EXPLORATION IN THE RAT AND THE MARMOSET: RELATIONSHIPS BETWEEN LEARNING AND OBJECT NOVELTY IN AN OPEN FIELD

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SUMMARY

The research reported in this thesis is concerned with exploratory behaviour, and conditions under which exploration occurs or is enhanced. A series of experiments were conducted, using rats (*Rattus norvegicus*) and common marmosets (*Callithrix jacchus jacchus*) as subjects. Methodologically, the studies followed the 'ethoexperimental' approach to the study of animal behaviour, an approach which aims to study animals in the laboratory, but with reference to natural problems confronting them. A number of learning tasks and forms of reinforcement were employed, as well as variations in the open field itself, from an 'exploration box' to the animals' own home cages.

The initial study examined effects of response generalisation and extinction on exploration in the rat. Bar-pressing responses (using the paws) and key-pushing responses (using the nose) were conditioned in an open field, and exploratory behaviour was measured in the form of activities directed towards various novel objects. Two main predictions were made: firstly, that learning would lead to increased object exploration, and secondly, that animals trained to bar-press would subsequently explore more with their paws, whilst animals trained to key-push would explore more with their noses.

Two subsequent experiments viewed exploration in the context of the 'behaviour systems' approach; that is, in relation to systems of processes which serve particular survival functions (as opposed to arbitrary behaviours used to deal with arbitrary environments). Exploration directed towards familiar and novel objects was observed during conditioning and extinction in the presence of a moving ball bearing, the aim being to examine object-directed and ball bearing-directed activities in conjunction with the rats' appetitive behaviour system.

A discussion of comparative aspects of exploration was derived from a pair of studies using two different species: the open-field activities of the rat and the marmoset were compared under conditions of varying object novelty during both operant conditioning and extinction.

A final study examined effects of food reward, social reward and the mere presence of novel objects on marmosets' exploration in their home cages, thus providing a contrast to the previous studies, which all used an experimental testing field in an isolated room. The aim of the study was to obtain data relevant to cage design and maintenance of marmosets held in captivity.

The thesis concludes with a general discussion which provides a rationale for attempts to enrich the behaviour of animals held in laboratories and zoos, reviews some of the problems associated with captivity, and interprets the findings of the six experiments as possible solutions to these problems.

STATEMENT

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University, and to the best of my knowledge and belief contains no material previously published or written by another person, except where due reference is made in the text of the thesis. If accepted for the award of the degree I consent to the thesis being made available for photocopying and loan.

Signed

Felicity C. Forster

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CHAPTER 1

DESCRIBING BEHAVIOUR

1.1. INTRODUCTION

The description and categorisation of events, made within a particular conceptual framework, forms a starting point for science. In the behavioural sciences descriptions are based on the assumption that predictions about behaviour can be made if a sufficient number of relevant variables can be understood and well defined.

The opening chapter of this thesis is intended firstly to provide a brief overview of two conceptual frameworks employed in describing behaviour, experimental psychology and ethology, traditions spanning almost a century. The focus of the chapter is on a third framework, the ethoexperimental approach, a means by which laboratory based behaviour can be systematically analysed within an ecological context. This new paradigm, a combination of experimental psychology and ethology, forms the conceptual framework for the behavioural descriptions in the present studies.

1.2. EXPERIMENTAL PSYCHOLOGY

During the nineteenth and early twentieth centuries much of psychology was couched in terms of various conceptualisations of the observable and measurable in mental life and behaviour, as opposed to introspection (Murphy & Kovach, 1972). This conception of the focus of attention in empirical psychology (particularly in the United States) originated with Watson (1914), and his definition of psychology as the 'science of behavior' is still being used today (McGovern, Furumoto, Halpern, Kimble, & McKeachie, 1991, p. 599). Thus, arguments in experimental psychology suggested that the mind could be reduced to its elements, that mental events could be reduced to behavioural events, and further, that behavioural events could be reduced to physiological events. It was in this climate that much attention was focused on the learning process, using explanations which went hand in hand with explanations in biology, anatomy and physiology.

The study of animal learning by experimental psychologists was dominated by authors such as Thorndike (1898), Watson (1914), Tolman (1938) and Hull (1943), who argued that learning was best studied in arbitrary situations; that is, situations as different as possible from those one might expect members of each species to encounter in their respective ecological situations. Of interest to such researchers was the formation of associations which were "free from the helping hand of instinct" (Thorndike, 1911, p. 30), as opposed to species-specific associative abilities.

Consequently, investigators using an arbitrary (or decontextualised) approach ensured that the experimental environment did not resemble an animal's natural environment. By isolating the process of learning from its natural context, descriptions were formulated in terms of arbitrary stimuli, responses and circumstances. Experimenters concentrated on artificial learning situations containing arbitrary stimuli and requiring responses that "could not have been previously experienced or provided for by heredity" (Thorndike, 1898, pp. 7-8), except in the sense of associations of acts with situations found in an animal's normal life.

According to Galef (1984), Thorndike's selection of environments in which to study animal learning was determined by theoretical rather than ecological concerns. In this way he was able to study general processes of learning, using an approach intentionally disparate from ecology. For example, Thorndike required his cats to get out of a puzzle box to obtain food, rather than the more ecologically usual task of opening a box to find food (Kline, 1899; Warden, Jenkins, & Warner, 1935). While Thorndike acknowledged that the animals' instinctive reactions to the puzzle box formed a basic repertoire from which the correct response developed, the circumstances he created meant that most of the cat's initial behaviours were persistently counter-productive. Thus, the animal was required to perform an ecologically unusual response, escaping from a box.

Pavlov also isolated subjects from the distractions of ordinary environments. In Pavlov's words, "any phenomenon of the external world can be made a temporary signal of the object which stimulates the salivary glands" (Pavlov, 1904, p. 56), and "it is obvious that the reflex activity of any effector organ can get hooked up with any of the inborn reflexes" (Pavlov, 1927, p. 17). This approach emphasised the arbitrary nature of the choice of stimuli and responses.

Similarly, Skinner (1938) focused on the role of the reinforcer in arbitrarily defining behaviour rather than 'botanising' the responses which the subject brought to a situation. In this analysis, any response could be brought about by means of reinforcement; a subject's responses were literally undefined until they were brought under operant control.

Overall, then, experimental psychologists using an arbitrary or decontextualised approach isolated the subject from its natural circumstances by an arbitrary choice of stimuli, responses and situations. As Seligman (1970, p. 406) stated:

> *What captured the interest of the psychological world was the possibility that laws of behaviour deduced from the study of animals in arbitrary situations might describe the general characteristics of behaviour acquired as the result of pairing one event with another.*

1.3. ETHOLOGY

In contrast to experimental psychology, ethology (from the Greek word *ethos*, meaning 'manner' or 'behaviour') emphasised the great diversity of species-specific variations in behaviour and the need for examining behaviour in species' natural environments. According to two of its early exponents, Lorenz (1970) and Tinbergen (1951), the field of ethology could be defined as 'the biology of behaviour', underlining the notion that animal behaviour has evolved phylogenetically and should be studied as one aspect of evolution (Von Cranach, Foppa, Lepenies, & Ploog, 1979).

Ethology's roots, according to Thorpe (1979), were in field studies such as those conducted by the naturalists Fabre, Selous, Eliot Howard, J.S. Huxley, Makkink and Vervey during the nineteenth and early twentieth centuries. Since the 1930s, however, ethology has expanded and developed especially rapidly (Hinde, 1982). The term 'ethology' came into general use in Europe during the 1930s, where a school of zoological workers (including Lorenz and Tinbergen) became concerned with animal behaviour, developing a unified set of ideas around such terms as 'innate releasing mechanism' and 'fixed action pattern'. Unlike research in the United States, where experimental psychologists tended to use animals as tools or objects for the study of the problems of general psychology, ethologists sought to answer questions about the way in which animals acted in their natural environment (Lehrman, 1974). White (1974) described the central theme of ethology as having an emphasis on the study of animals in their native habitat, and extended its role to the correction of psychiatric problems in humans.

Ethology, then, is the study of what animals do, and how and why they do it. This involves the accurate observation and description of an animal's behaviour, with the aim of understanding the reasons why an animal behaves as it does in its natural environment. Gould (1982) argued that biology has shown how environmental pressures have given rise to each animal's peculiar behaviour, and this explains why given behaviours observed under natural conditions are so well suited to each species' particular environment.

For ethologists, the environment is of the greatest importance; this includes the ecology of the physical surroundings, the animal's social interactions with its own and other species, the sensory world in which the animal lives, and the many series of environments through which and to which the animal has evolved (Gould, 1982). Ethological descriptions of behaviour therefore rely on inconspicuous observation in the field, drawing on information about an animal's evolution, ecology, social organisation and sensory abilities.

Ethologists typically ask questions about the adaptive value of behaviour; that is, how a particular behaviour helps the individual to survive and reproduce in its physical and social environment. As well as studying how behaviour develops over time within individuals (examining the role of genetic and environmental factors in behavioural development), ethologists study how behaviour develops in a species throughout the course of evolution (D'Amato, 1989).

A characteristic of ethological studies of animals and humans is the composition of behaviour catalogues, or 'ethograms'. An ethogram is a comprehensive list of items of behaviour (Brown, 1975), defined in terms of their constituent motor patterns; that is, in terms of physical movements, postures or cries (Hinde, 1982). For these catalogues, one selects functional units of behaviour which are constant in their physical form; for example, chasing, threatening, scratching or chewing (Lehner, 1979). The physical description of a behaviour pattern includes each physical detail of the event, and a greater accuracy of such measurement has recently been made possible by the use of video tape. One advantage of video tape is that behaviour can be reviewed again and again, soon after it occurs (Lehner, 1979), and in particular, this makes it possible to measure multiple aspects of behaviour occurring simultaneously (Renner, 1987), since tapes can be watched repeatedly. Other advantages are that behaviour patterns can be preserved and used for later comparison, and fast and slow motion allows for the analysis of data that would normally be inaccessible to direct observation. In order to record a sequence of movement patterns with respect to frequency, duration and relative position in time to one another, and without interrupting the continuity of observations, ethologists may use multi-channel event recorders. In this case, each of a number of previously selected behaviour patterns is represented by a particular key which records the event, either on paper or directly on to a computer file.

Ethologists often record behaviour according to its function or consequence, focusing on its goal rather than on the actions preceding it. For example, 'carrying in' or 'nest building' are functional terms (Hinde, 1959), as are 'seeking food' or 'hiding from the hawk' (Hinde, 1982). Hinde noted that categories like these involve some interpretation on the part of the observer, thus creating a certain risk.

1.4. THE ETHOEXPERIMENTAL APPROACH

The remainder of this chapter introduces the approach which was employed for the present study, a paradigm arising from the recognition that experimental psychology and ethology are equally valuable in describing and understanding behaviour, and that different environments are suitable for answering different questions. The material which follows consists of a section describing the complementary nature of experimental psychology and ethology, an outline of the historical origins of the ethoexperimental approach, and a final section suggesting some of the advantages associated with such an approach.

1.4.1. Complementary nature of experimental psychology and ethology

According to Brain (1989), a strength of experimental psychology is that it provides a means of studying behaviour where variables can be carefully controlled and systematically manipulated. Its disadvantage, however, is that the ecological relevance of the behaviours studied is questionable, and there is a tendency to focus exclusively on a limited range of responses. Brain went on to suggest that in studying behaviour in its natural context, in ethology, the responses may certainly be adaptive, and a broad range of behaviours may be recorded, but wide-ranging conclusions about behaviour are difficult to make. It may be claimed, however, that experimental psychology and ethology offer complementary approaches to the description of behaviour.

It is important to note here that there need not be anything inherently good or bad about laboratory or field approaches to the study of behaviour, and neither need be abandoned. As Galef (1989) pointed out, it all depends on the questions one is trying to answer.

Further, Brain (1989) recognised that there is no such thing as an optimal or 'typical' environment for a given species. Mice, for example, are able to adapt successfully to a very wide range of habitats (Brain, Mainardi, & Parmigiani, 1988). Studies of other species, such as the arctic fox, *Alopex lagopus* (Angerbjorn, Arvidson, Noren, & Stromgren, 1991) and the European wild rabbit, *Oryctolagus* *cuniculus* (Bell & Webb, 1991), have drawn attention to the wide range of physiological and behavioural variations displayed by these animals in response to seasonal factors. Examples such as these emphasise the variability of behaviour observed in the wild, implying a lack of static, optimal or typical environmental features.

This argument may be extended by suggesting that different environments may be suitable for answering different questions (Galef, 1989). For example, the rat's ability to dig, bury and construct tunnels may best be studied in the laboratory, using a glass-covered apparatus filled with digging materials. (Calhoun, 1962, noted the difficulty of observing the burying and digging behaviour of wild rats.) Blanchard, Blanchard and Flannelly (1985) and Lore, Nikoletseas and Takahashi (1984) each examined semi-natural colonies where animals were given the opportunity to dig, and Brain (1989) argued that such studies increase the richness of analysis in wild rat behaviour. Using the same logic, Brain also suggested that allowing laboratory rats the opportunity to defend nests within tunnels may provide valuable contributions to the study of aggression in defensive species.

It had already been argued by the 1970s that observations in the wild and in captivity complement each other, such that a discussion of the relative merits of each method would be superfluous (Eibl-Eibesfeldt, 1970). By way of example, Mason (1968b) argued that there is no reason why experimental research cannot be performed in the field, or why naturalistic data cannot be collected in the laboratory. Similarly, Miller (1977) suggested that the field can be a natural laboratory in which hypotheses can be tested, a view coinciding with Hinde (1966) in his book *Animal Behaviour; A Synthesis of Ethology and Comparative Psychology*. Thus, experimental control does not always require an artificial environment, and does not necessarily produce artificial changes in animals (e.g., artificial stimuli can be efficient releasers of instinctive responses); as a result, experimental manipulations may be carried out in the field and ecologically valid experiments may be conducted in the laboratory (Zayan, 1989).

Referring specifically to social behaviour in primates, Mason (1968b) maintained that for continuing progress to be made, a closer working relationship between experimental and ethological research is not merely desirable but an essential requirement. According to Mason, both approaches are indispensable, neither being complete without the contribution of the other. Thus, the biological perspective is not described as a mutually exclusive alternative to experimental psychology, but as a complement to it. As a consequence, new principles may be generated, and existing principles from each discipline may be augmented and restructured in accordance with those of the other (Murphy & Kovach, 1972).

1.4.2. A new paradigm: The ethoexperimental approach

Timberlake (1984) characterised recent developments in animal learning as representing an integration of ecological or functional accounts of behaviour within the classic laboratory approach, a contrast from previous approaches involving the use of arbitrary problems, stimuli and responses to generalise principles or laws of behaviour. Such an approach, according to Timberlake, involves examining behaviour as a functional system, and analysing where and how learning regulates the operation of that system. As a result, the data obtained are said to be relevant to issues in evolution, development and physiology, a characteristic not shared by the classic laboratory approach (Timberlake, 1984).

In achieving such an integrated approach in the laboratory, one suggestion is that experimenters employ methods from ethology. Ethologically derived observational techniques in particular have been seen as having an important role to play in laboratory experimentation (Lehner, 1979, p. 15):

> *...quantification and statistical analysis must not become the overlord of good quality observation. Sometimes initial observations cannot be quantified, but their value is not necessarily greatly diminished.*

Technological and methodological advances, particularly since the 1970s, have had a large influence: new measuring and visual recording equipment has allowed for complete records of behaviour, and these can be slowed to analyse details of movements or sped up to reveal patterns of behaviour not previously evident (Rosenblatt, 1989). This also applies to auditory recording.

Blanchard and Blanchard (1986) coined the term 'ethoexperimental' to describe the blend of experimental and ethological approaches. Historically, the ethoexperimental approach may be traced back to the learning theorists whose aim was to duplicate some essential aspect of the problems faced by animals in their natural environment. Kline (1899, p. 399), for example, noted that:

> *A careful study of the instincts, dominant traits and habits of an animal as expressed in its free life...should precede as far as possible any experimental study.*

Such an argument was also used by Small (1900, p. 131) in the early stages of the American tradition of animal psychology, when he stated that:

> *The chief difficulty of such experimentation lies in controlling the conditions of the problems without interfering with the natural instincts and predilections of the animals.*

From the beginning, then, there were arguments favouring the investigation of learning in ecological settings. Small (1901, p. 208) justified the use of his maze by referring to the rats' "propensity for winding passages", and argued that "experiments must conform to the psycho-biological character of an animal if sane results are to be obtained" (p. 206). Further, Galef (1984) argued that the work of Kline and Small influenced the early work of Watson, who showed an initial interest in the ecological orientation toward the study of learning in animals (1914, p. 45):

> *Before beginning upon the simplest problem in learning, it is necessary...to have some knowledge at least of the instinctive modes of response of the animal and of the receptors to which we are making appeal. In behaviour up to the present time, we have largely put the cart before the horse. In entire ignorance of instinctive capacity and sense organ functions, we have plunged in medias res and attempted to do satisfactory work on learning.*

Furthermore, Watson's early emphasis on the study of individual species, the need to use field studies to assess the adequacy of laboratory results, and the importance of treating learning as an adaptive faculty can all be seen, in retrospect, as factors characteristic of an ecological approach to learning.

Particularly since the 1970s, laboratory studies of behaviour have been influenced by the recognition that behaviour must be considered in its natural context, thus taking evolutionary, ethological and sociobiological principles into account (e.g., Timberlake, 1984; Blanchard & Blanchard, 1986). This, according to Bronstein (1989), means that details about an animal's ecology and personal history, along with informal, even playful, observations, are relevant to descriptions within animal research. Thus, the ethoexperimental approach, as propounded by these authors, represents a merging of laboratory and field approaches, and treats behaviour as part of a wider functional system.

1.4.3. Advantages of the ethoexperimental approach

A combination of laboratory and field techniques, including the use of less constrained experimental tests instead of constrained environments where animals must perform a specific behaviour in order to produce some outcome, and a combination of quantitative and qualitative description, has numerous advantages over the use of either of the two approaches separately.

Miller (1977), for example, defended the use of naturalistic laboratory settings in arguing that naturalistic observations can serve as a starting point from which to develop laboratory research programs (as well as being important for their own sake, in understanding how an animal behaves in its natural environment). As pointed out by Snowdon (1983), there are many cases where phenomena studied in the laboratory had their origins in field observations (e.g., the studies of 'imprinting', as described by Lorenz, 1966, pp. 57-59). Similarly, researchers such as Pereira, Macedonia, Haring and Simons (1989) and Snowdon and Savage (1989), have argued for the use of non-invasive techniques in order to complement field research.

A second advantage identified by Miller (1977) is that ethoexperimental findings can validate or lend substance to previous laboratory findings, as well as increasing the efficiency of laboratory work, by identifying possible biological constraints on the behaviour of particular species. For example, ethoexperimental studies of wild rats in semi-natural conditions helped to identify a number of specific behaviours which serve as responses to threats from predators, conspecifics and natural hazards (Blanchard & Blanchard, 1987). The naturalistic laboratory setting allowed for the systematic manipulation of threat stimulus, situational parameters, and the consequences of subject actions, thus helping to determine the relationship between these variables and changes in defensive behaviour.

Thirdly, Rosellini and Widman (1989) argued that the ethoexperimental approach produces more ecologically relevant information about animal behaviour. For example, it would be very rare for an animal to find itself confined to a novel area without some possibility of escape or finding cover (Russell, 1983). The ethoexperimental solution to this problem is to provide an open-field situation which is closer to the animal's natural habitat, including opportunities for escape and cover.

Another advantage of the ethoexperimental approach is that it produces a valuable and extremely detailed descriptive data base, thus providing links between a range of behaviours, situational and subject variables (Blanchard, Blanchard, Cholvanich, & Mayer, 1989). These authors go on to suggest that the systematic manipulation and control of variables in the laboratory means that hypotheses which emerge from this approach can be very detailed and close to the data.

Finally, Brain's position (1989) is that the ethoexperimental approach is more conducive to an appreciation of the *function* of particular actions. For example, an awareness of the impact of ecological factors in the field, such as seasonal flooding, temperature variation, parasite loads and starvation, has implications on interpretations of the function of laboratory-based behaviours. This awareness, according to Brain, should help to guard against inappropriate interpretations of the possible reasons for an animal's behaviour.

1.5. CONCLUSION

Chapter 1 began by providing an overview of experimental psychology, showing how careful control of an organism's genes and environment led researchers to undertake precise and reproducible experiments. A discussion of ethology followed, describing ethologists' desire for more ecologically relevant information. Brain (1989) characterised experimental psychology as originating in North America, using deliberately simplified apparatus and rigourous control over subjects, obtaining 'objective' measures of behaviour, and mainly concentrating on acquired behaviour. In contrast, ethology was characterised as originating in Europe, using natural environments or approximations to these conditions, with minimal control over subjects, producing detailed recording of 'behavioural elements' (using video equipment, for example), and concentrating on innate actions.

There are problems inherent in each of these approaches to the description of behaviour. For instance, laboratory investigators have acknowledged that the study of arbitrary situations might not lead to a complete understanding of the processes underlying behaviour acquisition in normal circumstances, and the control of an animal's physical environment in the laboratory (rather than in the 'uncontrollable chaos of nature', Gould, 1982) has led to a systematic under-estimation of the richness and subtlety of animals' capacities to learn about their environments (Galef, 1984). For Gould (1982, p. 12), a problem with the ethological approach is its questionable methodology, due to a lack of variable control and unquantifiable subjective data descriptions:

> *Moving out of the laboratory to study unrestrained animals in a world with countless uncontrolled variables was bad enough, but once there ethologists simply observed and took notes. Behaviorism was born with a healthy distrust of just subjective methods, and could point to a long list of cases in which the fond and overly romantic imaginings and expectations of observers had strongly biased the results of their observations.*

Another problem with ethology, according to Brain (1989), is that wild populations may be unrepresentative and descriptions may reflect a limited range of the capacity of the species over too restricted a time period.

In the mid-1970s there was a synthesis between experimental psychology and ethology, based on the acceptance by psychologists of the organic theory of evolution (Snowdon, 1983). As a result, experimental psychologists became more interested in descriptive natural history studies and field work. Simultaneously, ethologists became more interested in controlled experimentation and in understanding the development of behaviour within the individual, and semi-naturalistic environments were devised in order to provide a compromise between the field and the laboratory.

Blanchard and Blanchard (1986, 1987) described this general procedure as an experimental ethology, or an 'ethoexperimental approach' to the study of natural behaviours. The aim of this approach, as stated by Blanchard and Blanchard, is to provide full, detailed descriptions of relationships between species-specific behaviours and events which are antecedent and consequent to them. In Brain's (1989) description, the major aim of the ethoexperimental approach is to study *meaningful* behaviour in the laboratory, by applying ethological considerations to laboratory tests of behaviour. Thus, the contribution of the ethoexperimental approach is to create laboratory environments that are meaningful for particular species, and to develop inclusive, wide-ranging descriptions of animal behaviour which are minimally distorted by the nature of measurement.

If the basic aim of the psychologist is to achieve reliable descriptions of behaviour (Mason, 1968b), then an ethoexperimental approach to the study of behaviour is powerful, since its broad aim is the systematic investigation and description of naturalistic behaviours in ecologically relevant situations. It may be argued, however, that describing behaviour cannot be separated from explaining behaviour (Barnett, 1963), and *a fortiori*, that definitions of behaviour cannot be separated from theories used to explain behaviour. The ensuing chapter describes a particular type of behaviour, exploration; in doing so, explanations of its survival value will be offered and theories accounting for its occurrence in individuals and species will be discussed.

CHAPTER 2

CONCEPTS OF EXPLORATION

2.1. INTRODUCTION

Chapter 2 deals with concepts of exploration by first looking at the issue of definition, pointing out problems of definition itself, as well as problems in defining exploration in the psychological literature in particular. In describing the subject matter of this thesis, the chapter goes on to discuss the adaptive significance of exploration, and includes an historical outline of the contribution of experimental and ethoexperimental approaches to the study of exploration . The aim of the chapter is to contribute towards the definition of exploration; however, since no definition can be theory-neutral, that definition will itself be a product of the theoretical framework of the thesis.

2.2. THE PROBLEM OF DEFINITION

Beginning a chapter on exploration, one may first expect a definition of exploration. Indeed, definition or classification may be seen to be at the heart of many a scientific endeavour; to study natural phenomena, according to Hinde (1974), it is necessary first to describe and classify them. In biology, for example, classification has been described as its very basis, although such classification is not always clear-cut (Einon, 1983, p. 210):

> *Before we study a living organism we tend to describe it both in terms of its physical attributes and in terms of its relationships with other living organisms. We classify it, and in doing so we tend to emphasize those aspects of the organism that are easily described or that fit neatly into our categories...while placing less emphasis or even ignoring aspects of the organism that cannot so easily be categorized.*

Einon provided an example of this tendency to disregard certain characteristics by pointing out that we classify the platypus as a 'mammal', despite the fact that it lays eggs.

It is the purpose of the opening of this chapter to argue that the tendency to define and categorise is misleading in the study of exploration. Referring to the problem of definition, Eacker (1983) pointed out that questions like 'what is psychology?' (or some particular subject matter within psychology) seem to demand answers in the form of a statement of the 'essence' of the subject of the question. In other words, the subject matter is assumed to have a referent; in the case of psychology, that there is one thing which is psychology, to which the term 'psychology' refers. In the area of animal behaviour, Hinde (1974) argued against the straightforward categorisation of behaviour, stating that most categories are 'loose'. Welker (1971, p. 174) also suggested, with reference to play and exploration in particular, that these categories cannot be separated into distinct classes:

> *I find it virtually impossible to continue to think of play and exploration as unique behavioral categories with characteristics distinct from other phenomena within the behavioural repertoire of mammals...It is with their conceptualization and explanation that I find fault.*

Cowan (1983) supported this by arguing that exploratory behaviour is all-pervasive and therefore can never be evaluated in isolation from other aspects of behaviour and ecology. For example, exploration by one animal may influence the behaviour of other animals in the same area: animals whose territories overlap with neighbours often develop characteristic adaptive behaviours such as the maintenance of timetables for patrolling. This has been shown to occur in grey squirrels (Connolly, 1979) and a wide variety of species of small mammals (Baker, 1978). Exploratory behaviour may also be bound up with population dynamics; according to Gaines and McClenaghan (1980), when animals disperse from their native population, genetic variability and the exploration of new or more sparsely populated areas are facilitated.

Popper (1952, in Eacker, 1983, p. 10) provided a possible solution to the problem of definition by means of 'methodological nominalism', an approach characterised by descriptions of *how* things behave rather than what they are:

> *Instead of aiming at finding out what a thing really is, and at defining its true nature, methodological nominalism aims at describing how a thing behaves in various circumstances, and especially, whether there are any regularities in its behaviour.*

It is with this in mind that the present studies were conducted. This chapter, therefore, will review some of the psychological theories which attempt to account for exploration, and ask the question 'why do animals explore?'

2.3. ATTEMPTS AT DEFINING EXPLORATION IN THE PSYCHOLOGICAL LITERATURE

In the psychological literature dealing with exploration there exist a variety of different approaches, and these depend on the choice of initial research questions and the particular definition of exploration stipulated. In other words, definitions of exploration are bound up with theories of exploration. Maddi (1961), for example, described exploration in terms of orienting responses and investigatory responses, but indicated that each of these concepts used to explain exploration is embedded in a theory which interprets exploratory behaviour. Another example comes from Killeen (1975), who reported that most of the evaluations of exploratory behaviour have been made within the context of one or another theoretical paradigm. Some theoretically-laden definitions given to exploratory behaviour include the following: a by-product of conditioning by contiguity (Skinner, 1948), a derivative of optimal arousal (Dember & Earl, 1957), an adjunctive behaviour induced by a schedule of reinforcement (Levitsky & Collier, 1968), an integral part of the normal conditioning process (Sheffield, 1966), or a sign of frustration (Scull, 1973).

Assorted definitions of exploration, therefore, arise from the orientation of the researcher. It follows from this that two distinct paradigms, such as experimental psychology and ethology, will arrive at differences in descriptions of the subject matter under investigation, and consequently use different methods in which to study behaviour. For example, studying cause-effect relationships in exploration requires work on a single species, making systematic changes to the environment and viewing conditions under which exploration occurs, whilst formulating a description of specific movements made by animals while exploring and analysing the function of these movements requires work on more than one species, making cross-species comparisons within an ethological framework.

In the absence of a clear definition of exploration, difficulties in interpretation and comparison can occur. Hole and Einon (1984), for example, referred to the problem of knowing precisely what is being compared across species, since many authors do not define the phenomenon they purport to be measuring. In Chalmers' view (1984), researchers should not attempt to construct absolute dichotomies between behaviours, but rather tailor each particular definition to the investigation at hand. As a result, differing theoretical orientations and methodologies will necessarily require different definitions.

In the early 1960s Berlyne took steps towards producing a series of definitions of exploration by categorising his observations in terms of the perceived outcomes of exploratory behaviour. This represents a significant development in attempts at definition in this field; consequently, the following 4 sections summarise the definitions of exploration described by Berlyne (1960, 1963), and outline some of the difficulties these definitions generated.

2.3.1. Extrinsic and intrinsic exploration

Primarily, Berlyne made a distinction between *extrinsic* exploration and *intrinsic* exploration (1960).

Extrinsic exploratory responses were said to be directed towards a biologically significant event, thus corresponding to specific motivated behaviour. Appetitive behaviour is one instance of such an activity: the exploratory responses preceding the achievement of an end (a full stomach) were said to constitute extrinsic exploration. Wyckoff (1952), for example, studied observing responses, which were thought to provide information about the availability of food, and Barnett (1963, 1976) commented on a range of activities which preceded the achievement of a consummatory end, such as empty mammary glands or an optimum skin temperature.

Intrinsic exploration referred to responses which could not be so readily linked to a biological conclusion. This category accounted for the large proportion of time spent by animals in exploring and manipulating objects of no apparent biological significance (Berlyne, 1964). Barnett and Cowan (1976) supported this in describing movements which seemed to be not only independent of incentives, but often occurred after satiation. This form of exploration has been described as an end in itself (Berlyne, 1964), in which an animal may not necessarily be under an obvious primary drive state (such as hunger or thirst), but still engages in activities which supply information about its environment. Such a description is consistent with Hughes' (1965b) view of exploration. Hughes found that exploratory behaviour did not increase when an animal was deprived of food (although it was claimed that food-seeking behaviour may increase after deprivation).

According to Burghardt (1984), intrinsic exploration could be said to correspond to the concepts of 'curiosity' and 'play'. Some researchers studying curiosity used the notion of spontaneous alternation to account for the orderliness of exploration observed in animals exposed to unfamiliar areas. For example, in studies by Dember and Fowler (1958) and Douglas (1966), rats in a *T*-maze did not wander at random; rather, they turned left at the choice point on one trial, and right on the next. Independent of any incentive, then, an animal tends to move about in a methodical fashion. Brown (1969) supported this in describing the orderliness of patrolling behaviour displayed by small mammals.

2.3.2. Inspective and inquisitive exploration

A second distinction made by Berlyne (1960) was between responding *to* an environmental change, termed *inspective* exploration, and responding *for* a change, *inquisitive* exploration.

Inspective responses were said to involve increased contact (by means of exploration and play) with familiar objects entering an animal's stimulus field, thus providing the animal with information from familiar situations. Berlyne (1960, p. 80) defined this kind of exploration as behaviour which "brings the animal into contact with objects that are not already represented in the stimulus field." In other words, inspective exploration is concerned with objects which are familiar but out of the animal's visual range.

In contrast, inquisitive exploration was thought to bring an animal into contact with unfamiliar stimuli. According to Berlyne (1960, p. 80) inquisitive exploration "yields further stimulation from objects already acting on receptors." Thus, searching for food or nest materials, patrolling the home range, and excursions outside the home range constitute inquisitive exploration.

2.3.3. Specific and diversive exploration

Finally, Berlyne (1960) drew a distinction between *specific* exploration and *diversive* exploration. These categories were thought to involve different motivational pretexts, the former resulting from curiosity, and the latter resulting from boredom.

Specific exploration was defined as behaviour directed at obtaining specific information about a particular changed object or event, corresponding to Berlyne's notion of curiosity. An example of specific exploration is when a person sets out to solve a particular intellectual problem, motivated by a lack of information about a stimulus change.

Diversive exploration was said to be behaviour directed at obtaining stimulus change and information from any environmental source, motivated by a lack of stimulus change. For example, the case of a person seeking exposure to stimulus change, motivated by boredom, would constitute diversive exploration.

2.3.4. Difficulties with Berlyne's definitions of exploration

Berlyne's extensive classifications may be theoretically useful, if somewhat arbitrary (Halliday, 1968), but Birke and Archer (1983) argued that the categories do not necessarily provide us with a fruitful definition of exploration, since in practical terms exploration cannot be neatly broken down into a hierarchy of mutually exclusive categories.

Observations of animals in the field have shown that Berlyne's definitions can become indistinct. Birke and Archer (1983) showed how the distinction between extrinsic and intrinsic exploration becomes blurred in the case of activities which occur while an animal is patrolling its home range. It is difficult in this situation to know whether the activities while patrolling are directed towards a biologically significant event, or an end in themselves with no primary drive state. Similarly, Barnett (1981) argued that many animals move about in their living area when sated with necessities, and that they make use of the information they store much later. Thus, patrolling seems to supply animals with information which sometimes provides reinforcement, such as food and water, and sometimes not, in the case of information about the availability of cover and sleeping sites. Both of these types of information are relevant to an animal's survival, and so both could be said to be biologically significant. Russell (1983, p. 26) summed up this argument in the following way:

> *It is...doubtful whether, in the natural habitat, there is any such thing as a change that has no 'biological significance'. Any change is potentially important for survival...*

Cowan (1983) raised questions about the operational value of Berlyne's classifications due to the problem of identifying the 'motives' of animals, and subsequently argued that Berlyne's definitions have little reference to the history or ecology of the species concerned. Rather, Cowan suggested, Berlyne's categories ought to be thought of as purely descriptive behavioural observations.

A more reasonable goal in the pursuit of a definition of exploration, as put forward by Brown (1975), is to find out how exploration benefits individual animals and then to postulate how natural selection might have acted on a species to bring about its evolution. In other words, Brown's aim is to find out how exploratory behaviour is *adaptive*.

In the following section, ways in which exploratory behaviour can be of benefit to individuals and species will be discussed, arguing for the case that exploration is a highly adaptive means for survival.

2.4. THE ADAPTIVE SIGNIFICANCE OF EXPLORATION

From an evolutionary perspective, it may be argued that exploration has adaptive significance for a species. In addition, it may be argued that exploration is adaptive at the level of individuals. However, there is considerable debate regarding the standard of evidence for considering a trait as adaptive (D'Amato, 1989), and indeed the definition of 'adaptive significance' itself.

Calhoun (1962) defined adaptive significance as the attainment and maintenance of physiology conducive to growth, survival and reproduction, whilst adjustive significance, on the other hand, was described as the ability to accommodate to the exigencies of an existing situation sufficient for temporary survival irrespective of deleterious impact upon growth or reproduction. Within ethology, a behavioural trait is considered adaptive only after demonstration that it has an hereditary component and that it has been responsible for conferring fitness on its bearers (Hinde, 1975). Further, sociobiological theories regard current reproductive advantage as the most important variable, such that a behaviour is adaptive if it increases the animal's fitness (Tinbergen, 1963; Williams, 1966).

In practice, according to D'Amato (1989), theories of adaptive significance constantly face the criticism of 'adaptationism': the use of *post hoc* explanations to ascribe adaptive value to any biological trait. For the present purposes, adaptive significance is considered to include both adaptive and adjustive components, and to function at the level of species and individuals. Since most of the psychological literature dealing with the adaptive significance of exploration is concerned with analysis at the level of the individual, the following sections give greater emphasis to the benefits gained by individual animals. The adaptive significance of exploration has often been described in terms of a cost-benefit analysis (e.g., Russell, 1983; D'Amato, 1989), in which animals explore if the benefits outweigh the costs (Birke & Archer, 1983). The following section deals briefly with some of the costs of exploration, and sections 2.4.2 to 2.4.6 examine benefits thought to be gained by animals which explore.

2.4.1. Costs of exploration

Barnett (1976) suggested that energy expenditure and dangers, such as the risk of predation, are significant costs associated with exploring, particularly for species subject to predation in the wild. For such animals as these, danger from predation would be assumed to result in less exploration of novel environments. This was supported in a study of mice by Glickman and Morrison (1969), in which it was found that exploratory mice were more likely to be preyed upon by owls, compared to less exploratory individuals.

Exploration has also been shown to have maladaptive consequences for primates. According to Baldwin and Baldwin (1977) young primates risk greater chances of predation, poisoning, falls from trees, separation from the troop and maladaptive learning. Baldwin and Baldwin suggested that stimulus-seeking behaviour actually lies on a continuum between adaptive and maladaptive behaviour, although it is predominantly nearer the adaptive pole.

Once establishing costs such as those mentioned here, they can be weighed against the benefits gained by animals which explore, showing why, in a particular situation, an animal may be likely to explore its surroundings. Cowan (1983) defined benefits as being the reduction of factors influencing mortality (such as vulnerability to predation) and the increase of factors contributing directly to survival (such as the ability to find food by foraging). Benefits discussed in the following sections begin with the general claim that exploration provides information about the environment; following this, the discussion will turn to specific benefits (all of which are inter-related, rather than being mutually exclusive), including maintenance of familiarity with the home range, location of new resources, avoidance of predators and learning new strategies.

2.4.2. Acquisition of information about the environment

Suggestions of the benefits of exploration abound in the literature, beginning with the overall proposition that exploration provides animals with information about their environment and all of the stimuli within it. Bolles and Woods (1964), for example, wrote that locomotion, sniffing, orienting and manipulating all share the functional significance of expanding an animal's stimulation from the environment. Further, according to Russell (1983), proximate mechanisms of exploration such as arousal, curiosity and boredom (discussed later in sections 2.5.1 and 2.5.2 of this chapter) may have evolved in order to provide organisms with information about their environment. Richardson, Siegel and Campbell (1988, p. 492) supported the notion of exploration as information acquisition in stating that:

> *In addition to increasing fear and/or arousal, placing an animal in an unfamiliar environment undoubtedly increases information processing of environmental stimuli. From a purely adaptive standpoint, the more an animal knows about its environment the more likely it is to survive in that setting.*

For example, knowledge of the location of cover may be vital for survival, particularly for species which are susceptible to predation.

In describing the process by which animals are able to acquire information about their surroundings, Tolman (1932, 1948) proposed the term 'cognitive mapping', a process involving the formation of internal models or maps of an animal's world. Research based on Tolman's model has continued; for example, Inglis (1983) has developed a cognitive theory in which the function of exploration is that it provides a source of knowledge about the environment, a function of central importance to animals.

2.4.3. Maintenance of familiarity with the home range

Jewell (1966) showed that many animals show attachment to a home range (the home range being the area where activities such as feeding, sleeping and reproduction occur, Russell, 1983). This attachment is expressed in the form of the establishment and maintenance of familiarity with an area; for example, the accrual and storage of knowledge about the location of food, water and essential resources, sleeping and hiding places, heights, the presence of conspecifics and the likely whereabouts of predators (Russell, 1979). Russell described the adaptive significance of home range familiarity as 'insurance against danger', and according to Cowan (1983), sampling different patches of resources leads to topographical and other learning, which can be used later (e.g., in foraging), thus enhancing animals' survival chances. This idea was borne out in Glickman and Morrison's study (1969), in which the group of mice which were familiar with an area were more successful at avoiding predation by owls.

Russell (1983) further argued that since habitats usually change over time (due to seasonal and climatic factors, as well as the behaviour of other animals), maintenance of familiarity with the home range demands regular inspections. Barnett and Cowan (1976), for example, reported their observations of the systematic patrolling behaviour of rats, and Gordon (1988) found comparable patrolling patterns in the fire ant, *Solenopsis invicta*. Systematic patrolling of the environment (in which animals tend to visit those parts of the environment least recently visited), according to Russell (1983), may serve not only to 'refresh the animal's memory', but also to determine whether or not changes have occurred, so that the animal may alter its behaviour accordingly.

2.4.4. Location of new resources

The location of new resource sites is another benefit of exploration. Birke and Archer (1983) reviewed evidence which suggests that knowledge of the location of different resource sites (such as nest sites, food sites, mates, places of hiding and potential hazards) can be exploited some time in the future (e.g., Krebs, 1978). The benefit of the storage of resource site information may be only potential, or may not produce a change in behaviour until some time later. For example, an animal may remember the location of nesting materials, but not use this information until months later, when it is time to build a nest (Birke & Archer, 1983). Similarly, animals which cache food supplies (such as the nutcracker, *Nucifraga carycatactes*, Balda, 1980) are able to remember where the food is located many months afterwards. The benefit is that the animal is able to locate the remembered source when it is required, without having to spend time searching. As a consequence, an animal which is familiar with its environment has an advantage over one which has recently migrated to the area (Birke & Archer, 1983).

Studies of the ability of animals to efficiently store topographical information have given rise to a great deal of literature on 'optimal foraging' strategies (reviewed by Krebs, 1978). MacArthur and Pianka (1966), for example, suggested that foraging animals do not move randomly through their habitats, but consistently act to maximise resource utilisation. In this analysis, searching efficiency is maximised if the animal visits each resource point only once and travels by the shortest possible route (Pierce, 1987).

The optimal foraging model has, however, generated criticism, as summarised by Birke and Archer (1983). It may be the case, for example, that optimal strategies only come into operation when resources are critical (Pulliam, 1974). Other examples come from Christensen-Szalanski, Goldberg, Anderson and Mitchell (1980), who found that rats deprived of food do not always behave in the most efficient manner when obtaining food; Pierce (1987), who found that common shrews (*Sorex araneus*) do not forage systematically; and Timberlake and White (1990), who reported that animals may not even need a food reward in order to traverse an area efficiently (their food-deprived rats were able to efficiently traverse a maze despite the experience of being continuously unrewarded at the end). A possible explanation for these findings is that foraging may be based on a variety of specific mechanisms rather than a general optimising principle (Timberlake, Gawley, & Lucas, 1987). Instead of travelling as fast as possible, then, Gendron and Staddon (1983) suggested that there may be a trade-off between the rate at which prey are encountered and the forager's ability to detect them. Timberlake and White (1990) argued that this behaviour makes ecological sense, since in the wild considerable unrewarded locomotion is usually required to find food. Thus, animals which persistently explore their environment efficiently, regardless of the existence of rewards, would be said to be more likely to survive and reproduce than animals exclusively exploring to receive proximate food rewards.

2.4.5. Avoidance of predators

Evidence for exploration as a means for avoiding predators comes largely from research on small rodents, since predation is a significant factor in the lives these animals (Ambrose, 1972). It has been shown that if placed in unfamiliar surroundings, rats and mice become more vulnerable to predation (e.g., Shorten, 1954; Metzgar, 1967; Glickman & Morrison, 1969; Ambrose, 1972). As stated earlier, when mice are put into an unfamiliar area, they are preyed upon by owls significantly more than animals which are familiar with their environment.

Metzgar (1967) suggested several reasons to account for the advantage of animals which are familiar with their surroundings in comparison to new animals; for example, 'residents' may become aware of danger more readily than 'transients', and animals which know the terrain may escape more effectively. However, given the excellent hunting ability of owls, Ambrose (1972, p. 911) argued that these explanations are not plausible:

> *...a barn owl, approaching swiftly and silently from above in partial or complete darkness, probably gives little opportunity for detection by a Microtus in a runway and even less time for decision as to escape direction.*

An alternative explanation put forward by Metzgar (1967) is that new animals may be more active and hence more exposed to predation than resident animals. Ambrose (1972) supported this third explanation, reporting that mice released in a strange place tend to remain under cover for a period and then begin to explore their surroundings; in doing this, they become more active than residents in the same environment. This is also consistent with Cowan (1983), who argued that increased movement is a means of gaining knowledge about the topography of refuges.

Barnett (1976, p. 49) concluded that knowledge of the environment obtained through exploration is fundamental to predation avoidance in wild rats:

> *...their principle means of avoiding predators are the use of pathways under cover, and flight to a burrow or other place of concealment. These actions depend on previous experience of the topography of their living space. Given such experience, they can run from any point to any other, by the shortest route and in the least possible time.*

2.4.6. Learning new adaptive strategies

It has been argued that the most significant benefit from a knowledge of the surroundings may be that an animal can adapt its strategies appropriately (Birke & Archer, 1983). Since habitats are not usually static, animals need to adapt their behaviour so as to allow for environmental changes. One example of a habitat change is the yearly fluctuation in food type and availability. Davies and Houston (1981) showed that on days of high food abundance pied wagtail territory holders tolerated subordinates and intruders, whilst on days of low food abundance newcomers were evicted. The variation in wagtail behaviour suggests that the birds learnt an adaptive strategy according to the quantity of food available.

Baldwin and Baldwin (1977, 1978a, 1978b) stressed the importance of learning in the ontogeny of exploration, arguing that most of the adaptive functions postulated to result from exploration and play involve learning. Fiske (1961) also attributed a learning role to variable behaviour, reporting that exploration increases the likelihood of an animal making and learning a response by which it can cope most adequately with a given situation. In primates, for example, exploration and play provide animals with the practice of adult skills and ensure the learning of information about the environment, such as learning one's place in the social structure and learning how to manipulate objects that may be of potential use (Baldwin & Baldwin, 1977). Other learning benefits of exploration listed by Baldwin and Baldwin include the development of perceptual skills, the facilitation of adaptive innovation in new environments and the development of predator defences.

Research concerning differences in the behaviour of wild and domestic rats sheds light on the issue of learning adaptive strategies by exploring. In nature, fitness is determined by the ability to adapt to an ever-changing environment, whilst in the laboratory the environment remains relatively static (Huck & Price, 1975). An implication of this is that if wild rats exhibit any differences in behaviour compared to their laboratory counterparts, it may be a result of learned adaptations acquired by the former. Research has, in fact, confirmed this idea: studies of commensal rats and laboratory rats (reviewed by Boice, 1973) have yielded disparate results, indicating ways in which wild rats have adapted to changing environmental conditions brought about by humans (such as attempts at pest control). Avoidance of trapping and avoidance of poisoning are two commonly quoted learned behaviours exhibited by wild rats (Shorten, 1954; Rzoska, 1954; Calhoun, 1962; Cowan, 1977a).

Laboratory rats usually approach and investigate new objects in a familiar place (Barnett, 1976). This is known as *neophilia.* In contrast, commensal rats typically avoid such objects, *neophobia* (Barnett, 1958a, 1958b; Barnett & Cowan, 1976). Calhoun (1962) noted in his long-term wild rat project that it was frequently difficult to capture wild rats in many of the types of commercially available traps. This was attributed to the fact that traps represent a new object in the animal's environment: commensal rats have learned to avoid new objects in familiar places. Declines in the success of field poisoning operations against rabbits in Australia and New Zealand have also been attributed to increases in learned neophobia in the wild (Cowan, 1983). Cowan argued that selection as a result of human predation accounts for the learned behaviour; avoidance of unfamiliar objects provides protection from trapping and poisoning (Shorten, 1954).

Along a similar line, Price and Huck (1976) found support for the hypothesis that the domestication of rats (for laboratory purposes) has raised their threshold for avoidance-escape behaviour in response to a novel environment. Price and Huck observed wild rats in a novel open field and reported that the animals displayed rapid and vigorous motor activity compared to their domestic counterparts. This kind of behaviour was thought to be adaptive for the wild rat in times of danger, so that it could escape or increase its chances of finding shelter (Barnett, 1958b). In contrast, the lack of jumping by Price and Huck's domestic subjects and their more constant levels of activity suggested a rise in their threshold for avoidance behaviour in response to a totally new environment. Similarly, Price and King (1968) suggested that such behaviour may have arisen through selection for docility in captive animals.

The differing strategies learnt by wild and domestic rats demonstrate the adaptive quality of exploration, showing how animals can learn new responses and alter their behaviour in order to cope with a changing environment.

Having described various adaptive benefits of exploration, the discussion will now turn to an historical analysis of exploratory behaviour, aiming for a better understanding of the concept of exploration. The remaining half of Chapter 2 examines the contribution of experimental and ethoexperimental approaches to the study of exploration.

2.5. CONTRIBUTION OF EXPERIMENTAL PSYCHOLOGY TO THE STUDY OF EXPLORATION

Interest in the exploratory behaviour of animals within psychology dates back at least to 1899, with Small's *Notes on the psychic development of the young white rat*, in which the restlessness of infant rats was described as being 'premonitions of curiosity', and not merely a reflection of hunger. During the first half of the twentieth century, no systematic investigation of exploratory behaviour was carried out; rather, exploration was remarked upon in passing, as an interesting propensity of animals (in particular, rats).

Initially, exploration was conceived as a form of general activity, but this view began to change during the 1950s due to the finding that the opportunity to explore stimuli seemed to be reinforcing in itself (e.g., Berlyne, 1950; Fowler, 1965; Hebb, 1949; Montgomery, 1953). As a result, researchers (such as Berlyne, 1950; Montgomery, 1953) posited the existence of a 'curiosity drive' to explain exploration.

Alternative views interpreted exploration in terms of fear; some researchers argued that exploration results from a balance between fear and the tendency to approach novel stimulation (e.g., Montgomery, 1955), and others argued that a single process motivates exploration, such that mild fear increases exploration and strong fear inhibits it (e.g., Lester, 1967a; Halliday, 1966).

More recently, ethoexperimental interpretations of exploration have appeared in the literature (e.g., Suarez & Gallup, 1981a; Rosellini & Widman, 1989), suggesting that exploration in the laboratory actually represents an animal's response to a simulated predatory encounter (i.e., a response to being picked up and handled by a human), a reaction to social separation, and attempts to escape.

The sections which follow give details on two lines of theorising used to account for exploration within the context of experimental psychology: drive theories and fear theories. (It should be noted that these are not the *only* theories of exploration.) Following this, section 2.6 describes an ethoexperimental approach to laboratory studies of exploration, arguing that an awareness of possible ethological factors in the laboratory may lead to a better conceptualisation of open-field exploration.

2.5.1. Drive theories

From the early twentieth century onwards, the concept of drive was being used to explain behaviour. Moss (1924), for example, in his *Study of animal drives* theorised that drives were internal, biological disturbances which forced animals to behave in particular ways, thereby restoring their natural balance or equilibrium. In drive terms, behaviour was dominated by primary motives such as hunger, thirst, sex, pain, and extremes of temperature, and the resulting behaviour was assumed to sustain the biological well-being of the animal.

In attempting to account for the variability of behaviour which occurred in the absence of these primary drives, Tolman (1925) extended the drive conceptualisation to include *secondary* or *learned* drives (a move also consistent with Hull, 1943). According to Tolman, secondary drives operated through the action of stimulus substitution: those neutral stimuli in an animal's environment that were consistently associated with a primary drive state could come to elicit the drives that usually resulted from conditions of deprivation and external stimulation.

By the late 1920s the drive principle was being applied to curiosity and exploratory behaviour; for example, Dashiell (1928) and Nissen (1930) adopted the concept of drive to explain the restless activity of a food-deprived animal. Hull (1952) developed the concept of *drive reduction* as the theoretical mechanism of reinforcement; that is, the means by which a response becomes more strongly associated with a particular stimulus or set of stimuli. In this analysis, any behaviour occurring in close temporal contiguity to a reduced drive would become reinforced. Researchers in the field of exploration applied this concept to exploratory behaviour: in addition to drives such as hunger and thirst, animals were said to have 'exploratory drives', the reduction of which reinforced their subsequent occurrence. The existence of such a drive was used to explain why rats would cross an electrified grid in order to explore a novel environment (Dashiell, 1925; Nissen, 1930). The drive was secondary in that it was thought to serve one of the primary drives, for example, searching for food.

The concept of exploratory drive or 'curiosity drive' was also used by Berlyne (1950), Montgomery (1953) and Harlow (1950, 1953). It was thought that the exploratory drive was evoked by a novel stimulus situation, and that its strength would first decrease with continuous exposure and then recover during a period of non-exposure (Montgomery, 1953; Berlyne & Slater, 1957). In other words, the exploratory drive was thought to be homeostatic. Harlow (1950, 1953), however, objected to the tendency to view all behaviour as dependent upon secondary homeostatic drives which served primary drives: he reported that hand-reared monkeys which had never had to search for food or water nevertheless manipulated puzzles for long periods in the absence of a primary drive state. Consequently, Harlow argued for a 'manipulation motive' (1950) and a 'visual exploration drive' (1953).

An alternative concept to the curiosity drive was the 'boredom drive'. Rather than novelty motivating exploration, *lack* of novelty (in the form of familiar or unchanging stimuli) was said to motivate such behaviour. According to Myers and Miller (1954), the boredom drive was evoked by homogeneous, unchanging stimuli and reduced by sensory variety. In their description, this initiated the exploration of novel stimuli, and once sated, an animal would explore other more novel stimuli in order to reduce the boredom drive.

Attempts to account for exploration within the realm of classical drive theory met with many difficulties, not least due to the existence of data which contradicted drive interpretations (Birke & Archer, 1983). For example, depriving animals from any opportunity to explore does not always result in increased exploration, and further, Brown (1961) found that animals would begin running and pressing a bar for novel stimuli prior to the introduction of these stimuli. Such evidence caused difficulties for theories positing an exploratory drive.

In addition to the empirical criticisms of drive interpretations of exploration, there have been many objections on philosophical grounds. Bolles (1958, p. 23), for example, argued that drive has no explanatory power:

> *...where little is known about the conditions that control some behaviour (e.g., exploratory behaviour), the inference of a causal drive does little more than restate the facts to be explained.*

Brown (1961, p. 334) was also sceptical about the explanatory power of drive theories and challenged their adequacy for describing behaviour by suggesting that the concept was circular:

> *...the presence of a drive to explore is sometimes inferred from, and at the same time used to explain, behaviour of moving from one place to another, especially if there is no other apparent reason for the movement. The postulation of an exploratory drive in this way is quite circular, and therefore of questionable worth as a scientific explanation.*

2.5.2. Fear theories

To provide a contrast to the suggestion of drive as the mechanism of exploration, some of the experimental research suggesting that exploration is motivated by fear will now be discussed.

Early in the study of exploration it was suggested that animals' spontaneous activity may be inhibited by fear. For example, Higginson (1930) reported that the presence of a cat caused rats to 'freeze' (remain immobile for a period of time), and partly inhibited their exploratory behaviour; Patrick (1931) found that maze exploration was significantly reduced by the sound of two buzzers outside the maze; and Welker (1959) compared activity under two levels of illumination, and reported less activity with bright light. In these three studies, the presence of the cat, the buzzers and the bright light respectively were assumed to be frightening stimuli.

Apart from the presence of fear-inducing stimuli, it has also been suggested that food deprivation produces fear, thus inhibiting activity (Mowrer, 1960). This is consistent with the model above, positing that fear reduces exploration, an idea supported by Lester (1967a) in a study manipulating maze elevation and hunger in rats (both of which were found to induce reduced alternation behaviour).

Despite these findings, however, Welker (1957, 1959) suggested that fear initiates rather than inhibits exploratory activity. Welker found that exploration by rats increased significantly when the animals were confined to a novel situation, and diminished when the rats were allowed to move from an open field to an adjoining small dark box. From these findings it was inferred that the activity in the novel situation represented the rats' attempts to escape. Blanchard, Kelley and Blanchard (1974) extended Welker's findings, showing that forced pre-exposure to a novel situation reduces subsequent latencies to leave the home cage and enter the novel situation. Blanchard *et al.* concluded that reactions to novelty may be based largely, or even entirely, on a fear mechanism. The idea that the increased behaviour reflects attempts at flight or escape has also been reported by Takahashi and Kalin (1989).

An explanation for the disparity in the findings (i.e., some reporting that fear inhibits activity and others reporting that fear induces it) may be due to the variety of ways in which fear was evoked; for example, being placed in a novel enclosure, compared to being exposed to a cat. Thus, certain stimuli may be inherently incompatible with activity, despite their fearful quality; for example, electric shock is more likely to elicit freezing rather than approach to novel stimuli (Hayes, 1960). To allow for this, Bolles and Fanselow (1980) argued that fear ought to be seen as a set of responses rather than a motivational construct, and should therefore be properly defined in terms of those responses.

Hebb (1955) had earlier attempted a solution to the above problem by referring to differences in the level of fear invoked in particular experiments. According to Hebb, animals may seek stimulation from mildly fear-provoking objects because moderate levels of fear are rewarding; however, high levels of fear cause avoidance behaviour. This corresponds to the biphasic theory of fear proposed by Montgomery (1955), later investigated by Schneirla (1959) and Valle (1972). The theory stated that novel stimuli evoke both curiosity and fear, with exploration as the net outcome of competing tendencies to approach and avoid novel stimulation. The tendencies were said to reflect the interaction of two underlying motivational systems corresponding to the level of the 'exploratory drive' and the level of fear or anxiety. Evidence supporting the model was reviewed by Kish (1966), Russell (1973a) and Barnett and Cowan (1976).

A second theory, proposed by Lester (1967a, 1967b) and Halliday (1966) suggested that there is only one process motivating exploration, a single 'fear continuum' operating with a threshold. In the monophasic model, avoidance occurs at high fear levels and exploration occurs at low to moderate levels; studies by Lester (1968, 1969) produced data supporting this hypothesis.

The monophasic theory is consistent with the literature on arousal, in which exploration occurs in response to small or moderate increases in arousal, and withdrawal from stimulation in response to large increases in arousal (thus forming an inverted *U*-shaped function). According to such a model, whether the underlying motivation is above or below threshold depends upon factors such as the magnitude and nature of the environmental change (Russell, 1983). The existence of an inverted *U*-shaped function of exploration was supported in Lester's (1969) study, in which rats were exposed to parts of a maze that gradually changed from being closed to elevated. The animals showed an increasing tendency to approach the arm, and then a decreasing tendency as the level of fear increased.

There have been many criticisms of fear theories of exploration, largely based on the difficulty of separating differences due to fear from differences due to novelty (Russell, 1973a). As a consequence, differences between fear-motivated activity and novelty-motivated activity may remain impossible to define. Kish (1966) pointed out that since an animal in the open field is surrounded by novel stimuli, its behaviour may be interpreted as either approach or avoidance. There is a further difficulty in that animals may explore *despite* their fear, rather than because of it. Finally, Russell (1973a) argued that although fear may indeed facilitate exploration under certain conditions, this does not necessarily constitute evidence that *all* exploration is motivated by fear.

2.6. AN ETHOEXPERIMENTAL INTERPRETATION OF LABORATORY STUDIES OF EXPLORATION

Over the last decade the ethoexperimental approach to the study of behaviour has brought about changes in the way laboratory studies of exploration have been perceived. Gallup and Suarez (1980) gave an exposition of this new conceptualisation, analysing open-field behaviour within an ethological framework. In this section, it will be argued that exploratory behaviour, as observed in laboratory experiments, can be interpreted in an ethological sense, taking ecologically relevant and adaptive factors into account.

According to Rosellini and Widman (1989), recent advances in the ethoexperimental literature have emphasised the effects of laboratory stresses on the behaviour of experimental animals. Fanselow (1988), for example, showed that exposure to electric shock effectively simulates a predatory encounter, such that the resulting behaviour represents a reaction to predation. Earlier, Russell (1983) had argued that interpretations of exploratory behaviour in the laboratory may be better viewed in a wider context, taking a variety of goals into consideration, such as animals' attempts to escape from novelty and search for familiar stimuli, or their approach to novelty to seek information. The resulting description of exploration, according to Rosellini and Widman (1989), would be a more comprehensive account of laboratory findings.

Section 2.6.1 introduces the idea that open-field behaviour may be related to animals' attempts to escape, and section 2.6.2 reviews an ethologically derived model of open-field behaviour, in which exploration occurs as the result of a compromise between the tendency to evade predation and attempts to reinstate contact with conspecifics.

2.6.1. Escape

Early studies postulating a relationship between exploration and escape behaviour, such as those of Welker (1957, 1959), Johnston (1964), Whimbey and Denenberg (1967), Russell and Williams (1973) and Blanchard, Kelley and Blanchard (1974), were to influence ethoexperimental interpretations of open-field behaviour. These authors suggested that exploration in a novel environment may represent the animal's attempts to escape from the situation, and that the decreases in activity observed over time represented a gradual reduction of escape tendencies. To explain this position, exploration was said to have different goals, one of which is to search for and retreat to a familiar area or place of cover (Russell, 1983). Thus, one form of exploration was described as 'escape-directed'. Some of the evidence for the escape-directed nature of exploratory behaviour in a novel environment has come from observations of wild rats: when placed in a novel enclosure, wild rats have been shown to ambulate and jump vigorously, in apparent attempts to escape (Price & Huck, 1976).

In ecological terms, there is obvious adaptive significance for a species such as the rat (an animal susceptible to predation) to be able to escape from a novel environment, particularly if that environment is well lit and affords no cover (Russell, 1983). Rodents and other small mammals are at an advantage in familiar, covered or dark environments (as discussed in section 2.4).

The model of exploratory behaviour expounded by Suarez and Gallup (1981a) (discussed in the following section) was based on the idea that activity in the open field is not motivated simply by a tendency to explore the environment but, rather, by attempts to escape from the confines of the apparatus. Thus, in Suarez and Gallup's model open-field exploration was interpreted within an ecological framework.

2.6.2. Reaction to predation and social separation

The ethoexperimental interpretation of open-field exploration developed by Gallup and Suarez (1980) and Suarez and Gallup (1981a, 1981b, 1983) hinged upon two previously unacknowledged features of the testing situation. The first of these was that most animals are subjected to sudden social separation from familiar and/or imprinted conspecifics when they are removed from their home cages and tested in isolation. Secondly, animals are typically, albeit unintentionally, exposed to a simulated predatory encounter due to contact and restraint by a human being upon removal from the home cage and placement in the open field. In Suarez and Gallup's view, open-field behaviour may therefore be viewed as an interaction or compromise between the opposing tendencies of evading further predatory activity and reinstating social contact.

One way of determining whether open-field behaviour does represent a reaction to predation and social separation is by examining effects of actual predation and social separation on animals. Many studies have been designed in order to assess the effects of the presence of a natural predator on subsequent activity patterns. For example, Noble (1931) found that threat of predation suppressed vocalisation and movement in amphibians, and Blanchard and Blanchard (1971) found that the presence of a cat elicited freezing in rats, even though they had never seen a cat before. Other studies yielding similar results (i.e., inhibition of movement) have been reported by Griffith (1920), Leopold (1944), Armstrong (1955), King (1956), White and Weeden (1966), Hofer (1970), Price (1970), Gallup, Nash, Donegan and McClure (1971), Gallup (1973) Blanchard, Mast and Blanchard (1975), Satinder (1976) and Gallup and Suarez (1980).

It has been suggested that prey progress through several distinct behavioural stages during a predatory encounter (Ratner, 1967). First, according to Ratner, animals freeze and become silent, their principle means of minimising detection. If the predator moves closer the prey may attempt to flee, and if contact occurs, fighting and struggling usually result. During prolonged contact, however, the prey may enter a condition of tonic immobility: a state of complete motor inhibition, a suppression of vocalisation and in some cases, eye closure (a method of concealment for species in which the eyelid matches the colouration of the surrounding skin, Cott, 1940). Ratner (1967) and Gallup (1974, 1977) described tonic immobility as being hypnotic or catatonic-like in nature, and easily induced by holding an animal down for a brief period. The adaptive significance of this behaviour is that prey movement and sound is often a necessary condition for eliciting and maintaining attack (Drummond, 1979); hence suppression of these may avoid detection and contact. Such a state has been shown to be elicited (but not maintained) by physical restraint in ducks (Sargeant & Eberhardt, 1975), quail (Thompson, Foltin, Boylan, Sweet, Graves, & Lowitz, 1981), a wide variety of zoo animals (Hediger, 1955), and perhaps even in humans (Suarez & Gallup, 1979). In addition, *simulation* of a predatory encounter has been shown to result in less locomotion and vocalisation in rats (Williams & Lierle, 1988).

In a series of experiments by Suarez and Gallup (1981a) designed to define the predatory overtones of open-field testing, it was found that visibility of the predator's eyes and the presence of sudden noise were particularly salient features in eliciting immobility. Results showed that birds tested in the presence of artificial eyes took three times longer to begin ambulating and distress-calling than birds for whom the artificial eyes were masked. An even more pronounced effect occurred when birds were subjected to a sudden noise: they took a hundred times longer to attempt to escape and begin distress-calling. Other findings supporting the effects of eyes have been reported by Gallup (1973), Gallup, Nash, Donegan and McClure (1971); and evidence supporting Suarez and Gallup's study on effects of noise has been reported by Miller and Murray (1966), Edson and Gallup (1972), Gallup, Nash, Potter and Donegan (1970) and Nash, Gallup and McClure (1970).

The significance of these findings in relation to the issue of open-field behaviour is that the presence of an *experimenter* has been shown to produce the same predator defense strategies (Williamson, 1950; Cornwell & Bartonex, 1963; Edson & Gallup, 1972; Gallup, Cummings, & Nash, 1972). This strongly suggests that open-field testing may bring with it overtones of predation (Suarez & Gallup, 1981a).

Adding weight to this suggestion is research supporting the idea that handling is an aversive stimulus for many animals. Candland, Foulds, Thomas and Candland (1960), for example, demonstrated that rats learnt discrimination and reversal problems purely to avoid being picked up and stroked. Abel (1971) reviewed such evidence and came to the conclusion that a combination of handling and the open field may induce greater fear than the open field itself. Consistent with Suarez and Gallup's (1981a) proposal that human contact simulates a predatory encounter, Abel (1971) found that elimination of handling diminished the occurrence of predator evasion behaviour.

In Suarez and Gallup's model (1981a, 1981b), open-field behaviour represents a compromise between attempts to avoid predation and to reinstate social contact. The remainder of this section deals with the issue of social reinstatement, showing how animals' reactions in the wild may be similar to reactions in the open field.

In natural conditions, according to Suarez and Gallup (1983), the young of many avian species ambulate and emit distress calls when separated from their mother or brood-mates. For example, Suarez and Gallup found that chickens ran faster down a straight alley if the goal-box contained one or more conspecifics, as opposed to when the goal-box was empty or contained a guinea pig. The adaptive significance of such behaviour is that it facilitates detection by the mother or conspecifics, thereby re-establishing social contact (Collias, 1952; Guiton, 1959; Sluckin, 1965). As argued above, however, threat of predation in the wild may suppress these responses, resulting in a reduction of movement and vocalisation. Thus, behaviour produced in an open-field represents a compromise between these two opposing tendencies: the likelihood of freezing in response to predation, but increased activity in response to social separation.

Rosellini and Widman (1989) supported the general analysis made by Suarez and Gallup (1983), and added that qualitative aspects of exploratory behaviour may be due to particular animals' sensitivity to predation. Exploratory behaviour, according to Rosellini and Widman can be viewed as arising from competition between the tendency to acquire information about the environment (such as the location of conspecifics) and the need to avoid the stress of predation.

2.7. CONCLUSION

The aim of Chapter 2 was to contribute towards a definition of exploration. Given the problems inherent in defining any psychological phenomenon, the approach taken here was to describe concepts of exploration by discussing adaptive benefits and theories in the experimental and ethoexperimental literature.

In experimental psychology, theories of exploration have relied on hypothetical motivational constructs such as curiosity, boredom, drive, arousal and fear. It may be argued that these only allow for limited prediction and testing, since they are not linked to independently measurable events (Russell, 1983).

Ideally, as Cowan (1983) argued, exploration should not be evaluated in isolation from other aspects of behaviour and ecology. An awareness of the relevance of adaptive and ecological factors allows for a better understanding of the role of exploration in an animal's behavioural repertoire, and it was argued in this chapter that this has been the aim of ethoexperimental studies of exploratory behaviour. Considerations of behaviour in its ecological context widens the concept of exploration, showing how it plays a role in an animal's survival strategies. For example, it has been proposed here that exploration in the laboratory may unintentionally subject animals to predatory contact from the experimenter, as well as sudden separation from conspecifics; and as a result, activity may actually represent the animal's opposing tendencies to evade predation and reinstate social contact (Suarez and Gallup, 1981a, 1981b).

In practice, 'exploration' is a unifying term describing a variety of activities with certain features in common, and it may be defined according to its observed physical attributes, its consequences, its adaptive significance or its theoretical function. Each concept of exploration is embedded in a theory which interprets it, and so diverse definitions arise according to the orientation of the researcher.

Chapter 3 describes the orientation of the research done in this thesis: the study of exploration in the open field.

CHAPTER 3

THE OPEN FIELD AS A METHOD FOR STUDYING EXPLORATION

3.1. INTRODUCTION

Chapter 3 introduces the open field as a method for studying exploration, and is divided into two broad sections. The first deals with independent variables inherent in any open-field study, namely, apparatus characteristics, testing procedures and experimental designs; and the second covers some of the dependent variables commonly measured in the open field. These include ambulation or activity, parameters other than whole body movement and measures derived via physiological techniques. The chapter concludes with an indication of the methods used in the present studies.

3.2. THE OPEN FIELD

Suarez and Gallup (1983) defined the open field as a novel enclosure that is larger than the home cage. During the years following its origin in the 1930s, the open field has become a widely used tool for measuring the behaviour of a variety of animal species. A detailed review by Walsh and Cummins (1976) critically examined the use of this instrument, especially regarding the development of a standard form for its use.

According to Walsh and Cummins, since its introduction by Hall (1934a), the open-field test has become one of the most widely used instruments in animal psychology. The rationale originally underlying its use stemmed from the measurement of emotional reactivity, or 'emotionality', in rodent species, by recording activity, freezing (immobility) and defecation. According to Denenberg (1969), to obtain such measurements an animal was introduced into an environment which was different from any environment it had previously encountered, thus triggering behaviour in response to mildly noxious surroundings. Some of the difficulties encountered in interpreting open-field activity and defecation in terms of emotionality have been discussed by Archer (1973) and Denenberg (1969) in reviews of the open-field literature. One example comes from Corman and Biondo (1969), who were sceptical about the assumed correlation between emotionality and the open-field measures of locomotion, latency and time in the centre of the apparatus.

Behaviour observed in the open field depends on a variety of factors and their interactions. Denenberg (1969), for example, described variations in test factors such as home-cage removal and transfer to the open field, exposure to the open field and its surroundings, and all prior experiences of the test situation. As stated by Denenberg, any behaviour elicited must be a function of the multi-way interaction of such factors, together with the varying genetic and experiential backgrounds of the animals tested.

Sections 3.3 and 3.4 describe independent and dependent variables respectively, indicating in the first instance how changes in the apparatus, testing procedures and experimental designs can influence subsequent behaviour, and secondly, describing measures commonly used in open-field testing.

3.3. INDEPENDENT VARIABLES

There may be many variations in the open field itself, as well as variations in testing procedures and designs, and each of these has effects on the behaviour being measured. The following sections deal with variations in apparatus characteristics, testing procedures and experimental designs.

3.3.1. Apparatus characteristics

Walsh and Cummins (1976, p. 483), in their discussion of the standardisation (or lack thereof) of open-field testing, stated that:

> *Almost every physical characteristic of the apparatus, its surroundings, and every procedural step have been widely varied, so that although standardization may have been established within individual laboratories, there is a disturbing lack of conformity in procedure and results within the literature as a whole.*

The extensive range of open-field apparatus characteristics include variations in its size, shape, colour, subdivision, wall height, floor texture, odour, and nature and location of the starting area; the presence, absence and nature of additional inherent stimuli; variations in the surroundings, such as the nature, intensity and position of light, sound and odour sources; and lastly, the visibility and position of the observer. In summary, "it is hard to think of any facet which has not been modified" (Walsh & Cummins, 1976, p. 483).

The following subsections give details on some of the most commonly reported variations in open-field design: size and shape, ambient noise, environmental odours and level of illumination, and addition of objects.

Size and shape

Buhot (1989) reported that the size of nest boxes induces contrasting effects on the exploratory behaviour and nest establishment of mice, and Krsiak and Janku (1971) observed changes in exploratory behaviour in mice as a function of the size of the test enclosure. Such results suggest that animals pay attention differentially to the spatial features of their environment. In other words, the size and shape of the apparatus is important.

Open-field size has varied for different species; for example, a whole room has been used for human infants (Rheingold, 1969), while a small field has been used for mice (Manosevitz, 1970). Variations in open-field size have been shown to produce significant effects on subsequent behaviour. In a large open field, for example, many researchers have observed great increases in ambulation (e.g., Broadhurst, 1957; Montgomery, 1951; Oldham & Morlock, 1970; Blizard, 1971; Buhot, 1987).

Evidence relating to open-field shape has been reported by Valle (1970) in his studies of thigmotaxis (or 'wall-hugging'). Some animals have a tendency to remain in corners, suggesting that circular designs (e.g., Barnett & Cowan, 1976) may be preferable to square or rectangular designs. Another study, reported by Phelps and Roberts (1989), showed that characteristic patterns in rats' food-hoarding and food-carrying behaviour occurred according to the shape of a 4-arm maze and the amount of food available. As the size of the food increased, rats tended to carry it to the centre of the maze, and blocking one of the arm entrances resulted in faster locomotion towards the centre.

Ambient noise, environmental odours and level of illumination

Exploratory behaviour has been shown to be influenced by the intensity of ambient noise, environmental odours and level of illumination present at the time of testing. In the first category, Broadhurst (1957) found that exploration was affected by high noise intensity. Similarly, Hofer (1970) reported that any abrupt noise can inhibit locomotion and induce prolonged immobility in a variety of species. Some researchers (e.g., Halliday, 1968; Ivinskis, 1968) have argued for the use of a white noise of low intensity, as this masks any extraneous sounds which may be disturbing to the animal.

Regarding environmental odours, Russell and Chalkly-Maber (1979) found that animals were responsive to the former presence of a conspecific in a particular section of an open field, and they were also affected by the degree of stress experienced by the predecessor. Earlier, McCall (1969) demonstrated the importance of human odour in rat exploration, by showing that rats tend to spend more time on the side of the field nearest to the experimenter who had reared them, rather than near an experimenter who had had no previous experience of the rats. To overcome such biases, it has been suggested that the apparatus be washed between trials (Whittier & McReynolds, 1965), and that observations be made from behind a screen (Nielson, 1970) or through a one-way mirror (Fox & Spencer, 1969).

Most studies varying level of illumination (e.g., those reviewed by Archer, 1973; Russell, 1973b) have shown that bright light reduces ambulation. High levels of illumination have also been associated with diminished rearing and thigmotaxis (Valle, 1970), which, according to Russell (1973b), probably reflects the aversive influence of bright light.

In contrast, low light intensity has been shown to have reinforcing properties (Kling, Horowitz, & Delhagen, 1956) and to cause increases in exploratory behaviour (Krsiak & Janku, 1971), particularly in mice. Despite this effect, early experience with bright light can lessen its aversiveness, until animals prefer it no less than dim light (Levin & Forgays, 1959). This reflects the interactional quality of the variables of lighting intensity and rearing environment, as reported by Livesey and Egger (1970) and Sackett (1967a). Furthermore, it should be noted that effects of illumination differ for different strains: albino rats are more sensitive than pigmented rats (Dixon & DeFries, 1968a); and different species: many children, for example, are afraid of the dark (Russell, 1979).

Addition of objects

In line with the less constrained and more ecologically valid measures of animal exploration suggested by Rosellini and Widman (1989), objects may be included in the open field. These provide measures of physical interaction and general quantification of activity (Renner & Rosenzweig, 1986; Renner, 1987), indicating investigatory behaviour and object preferences. In the past, objects such as nuts and bolts, door stops and mirrors have been used in the open field (e.g., Ehrlich & Burns, 1958; Furchtgott, Wechkin, & Dees, 1961). Other researchers quantifying exploration by means of object interactions include Foshee, Vierck, Meier and Federspiel (1965), Russell and Williams (1973), Einon and Morgan (1976) and Millar, Evans and Chamove (1988).

Studies involving the use of novel objects will be discussed in more detail later in this chapter, and in Chapter 4.

3.3.2. Testing procedures

The usual methods of testing in an open field have been described (e.g., Walsh & Cummins, 1976; Barnett & Cowan, 1976) as consisting of removing the animal from its home environment, carrying it to the test area (which the animal has not previously experienced), and placing it in the open field. The animal's movements are then recorded and defined, often in terms of exploratory behaviour, grooming, defecation and freezing. The procedure may vary in terms of the specific method of transport and placement used and the duration of the experimental trials, and, as summarised by Walsh and Cummins, each of these influences the subsequent open-field behaviour produced.

Animal transport and placement in cage

Most animals are assumed to be transported by hand, but details of animal removal and transfer are rarely reported in the literature (Walsh & Cummins, 1976). However, effects of handling stress have been well documented: Candland, Foulds, Thomas and Candland (1960) and Abel (1971), for example, argued that handling remains an aversive stimulus in rats, even after frequent exposure. Stellar (1960) described the marmoset's reaction to handling as extremely stressful, resulting in wild struggling to the point of physical exhaustion. As a result, many researchers have favoured less distressing methods of animal transport; for example, a box (Nielson, 1971; Tighe, 1965; Epple, 1970), a tube (Dixon & DeFries, 1968b), or a transport cup (Hofer, 1970). Another less stressful method of transport is where animals are habituated to the transport container and the carrying procedure prior to testing (Nielson, 1970). Abel (1971) reported that such familiarisation may produce increases in ambulation at the start of the open-field trial.

Animals are usually placed into the centre of the open field at the beginning of their experimental trial (e.g., Clark, Gorman, & Vernadakis, 1970), or otherwise against the retaining wall (e.g., King, 1970). It is important to note that rats tend to remain on the side of the field on which they are originally placed (Satinder, 1969).

Trial duration

There has been considerable variation in the length of time during which animals have been observed in the open field; for example, trials of a few minutes (e.g., Krsiak & Janku, 1971), or trials of one hour (e.g., Russell, 1973b).

In many cases behaviour is summed, either over each trial, or over all trials. The latter of these procedures has come under criticism: Suarez and Gallup (1981b), for example, argued that initial open-field activity measures something different from that of subsequent days. In this case, collapsing measures across days would lose valuable effects present in the data, and the representation of behaviour would not be as accurate as it might have been. In order to avoid this, Suarez and Gallup advocated the use of a single trial, thus eliminating habituation effects. However, multiple trials have often been used, with the advantage of greater reliability and the opportunity for temporal analysis (Walsh & Cummins, 1976). Most experimenters using multiple trials have used around four, although up to sixty have been used (Bronstein, 1972).

Inter-trial intervals have been shown to have an influence on activity patterns; for example, Battig (1969) found that short inter-trial intervals (e.g., 3-12 minutes), as opposed to longer intervals (e.g., 2 hours), produced a milder inhibition of ambulation on subsequent testing. The usual interval between trials is 24 hours, an interval which, according to Walsh and Cummins, avoids the complications of diurnal rhythms.

3.3.3. Experimental designs

A detailed review on experimental designs used in studies of exploration has been provided by Russell (1983). Section 3.3.3 is based on this review, summarising methods by which psychologists have studied open-field exploration. As a general rule, open-field studies involve exposing an animal to a novel environment. In practice, this may be brought about by confinement to a novel area, exposure to discrete, localised environmental changes in a familiar area, access to a new area adjacent to a familiar one, alternation between different environmental areas or response for environmental change. Each of these possibilities will be discussed in the following subsections.

Confinement to a novel area

A common method for studying exploration is to place an animal into a novel environment; this method is referred to as a 'forced exploration' test, since the animal has no opportunity to escape from the situation. The method has been shown to induce greater amounts of activity compared to that produced in 'free exploration' tests (in which animals have access to novel stimuli in a familiar place): Moser, Moser, Wultz and Sagvolden (1988), for example, stated that if conditions allow, rats in a forced exploration test attempt to leave the area by burrowing or leaping on to the surrounding wall. Welker (1957) and Hayes (1960) explained this finding in terms of fear generated by the forced situation.

Criticisms of the forced exploration test may be based on adaptive considerations: in the wild, animals rarely, if ever, find themselves in a novel environment with no means of escape. According to Russell (1983), even animals which are captured by predators have at least the possibility of relocating a familiar area. Thus, the forced exploration test does not correspond particularly closely to situations typical of the environment of wild animals, and could therefore be said to have little ecological validity. In other words, confinement to a novel area with no opportunity for escape and no objects to explore does not conform to an ethoexperimental approach to the study of exploration. In fact, the use of forced tests was largely dictated by the convenience and ease of recording behaviour (Russell, 1983).

One attempt to overcome the problem has been to provide holes or recesses into which animals can poke or dip their heads. The 'hole-board' has been used by File and Wardill (1975a, 1975b), Makanjuola, Hill, Maben, Dow and Ashcroft (1977) and Weinberg, Krahn and Levine (1978). Another method has been to provide objects to encourage exploration (see section 3.3.1).

It may be argued that tests involving a choice between novel and familiar stimuli have more ecological relevance; for example, where animals are exposed to changes in a familiar place.

Exposure to discrete, localised environmental changes in a familiar area

Russell (1983) described a more ecologically sound alternative to the forced exploration test as being the presentation of discrete, localised novel stimuli to an animal in familiar surroundings. Such an experimental design allows an animal the opportunity to display preferences for some stimuli over others, and, perhaps more importantly, it constitutes a much closer parallel to conditions under which animals normally encounter novelty (such as new objects or odours from other animals) in the wild.

An effective method for introducing discrete, localised novel stimuli into a familiar environment is by placing one or more new objects in or adjacent to the home cage. Alternatively, novel stimuli may be introduced into an area to which the animal has been 'pre-familiarised' prior to the testing time. Studies of reactions to object novelty are discussed at length in Chapter 4 (section 4.3.1); it suffices to mention here that novel objects typically elicit approach and exploration (e.g., Berlyne, 1955; Glickman & Sroges, 1966; Barnett & Cowan, 1976; Poucet, Durup, & Thinus-Blanc, 1988; Millar, Evans, & Chamove, 1988).

The usual method for measuring exploration in an open field containing novel objects is to record the frequency and duration of object contacts. Such a procedure allows for the potentially important distinction between object exploration and general activity. Leyland, Robbins and Iverson (1976) reported a dissociation between these two behavioural measures, emphasising the differences each imply: for example, higher levels of locomotion do not necessarily indicate higher levels of exploratory behaviour. Differences between ambulation and exploration are discussed further in this chapter (in section 3.4, which deals with dependent variables).

Access to a new area adjacent to a familiar one

This type of experimental design is similar to the previous one, except that instead of novel objects, the animal is permitted access to a novel area: a second kind of 'free exploration' test (the first being exposure to novel objects in a familiar place).

This may be achieved by removing a barrier between the animal's cage (or some other area with which it is familiar) and an adjoining section of environment. The technique has been shown to result in movement into the new area (Barnett & Cowan, 1976; Barnett & Spencer, 1951; Hughes, 1965a, 1968; Russell, 1975), sometimes after a delay due to fear (Blanchard, Kelley and Blanchard, 1974; Montgomery, 1955; Williams & Wells, 1970).

There has been much debate in the literature on differences between free and forced tests of exploration, and it has been argued that the two methods produce entirely different results. Lore and Levowitz (1966), for example, reported that rats are often slow to emerge from a familiar start box, and therefore judged as being less exploratory, whilst animals placed directly into an open field are usually more active, and therefore judged as being more exploratory. In support of this, Welker (1957, 1959) had earlier compared the activity of animals forced to remain in an open field with the activity of animals that were allowed free access to, but were not forced into, an open-field test situation. Welker found that forced animals were significantly more active in the field than free animals, suggesting that fear and attempts to escape play important roles in forced exploration (as discussed in Chapter 2). Other investigators have supported this analysis (e.g., Hayes, 1960; Kish, 1966; Valle, 1972; Blanchard, Kelley, & Blanchard, 1974). Moser, Moser, Wultz and Sagvolden (1988) concluded that the free exploration technique provides a better and more ecologically-relevant measure of exploratory behaviour as it occurs in the wild.

Alternation between different environmental areas

Studies of alternation behaviour may involve any of the open-field methods discussed above; for example, alternation has been observed in animals confined to a novel area (Dennis, 1939; Glanzer, 1953a, 1953b; Montgomery, 1952) and in animals more familiar with their environment, including animals in the wild (Barnett & Cowan, 1976).

The phenomenon of 'spontaneous alternation' was first described by Tolman (1925), to account for the predictable movement of animals about their living space: animals tend to enter the area visited least recently, rather than move at random. In the laboratory, alternation behaviour has been studied in a *T*-maze (a confined novel environment), in which an animal is placed in a start arm and allowed to move to one of two choice arms. According to alternation theory, on replacement in the start arm an animal is more likely to enter the unvisited arm or the same arm if it is changed in some way (Montgomery, 1952; Glanzer, 1953b; Dember, 1956; Kivy, Earl and Walker, 1956; Sutherland, 1957; Dember & Fowler, 1958; Hughes, 1965b).

In the wild, regular systematic patrolling observed in rats has been described as alternation (Barnett & Cowan, 1976; Cowan, 1977b). Such patrolling involves an orderly sequence of visits to different parts of the environment, behaviour characteristic of alternation in the laboratory. Alternation has been studied in other species as well; for example, fish, rats and humans (Neiberg, Dale, & Grainger, 1970), chicks (Hayes & Warren, 1963; Cogan, Jones, & Irons, 1979) and hamsters (Sinclair & Bender, 1978).

Response for environmental change

A fifth procedure for studying exploration is a method by which an animal can bring about environmental change by responding in a particular way. The crucial feature of such testing is that the novel stimulus or change does not impinge on the animal until after the animal has responded.

This approach originated from laboratory studies employing operant procedures: for example, a rat may press a lever to instigate an environmental change, such as a brief period of illumination, light offset, sound or mild electric shock (such procedures have been reviewed by Berlyne, 1960, Fowler, 1971, and Kish, 1966). An alternative is a discrete trial situation, in which an animal must enter the arm of a *T*-maze containing novel stimuli (Montgomery, 1954; Montgomery & Segall, 1955).

Other procedures require an animal to respond correctly in order to view the environment outside the test apparatus. Halliday (1968) reported that this is a standard technique in primate research (e.g., Butler, 1953, 1957, 1958, 1965; Butler & Woolpy, 1963), and it has also been used for pigeons (Stahl, O'Brien, & Hanford, 1973). Studies by these researchers suggested that visual exploration is a reinforcer, in the same sense as conventional reinforcers such as food or water (Kish, 1966; Halliday, 1968). Supporting this idea is the finding that the sensory reinforcement effect can be maintained for some time, with response rates following the conventional extinction patterns when the light contingency is terminated (Barnes & Baron, 1961; Kling, Horowitz, & Delhagen, 1956).

3.4. DEPENDENT VARIABLES (MEASURES IN THE OPEN FIELD)

Techniques of measurement in open-field studies vary from automatic recording of behaviour (e.g., Battig, 1969) to verbal descriptions of behaviour (e.g., Blurton Jones & Woodson, 1979). Automatic recording devices have come under considerable criticism (e.g., Prescott, 1970), since their use usually results in the loss of much valuable qualitative data. According to Prescott, the use of descriptive methods (by means of direct observation) avoids problems inherent in the use of automatic recording devices, and can provide a basis for clarifying the nature of any behavioural changes which occur. The most common descriptive method is to record the frequency and duration of behaviours with an event recorder, either from watching video tape or watching animals directly (e.g., Renner, 1987; Roder, Timmermans, & Vossen, 1989). Video tape is often preferred over live observation since it allows more accurate measurement due to the possibility of repeated observations of the same event (e.g., by a number of independent judges), or the viewing of multiple aspects of behaviour occurring simultaneously (Renner, 1987).

The variety in the types of description and the number of dependent variables used to analyse open-field behaviour has increased a great deal since the early work of Hall (1934a). Walsh and Cummins (1976) classified dependent variables in terms of behavioural and physiological parameters; each of these will be discussed in the sections which follow, under the headings 'ambulation or activity', 'parameters other than whole body movement' and 'physiological techniques'. In each category it is possible to identify causal, functional and descriptive aspects of the behaviour being described. Blurton Jones and Woodson (1979) recognised the merits of each of these features, arguing that it is not enough to simply describe behaviour without reference to its possible cause and function. For example, Baenninger (1967) categorised exploration in terms of its social or non-social aspects; that is, according to its function within a group of animals.

3.4.1. Ambulation or activity

Perhaps the most favoured open-field measure has been ambulation or activity, probably because of its ease of quantification and the face validity for interpretive constructs of exploration and arousal (Walsh & Cummins, 1976). In this section ambulation will be discussed as an open-field measure of exploratory behaviour, and then attention will be drawn to some of the problems inherent in its use, particularly as an indicator of exploration.

Ambulation is usually scored spatially; that is, according to its locality. Most frequently, the open field is subdivided into a number of regions (e.g., inner or peripheral areas of the apparatus, floor squares or maze arms), and the experimenter counts the number of subdivisions entered. This method has been employed by investigators such as Ehrlich and Burns (1958), Ivinskis (1968), Morrison and Thatcher (1969), Valle (1970) and Renner (1987).

Walsh and Cummins (1976) suggested alternative ways of measuring ambulation; for example, by recording the amount of time spent ambulating (e.g., Russell & Williams, 1973), or according to characteristics of the apparent aim of ambulation (such as escape attempts, Ehrlich & Burns, 1958). A third possibility is when object or conspecific interactions are measured in connection with locality of ambulation: Fox and Spencer (1969), for example, measured the frequency and duration of activity occurring within the same square as an inanimate object. A similar technique was employed by McCall, Lester and Dolan (1969), who examined not only frequencies and durations, but qualitative differences in responses to objects. Latane, Cappell and Joy (1970) applied this method to a measure of 'interaction with conspecifics' by scoring the distance between two animals and the time they spent in contact with one another. Ambulation has also been measured in association with specifically defined behaviours such as walking, rearing and sniffing (Prescott, 1970), the assumption being that increased 'activity' consists of increases in behaviour related to the sampling of environmental stimuli.

It is also possible to score activity by its absence. This is achieved by measuring latency and freezing, behaviours negatively correlated with ambulation. Latency, according to Walsh and Cummins (1976), is measured by the time taken from the start of a trial until the occurrence of a certain type of behaviour (usually ambulation). Ivinskis (1968, 1970), Poley and Royce (1970) and King (1970) used 'latency to emerge from the home cage' as an index of emotionality, the latter showing that it was negatively correlated with activity. Alternatives are to measure the latency to reach the periphery of the open field from the centre (Tobach, 1966), or to reach the centre from the periphery (King, 1970).

Freezing, defined as the sudden interruption of activity in favour of immobility (Renner, 1987), has been widely used as an indicator of a high-stress state (Walsh & Cummins, 1976). It has been shown to occur in a vast range of species (as reported in Chapter 2, section 2.5.2), particularly as a response to danger or physical restraint (Suarez & Gallup, 1981b). Walsh and Cummins noted that it should not be forgotten that another cause of prolonged immobility is sleep.

Since measures of latency and freezing are normally negatively correlated with ambulation (Prescott, 1970), they provide a valuable alternative means for measuring open-field activity.

Problems with measures of ambulation as indicators of exploration

Greater levels of locomotor activity have often been thought to reflect more exploration of environmental stimuli, the assumption being that in order to explore the environment the animal must move about (Russell, 1983). However, there is considerable debate as to whether locomotion is an index of exploration.

Halliday (1968) argued that it may not be true that the animal with the highest level of locomotion is exploring to the greatest extent, just as the person who moves around a museum the most may not be the one who is seeing the most exhibits. A dissociation between ambulation and exploration has been reported in many open-field studies. A common finding is that animals may show an increase in object investigation as a function of increases in object novelty or complexity (e.g., by sniffing), but no corresponding increases in ambulation (Fowler, 1965; Sheldon, 1968a; Corman & Shafer, 1968; Leyland, Robbins, & Iverson, 1976). Demonstrations such as these, where effective manipulators of exploration have no effect on locomotor activity, strongly suggest that ambulation and exploration are not correlated.

Other researchers have dissociated ambulation and exploration by showing that increases in locomotor activity need not be accompanied by increases in exploratory and orienting responses (e.g., Foshee, Vierck, Meier, & Federspiel, 1965; Leyland, Robbins, & Iverson, 1976; File, 1978). One result of this has been the exclusion of measures of ambulation in studies investigating exploratory behaviour (e.g., Poucet, Durup, & Thinus-Blanc, 1988).

Rather than reflecting exploration, then, ambulation may simply correspond to 'spontaneous activity' or 'exercising' (Berlyne, 1960; Fowler, 1965; Halliday, 1968), although Berlyne (1960) suggested that environmental ambulation may be qualitatively different from, say, the exercise rats receive in wheel-running. Alternatively, ambulation may reflect avoidance, emotional flight responses, or attempts to escape (Whimbey & Denenberg, 1967). Given that exercise and attempts to escape both provide animals with information about their environment, these forms of ambulation may therefore be thought of as related to exploration. However, the difference is that these types of exploration probably provide animals with different sorts of information about the environment (Russell, 1983).

In summary, discrepancies in data using locomotion as an index of exploration suggest that there are difficulties in using 'ambulation' synonymously with 'exploration'. Maier, Vandenhoff and Crowne (1988) argued, as a consequence, that the terms should not be used interchangeably, but regarded instead as conceptually separate.

3.4.2. Parameters other than whole body movement

According to Kish (1966), a better method of obtaining data on exploration is to make fine distinctions between behaviours which do not necessarily involve whole body movement. Section 3.4.2 describes dependent variables which fall under this category: self-directed activities (e.g., grooming, washing and teeth-grinding); vocalisation; activities directed towards the open field (e.g., scratching and digging, rearing, propping and head-dipping); and activities directed towards objects (e.g., visual exploration, sniffing and manipulation of objects).

Self-directed activities: Grooming, washing and teeth-grinding

Grooming, washing and teeth-grinding are behaviours which are self-directed; they have been shown to be negatively correlated with indices of high activity states (Prescott, 1970). These behaviours include self-washing, licking and scratching movements (Russell, 1973b). According to Hughes (1969), teeth grinding may possibly indicate anxiety, on the grounds that it may represent a 'tooth sharpening defensive behaviour'.

Vocalisation

Vocalisation, like teeth-grinding, has been taken as an indication of distress; indeed, the vocalisation emitted by animals placed in the open field has sometimes been called 'distress calling' (e.g., Candland & Nagy, 1969). According to Candland and Nagy, distress calling has been used as a major index of emotionality, especially in species for which ambulation and defecation are not reliable, such as the cat and domestic fowl.

Marmoset and tamarin vocalisations have been described in detail by Epple (1968). Epple suggested that the vocalisations of these species have social significance as a means of communication, as well as being indications of distress. In analysing the vocal repertoires of animals, it is necessary to observe the situations which elicit each vocalisation and the reactions they produce, taking ecological factors into account. For example, marmoset twitters and trills are associated with short-range contact with conspecifics, whilst short, high-pitched and very sharp whistles are associated with danger warnings (Epple, 1968). Another situation in which vocalisation occurs is in the presence of a novel object. Millar, Evans and Chamove (1988), for example, observed this form of vocalisation in their study of marmosets' and tamarins' responses to novel objects.

Activities directed towards the open field: Scratching and digging, rearing, propping and head-dipping

According to Walsh and Cummins (1976), the terms 'scratching' and 'digging' probably refer to essentially the same behaviour, associated with conditions of hard and loose floor material respectively. Digging has been described as a correlate of high activity (Prescott, 1970), a sign of frustration when a reward is anticipated (Timberlake, 1982), a defensive reaction (Pinel, Symons, Christensen, & Tees, 1989) or an adjunctive behaviour occurring during post-reinforcement pauses (Litchfield, 1987). It may occur at floor level, although Renner (1987) included digging and scratching motions at the wall of the arena in the same category.

The categories of 'rearing', defined as standing on the hind legs with the forepaws in free air, and 'propping', where the forepaws are against the wall of the arena (Renner, 1987), have also been widely used (e.g., Ivinskis, 1968, 1970; Russell, 1973b; Litchfield, 1987). In combination with ambulation, rearing and propping have been employed to provide measures of activity or excitability.

A measure called 'head-dipping' has been used by Blanchard, Shelton and Blanchard, (1970) and File and Wardill (1975b) in measuring activity and exploration. The head-dipping response is usually observed in a hole-board apparatus, where an animal may look into holes in the floor. Blanchard *et al.* reported that head-dipping reflected novel aspects of the environment, since novel objects were present below the holes.

Activities directed towards objects: Visual exploration, sniffing and manipulation of objects

Visual exploration has been measured in cats (Riesen & Aarons, 1959), mice (Barnes & Baron, 1961) and pigeons (Stahl, O'Brien, & Hanford, 1973), but measures of vision have particularly been developed in work with primates (e.g., Butler, 1953; Stellar, 1960; Anderson & Chamove, 1984). This arises from the observation that monkeys engage in considerable amounts of visual inspection of objects, animals and people in their environment. For this reason, visual exploration has been used as a means of reinforcement (e.g., Butler, 1953, 1957, 1958, 1965; Butler & Woolpy, 1963).

Sniffing has been widely used as a measure of exploration. It may be directed towards any part of the open field, including sniffing the air (Russell, 1973b), or may be directed towards stimulus objects (Bolles & Woods, 1964; Renner & Rosenzweig, 1986; Renner, 1987; Rosellini & Widman, 1989). In cases where sniffing accompanies another behaviour, such as manipulation of objects, the latter category is usually applied.

The inclusion of novel objects in an open field allows for the measurement of stimulus interaction not covered by any of the dependent variables discussed above, since objects supply foci for exploratory responses (Russell, 1983), thus providing a contrast to measures of ambulation alone (Poucet, Durup, & Thinus-Blanc, 1988). According to Kish (1966), exposing animals to novel objects provides a refinement of purely locomotor exploration, thus minimising the possibility of a contaminating factor in the measurement of activity level.

A measure of object interactions provides valuable information about a broad range of investigatory behaviours, including movements in space as well as exploration directed towards objects in an animal's environment. Renner and Rosenzweig (1986) argued that object interaction measures are necessary if one is to capture the complexity inherent in spontaneous exploratory behaviour. To take this one step further, Rosellini and Widman (1989) used objects which varied in manipulability; thus, one object was of a size and weight such that it could be manipulated by the animal, whereas a second object could neither be moved nor manipulated by the animal. This allowed for the occurrence of an even wider range of exploratory behaviours, consistent with Renner and Rosenzweig's conception of a broad measure of exploration.

The following list consists of examples of objects used in experiments measuring stimulus interaction as a dependent variable, included here to give an indication of the diversity possible in studies with objects: a door stop and a flashlight battery (Furchtgott, Wechkin, & Dees, 1961), a polished brass finial (Ehrlich & Burns, 1958); a mirror, a toy puppy and a flashing light (Fox & Spencer, 1969); a chrome-plated microphone connector (Foshee, Vierck, Meier, & Federspiel, 1965); branches, swinging ropes, nest boxes and shelves (Epple, 1970); a plastic cylinder (Russell & Williams, 1973); a plastic flower pot, a cardboard tube, the lid of a mouse cage, crumpled paper, cotton wool, a kettle whistle and a plastic ball (Einon & Morgan, 1976); a metal swing and a chain with hooks (Candland, Weldon, Lorinc, & O'Connor, 1978); hanging toys (Renner & Rosenzweig, 1986); junk objects kept in the laboratory (Renner, 1987); a cotton wool ball, a non-ticking clock, keys, a plastic flower, a paperweight and a paper cup (Millar, Evans, & Chamove, 1988); a glass jar, a copper weight, a bowl and a cup (Poucet, Durup, & Thinus-Blanc, 1988); a stainless steel house, a slide and a tunnel (Forster, 1986; Litchfield, 1987); hoses, child-development toys, plastic milk crates, a hanging chain, plastic pails, mirrors and pebbles (O'Neill, 1989); a colour-and-sound game consisting of ropes, lights and sounds (Markowitz & Line, 1989); a trapeze, a hammock, a radio, a television, soccer balls and soft children's toys (Blackmore, 1989); golf balls, rawhide dog bones, a *Fisher-Price* 'Butterfly Ball' (a clear plastic ball which, when rolled, spins a colourful butterfly which is enclosed in it), a stainless steel chain and stainless steel cat feeding bowls (Gilbert & Wrenshall, 1989); magazines, brushes, toys, stickers, unbreakable plastic mirrors, perfume samples, whistles, rubber-bands, cardboard, cloth sacks and balloons (Fouts, Abshire, Bodamer, & Fouts, 1989); a plastic windmill, a transparent plastic tunnel and a piece of wire grid (Forster, 1990).

Measurement of object manipulation has been recorded by means of a variety of behavioural categories. For example, Renner (1987), in observing the rat, formed the following categories of object manipulation, as observed in the rat: low risk investigation (sniff or nose contact), paw contact (single paw contact, lean on object, grab object), climb or enter object (weight on object, all four paws on object), contacts with mouth (bite object, drag object), accidental contacts (collide with object moving forward, collide with object moving backward), object 'behaviour' (object moves). For Renner, any combination of categories could occur during any given interaction with an object; for example, an animal could be scored as sniffing an object as well as leaning on it.

The measures of object interactions employed necessarily differ depending on the animal being studied. For example, in primate studies it may be appropriate to observe facial expressions and head movements in combination with measures such as those mentioned above. Stevenson and Poole (1976), in their ethogram of the common marmoset, described the many facial expressions exhibited by these animals in the presence of novel objects; for example, staring with the eyes wide open, movement of the head from side to side and flattened ear tufts.

3.4.3. Physiological techniques

A third way of measuring dependent variables in the open field is by means of physiological techniques. For the present purposes, these will be described only briefly, since such techniques were not used in the experimental studies described in this thesis.

Measures of heart and respiration rates (Hofer, 1970) and EEG measures (Lat & Gollova-Hemon, 1969) have commonly been combined with data describing motor behaviour, thus providing a broader understanding of open-field activity and responses to novelty. Candland and Nagy (1969) argued further that physiological measures may be used to validate other behavioural measures (such as ambulation and defecation).

Originally, the open field was designed to measure emotionality, and defecation has remained a widely used index of this (Walsh & Cummins, 1976). Measures of defecation and digestive transit time (the time interval between consumption and defecation) are examples of physiological techniques employed to describe open-field behaviour (e.g., Tobach, 1966). The reliability of defecation as a measure of emotionality has been reported by Broadhurst (1960) and Whimbey and Denenberg (1967). Urination is another possible physiological measure (Singer, 1963; Werboff & Havlena, 1962), scored by frequency, presence, absence or amount, and may be combined with defecation to yield a composite elimination score (Tobach, 1966).

Biochemical parameters, such as adrenal gland function, have also been used in open-field studies (e.g., Morgan & Stellar, 1950; Fuller, Chambers, & Fuller, 1956; Moyer, 1958; Paul & Havlena, 1962; Pare & Cullen, 1965; Levine, Haltmeyer, Karas, & Denenberg, 1967). The general assumption has been that adrenal gland function and emotionality are interrelated, with larger or more active adrenal glands being associated with greater emotionality (Morgan & Stellar, 1950; Moyer, 1958; Levine, Haltmeyer, Karas, & Denenberg, 1967). Levine *et al.*, for example, suggested that exposure to novel stimuli results in an increase in circulating adrenal steroids, whilst less emotional animals (e.g., those handled in infancy) show a reduced physiological response in the same novel situation. This demonstrates how physiological techniques can be used to expand descriptions of open-field behaviour.

3.5. CONCLUSION

In this chapter the open field was introduced as a method for studying exploration. The first half of the chapter described independent variables common to open-field testing, showing how changes in the apparatus, testing procedures and experimental designs can influence subsequent behaviour. The second half of the chapter dealt with dependent variables, outlining some standard open-field measures.

For practical and theoretical reasons only certain responses can be measured in the open field, out of the many which actually occur. Responses commonly measured may be divided into categories such as ambulation, parameters other than whole body movement and behaviour described in physiological terms. The use of these measures, together with the interaction of the particular test characteristics applicable to the open-field situation (the apparatus, procedure and design), means that the behaviour observed is a function of such factors.

In the experiments reported in Chapters 5 to 8, animals were given access to sets of novel objects in a familiar open field (an exploration box or cage). This method corresponds to the category 'exposure to discrete, localised changes in a familiar area', a test of free exploration. In Chapter 8, this method was adopted in conjunction with the method 'response for environmental change'. The dependent variables varied in each experiment, and included behavioural categories such as general locomotion, sniffing, digging, grooming, vocalisation, visual exploration, touching objects with the nose or paws and biting objects. In other words, the methodology for the present studies employed the categories of 'ambulation or activity' and 'parameters other than whole body movement', as described in sections 3.4.1 and 3.4.2.

The chapter which follows discusses factors affecting the open-field behaviour contained within these categories. Thus, it acts as a detailed introduction to the experimental research reported in Chapters 5 to 8.

CHAPTER 4

FACTORS AFFECTING OPEN-FIELD BEHAVIOUR

4.1. INTRODUCTION

In Chapter 3 the open field was discussed as a method for studying exploration. The present chapter is concerned with the outcome of the use of this methodology by discussing investigations which have focused on the open field, and variables likely to be of importance in affecting open-field behaviour.

As noted in Chapter 2, describing and explaining behaviour involves interpretations of the adaptive significance of such behaviour, as well as variables immediately influencing an animal's activities during its lifetime. This chapter is concerned with the latter category of explanations, and aims to systematically examine factors affecting open-field activity.

Baldwin and Baldwin (1977) reported that the motor patterns associated with exploratory behaviour are extremely varied and are influenced by numerous complex and interacting factors including genetic, physiological, maturational and environmental variables. Thus, a causal network of variables contributing towards the ontogeny of exploration includes an animal's age, sex, past learning experiences, social relationships, physical environment and personal idiosyncrasies.

It may be said of any behavioural test that the activities observed represent the interaction of the subject with the experimental situation (Walsh & Cummins, 1976). This chapter focuses first on subject variables, classified under genetic and experiential headings, and interactions between the subject and the environment. The second feature of this chapter is a discussion of some of the experimental situations purported to affect open-field behaviour, and in particular, exploratory behaviour.

4.2. SUBJECT VARIABLES

Subject variables may be divided into genetic and experiential categories, and interactions between these. Differences in open-field behaviour arising from differences in genetic factors will be discussed here under the subheadings of 'species and strain differences in open-field behaviour', and 'sex differences in open-field behaviour'; experiential factors will be discussed under the subheadings of 'handling effects', 'enrichment with objects', 'enrichment with natural cage design', and 'social enrichment and early social experience'. A final section, labelled 'interactions amongst subject variables', deals with interactions between some of the variables previously discussed, focusing on sex, strain and early experience.

4.2.1. Genetic variables

In studying genetic influences in open-field behaviour, the technique of selective breeding has been employed (e.g., Hall, 1951; Broadhurst, 1958; Levine & Broadhurst, 1963; Whitney, 1970). Much of the research on genetic differences has been concerned with the concept of emotionality, indicating the significance of hereditary factors in the emotional reactivity of rats and mice (e.g., Broadhurst, 1960). Species, strain and sex differences will be discussed in the subsections which follow.

In conjunction with genetic influences, it may be briefly noted here that researchers have also examined developmental variables, thus describing the ontogeny of exploratory behaviour in individuals. Furchtgott, Wechkin and Dees (1961), for example, showed that older rats tend to direct less attention to novel objects than young rats. Similar findings have been presented by Bronstein (1972), who described a critical period in the development of ambulation in rats, and Bolles and Woods (1964), who argued for the importance of various social phases in the development of exploratory behaviour in the rat (such as social grooming, fighting and playing). Eilam and Golani (1988) have continued this line of research, in describing the ontogeny of exploration in the house rat (*Rattus rattus*).

Species and strain differences in open-field behaviour

Open-field behaviour has been studied in a variety of species, a common focus being on differences in responses to novelty. Glickman, Sroges and Hoff (1961), for example, studied a range of reptiles and mammals and found that differences in their responses to novel stimulation seemed to be a function of each animal's position in the evolutionary series, with primates exhibiting the greatest responsiveness to novelty. In presenting novel objects to different species in zoological gardens, Glickman and Sroges (1966) reported differences in object exploration expressed in the form of object contact time. Similarly, Glickman and Hartz (1964) found significant differences in the locomotory and exploratory behaviour of seven species of rodents in an open field: albino rats and guinea pigs tended to leave an open field in a free exploration test in which escape was possible, whilst albino mice, chinchillas, hamsters, gerbils and African spiny mice stayed in the open field for longer, engaging in more locomotor exploration, biting objects, scratching the floor, rearing, grooming and defecating.

Other experiments reporting species differences include those of Garcha and Ettlinger (1978), who found that chimpanzees learned to sort different coloured objects more rapidly than rhesus monkeys, and Fragaszy (1979), who pointed to significant species differences in the activity levels, social cohesion, vocalisation and feeding style of titi monkeys and squirrel monkeys in a novel environment, the former being less active, showing greater social co-ordination, vocalising more and feeding more slowly. One final example is that of Millar, Evans and Chamove (1988), who reported species differences in the exploratory behaviour of the common marmoset (*Callithrix jacchus jacchus*) and the cotton-top tamarin (*Saquinus oedipus oedipus*): when presented with small objects, marmosets began manipulating them almost immediately following approach, whilst tamarins approached with more caution, allowing more time for sniffing and visual inspection. In addition, Millar *et al.* noted a species difference in the threatening and/or aggressive behaviour of the animals: marmosets raised their tails, and tamarins exhibited frowning.

One consequence of such studies examining species differences in open-field activity is the argument that information about species characteristics ought to be taken into account before making general statements about possible causes of observed behaviour (Kish, 1966). Kish pointed to evidence indicating that different species have different sensory capacities and differences in their fearfulness and general responsiveness, thereby implying that such variations should enter into any discussion of responses to stimulation.

An alternative implication, and one consistent with an ethoexperimental interpretation of species differences, is that ecologically relevant factors, such as differences in species' susceptibility to predation and the likelihood of encounters with novel areas in a species' natural habitat, have an important role to play in explanations of open-field behaviour observed in laboratory settings (this view is consistent with Bolles, 1970; Seligman, 1971; Russell, 1983; Roder, Timmermans, & Vossen, 1989). For example, a species highly susceptible to predation, such as the rat or guinea pig, may be expected to attempt to escape from an open-field enclosure (as was the case in Glickman & Hartz's 1964 study). For another species, such as the domestic chick, freezing may be an effective defence against predation, and may therefore occur in a novel open field (Salzen, 1962; Candland & Nagy, 1969). It may be argued, then, that all studies ought to take such factors into account. In addition, it may be argued that the choice of novel objects in any given study should not be arbitrary, since different species display different reactions towards novel stimuli. Roder, Timmermans and Vossen (1989), for example, used a paper bag filled with woodchips for their open-field experiment using young monkeys, since this was not thought to represent a prepared stimulus complex or contain a species-specific sign-stimulus for danger.

Within a species, open-field behaviour may also differ across various strains. Early descriptions of emotionality in rats were often attributed to genetic determinants involving coat colour (e.g., Keeler, 1948). Broadhurst (1958) was able to differentiate (by means of a test of emotionality) two groups of rat strains according to a gene pair determining coat colour. Studies of this kind not only provide information about the sensitivity of open-field testing to strain differences, but also contribute towards discussions of effects of domestication on open-field behaviour. Domestication, according to Keeler (1948) has selected for characteristics such as docility and tameness, thus linking these traits with genes determining coat colour, and producing new strains of animals (such as albino and hooded rats).

Differences in exploration between commensal and laboratory rats were mentioned in Chapter 2, indicating possible adaptive benefits of such differences in behaviour. Barnett (1958a), for example, observed differences in reactions to novel stimulation by wild, hooded and albino rats. Albino rats were found to explore a novel object in their home cage without hesitating, whilst hooded rats showed more hesitancy, and wild rats were highly fearful and did not eat for several days following the introduction of a novel stimulus. Ivinskis (1968) supported this finding in a study of strain differences in ambulation, rearing, inner circle activity and defecation in Wistar albino and hooded rats. Kish's (1966) explanation for such differences was in terms of greater individual variation in wild strains compared to the more inbred laboratory strains; Henderson (1970), however, accounted for differences in the open-field behaviour of different strains of mice by suggesting that rearing laboratory mice in standard cages makes their behaviour more uniform, thus obscuring effects of genetic variation among them. Differences in response to novelty by laboratory and wild rats are discussed in greater length in section 4.3.1.

Thus, strain differences in open-field behaviour have been explained according to a variety of causal factors: in terms of differences in photophobia (Dixon & DeFries, 1968a), differences in the environment in which the animals are reared (Barrett & Ray, 1970; Freeman & Ray, 1972), differences in emotionality (Broadhurst, 1957, 1958; Chamove & Sanders, 1980), interactions between emotionality and maternal stimulation (Poley & Royce, 1970), or interactions between emotionality ('hypertensivity') and a wide range of environmental conditions (Rogers, Sink, & Hambley, 1988). As a result, in addition to the recommendation that species characteristics be taken into account in any study reporting differences in open-field activity, strain variables should also enter into descriptions and explanations of behaviour, since there is experimental evidence to suggest that responses to novelty differ among different strains as well as different species.

Sex differences in open-field behaviour

There is a considerable amount of literature dealing with sex differences in open-field behaviour; for the present purposes a selection of the some of the research concerning sex differences in rats will be reviewed, since much of the research using rats has focused on exploratory behaviour and responses to novelty as dependent variables.

Lester (1967b, 1967c) argued for the importance of the existence of a sex difference in exploration, reporting that male and female rats differ in their characteristic levels of fear. A possible test of the fear levels of male and female rats is to measure defecation levels; using this variable, Tobach (1966) found that male rats defecated more than female rats, regardless of prior handling conditions, a result interpreted as an indication of the higher levels of fear in male rats compared to females. Russell (1973b), however, pointed out that defecation scores may not be valid measures, since all the determinants of defecation are not known. As a consequence, there are difficulties in determining whether male and female rats do differ in their basal levels of fear.

It has commonly been reported that female rats are consistently more exploratory than males, represented by greater relative amounts of ambulation, rearing and sniffing in a novel environment, and less grooming, eating and drinking (Russell, 1973b). This result supports previous studies by Hall (1934b), Munn (1950), Broadhurst (1957), Woods (1962), Martin (1967), Hughes (1968) and Sheldon (1969). Further, Archer (1975) reported that this trend was apparent for rats of various strains. Some studies have reported less obvious sex differences in open-field behaviour; for example, Gray (1965) found only limited genetic effects for rearing, walking, exploration, grooming, lying and sitting, observing that although females exhibited more rearing than males, they did not ambulate more. More recently, Rogers, Sink and Hambley (1988) reported no *strong* sex differences in two strains of rat on a variety of tests. Despite these variations, the general trend remains, and such sex differences in open-field behaviour have been explained in terms of the priority of certain activities over others: Russell (1973b) suggested that male rats may indulge in more grooming, eating and drinking than females because these are essential 'maintenance' activities, with greater priority over exploratory behaviour.

Once new variables, such as deprivation or stimulus novelty, are introduced into experimental designs concerning sex differences in open-field behaviour, the findings and their subsequent interpretations become more diverse. Experiments by Thompson (1953) and Lester (1967c), for example, suggested that female rats are more likely to leave their home cage when sated rather than deprived of food, but males tend to leave sooner when deprived. Other experiments varying levels of food deprivation, however, have reported no differences in locomotory or exploratory behaviour between the sexes (e.g., Zimbardo & Montgomery, 1957b; Bolles & DeLorge, 1962; Meyers, 1965; Williams & Wells, 1970).

When varying novelty in an open field, experimental results relating to sex differences in exploration are similarly diverse. Hughes (1968), for example, reported that when male and female rats were given a choice between a novel and a familiar area, females exhibited more exploration in the novel area than males, and yet there were no differences in preferences for novelty over familiarity. Russell (1975), on the other hand, compared the time spent by male and female rats in novel compartments and found that females showed a stronger preference for novelty than males (regardless of total amounts of activity), contradicting Hughes' results. Russell interpreted the females' preference for novelty (as indicated by a higher frequency of ambulating, rearing and sniffing in a novel compartment) as being a possible indication of differences in the fearfulness or curiosity of male and female rats. This interpretation is consistent with J. A. Gray (1971), who suggested that male rats are inherently more fearful than females, and Sheldon (1968b), who reported that exploration of novel stimuli is more likely when fearfulness is reduced. In addition, Russell's finding suggests that sex differences in response to novelty may be independent of possible activity differences such as those referred to earlier in this section. A later experiment by Russell (1977) was consistent with this interpretation: using a head-poking response as an indication of exploration, Russell found that although male and female rats exhibited a similar number of exploratory bouts when exposed to a novel open field for a short time, the exploratory bouts of the females were consistently longer in duration. According to Russell, this implies that the difference is independent of a simple activity difference. When the exposure to the novel apparatus was increased, however, males engaged in more exploration, and with familiarisation of the apparatus, the differences disappeared completely. Russell accounted for this result in terms of a higher susceptibility of male rats to inhibitory influences, such as disturbance and extreme novelty.

It may be concluded that there is no unanimous evidence on the topic of sex differences in the open-field behaviour of the rat, but the general trend is for females to engage in more exploratory behaviour than males, represented by greater amounts of ambulation, rearing and sniffing, and less grooming, eating and drinking. The introduction of new variables into the equation, such as deprivation and novelty, create new interactions and alter the open-field behaviour produced. As a consequence, it may be argued that any theory of exploration needs to take such variables and their interactions into account.

4.2.2. Experiential variables

A second category falling under the heading of subject variables affecting open-field behaviour is that of experiential variables. These refer to the experience gained by subjects prior to testing in the experimental situation, as well as the developmental stage at which it occurs, and may be classified according to a variety of criteria. Denenberg, Karas, Rosenberg and Schell (1968, p. 3), for example, broadly referred to an understanding of an animal's "total accumulated experience" as being necessary for the interpretation of particular adult behaviour patterns. More specifically, Walsh and Cummins (1976) described distinct categories of experiential variables: experience gained prior to testing, manipulation of the subject involved in bringing it to the experimental situation, and the subject's experience of the experimental situation up until the time when the behaviour is measured. Theoretically, such variables have been seen as being important in an evolutionary sense, in that learning from experience would be assumed to have selection value for a species as well as for individuals (Renner & Rosenzweig, 1986).

In practical terms, measurement of experiential variables may be difficult to achieve. Careful control and programming of the entire life experiences of experimental animals has been advocated as one possibility (Denenberg, Karas, Rosenberg, & Schell, 1968; Denenberg & Whimbey, 1968; Denenberg & Rosenberg, 1968; Dixon & DeFries, 1968b). Such control and programming may include (in the case of rats, for example) manipulation of the handling of the mother, the kind of environment in which pups are born and reared until weaning, the nature of the post-weaning environment, handling of the pups during infancy, avoidance conditioning training, and food or water deprivation. Difficulties with this ambitious approach arise from the extensive number of developmental and social variables which one would have to control. Thus, should it be the case that young animals are more interested in novel objects than older animals (e.g., Paquette & Prescott, 1988), the control of life experiences would need to take this into account. Similarly, researchers would need to control for social factors such as the possible effects of dominance hierarchies on behaviour. (In this area, Chamove, 1983, and Millar, Evans and Chamove, 1988, have shown that the exploration of novel objects by macaques, tamarins and marmosets is influenced to a large extent by each animal's position in the dominance hierarchy, and that a particular individual usually contacts objects first.)

Studies focusing on ways in which early experiences affect later behaviour have been diverse, covering a very wide range of topics. For example, researchers have examined prenatal stimulation effects on later open-field behaviour (Thompson &

Olian, 1961; Weir & De Fries, 1964; De Fries, Weir, & Hegmann, 1967); infantile trauma effects on temperament characteristics (Lindzey, Winston, & Manosevitz, 1963); prior shock and handling effects on subsequent open-field behaviour (Henderson, 1967); early treatment effects on later aggressive behaviour (Ginsburg, 1965, 1967); and effects of early pre-weaning experience on the way in which hormones act on the brain (Lehrman, 1971).

Much of the literature dealing with experiential variables contains descriptions couched in terms of 'enrichment'. This is often contrasted with 'impoverished conditions' or 'social isolation'. One strategy has been to compare the behaviour of animals reared in enriched social groups with animals reared in isolated environments, the suggestion being that animals with a history of enriched environments gather and process information differently from their impoverished litter-mates (e.g., Greenough, Wood, & Madden, 1972; Einon & Morgan, 1976; Renner & Rosenzweig, 1986).

A wide variety of behavioural changes resulting from enriched or impoverished laboratory conditions during development have been reported (e.g., Rosenzweig, Krech, Bennett, & Diamond, 1962; Greenough, Fulcher, Yuwiler, & Geller, 1970; Manosevitz, 1970; Rosenzweig, 1971; Greenough, Wood, & Madden, 1972; Renner & Rosenzweig, 1986; Renner, 1987). Such changes may involve differences in amounts or types of exploratory behaviour, differences in learning and memory, differences in information-gathering, or differences in activity levels. It is important to note at the outset, however, that 'enrichment' may refer to any one of a number of experimental manipulations (or, as is often the case, a combination of manipulations); for example, increasing the size of an animal's living area, placing novel objects into an enclosure, or housing animals in groups rather than in restricted individual enclosures. Likewise, impoverishment may refer to a small cage size, an absence of objects or social isolation.

Morgan (1973) argued that effects of object enrichment and social enrichment may be completely different from each other, producing entirely different behavioural patterns in animals' later adult behaviour. In the following subsections, therefore, a range of types of enrichment will be examined under separate headings, as well as a subsection dealing with handling, an experiential variable not necessarily designed to be enriching. The subheadings are labelled 'handling effects', 'enrichment with objects', 'enrichment with natural cage design' and 'social enrichment and early social experience'. It should be noted before proceeding that these categories represent only part of the very wide range of factors which have been manipulated in early experience studies. For example, a large portion of early experience literature focuses on the effects of various drugs on the subsequent development of locomotory and other behaviours (e.g., Battig, 1969; Clark, Gorman, & Vernadakis, 1970; Ammassari-Teule, D'Amato, Sansone and Oliverio, 1988).

Handling effects

Many studies varying the presence/absence or relative amounts of handling of experimental animals have pointed to its extensive effects on subsequent behaviour. Candland, Foulds, Thomas and Candland (1960), for example, argued for the reinforcing effects of 'gentling', and Levine (1962) claimed that just a few minutes spent in handling a rodent each day between birth and weaning can have significant and lasting effects on both its physical and behavioural development, resulting in observable differences in a variety of behaviours in adulthood, from brain chemistry to exploration. Along a similar line, Levine, Haltmeyer, Karas and Denenberg (1967) reported that handling affects responsiveness to novel stimuli, both at physiological and behavioural levels. Another parameter purported to be affected by early handling is maze learning (Lindzey & Winston, 1962).

Effects of handling on ambulation and exploratory behaviour have been well documented, particularly as applied to the rat. Williams (1970) measured rats' emergence from their home cages, and found that animals which had been handled daily between birth and weaning were more likely to leave their cages sooner than animals which had been left undisturbed during this period. Similarly, Abel (1971) reported that infant handling affected latency to move in an open field, suggesting that handled rats are less fearful in test situations compared to non-handled rats. (Abel's interpretation was that handled rats have less to react to in an open field than previously non-handled animals.)

Increases in exploratory behaviour have often been interpreted as being a direct consequence of the early handling of mice (e.g., Lagerspetz, Kvist, & Lagerspetz, 1980), as well as rat pups and their mothers (e.g., Whimbey & Denenberg, 1967). Further, according to Wells, Lowe, Sheldon and Williams (1969), handling has been shown to have interactive effects when combined with other 'enriching' variables, such as the addition of tactile and visual stimulation (DeNelsky & Denenberg, 1967a, 1967b), resulting in an increase in exploration for handled rats and a decrease for non-handled rats. Variations in stimulus novelty will be discussed later in section 4.3.1.

Contrary to interpretations of handling as a means of reducing fear (e.g., Abel, 1971), researchers favouring an ethoexperimental approach have viewed handling as a form of stress. Consequently, any effects of handling on exploration may be seen as effects of stress on exploration. As argued in Chapter 2 (section 2.6), open-field behaviour may be described in terms of a reaction to predation (e.g., Gallup & Suarez, 1980). The physical restraint brought about by the experimenter in handling animal subjects may thus bring about reactions against such restraint, displayed in the form of initial struggling and attempts to escape, possibly followed by tonic immobility (Russell, 1983). In experiments reported by Nash and Gallup (1976) and Suarez and Gallup (1981a), the repetitive stress of handling was said to reduce open-field freezing in chickens. This interpretation is consistent with the findings discussed earlier in this section; that is, that handling increases exploration. Thus, any observed increases in exploration may not be due to the 'enriching' effects of handling so much as the fearful escape-directed attempts brought on by exposure to a stressful stimulus.

Aside from research on chickens, handling has been shown to be a mildly stressful stimulus in rats, affecting females more than males (West & Michael, 1988). Such a result accounts for the greater amounts of exploratory behaviour usually observed in female rats (as discussed earlier in section 4.2.1). Studies of marmosets also indicate that handling is stressful: marmosets react to restraint by vocalising and struggling wildly, sometimes continuing such displays to the point of physical exhaustion (Stellar, 1960); a kind of reaction assumed to have an effect on subsequent behaviour. It may be suggested that any effects of handling on subsequent open-field behaviour need to be interpreted within the context of the species being studied: for some species handling may be more stressful than for others.

Enrichment with objects

A second way in which the life experiences of an animal may be manipulated prior to open-field testing is by means of enrichment with objects. The idea of enrichment by adding objects to an animal's environment may be seen partly as an outcome of studies of sensory deprivation. As a general rule, it has been reported that an animal's level of activity and exploration in a novel environment are affected by the degree of sensory restriction experienced by that animal during rearing (e.g., Sackett, 1967a, using rats; Anderson & Chamove, 1984, using stumptailed macaques). Thus, animals severely deprived of visual and/or tactile stimulation subsequently show little interest in novelty or complexity when it is introduced into their surroundings. It is important to note, however, that the effects of early sensory deprivation have not been found to be irreversible: Sackett (1967a) returned deprived rats to normal colony conditions for 30 days, and found that these animals explored maximally complex stimuli, as did their normally-reared counterparts. The reversibility, or malleability, of the result shows that experimental manipulations can be effective at more than one developmental stage, and this provides a basis for experiments in which attempts are made to manipulate animals' sensory stimulation in order to enrich their environments.

Early studies manipulating sensory stimulation (e.g., those reviewed by Kish, 1966) were often carried out by means of the addition of various objects in animals' home cages. Zimbardo and Montgomery (1957a), for example, reared rats in normal cages and in cages enriched with blocks, marbles, trapeze-swings, a tunnel, a hollow cube-shaped figure with steps, an inverted *V*-shaped object and an upright board with holes. Comparisons between the two groups' exploratory behaviour indicated a significant interaction between rearing conditions and sex: females raised in normal cages showed the greatest amount of *Y*-maze exploration, but normal males and enriched males and females exhibited the same degree of exploration. Another interaction effect was reported by DeNelsky and Denenberg (1967a), who found that as the degree of stimulus variation increased, the exploratory behaviour of handled rats increased whilst that of non-handled rats was depressed.

Since these studies, a number of experiments have drawn attention to the increases in the diversity of behaviour (including enhancements in learning and exploration) which can occur after an animal experiences environmental enrichment in the form of contact with objects. For example, Greenough, Fulcher, Yuwiler and Geller (1970), Rosenzweig (1971) and Greenough, Wood and Madden (1972) argued that animals reared in complex environments are superior on learning tasks compared to animals raised in isolation. Increases in general activity, such as ambulation, rearing and grooming, have also been widely reported. Manosevitz (1970, p. 459), for example, compared the behaviour of mice exposed to an early enrichment experience with controls, and found "pervasive" and "relatively permanent" increases in open-field activity, including behaviour on a running wheel and competition for food. Such results do not only apply to mice: activity increases for rats reared in an enriched environment have been reported by Huck and Price (1975). These researchers found that early post-weaning experience in an enriched environment increased activity and body weight in both wild Norway rats and domestic rats, with a greater effect observed in the former. Studies with primates have also emphasised the effectiveness of novel objects in eliciting play and investigation (e.g., Candland, Weldon, Lorinc, & O'Connor, 1978; Bramblett, 1989; O'Neill, 1989).

Behavioural enrichment by means of providing objects in animal cages may be seen as having important practical relevance (in addition to theoretical interest) because it may be employed to ensure the well-being and behavioural diversity of animals kept in captivity. This point will be expanded upon later, in section 4.3.1, and further in

Chapter 9, in which it will be argued that enrichment with objects can have significant benefits for laboratory and zoo animals.

Enrichment with natural cage design

An alternative form of enrichment during rearing may be achieved by altering features of an animal's cage to make it resemble the natural conditions that animal is likely to encounter in the wild. Such alterations may be brought about in a number of ways; for example, by creating environments which are 'unrestricted' (as opposed to 'restricted'), 'free' (rather than 'forced'), 'complex' (rather than 'simple'), or combinations of these. It is often difficult to separate enrichment studies according to these categories, since many use the terms synonymously, and the distinctions become blurred; it should also be noted here that enrichment with natural cage design may overlap with the previous category of enrichment with objects, since novel objects can be employed as a means of creating a more natural, complex environment.

Studies using rats as subjects, such as those of Whimbey and Denenberg (1967) and Denenberg, Karas, Rosenberg and Schell (1968) have shown that enriched housing conditions (e.g., 'free-environment boxes') between birth and weaning, as well as after weaning, can result in increases in play and exploratory behaviour in an open field. Specifically, it has been suggested that animals which are raised in small, restricted areas are subsequently disadvantaged compared to animals raised in larger areas (e.g., Denenberg, Woodcock, & Rosenberg, 1968; Denenberg, Karas, Rosenberg, & Schell, 1968; Forgays & Read, 1962). This is consistent with Smith (1972), who measured error scores on a Hebb-Williams maze for rats which had been reared in enriched or restricted environments during pre- and post-weaning periods. Smith reported that animals from the enriched environment engaged in greater amounts of activity and produced fewer errors than those from the restricted environment. (Such a finding may also be relevant to research on prior experience with light and dark; it has been reported that kittens reared in the dark are slow to learn spatial cues and slow to learn visual discrimination habits compared to normally reared animals, Riesen & Aarons, 1959.)

Another study highlighting effects of enrichment and restriction during rearing on subsequent behaviour is that of Menzel, Davenport and Rogers (1963). These investigators examined the behaviour of chimpanzees which had been reared in the wild and chimpanzees which had been reared in a restricted environment. The result was that restricted animals explored less, spent less time in contact with novel objects, exhibited fear reactions to any novel stimulation, and engaged in more stereotyped self-directed activity. After allowing the restricted animals to live outdoors in a colony for one year, however, these effects were reversed. This shows that general living conditions throughout an animal's life, as well as initial rearing conditions, are influential in contributing towards behavioural development.

Methodologies involving variations in cage complexity have also been employed in early experience studies designed to enrich animal cages. Chamove (1989a), for example, manipulated the housing environment of a group of laboratory mice by including different numbers of vertical dividers and a horizontal platform in their cages. The study indicated that mice reared in the most complex cages (those with the most partitions and the platform) gained more weight, were more active, emerged from a novel box faster, were faster to leave the complex cage to enter an open area, walked more, defecated less and groomed less than mice reared in the open cages. This finding was interpreted in terms of a preference for natural cage design, resulting in healthier and less emotional animals. The idea of reducing the stressfulness of caging will be discussed further in section 4.3.

Another method used to simulate natural conditions was described by Snowdon and Savage (1989), whereby an animal's enclosure undergoes various changes over time. In cages designed for marmosets and tamarins, for example, the branches and ropes may be removed and replaced every few months, thus giving animals a varied environment which both reduces stereotyped actions and allows for the learning of new routes within the cage.

Social enrichment and early social experience

A fourth category of early experience studies consists of experiments manipulating social factors. The importance of social factors during rearing has been emphasised insofar as it has been shown that manipulation of such factors can induce a number of behavioural and neurochemical changes (e.g., Brain & Benton, 1979; Valzelli, 1973; Gentsch, Lichtsteiner, Frischknecht, Feer, & Siegfried, 1988). Many studies examining social factors have involved either the manipulation of the mother-infant relationship, or social aspects of the housing conditions; these will be the focus of this subsection.

Much of the early experience research on primate social and cognitive development has concentrated on the importance of the mother-infant relationship, studied by means of isolation or separation (Fairbanks & McGuire, 1988). This relationship has been seen as important largely as a consequence of studies reporting profound and long-lasting detrimental effects on infants deprived of their mothers (e.g., Arling & Harlow, 1967; Sackett, 1967b; Mitchell, 1968; Soumi, Mineka, & De Lizio, 1983).

It has been shown that exploratory behaviour and reactions to novel environments in particular can be affected by variations in the nature of the mother-infant relationship. Hinde and Spencer-Booth (1971), in a study of rhesus monkeys, reported that even a brief separation between a mother and her offspring has a detrimental effect on the infant's response to novelty later in life. Rearing in the complete absence of a mother has often been shown to result in an avoidance of novel stimuli (e.g., Menzel, 1964; Sackett, 1972; Paquette & Prescott, 1988). Not only is the presence of the mother important, but it has also been shown that the social experience of the mother can have an effect on the behaviour of the offspring. Sackett (1972), for example, observed differences between feral-reared monkeys and monkeys which had been reared to varying degrees by their mothers (complete rearing, partial rearing or complete deprivation) in captive social groups. Sackett reported that animals from the feral group were faster (compared to normally reared animals in captivity) to explore a novel apparatus when they were young adults, while animals partially or completely deprived of a normal mothering experience were much less likely to explore. Fairbanks and McGuire (1988) added to this finding in their research on mothering style, showing that overly protective mothering (measured in terms of approach, contact, restraint and inspection by the mother) led to juveniles engaging in less visual exploration and exhibiting longer latencies to enter a novel environment.

In studies examining social variables in housing conditions (i.e., studies manipulating the general social conditions of an animal's living space, as opposed to merely the mother-infant relationship), the terms 'enrichment' and 'impoverishment' are often used. In this case, 'enrichment' typically refers to group housing conditions during rearing, while 'impoverishment' is its opposite, referring to individual housing or isolation. However, the extent to which such definitions are appropriate (i.e., the extent to which enrichment is positive and impoverishment is negative) is unclear, since some studies have reported that isolation leads to more object contacts and hyperactivity in response to novelty, while others indicate the reverse.

There is an abundance of data on object contacts of socially impoverished and enriched rats, indicating some of the inconsistencies. Some researchers have reported that socially impoverished animals engage in more object exploration, contacting more novel objects in an open field than socially reared animals (e.g., Baenninger, 1967; Latane, Cappell, & Joy, 1970; Einon & Morgan, 1977; Einon, Morgan, & Kibbler, 1978; Siegfried, Alleva, Oliverio, & Puglesi-Allegra, 1981; Gentsch, Lichtsteiner, Kraeuchi, & Feer, 1982; Gentsch, Lichtsteiner, Frischknecht, Feer, & Siegfried, 1988; Paquette & Prescott, 1988). Such results appear to support the claim that animals reared in isolation actively seek out sensory stimulation in order to maintain an optimal level of CNS stimulation (Walsh & Cummins, 1975).

However, another set of studies have provided evidence to suggest that socially impoverished animals make less object contacts than group-housed animals. A sample of reports from researchers in this category are as follows: socially reared animals (e.g., dogs which interact with a human during rearing) are more 'exploratory' and less fearful of a novel environment than animals reared in isolation (Fox and Spencer, 1969); group-housed rats contact a larger variety of novel objects in a variety of different ways compared to isolated rats (e.g., Walsh & Cummins, 1975; Einon & Morgan, 1976); and socially reared rhesus macaques are more responsive to visual social stimuli (slides depicting conspecifics rather than inanimate scenes) than isolation-reared monkeys (Sackett, 1966). Further to Sackett's report is a study by Anderson and Chamove (1984), showing not that socially reared animals are more exploratory, but that their behaviour (their responses to novelty and complexity, their aggression, and other social behaviours) is more 'appropriate' after social rearing. In Anderson and Chamove's study, juvenile stumptailed macaques which had been reared with a peer responded more appropriately to slides of conspecifics, compared to infants reared with a mirror as their primary source of social input.

The discrepancies in the enrichment/impoverishment data described above have been accounted for in a variety of ways. First of all, it has been suggested that isolation may indeed lead to increased motor activity, but reductions specifically in exploration and orienting responses (File, 1978). Thus, an animal from an impoverished environment may indeed move around more, but contact objects less than an animal from an enriched environment.

There are at least two other accounts for the apparent inconsistencies: one couched in terms of differences in speed of habituation between enriched and impoverished animals, and another in terms of overcrowding stress. In the former category, it has been demonstrated that socially reared animals show more rapid habituation of object contact than individually housed animals; that is, an habituation of the enrichment effect (Einon & Morgan, 1976). Initially, then, group-housed animals may indeed contact objects more than isolated ones, but over time the result will appear to be reversed, since the group-housed animals become habituated to the objects but the isolated subjects do not. Here, Einon and Morgan imply that the discrepancies in the behaviour observed following enrichment and impoverishment are a function of the particular time at which the groups are tested and the length of the trials. This explanation has been used to explain any data which indicate that isolated animals show heightened levels of exploration.

In the latter category, differences between group-reared and isolated animals (in which animals reared alone show heightened exploration) have sometimes been said to be due to effects of possible overcrowding stress. It could be argued that social enrichment may be achieved by grouping an 'optimum' number of animals together, and once this number is exceeded conditions become stressful, and hence can be described as impoverished. Thus, 'social enrichment' needs a more specific definition than just 'the presence of other animals during rearing'. Latane, Cappell and Joy (1970) and Stevenson (1983), for example, argued that animals may develop social repulsion through overcrowding, due to competition for food, water and space, and this may lead to less activity and even abnormal responses to stimuli later in life. Latane *et al.* showed that rats housed alone (in relatively unchanging environments, and deprived of stimulation), were more gregarious and produced more exploratory behaviour than rats housed in groups. The study could thus be said to involve 'social enrichment' at an extreme end of the scale, where the presence of other animals in fact becomes detrimental to later exploratory behaviour. An experiment by Gentsch, Lichtsteiner, Frischknecht, Feer and Siegfried (1988) also falls into this category, and these researchers found that socially housed rats were more sensitive to the novelty of the test environment compared to their individually housed rats.

Research of this nature has practical implications for the maintenance of animals in captivity (e.g., in laboratories and zoos). In mongooses, overcrowding has been shown to induce changes in the frequency of social interactions, infanticide and loss of locomotor activity (Rasa, 1979); in tree shrews, it has been reported to cause abnormally long periods of immobility and piloerection of the tail (Von Holst, 1976); and in baboons, it has resulted in social withdrawal and increases in self-directed behaviour (Elton, 1979). To some extent, the control or even eradication of such behaviours may be brought about by enrichment with objects or natural cage design, as discussed earlier in this section.

4.2.3. Interactions amongst subject variables

The two previous sections have focused on some of the subject variables which have been manipulated in studies measuring open-field behaviour, namely genetic and experiential factors. In this concluding section on subject variables, a sample of studies examining interactions amongst subject variables will be discussed. Walsh and Cummins (1976, p. 499) supported the study of interactions (rather than studying variables separately) since, in their analysis:

> *...any behavior represents the determinant of the interaction of genetic background, maturation, biological rhythms, experience prior to testing, stimulation involved in bringing the subject into the experimental situation, stimulation afforded by the experimental apparatus, stimulation afforded by the test environment, experience of the test situation up to the instant of measurement, and method of measurement.*

Experiments concerned with interactions between numbers of subject variables are necessarily complex; for example, to study effects of genetic variables in combination with consequences of changes in the early environment, several factors must be manipulated at once (Hinde, 1974). The issue of the inherent complexity of interactional studies had been raised earlier by Henderson (1968), who argued that such studies involve a series of factors which vary considerably even in populations of the same species; hence the variation of such factors increases to a much greater extent when interactions are taken into account. Thus, any dependent variable, such as maze exploration, is affected by factors such as the age of the animal, its sex, the degree of deprivation, and the complexity of the maze.

One example of a study dealing with interaction effects is that of Cooper and Zubeck (1958), who demonstrated that 'maze-bright' and 'maze-dull' rats (two genotypes) responded differently to enrichment and impoverishment: maze-bright animals did not improve in their maze performance as a result of an enriched environment, while maze-dull animals did; and a deprived environment had little effect on maze-dull rats but was detrimental to maze-brights. Other examples reporting interactions between variables come from Denenberg, Karas, Rosenberg and Schell (1968), Denenberg and Rosenberg (1968) and Denenberg and Whimbey (1968), who each measured rats' ambulation in an open field, and reported interactions between handling, pre-weaning/post-weaning environment, and sex.

The remainder of this section gives examples of studies reporting interaction effects amongst some of the subject variables discussed above. For the present purposes the sample of studies will be limited to those discussing interactions between sex, strain and early experience. (As Henderson, 1968, p. 150, pointed out, the diversity of both genetic factors as well as manipulations of early experiences of animals means that the permutations for interaction effects are very complex and therefore sometimes "chaotic". It is beyond the scope of this thesis to enter into a more detailed discussion of this area.)

Henderson's (1968) review of the literature dealing with *genetic x treatment* interactions states that there are a large number of early experience studies on rodents where an interaction between treatment and sex occur. According to Henderson, such interactions are to be expected, since the two sexes respond in diverse ways to environmental stimuli, and develop different territorial behaviour. As a result, differing effects of early stimulation should be expected.

Experimental treatments such as handling and the addition of objects into an animal's environment (as discussed in the previous section) have been found to interact with effects of sex. In an experiment combining handling and the addition of objects, Weinberg, Krahn and Levine (1978) examined sex differences in the exploratory behaviour of handled and non-handled rats, under conditions of high and low stimulus variation. These researchers found that handled animals maintained a head-dipping response over time (whereas this response decreased in non-handled animals), and the particular pattern of head-dipping differed for males and females depending on whether objects were present or absent.

Studies such as these indicate the interaction between the genetic variable of sex and the experiential and environmental variables of handling and the addition of objects. Another study (Wells, Lowe, Sheldon, & Williams, 1969) gave an account of the interaction between handling and environmental familiarity, in an experiment examining exploration following rats' experience of handling during infancy. Williams and Russell (1972) also reported interactions in their study testing for effects of pre-weaning handling, sex and repeated testing on the open-field behaviour of rats. Williams and Russell found that ambulation increased in handled rats, but initially declined and then increased in non-handled rats.

Similarly, strain effects have been shown to interact with experiential variables. Levine and Broadhurst (1963), for example, found a *genetic x treatment* effect when manipulating infantile stimulation in two strains of laboratory rat. Henderson (1968) examined the effects of environmental enrichment/impoverishment (cages with or without objects) on nearly 40 genetic combinations of mice, and reported that subjects reared in enriched cages were superior to control subjects on a variety of discrimination tasks. Experiments by Barrett and Ray (1970) and Freeman and Ray (1972) showed that problem-solving ability in the rat (as measured in appetitive and aversive learning trials in open-field shuttle-boxes and mazes) depended on the strain of the animal, and that this factor interacted with sex and environmental factors such as differential rearing conditions (an enriched or isolated environment).

This concludes the discussion of pre-test subject variables in studies of open-field behaviour. The rest of this chapter is devoted to factors which may be manipulated in the experimental situation itself, laying the foundations for the experimental chapters to come.

4.3. EXPERIMENTAL SITUATION: NOVELTY, COMPLEXITY AND LEARNING

In the second half of Chapter 4, some of the experimental research examining factors which affect open-field behaviour will be described. The factors discussed are firstly, novelty and complexity, and secondly, learning. These are the principle independent variables which were investigated in the six experiments reported in Chapters 5 to 8. Thus, these sections, together with the experimental findings, form the basis for discussion in the final chapter of this thesis.

Open-field studies using objects as foci for exploration have traditionally been concerned with two features, novelty and complexity, each of which has been seen to play an important role in determining exploratory behaviour. 'Novelty' is a term which has been used in a variety of ways, mostly to refer to 'unfamiliarity' (definitions of this term will be discussed in section 4.3.1). Stimulus complexity has also been a focus of attention in this field; it has been argued that the physical characteristics of an object itself (e.g., its physical complexity) must determine at least in part what an animal actually does once it is interacting with it (Renner & Rosenzweig, 1986). Finally, it has been argued that there is a connection between learning and activity, with enhancements of exploration occurring after learning (Kvist, 1983), as well as general behavioural enrichment (Chamove, 1989a, 1989b).

The first aim of section 4.3 is to present some of the research on novelty and complexity. The section begins by describing the concept of novelty, showing how it may serve to influence and/or reinforce the exploratory behaviour of a wide range of species. Following this, the review turns to the habituation of novelty, reports of novelty as fear-inducing, complexity, and the preference for moderate levels of novelty and complexity. The topic of novelty and complexity is concluded with a discussion of how the control and manipulation of these factors can be used for behavioural enrichment for captive animals. Lastly, learning is discussed with reference to open-field behaviour, arguing that it, too, can be used for purposes of behavioural enrichment. The material relating to enrichment forms a significant part of the theoretical background to the experiments conducted for the present study.

4.3.1. Novelty

Before reviewing research which has focused on novelty and its influence on exploratory behaviour, this section will begin with a few words on definitions of novelty.

Usage of the term 'novelty' has varied widely from experiment to experiment; for example, diet variations (Welker, 1961), changes in illumination (Moon & Lodahl, 1956), changes in odour due to the former presence of conspecifics (Russell & Chalkly-Maber, 1979), the introduction of new apparatus characteristics (such as a checkerboard, Fowler, 1965; or an elevated maze, Halliday, 1967), and opportunities to view other animals (Butler, 1953, 1957, 1958). A feature which these experimental manipulations have in common is the imposition of some kind of *change* in the environment, thus bringing unfamiliarity to the situation. Thus, novelty is not a stimulus variable, but a transactional concept referring to a ratio of past-to-present experience with a particular stimulus (Welker, 1971). For Berlyne (1960), novelty could be broken down into different classes: relative to an animal's total life span ('complete novelty') or relative to an animal's last exposure to a stimulus ('short-term novelty'); it could incorporate familiar elements in an unfamiliar combination ('relative novelty'), or contain elements never before perceived by an animal ('absolute novelty'). Thus, as summed up by Kish (1966), novelty may be seen as a relationship between a perceiving animal and stimulation, assessed in terms of that animal's short-term and long-term experiences with the stimulation. In the experiments reviewed in this (and other) sections, it is not always clear which definition of novelty the authors are adhering to. For the present purposes, the wider definition of 'novelty' as 'change' or 'the introduction of an unfamiliar stimulus' will suffice.

It has been well documented that most mammals display increased activity and marked exploratory reactions when placed in a novel environment (e.g., Glickman & Sroges, 1966; Poucet, Durup, & Thinus-Blanc, 1988; Rogers, Sink, & Hambley, 1988). According to Fowler (1971), a novel environment provides a change in stimulation, and elicits consistent reactions such as orientation, approach, investigation and manipulation. (Orientation and information processing as reactions to novelty have been described in depth by Richardson, Siegel and Campbell, 1988, who outlined some of the physiological events associated with such behaviour.)

Such activity reactions have been interpreted in a variety of ways, as discussed in earlier theoretical sections of this thesis (Chapter 2); for example, indications of curiosity or attempts to escape. An alternative interpretation is in terms of reinforcement value: it has been suggested that novelty may function as does any other conventional incentive, such as food or water (Chapman & Levy, 1957; Fowler, 1965; Baldwin & Baldwin, 1978a). Thus, it may be proposed that novelty can influence exploratory behaviour in the same way as hunger or thirst. (However, it may be noted that hunger has been reported to enhance exploration, Glickman & Jensen, 1961, Bolles, 1967; depress exploration, Zimbardo & Montgomery, 1957b; and have no effect on exploration, Hughes, 1965b.)

In particular, stimulus change may be used to reinforce exploratory behaviour (Taylor, 1974). A study of golden hamsters, *Mesocricetus auratus*, by Schneider and Gross (1965) is relevant to this idea: animals were able to run down an alley from a start box to either constant or changing objects. It was found that their exploratory behaviour directed towards the constant objects declined more rapidly over time than their behaviour directed towards the changing objects. Further, novel and complex stimuli were found to evoke more exploratory behaviour than merely complex stimuli. Hebb and Thompson (1954) and White (1961) extended the reinforcement theory of novelty to humans, arguing that a liking for games, sports or roller coasters indicates that novel stimulation (including stimulation invoking fear) is reinforcing. This point is developed further in section 4.3.3, in which novelty is viewed as fear-inducing.

The remainder of this section presents experimental evidence on animals' reactions to novelty, first suggesting that novelty is an important factor influencing the open-field behaviour of a variety of species, and secondly, emphasising species differences in reactions to novelty.

Berlyne (1955) conducted an experiment in which rats' nosing behaviour was measured under three conditions: in an empty compartment, a compartment containing a wooden cube to which animals had been pre-exposed, and a compartment containing a completely novel cube. The result was that rats produced the most nosing behaviour in the novel object group and the least nosing in the empty compartment, with an intermediate amount of nosing in the familiar cube group. Many other studies using rats and novel objects have yielded similar results, indicating the rat's interest in novelty; for example, Einon and Morgan (1976), Harcourt (1983), Gojak (1984), Forster (1986), Renner and Rosenzweig (1986), Renner (1987), Litchfield (1987) and Rosellini and Widman (1989).

Such an activity increase and a general interest in novelty has been confirmed in many studies, and in a variety of species. For example, Jowaisas (1969), using golden hamsters as subjects, found activity increases (scratching and biting the floor and walls) and decreases in non-object sniffing in the presence of novel objects in an open field. Leyland, Robbins and Iverson (1976) were able to maintain an enhancement in exploration by providing rats with novel stimuli every day. Candland, Weldon, Lorinc and O'Connor (1978) supplied their macaque colony with novel objects, and this resulted in substantial play, object modification and defence of the objects, especially by juveniles. Welker (1956) introduced 'play objects' (stimuli varying in shape, size, manipulability, texture and brightness) to a chimpanzee, and found increased responsiveness towards the objects, as measured by manipulations during a given period of time. Further, the same increase in responsiveness returned after the animal had not seen the objects for an interval of time. Glickman and Sroges (1966) conducted a study in which novel objects were presented to a variety of animals in zoological gardens, and found that primates, in particular, spent a great deal of time visually inspecting and manipulating the objects. A study of the object manipulations of chimpanzees by Litchfield (1991a, 1991b, 1991c) supported this finding, showing that object novelty in a zoo enclosure can result in marked exploratory reactions and play behaviour by chimpanzees (sometimes leading to the destruction of the objects). Similarly, Millar, Evans and Chamove (1988) presented a series of novel objects to a group of marmosets and tamarins, and found that this resulted in vocalisations, headcock stares, piloerection and/or threatening aggressive displays (tail-raising by marmosets and frowning by tamarins), followed by approaching, sniffing and contacting the objects. Bramblett (1989) reported that novel objects provide hours of attention and manipulation in guenons. Other studies reporting primates' extreme interest in novel objects include those of Menzel (1978), Fragaszy and Mason (1978), Menzel and Menzel (1979), Wilson (1982), Chamove (1983), O'Neill (1989) and Forster (1990).

The preceding paragraph re-introduces the notion of species differences in animals' responses to novelty (referred to earlier in section 4.2.1, which dealt with effects of subject variables on exploratory behaviour). It is relevant at this point to expand on some of the studies reporting an interaction between novelty and species.

Jolly (1964) conducted a study of prosimians, and found that insectivorous primates were more likely to observe novel stimuli than folivorous or frugivorous primates, and that the former were less likely to manipulate stimuli than the latter. An interpretation of this behaviour is that visual attention is more important, and therefore more developed, in insectivorous animals because they need to capture moving targets, whilst tactile manipulation is more important to fruit-eaters. This accounts for the visual attention of the insectivores and the manual exploration of the folivores and frugivores. Such a species interaction draws attention to the idea that species differences in novelty responses may reflect animals' differing adaptive skills or requirements. Another example of a study of responses to novelty in which adaptive considerations were taken into account is that of Jaenicke and Ehrlich (1982). These researchers found that monkeys' and prosimians' latency to contact novel objects was influenced by the location of the objects, with a preference for objects above the ground. Millar, Evans and Chamove (1988) cited this study, and, as a consequence, presented their primate subjects with novel objects at least one metre above the ground, accessed by a network of branches and platforms.

Further examples come from studies specifically comparing marmosets and tamarins. Descriptions of marmosets have placed a great deal of emphasis on their curiosity, alertness and capacity for visual exploration (e.g., Stellar, 1960), as have descriptions of tamarins (e.g., Menzel & Menzel, 1979). However, Millar, Evans and Chamove (1988) pointed out that since the common marmoset, *Callithrix jacchus jacchus*, is specialised for eating gum from the bark of trees, whilst cotton-top tamarins, *Saquinus oedipus oedipus*, are more insectivorous, one might expect their responses to novelty to be in line with the account given above by Jolly (1964). This is in fact what was found by Millar *et al*: marmosets began manipulating objects almost immediately during all trials, whereas tamarins contacted objects immediately on only half of the trials, approaching more cautiously, and visually inspecting objects before making contact.

4.3.2. Habituation of novelty

An important consideration in studies of novelty is habituation. Over time, effects of novelty change as subjects become habituated to stimuli: habituation has been defined by Zayan and Lamberty (1989, p. 692) as "the relatively persistent waning of a response as a result of repeated stimulation." Berlyne's (1950) account of habituation was in terms of a decrease in curiosity; he supported this with evidence that rats spend more time exploring novel stimuli than stimuli which they have previously been able to explore, and they spend less time exploring stimuli on a second presentation. An alternative interpretation has been suggested by Richardson, Siegel and Campbell (1988), who explained habituation in terms of a decrease in fear or distress caused by an unfamiliar environment.

It has been well documented that repeated or continual exposure to a stimulus leads to a general decrease in activity, thought to be due to habituation (e.g., Hutt, 1967b; Ratner, 1970; Ivinskis, 1970; Rogers, Sink, & Hambley, 1988). However, it has been suggested that habituation applies specifically to exploratory activity rather than general activity (O'Keefe & Nadel, 1978; Ellen & Weston, 1983; Poucet, Durup, & Thinus-Blanc, 1988). Studies by Ehrlich and Burns (1958) and Corman and Shafer (1968) are consistent with this account: the former reported little decline in locomotor activity by black-footed ferrets during the first three days of presentation of a novel object; the latter reported that habituation over trials led to a decrease in rats' exploratory behaviour, but not in their total locomotor activity. This has been explained in terms of decreases in orienting and defensive responses in the presence of novel stimuli (Richardson, Siegel, & Campbell, 1988). In other species, behavioural responses apart from exploration have been reported to decrease upon repeated presentation of stimuli; for example, vocalisations, head movements and facial expressions (such as frowning) in tamarins, and declines in tail-raised presenting in marmosets (Millar, Evans, & Chamove, 1988). Thus, species differences in habituation need to be taken into account.

It should be noted that it is possible to offset effects of habituation: Corman and Shafer (1968) found that if the centre of an open field was changed from black to white, exploratory behaviour resumed, despite habituation in the area. Similarly, Welker (1956) reported that following habituation to a complex stimulus array, merely changing the colour of the presentation board renewed responsiveness to the array. These findings also accord with a series of studies of hamsters, in which it was found that animals actively re-investigated objects after two sessions of habituation, provided the spatial relationships between the objects were changed (Poucet, Chapuis, Durup, & Thinus-Blanc, 1986; Thinus-Blanc, Bouzouba, Chaix, Chapuis, Durup, & Poucet, 1987).

These last examples refer to effects of habituation on exploratory behaviour in particular, and this will be the topic for the rest of this section. Typically, according to Thor, Harrison, Schneider and Carr (1988), the exploratory behaviour exhibited by a rat exposed to a novel environment begins with several bouts of sustained investigation, and upon habituation the animal directs its attention away from the novel stimulus to itself and engages in repeated bouts of self-grooming. This description is consistent with other accounts of habituation in rats, hamsters and gerbils, provided by Poucet, Durup and Thinus-Blanc (1988). According to these researchers, exploration involves a burst of activity directed towards a set of novel objects at the beginning of each session, followed by habituation (less activity) during the session. Thus, habituation was not described as occurring gradually over time (in which case there would be no initial bursts of activity in every session); rather, it had a *within-session* effect, and a slower overall *between-sessions* effect.

Other researchers have claimed that habituation on one occasion may not carry over at all into the subsequent day's testing (i.e., that *between-sessions* habituation does not necessarily occur). For example, Renner and Rosenzweig (1986) reported that a rat's previous day's experience with a set of objects only had a limited effect on the subsequent day's behaviour (measured in terms of number of bouts of interaction and total time of interaction). According to Renner and Rosenzweig, one possible reason for this is that an opportunity (e.g., 10 minutes in an open field) to explore novel stimuli does not produce an overwhelming familiarity with the objects; thus the objects remain relatively novel for the second session of testing. This explanation may be used to account for Welker's (1956) chimpanzee study; therefore, Paquette and Prescott (1988) suggested that maximal object exploration over a series of sessions could be achieved by reducing the daily exposure period. An alternative way to achieve this result follows from Hinde (1966), who stated that habituation occurs more rapidly with the reduction of time intervals between stimuli. This implies that maximal exploration can be achieved by increasing the time intervals between the presentation of objects. Thirdly, since decreases in exploration of novel stimuli have been thought to be related to the complexity or diversity of the stimuli (Hutt, 1967b), the fact that Welker used objects which were movable, bright, configurally heterogeneous, and capable of producing auditory or visual changes accounts for the long habituation periods displayed by the chimpanzees. A final consideration in the discussion of *between-sessions* effects is that of species differences in habituation. Millar, Evans and Chamove (1988), in their study of tamarins' and marmosets' responses to novelty, observed a difference in the latency to first contact objects after repeated presentations. This was accounted for in terms of the "more cautious nature" of cotton-top marmosets (p. 95). Another example is that of Richardson, Siegel and Campbell (1988), who characterised the orienting responses of black-footed ferrets as being limited by their information processing capacity.

At the *within-sessions* level, species differences have also been seen as important. It has been argued that satiation of interest in novel stimuli may be more prevalent in species with a short attention span, since such animals tend to be rapidly sated, despite being attracted to novelty (Welker, 1961). Loizos (1967), in a study of chimpanzees, described these animals as responding to only one aspect of the experimental situation, shifting their attention rapidly from one object to another and from feature to feature of the same object; a description which seems to accord with Welker's suggestion. Such an explanation has also been offered as a possible reason for differences in habituation to novel environments by wild polecats and domestic ferrets, the former habituating faster than the latter (Poole, 1972).

One complication in the interpretation of habituation during single sessions and on successive sessions is that there may also be within- and between-species interactions, as suggested by Poucet, Durup and Thinus-Blanc (1988). Another consideration is that repeated exposure to novelty may interact with sex differences in exploratory behaviour. For example, Russell (1977) suggested that while female rats have a stronger preference for novelty than males, this preference is reversed with repeated exposure; and further, the length of the habituation period produces interactional effects, with females exploring stimuli more than males if the familiarisation period is short, but no sex differences if the familiarisation period is long. Still another possibility is that habituation interacts with prior experience (as suggested in section 4.2.2 dealing with social enrichment and early social experience): Einon and Morgan (1976) suggested that animals housed in social groups show more rapid habituation to objects than individually housed animals.

4.3.3. Novelty may induce fear

As argued in Chapter 2 (section 2.6.2), an ethoexperimental approach to open-field exploration involves an interpretation whereby an interaction between separation from conspecifics and threat of predation is postulated. These two variables could be said to be fear-inducing, leading to the hypothesis that novelty induces fear. Hayes (1960) supported this hypothesis, arguing that the strange environment encountered by a rat placed in an open field gives rise to a fear reaction. The avoidance responses of some animals to novel stimulation (especially those reared in deprived conditions) have been described by a number of investigators (e.g., Rowell & Hinde, 1963; Baldwin & Baldwin, 1977; Russell, 1979; Stevenson, 1983). Further, Richardson, Siegel and Campbell (1988) provided physiological evidence (increases in sympathetic and adrenocortical activity) pointing to the existence of a distress reaction by animals placed in an unfamiliar environment. However, whether such a fear reaction would result in freezing or escape-directed responses is less clear. (In Chapter 3, section 3.3.3, it was suggested that a 'forced situation' results in increased activity and escape attempts, whilst a 'free situation', in which animals have access to a familiar environment, results in less activity, Moser, Moser, Wultz, & Sagvolden, 1988.)

Kish (1966) reviewed some of the evidence relating to fear, arguing that anxiety plays an important role in sensorily reinforced behaviour such as exploration. Thus, as argued in Chapter 2, locomotor exploration may reflect an animal's attempts to escape from fear-inducing novel stimulation (Blanchard, Kelley, & Blanchard, 1974; Takahashi & Kalin, 1989). This accounts for findings such as those of Hudson (1940), who reported that rats react with avoidance responses to strange objects placed in their home cages. Such responses may be characterised by cautious approach, withdrawal, and the pushing of sawdust towards the objects. Similarly, King (1970) reported that rats avoid novel stimulation at the end of a runway, explaining this in light of the hypothesis that fearful rats stay in the same place until their fear has habituated. A series of studies by Rheingold (1969) examined the effect of a 'strange environment' on human infants, and also yielded results consistent with distress-induced novelty. In Rheingold's studies, emotional distress was characterised by crying and inhibited locomotor activity. More recently, research on fear-inducing aspects of novel stimulation has been followed up by Roder, Timmermans and Vossen (1989). In their experiments young surrogate-reared cynomolgus monkeys were confronted with a harmless novel object in their familiar home-cage environment, and the result was persistent avoidance behaviour (which the researchers labelled as 'maladaptive', compared to the approach behaviour of mother-reared monkeys).

In addition to freezing or escape/avoidance as fear-induced reactions to novelty, a number of studies have referred to burying behaviour as a significant part of the rat's defensive repertoire when faced with a novel situation. Pinel and Treit (1978), for example, reported that rats placed in an open field and subjected to shock almost always attempt to bury the shock source. It should be noted that there is currently a growing debate as to whether burying behaviour is solely a defensive response or whether it occurs in non-aversive situations, or both. An outline of some of the research in this area is given here, in view of the fact that many studies in this field interpret burying as a reaction to variations in stimulus novelty.

Burying behaviour has been shown to occur in response to a variety of novel stimuli, shock being only one such example. Terlecki, Pinel and Treit (1979) found that when rats first encountered a mouse-trap or a flashbulb in a familiar environment, they buried it with bedding material from the floor of the open field. Once habituated to these objects, however, the burying disappeared; thus, novelty seemed to be the distinguishing feature of the situation. It has also been reported that rats bury novel food substances which are noxious (Wilkie, MacLennan, & Pinel, 1979). These results seem to correspond to Barnett and Cowan's (1976) model (relating to the adaptive significance of exploration put forward in Chapter 2, section 2.4.6), suggesting that rats avoid new objects in familiar places, although Barnett and Cowan were referring only to wild rats. The result is contradictory to Barnett's (1976) description of laboratory rats, which typically approach and investigate new objects in a familiar place.

A study by Poling, Cleary and Monaghan (1981), in which rats were exposed to an extensive variety of stimuli - not all novel, and not all aversive - seemed to indicate that burying is not a species-specific defensive reaction, since it occurred in a wide range of conditions having little in common. For example, they found that rats would bury marbles, even though no obvious biological significance for this could be detected. Litchfield (1987) also observed such seemingly unexplained burying: rats filled up their food troughs with sawdust whilst in the conditioning phase of an experiment involving bar-pressing for food. It was suggested in this particular case that the behaviour was a by-product of the conditioning process.

Pinel, Symons, Christensen and Tees (1989) favoured a species-specific interpretation of burying, having reviewed research by Owings and Coss (1978) on the defensive behaviour of ground squirrels when confronted by snakes in naturalistic environments. There are several other reports favouring the species-specific explanation (e.g., Pinel & Treit, 1978; Terlecki, Pinel, & Treit, 1979; Wilkie, MacLennan, & Pinel, 1979), but Poling, Cleary and Monaghan (1981) argued that since burying occurs in response to novel stimuli which are not aversive (such as normal food or marbles), this interpretation does not suffice. Rather, different explanations may apply to different stimuli; for example, the burying of noxious food may be a defensive reaction, and the burying of marbles may be related to hoarding, a behaviour which is to be expected in a burrowing species such as the rat or squirrel (Calhoun, 1949; Barnett, 1976).

In concluding this section, it should be emphasised that novel stimuli do not *always* evoke fear-induced exploration. Rather, they can be seen as evoking both approach and avoidance, with exploration as a reflection of the balance and interplay between the two tendencies (Kish, 1966); and more importantly, the context of the presentation of the stimuli is important, as is the specific nature of those stimuli, be they aversive or non-aversive. Differences in reactions to novelty also need to be taken into account, since fear is not a universal response to a novel environment in all species. Further, fear responses are not necessarily the same in wild and domestic animals: Poole (1972), for example, reported that when wild polecats were moved to an unfamiliar environment, they expressed extreme caution, whilst domestic ferrets in this situation showed no fear responses and explored immediately upon introduction to their new cage.

4.3.4. Complexity

As stated at the beginning of section 4.3.1, open-field studies involving objects have traditionally manipulated complexity as well as novelty, one assumption being that the physical characteristics of objects used in open-field experimentation determine in part what the animals do once they are interacting with them (Renner & Rosenzweig, 1986). This section is concerned with stimulus complexity and its role in determining exploratory behaviour, beginning with a definition and then moving on to experimental research on complexity.

According to Berlyne (1960) and Walker (1970), stimulus complexity refers to the number of distinguishable elements composing a pattern or object, and the dissimilarity of those elements. Thus, as the number of elements and dissimilar features increases, so too does the complexity of a particular stimulus. Conversely, the greater the possibility of integrating a pattern into a unitary percept (or Gestalt), the lesser the degree of complexity (Berlyne, 1960). In practical terms, increases in complexity have been said to result in longer periods of attention and exploration, since the more complex a stimulus is, the longer it should take for such a stimulus to become familiar, and hence for the animal to be sated (Walker, 1970). Taylor (1974) expanded on this point, alluding to the *effectiveness* of changes in complexity in providing incentives for exploration: a physical stimulus change to a lesser stimulus complexity was described as being less effective in producing exploration than a similar change to a stimulus of greater complexity. This modifies a previous idea (e.g., Fowler, 1971) that *any* change (an increase or decrease) in complexity is an effective incentive for exploratory behaviour.

Empirically, stimulus complexity has been shown to play an important role in influencing open-field exploration. Many of the experiments reported in the subsections on enrichment with objects and novelty (in section 4.2.2) also systematically varied complexity, and these will be briefly referred to again here. For example, Leyland, Robbins and Iverson (1976) found that the increases in exploratory behaviour which were observed when rats were exposed to novel stimuli were enhanced by increasing the complexity of the stimuli. These enhancement effects persisted provided that a new stimulus was provided each day. Williams and Kuchta (1957) had reported earlier that rats spent more time exploring a maze arm which contains a number of different objects rather than an empty arm. Similarly, Taylor (1974) allowed rats to choose between a novel and a familiar arm of a *T*-maze, and found that animals' preference for the novel arm was greatest when it was more complex than the familiar one. Taylor interpreted this in terms of the greater amount of information to be assimilated in the complex arm.

Experiments manipulating complexity have also been carried out on primates. Welker (1956), in a chimpanzee study, found that animals preferred more movable, larger, brighter, heterogeneous and changing auditory and visual stimulus configurations over less complex stimuli. This emphasises the animals' attraction to qualitative characteristics of the stimuli, in addition to the fact that they are novel. In section 4.2.2, Chamove's (1989a) study on enrichment by natural cage design was discussed with reference to the reduction in stress associated with the presence of vertical partitions. A further interpretation of this study is that the mice preferred the more complex of the cages; that is, the cages with more divisions (and moreover, that this leads to healthier animals).

In summary, an animal's response to environmental change depends not just on novelty but also on the exact nature of the change. Experimental evidence suggests that complex stimuli evoke more exploration than simple stimuli, and that complexity is preferred in choice situations.

4.3.5. Preference for moderate levels of novelty and complexity

It has been shown that individual animals do not always prefer the most complex of a set of stimuli (Dember, Earl, & Paradise, 1957); rather, highly complex stimuli tend to be ignored or avoided, as are very simple stimuli (Leuba, 1955; Glanzer, 1958; Berlyne, 1960; Dember & Earl, 1957; Fiske & Maddi, 1961; Walker, 1964; Baldwin & Baldwin, 1978a). Walker (1970) extended this to humans, in arguing that for any array of stimuli, subjects order them from least to most complex, and subsequently prefer stimuli near an 'optimal complexity level'.

Such a theory has not only been applied to studies of stimulus complexity; there is also evidence to suggest that animals prefer moderate levels of novelty, rather than the most novel of a set of stimuli. Menzel, Davenport and Rogers (1961), for example, found that, up to a point, degrees of novelty enhanced the investigatory behaviour of chimpanzee subjects, but beyond this, the novel objects provoked fear and caution. Similarly, Loizos (1967) studied the exploratory activity of chimpanzees raised under conditions of almost total perceptual restriction, and reported that they found even the simplest object so novel that exploration was totally inhibited, and the animals huddled fearfully in a corner while the object was present. To account for this, and data on stimulus complexity, it has been suggested that animals prefer moderate levels of novelty and complexity, thereby maintaining an 'optimal arousal zone' (Baldwin & Baldwin, 1978a). In Berlyne's words (1964, p. 23):

> *There are plenty of indications that the nervous system, and in fact the whole body, of one of the higher animals is tailored to a moderately high influx of novelty, complexity or information, such as it usually receives in normal environments.*

In practice, according to Berlyne, the actual levels of novelty and complexity which are preferred vary within wide limits, and depend on factors such as an animal's physiological state and experiential history.

Implications of this theoretical viewpoint are relevant to the study of exploratory behaviour: if animals prefer stimuli of moderate novelty and complexity, it follows that they will maintain their interaction levels and frequently approach moderately complex stimuli (Dember & Earl, 1957). This hypothesis has been supported by Menzel, Davenport and Rogers (1961), who noted that chimpanzees manipulated moderately novel objects for longer periods of time than highly novel or highly familiar objects (which provoked a great deal of fear or very little fear respectively). Regarding complexity, Sales (1968) measured rats' inspection times for a set of relatively simple, highly complex and moderately complex stimuli, and found that the former two evoked comparatively brief observation periods, whereas the latter evoked much more extended observation.

One criticism of studies such as those mentioned here is that the researchers did not discuss the context in which the novel or complex stimuli were encountered, the content of such stimuli, or the situation appropriate to the exploratory behaviour. Russell (1983) argued that stimuli which are often employed in experiments manipulating novelty and complexity (such as visual patterns and objects) are, from the animal's point of view, relatively arbitrary or meaningless. In the natural habitat, then, novelty and complexity *per se* cannot be interpreted independently from their content and the context in which they are encountered; thus, as summed up by Russell, a reaction to a complex image such as an approaching predator will differ from a reaction to a conspecific or a wind-blown leaf, since reactions to these are not merely reactions to complexity, but behaviours relevant to life in the wild.

4.3.6. Novelty and complexity used for behavioural enrichment

The final section dealing with novelty and complexity will discuss ways in which manipulations of these factors can be used for behavioural enrichment. This section is intended to be a complementary section to the earlier discussions of 'enrichment with objects' and 'enrichment with natural cage design' (section 4.2.2). Some of the present material overlaps with the previous enrichment sections, since enrichment has been used both as a subject variable (i.e., manipulation of the subject's experience prior to testing) and an experimental manipulation during testing. In this section, therefore, the previous discussion will first be briefly summarised and then integrated with the present material on novelty and complexity.

In section 4.2.2, enrichment (by means of the addition of objects, natural cage design or social manipulations) was discussed in terms of experience gained by animals prior to testing in the experimental situation. It was argued that early exposure to enriching conditions can result in later benefits, such as increases in exploratory activity (e.g., Manosevitz, 1970), superiority at learning tasks (e.g., Greenough, Wood, &

Madden, 1972), increased play and behavioural diversity (e.g., Denenberg, Karas, Rosenberg, & Schell, 1968; Bramblett, 1989), and improvements in general health (e.g., Chamove, 1989a, 1989b; O'Neill, 1989). The present section views novelty and complexity as a form of behavioural enrichment applied during testing, and emphasises the practical value of improving conditions for captive animals.

A significant proportion of information about the effects of novelty and complexity on the behaviour of captive animals has come from studies conducted in zoos. It has been argued that enrichment in zoo enclosures is particularly important, largely because unlike their wild counterparts, animals maintained in captivity are under little pressure from the environment (Loizos, 1967). Zoo animals, according to Loizos, are provided with all of the requirements they would normally have to go about finding or avoiding for themselves; for example, a suitable climate, food supplies and a lack of predators. Since zoo animals do not operate at optimal levels, Loizos went on to argue, they should therefore be provided with stimulation appropriate to their potentials. In general terms, it has been shown that a lack of novel stimulation for exploration can result in distortions in behaviour (such as stereotyped pacing and rocking, Eibl-Eibesfeldt, 1970). In discussing the chimpanzee in particular, Loizos (1967) argued that since these animals are capable of performing extremely involved tasks (ranging from opening puzzle boxes to taking part in manned space-flight programs), they ought to be provided with a wide range of novel objects in their enclosures.

Similar suggestions for other primate enclosures are plentiful. Many studies have pointed to lack of novel and/or complex stimulation as being responsible for inactivity and abnormal behaviour in primates (e.g., Morris, 1964; Erwin & Deni, 1979; Maple, 1979, 1980; Maple & Hoff, 1982; Clarke, Juno, & Maple, 1982; Bramblett, 1989; O'Neill, 1989; Markowitz & Line, 1989; Gilbert & Wrenshall, 1989). Erwin and Deni (1979) provided descriptions of some of the abnormal behaviours said to be induced by captivity: bizarre postures (e.g., floating limb, self-biting, self-clasping, self-grasping and saluting), stereotyped motor acts (e.g., pacing, head-tossing, bouncing in place, somersaulting and rocking), appetitive disorders (e.g., copraphagia and paint-eating) and sexual disorders (e.g., inappropriate orientation and sexual dysfunction).

Such behaviours have been argued to be particularly problematic in a species such as the chimpanzee, which has been characterised as a highly curious, manipulative animal, often subject to boredom or lack of occupation (Kohler, 1927; Goodall, 1965; McGrew, 1977). Paquette and Prescott (1988) conducted an experiment to attempt to enrich the behaviour of captive chimpanzees, by simply allowing a small group to manipulate different quantities of novel objects. The result of the study was that manipulation frequency increased, and inactivity, self-grooming and abnormal stereotyped behaviour decreased. This finding, along with a decrease in aggression, led Paquette and Prescott to conclude that distributing objects was an effective way to occupy captive chimpanzees, particularly when the number of available objects exceeded the number of animals. Litchfield (1991a, 1991b, 1991c) supported the notion that novel stimulation can have an effect on aberrant behaviours in chimpanzees, reporting a dramatic reduction in fecal smearing and copraphagia in the first few days following the introduction of a set of objects. Clarke, Juno and Maple (1982) reported similar effects associated with the the use of objects in chimpanzee enclosures.

Prior to these studies, novelty and complexity have been purported to enrich the behaviour of a wide range of animals and humans (as discussed earlier, in sections 4.3.1 and 4.3.4, e.g., Butler, 1965; Hutt, 1967a; Welker, 1956, 1971; Taylor, 1974; Leyland, Robbins, & Iverson, 1976; Maple, 1979; Wilson, 1982; Poucet, Durup, & Thinus-Blanc, 1988; Rogers, Sink, & Hambley, 1988; Millar, Evans, & Chamove, 1988). As an additional observation, it has often been noted that effects of habituation can be countered by means of a periodical substitution of the objects from time to time. Thus, as suggested by Welker (1956), Leyland, Robbins and Iverson (1976) and Paquette and Prescott (1988), presenting a different set of objects each day, and maintaining object presentation in a cycle, effectively maximises the use of a limited bank of toys.

In conclusion, novelty and complexity have been shown to be important factors in eliciting exploration, and since these can be supplied in the form of objects and natural cage designs, it has been suggested that the environment of captive animals may be enriched accordingly.

4.3.7. Learning

The word 'learning' has diverse meanings in both scientific writing and ordinary speech, referring sometimes to internal processes and sometimes to observed behaviour (Barnett, 1976). In the present context it is used according to its usual meaning in operant conditioning; that is, "a relatively permanent change in response potentiality which occurs as a result of reinforced practice" (Kimble, in *The Penguin Dictionary of Psychology*, Reber, 1985, p. 395). Thus, operant conditioning and extinction are included under the title of 'learning'. Later in the section, however, learning is viewed in more general terms, in the sense of 'acquiring information about the environment'.

This final section in Chapter 4 deals with experimental evidence relating to learning and open-field behaviour, arguing that behavioural enrichment can be achieved through operant conditioning and extinction. The section begins with a short subsection on behaviours associated with the operant conditioning process, making particular mention of 'adjunctive behaviours', and following this, effects of extinction on open-field behaviour are examined. Finally, the discussion turns to relationships between learning and activity (based on the work of Kvist, 1983, 1984, 1986), proposing that learning activates the learner. In this context, both conditioning and extinction are examined, arguing that these have implications for programs of enrichment for animals in captivity. The discussion of enrichment completes the theoretical framework for the experimental research reported in Chapters 5 to 8.

Some behaviours associated with the operant conditioning process

A number of studies have examined behaviours which may occur in conjunction with the conditioning process; such schedule-induced 'adjunctive' behaviours have been reviewed by Falk (1971) and Lucas, Timberlake and Gawley (1988). The behaviours have been termed 'adjunctive' or 'schedule-induced' because they are not instrumental in producing food. Examples of behaviours induced as adjuncts to behaviours under schedule control have been observed in a variety of species (e.g., rats, pigeons, monkeys and chimpanzees), perhaps the most commonly reported being excessive drinking or 'polydipsia' (Falk, 1971; Roper, 1981; Timberlake & Lucas, 1991). The phenomenon of polydipsia is said to occur when food-deprived animals are fed small amounts of food every few minutes, resulting in the ingestion of as much as half an animal's body weight in a three-hour period (Falk, 1971).

Other adjunctive behaviours in rats include pica (ingesting wood shavings of the floor of the living space, Killeen, 1975; Roper, 1978), wheel-running (King, 1974; Levitsky & Collier, 1968), air-licking (Mendelson & Chillag, 1970), propping (placing the paws against the side walls of the apparatus) and jumping at the lid of the apparatus (Litchfield, 1987); as well as aggression and escape in monkeys (Hutchinson, Azrin, & Hunt, 1968; Falk, 1971, 1972; Segal, 1972); and pacing and cigarette smoking in humans (Wallace & Singer, 1976). Adjunctive behaviours have been interpreted as species-specific appetitive reactions, classed in the same category as the species-specific 'instinctive drift' behaviours reported by Breland and Breland (1966; see also Chapter 6), which emphasise the difficulties involved with certain species in certain conditioning situations (such as getting an animal to stand still using food as a reward).

Effects of extinction on open-field behaviour

In addition to the studies reporting a relationship between conditioning and open-field behaviour, there are many reporting characteristic effects of extinction on subsequent behaviour. Much of the literature on extinction refers to increases in response variability during the extinction process (in contrast to decreases in variability during conditioning). Response variability has been described as exploration of various members of the operant response class and various aspects of the testing situation (Miller & Stevenson, 1936; McFarland, 1966; Wong, 1977).

It has been shown, for example, that a pigeon trained to peck a key for food tends to become more and more stereotyped in its actions during conditioning, but during extinction the topography of this behaviour changes, such that the responses become novel in form (Antonitis, 1951; Eckerman & Lanson, 1969). According to Frick and Miller (1951), not only is this disruption in the behaviour pattern sharp and immediate, but the responses made after the first half hour of extinction become so variable that even the gross direction of movements becomes difficult to predict. Skinner (1938) suggested that an increase in the variety of response topographies has practical value in that it leaves more possibilities open for the conditioning of the novel response forms by selective reinforcement; this indicates the adaptive significance of response variability during extinction (Antonitis, 1951). There are also studies examining response variability during the different kinds of schedule (e.g., fixed interval, variable interval), and although these will not be discussed here, it may be noted that variability has been found to increase for all schedules other than those supplying continuous reinforcement (Eckerman & Lanson, 1969).

Apart from variability in the conditioned response itself, a variety of extinction-induced behaviours have been reported; for example, aggression (Azrin, Hutchinson, & Hake, 1966), agitated behaviour (Miller & Stevenson, 1936), escape (Rosellini & Seligman, 1975), displacement activities (McFarland, 1966), adjunctive drinking (Falk, 1971), sand-digging (Wong, 1977), vocalisation (Azrin & Lindsley, 1956), and exploration (Harcourt, 1983; Forster, 1986; Litchfield, 1987). Many reports, according to Azrin, Hutchinson and Hake (1966), have inferred the existence of a 'frustrating' or 'emotional' state during extinction. For the present purposes, the extinction-induced behaviour of aggression will be elaborated upon, since this has been reported most frequently.

A study by Azrin, Hutchinson and Hake (1966) tested for effects of extinction on pigeons' attacking behaviour by locating either a second pigeon or a stuffed model of a pigeon near the subject during the trial (in which key-pecking was the operant response). It was found that at the moment of transition from continuous reinforcement to extinction, the birds' frequency of pigeon-directed attacks increased, and this repeated each time the continuous reinforcement schedule was changed to extinction. This result suggested that the transition was an aversive event. Azrin *et al.* ruled out the pigeons' past history of social competition as an explanation, since socially deprived animals also attacked at the onset of extinction, and attacks were equally likely for real pigeons and stuffed model pigeons; however, hunger was found to be a factor, insofar as prior satiation reduced the attacks.

A later study (Hutchinson, Azrin, & Hunt, 1968) used squirrel monkeys as subjects, and examined instances of aggressive behaviour directed towards a rubber hose in conjunction with extinction (and various fixed ratio schedules) using lever-pressing as the operant response. Attacks consisting of biting behaviour were observed during the post-reinforcement pause, after transition to higher values of the fixed ratio requirement, and during extinction. This expanded the previous findings (Azrin, Hutchinson, & Hake, 1966) by showing that extinction-induced aggression occurred in primates as well as pigeons, and that the post-reinforcement pause and some features of ratio schedules are aversive. Such an interpretation is consistent with Azrin (1961), Thompson (1965) and Thompson and Bloom (1966); and further, Gentry (1968) went on to postulate that extinction-induced aggression may depend in part on the availability of certain responses and on the presence of a second animal.

A stage model of extinction developed by Wong (1977, 1978) proposed that extinction-induced response variability is theoretically similar to accounts of frustration (e.g., Amsel, 1958; J. G. Gray, 1971; Miller, 1959). In Wong's model, three distinct stages were said to occur during extinction: 'habit', 'trial and error' and 'resolution'; and each of these stages was characterised by particular behaviour patterns. 'Habit', was said to be characterised by response persistence and the absence of competing behaviour (i.e., persevering with habitual behaviours); 'trial and error' resulted in an increase in investigatory behaviour (response variation and exploration) and aggressive behaviour; and 'resolution' was associated with a decrease in the competing responses of the second stage. The model therefore accommodated previous research on aggression as an outcome of extinction, placing it under the category of 'trial and error'. Moreover, the model predicted an inverted *U*-function for exploratory and aggressive behaviour during extinction, and this was supported in Wong's experiments (1977, 1978).

To conclude this subsection, extinction, according to Wong (1978), may be thought of as a process involving a broadening of behavioural possibilities, in which behaviours which may have ceased during acquisition of the operant response often re-emerge, as well as displacement activities specific to the extinction situation (such as aggression). Thus, the extinction process can induce a wide range of behaviours, and these are particularly prevalent at the immediate onset period.

Learning activates the learner

One of the themes of the work of Kvist has been that "learning activates the learner" (1983, p. 313), and such a position has come about after a history of experiments reporting a connection between learning and activity. Some of the early studies of exploration carried out in the 1950s and '60s pointed to a connection between subjects' conditioning history and their subsequent exploratory behaviour (thus studying learning within the paradigm of early experience research). Butler (1954), for example, reported significant effects of monkeys' prior learning experiences on both their visual and auditory exploration. Other investigators reporting a connection between learning and activity include Rundquist and Heron (1935), Munn (1950) and Satinder (1968). More recently, relationships between early experience and amounts of exploration have been studied, with the argument that early learning (e.g., in enriched or impoverished conditions, as discussed in section 4.2.2) alters the character of later exploratory activity (Renner & Rosenzweig, 1986).

In particular, the existence of an *increase* in activity in conjunction with the learning process has been reported by Lagerspetz, Raitis, Tirri and Lagerspetz (1968); this is consistent with the models referred to in Chapter 2 (section 2.3), in which activity was described as an integral part of the normal conditioning process (Sheffield, 1966), a by-product of conditioning by contiguity (Skinner, 1948), a sign of frustration (Scull, 1973), a derivative of optimal arousal (Dember & Earl, 1957), or an adjunctive behaviour induced by a schedule of reinforcement (Levitsky & Collier, 1968). Other studies referring to activity increases following learning have been conducted by Mitani, Ando and Nagata (1972), who found that rats trained in a food-reinforced runway produced increased activity in an activity wheel; and Milkovic, Paunovic and Joffe (1976), who reported enhanced open-field activity by rats after avoidance conditioning. It has been shown that such behaviour is not restricted to rats: Killeen (1975) reported a series of experiments demonstrating that an increase in activity in pigeons was a fundamental consequence of the acquisition of a learned response, and that such an increase reached its maximum soon after a signal of impending reward. Killeen interpreted this behaviour as a species-specific appetitive reaction (similar to an adjunctive behaviour, as mentioned above).

More recent studies by Lagerspetz, Kvist and Lagerspetz (1980) and Kvist (1983, 1984) provided more details on the nature and context of the increases in activity following learning by mice. These studies examined possible increases in activity following various types of learning: conditioned passive avoidance responses, maze learning, or the learning of aggression and non-aggression. Factors assessed were the duration of activity increases, the influence of the familiarity of the environment, the influence of the floor texture, and the result of motor activation *per se* compared to the result of learning. Increases in ambulatory activity (lasting 60 minutes) were observed under all conditions (compared to control groups undergoing no learning), showing that the trend was not restricted to any specific type of learning procedure, and giving support for an enhancement of activity after learning. The result was explained on the basis of an increase in the arousal level caused by the acquisition of a new response (and was thought to apply especially to albino strains of mice, inferring that the thresholds in the arousal-motor activation systems differ between different strains, Kvist, 1984).

One criticism of the interpretation of activity increases in such situations has been that the behaviour may simply be due to hunger rather than learning (e.g., Glickman & Jensen, 1961; Bolles, 1967, mentioned earlier in section 4.3.1). However, the experimental animals in Kvist's studies (1983, 1984) were fed before the activity recordings, thus eliminating this possibility. Secondly, in reply to the criticism that the activity increases merely reflected the motor activity involved in maze learning, Kvist (1986) pointed out that the same result occurred in connection with passive avoidance conditioning, in which animals were not required to move.

A third criticism of the interpretation of the increases in activity is that the behaviour may actually be due to coping with stress during the learning procedure (consistent with the fear theory of exploration in Chapter 2, and the idea that novelty induces fear, section 4.3.3) rather than due to the learning procedure itself. Kvist (1986) conducted an investigation to clarify this distinction: open-field activity was measured following maze learning (which was claimed to involve psychological coping with a task), and this was compared to two 'stress' groups; the first measuring behaviour following a light-sound stress (a harmless physical stressor involving physiological coping by reflex action from eyes and ears), and the second exposing an animal to another animal's aggressive attacks (a harmful stress for which there was no effective coping possible). Kvist's findings indicated that the experimental procedures affected open-field activity in various ways. Maze learning was found to result in an increase in activity, but the activity level of the light-sound stress group was not affected, and the activity of the attacking stress group decreased. This supports a model in which 'learning activates the learner'.

The importance of the role of learning in the behaviour of captive animals has been emphasised (e.g., Eibl-Eibesfeldt, 1970; Chamove, 1989a, 1989b; Bramblett, 1989). It has frequently been observed that a lack of opportunity to learn skills (such as hunting for food) leads to distortions in the behaviour of captive animals, particularly in mammals which are normally quite active. For example, a lack of opportunity to learn may result in pacing back and forth (thereby retracing the same paths in an enclosure), engaging in repeated swinging movements, or other stereotyped actions (Eibl-Eibesfeldt, 1970). In some zoos, attempts have been made to reduce such behaviour by implementing programs of 'work therapy'. In these programs, animals are given the opportunity to carry out chains of behaviour, receiving food reinforcement upon completion of the activity (Eibl-Eibesfeldt, 1970). For example, Molzen and French (1989) used a novel foraging device containing raisins for their golden lion tamarins, Bloomsmith (1989) used a similar food puzzle device for chimpanzees, and Rumbaugh, Washburn and Savage-Rumbaugh (1989) taught two chimpanzees to use joysticks to play a video game. Rumbaugh *et al.* also reported that animals in fact *prefer* to work for food, rather than receiving identical rewards for free.

As an alternative to food-reinforced learning, it has been argued (e.g., Smith & Simon, 1984) that aberrant behaviour can be alleviated by the learning which accompanies play behaviour. According to Bruner (1972, p. 693), play serves several centrally important functions, since it "is a means of minimizing the consequences of one's actions and of learning, therefore, in a less risky situation" and it "provides an excellent opportunity to try combinations of behavior that would, under functional pressure, never be tried." This is consistent with the suggestion that exploration is enriching.

To conclude the present section, it may be argued that since wild animals need to learn the characteristics of their environment in order to find food, threaten and avoid conspecifics, and flee from predators (Chamove, 1989a), then it follows that learning procedures could be effectively implemented in zoos and laboratories, thus ensuring the continued maintenance of a variety of behavioural repertoires. In other words, behavioural enrichment could be achieved by providing increased psychological space in the form of opportunities to learn. Such an idea supports Smith and Simon (1984) and Renner and Rosenzweig (1986), who suggested that by creating situations in which learning is likely to take place, animals are able to modify their own strategies of behaviour, thereby enriching naturally occurring behaviours such as those involved in exploration.

4.4. CONCLUSION

The aim of this chapter was to examine factors affecting open-field activity, beginning with subject variables (genetic and experiential), and then focusing on the experimental situation, discussing the influence of novelty, complexity and learning on activity and exploration. Since these factors interact - resulting in all features of behaviour being inescapably influenced both by heredity and environment (Barnett & Cowan, 1976) - it has not been the intention to argue that one or other is more important. Rather, the aim has been to indicate the complexity involved in open-field studies, showing that a wide range of variables can play significant roles in the nature of behaviour produced.

A theme arising from both the discussion of subject variables and the experimental situation is that of enrichment. It has been argued that behavioural enrichment can be achieved by manipulations of the early experience of captive animals (e.g., by the addition of objects, natural cage design and social enrichment), and by manipulations during the experimental situation (e.g., by providing stimulus novelty and complexity, and the opportunity to learn). It follows from this that combinations of these factors may be used in attempting to improve the welfare of captive animals, thus altering behaviour so that it is within an animal's normal range (Chamove, 1989b). The experiments reported in the following four chapters concentrate particularly on learning and variations in stimulus novelty, the aim being to identify possible relationships between these, and to provide information about the enriching effects these variables may produce.

CHAPTER 5

EXPLORATION AND EXTINCTION

5.1. INTRODUCTION

Chapter 5 is the first of four chapters dealing with the present experimental research. The format for each of the experimental chapters is the same: first, a description of the experiment, indicating the hypotheses to be tested, next a description of the methodology employed, and then a single 'Results and Discussion' section, in which the findings are presented and discussed with reference to the initial hypotheses. A concluding section sums up the experimental findings and provides a link to the subsequent experimental chapter.

Methodologically, the present experiments were based on a number of specific procedures used by various investigators interested in exploration. The following general apparatus and techniques were employed in the six experimental studies. (Any departures from these are clarified in each 'Method' section.)

The design of the open fields varied for each experiment, according to the species involved and the purpose of the study. Generally, the open fields for the rats were either square or rectangular enclosures, all similar in size (but incorporating variations where necessary), and the marmoset enclosures were upright rectangular cages.

The use of objects as a means for measuring exploration followed from a group of studies focusing on novel object interactions by rats; for example, those of Renner and Rosenzweig (1986), Renner (1987) and Rosellini and Widman (1989). Common to these researchers is the idea that object interactions provide a great deal of information about complex patterns of exploratory behaviour, and that such information can be enhanced by the addition of other measures of behaviour, such as general activity levels or movements in space. Consequently, the behavioural measures selected for the present studies incorporated both object-directed and non-object-directed behaviour, aiming to capture a wide spectrum of exploration.

A further distinction in the work of Rosellini and Widman was the choice of objects which varied in manipulability: some of their objects were of a size and weight such that they could be manipulated by the animal, and some could neither be moved nor manipulated. Thus, the design of objects for the present experiments incorporated variations in manipulability.

The design and construction of objects differed according to the particular animal participating in each experiment; adaptations were incorporated where appropriate for use by rats or marmosets. For example, objects for rats were clipped on to the floor and many featured tunnels, an attempt to replicate a feature of the rat's natural environment. In contrast, marmosets were provided with hanging objects, since much of their behaviour occurs near the tops of their cages. This was an attempt to provide these animals with the opportunity to carry out behaviour resembling the activities involved in swinging from tree branches.

The use of recording equipment to produce video tapes for later scoring followed from Rosellini and Widman's (1989) study. Indeed, such a procedure has been employed by ethologists ever since the invention of video tape, providing advantages such as the opportunity to view behaviour over and over again (also making it possible to measure multiple aspects of behaviour which occur simultaneously), preservation for later comparison, and fast and slow motion for the analysis of every detail of the behaviour under observation (Lehner, 1979; Renner, 1987).

The procedures for scoring the behaviour of the rats and marmosets in the present studies were modelled after those of Renner (1987) and Roder, Timmermans and Vossen (1989), who recorded frequency and duration of behaviours with an event recorder (and again, event recording techniques have been used by ethologists, as outlined in Chapter 1, section 1.3).

Renner's behavioural categories were developed in order to measure the object-directed exploratory behaviour of the adult rat, *Rattus norvegicus*. The categories (which were also adopted by Rosellini and Widman, 1989) included sniffing (investigation of the arena itself as opposed to objects in it), grooming, withdrawal (sudden retreat from the arena into the start box), freezing (sudden interruption of ongoing activity in favour of immobility), immobility (periods in excess of 5 seconds without motion), locomotion (ambulation without changes of zones), digging (digging motions at the floor or wall of the arena), rearing (standing on the hind legs with the forepaws in free air), and propping (one or both forepaws against the wall of the arena or start box, with or without sniffing the adjacent wall). Renner recorded interactions with the objects under the following categories: low risk investigation (sniff/nose contact), paw contact (single paw contact, lean on object or grab object), climb/enter object (weight of all four paws on object), contacts with mouth (bite or drag object), accidental contacts (collide with object moving forward or backward), object 'behaviour' (movement of object). Any combination of categories could occur during any given object interaction; for example, an animal could be scored as sniffing an object as well as leaning on it.

Categories comprising subsets or extensions of these (often according to the particular species under investigation) have been used in many animal studies, as reviewed in Chapter 3, section 3.4; for example, by Berlyne (1955), Welker (1956), Glickman and Sroges (1966), Jowaisas (1969), Russell (1973b), Gojak (1984), Poucet, Durup and Thinus-Blanc (1988), Millar, Evans and Chamove (1988), Paquette and Prescott (1988), Litchfield (1987, 1991a, 1991b, 1991c) and Forster (1986, 1990).

The present experiments adopted a selection of Renner's (1987) behavioural categories, and some were modified for the measurement of marmoset behaviour. In response to the debate on activity versus exploration (Chapter 3, section 3.4.1), the experiments incorporated not only measures of object-directed behaviour, but also non-object-directed behaviour, with the aim of covering both 'general activity' and 'exploratory behaviour'. The particular categories employed for each experiment are described in detail in each respective 'Method' section.

5.2. EXPERIMENT 1: EFFECTS OF RESPONSE GENERALISATION AND EXTINCTION ON EXPLORATORY BEHAVIOUR IN THE RAT *(RATTUS NORVEGICUS)*

Experiment 1 examined effects of response generalisation and extinction on exploration in the rat (*Rattus norvegicus*) by means of observation of animals in an open field containing various novel objects. The purpose of the experiment was to investigate the relationship between extinction and exploration in the form of object interactions; or, more specifically, to determine whether object-directed exploratory behaviour could be induced by extinction. The reasoning for such a postulated relationship can be described in terms of the adaptive significance of exploration, as argued in Chapter 2, section 2.4: exploratory behaviour provides animals with information about the environment, including maintenance of familiarity with the home range, location of new resources, avoidance of predators and the opportunity to learn new strategies.

In the experiment, animals' object interactions and operant responses were observed following continuous reinforcement, and the role of response generalisation and extinction were examined by comparing object interactions following reinforcement of either bar-pressing with the paws, or key-pushing with the snout. The bar-pressing response was selected since it has been a standard operant for use with rats (e.g., Skinner, 1938), and a nose-key was designed in order to provide animals with a naturally occurring response, since rats often poke their noses into small holes and crevices during their wanderings (Barnett, 1981).

Firstly, in accordance with work on the habituation of novelty (Chapter 4, section 4.3.2), it was expected that object interactions would decrease as object novelty decreased, regardless of experimental conditions. Such a finding would be consistent with reports of Hutt (1967b), Ratner (1970), Ivinskis (1970), O'Keefe and Nadel (1978), Ellen and Weston (1983) and Rogers, Sink and Hambley (1988); and also with the theory of optimal arousal, in which repeated exposure to the same stimuli results in less arousal as animals become familiar with those stimuli, therefore directing less attention towards them (Berlyne, 1950; Dember, Earl, & Paradise, 1957; Montgomery, 1953).

Predictions for each individual session of extinction were based on descriptions by Thor, Harrison, Schneider and Carr (1988) and Poucet, Durup and Thinus-Blanc (1988), in which exploration begins with a burst of sustained object-directed investigation, followed by attention directed away from the novel objects. Regarding *between-sessions* effects, the experiment was also a test of Renner and Rosenzweig's (1986) hypothesis that habituation on one occasion does not necessarily carry over into the subsequent day's testing.

The second set of hypotheses concerned effects of extinction on exploratory behaviour, with the aim of testing the claim that learning activates the learner (Kvist, 1983). It was expected that animals undergoing extinction following the reinforcement of bar-pressing and key-pushing responses would show a higher initial rate of object interactions than untrained animals. This may be explained partly in terms of the finding that animals from enriched environments display a greater number of different behaviours in interacting with objects than impoverished litter-mates (Renner, 1987), if one defines the learning tasks as 'enriching'. In any case, the hypothesis rested on the idea that the extinction process not only induces changes in the form of the conditioned response (Antonitis, 1951; Frick & Miller, 1951; Eckerman & Lanson, 1969), but also induces a variety of new behaviours, such as aggression (Azrin, 1961; Thompson & Bloom, 1966; Gentry, 1968; Azrin, Hutchinson, & Hake, 1966) and exploration (Harcourt, 1983; Forster, 1986; Litchfield, 1987).

The existence of exploratory behaviour during extinction corresponds to the second stage of a model developed by Wong (1977, 1978); that is, 'trial and error', in which an animal investigates and explores its environment (as well as exhibiting aggressive behaviour). According to Wong, such behaviour reflects a widening of behavioural possibilities. A prediction consistent with this model is that exploration ought to follow an inverted *U*-function; in the present experiment this would be indicated by a higher level of exploration during the middle session of extinction, with lower levels before and afterwards. In addition, it was predicted that a sudden rise in exploration would occur at the onset of extinction. This prediction is consistent with accounts of extinction-induced aggression or attacking behaviour, which are typically observed at the precise moment of transition between continuous reinforcement and extinction (Hutchinson, Azrin, & Hunt, 1968). Indeed, the transition moment itself has been described as the most aversive event associated with the extinction process (Azrin, Hutchinson, & Hake, 1966).

The third and final set of hypotheses involved the role of the phenomenon of response generalisation on the exploratory behaviour produced during extinction. It was expected that animals trained to bar-press would subsequently explore objects more with their paws, whilst animals trained to key-push would produce more nosing actions. This hypothesis was partly derived from an experiment by Renner (1987), in which rats from enriched environments subsequently manipulated a set of novel objects more than animals from an impoverished environment; but it was primarily a test of the phenomenon of response generalisation, in which animals are said to carry out various members of the operant class (as well as exploring various aspects of the testing situation) during extinction (McFarland, 1966; Miller & Stevenson, 1936; Wong, 1977).

METHOD

Subjects

The subjects were 18 male Hooded Wistar rats (*Rattus norvegicus*) obtained from the Central Animal House of the Waite Institute, University of Adelaide, South Australia, at 90 days of age. They were housed in separate cages (28cm x 19cm x 18cm) in an animal holding room in the Psychology Department, University of Adelaide. 2 extra rats served as subjects for a pilot experiment, in order to test the apparatus and procedures.

The temperature of the animal holding room was kept constant, and lighting followed a 12/12 light-dark cycle (lights on 6.00am, off 6.00pm). All animals had *ad libitum* access to water via a drinking bottle.

Rats were individually handled for 5 days prior to the beginning of the experiment. The purpose of this was to familiarise the animals with the experimenter and the procedure of being removed from their home cages. Handling consisted of taking a rat out of its home cage, gently stroking it for 10 minutes, and then returning it to its cage. Throughout the 5 days of handling, food was supplied *ad libitum* in the form of rodent food pellets. For the duration of the study, the animals were given free access to food for an hour following each experimental session.

The rats were randomly allocated to one of three groups, each group consisting of 6 animals. There were two experimental groups: BAR and NOSE-KEY; and one control group: CONTROL.

Apparatus

Experimental apparatus

The experimental apparatus consisted of a box measuring 49cm x 49cm x 30cm (Figure 5.1). The box was made of stainless steel, and had a transparent plastic cover. Three removable partitions were used for the three experimental conditions respectively:

(a) a partition fitted with a bar (50mm x 12.5mm), feeding trough and light (Group BAR) (Figure 5.1);

(b) a partition fitted with a nose-key (diameter 1cm), feeding trough and light (Group NOSE-KEY) (Figure 5.2);

(c) a plain wall panel (Group CONTROL).

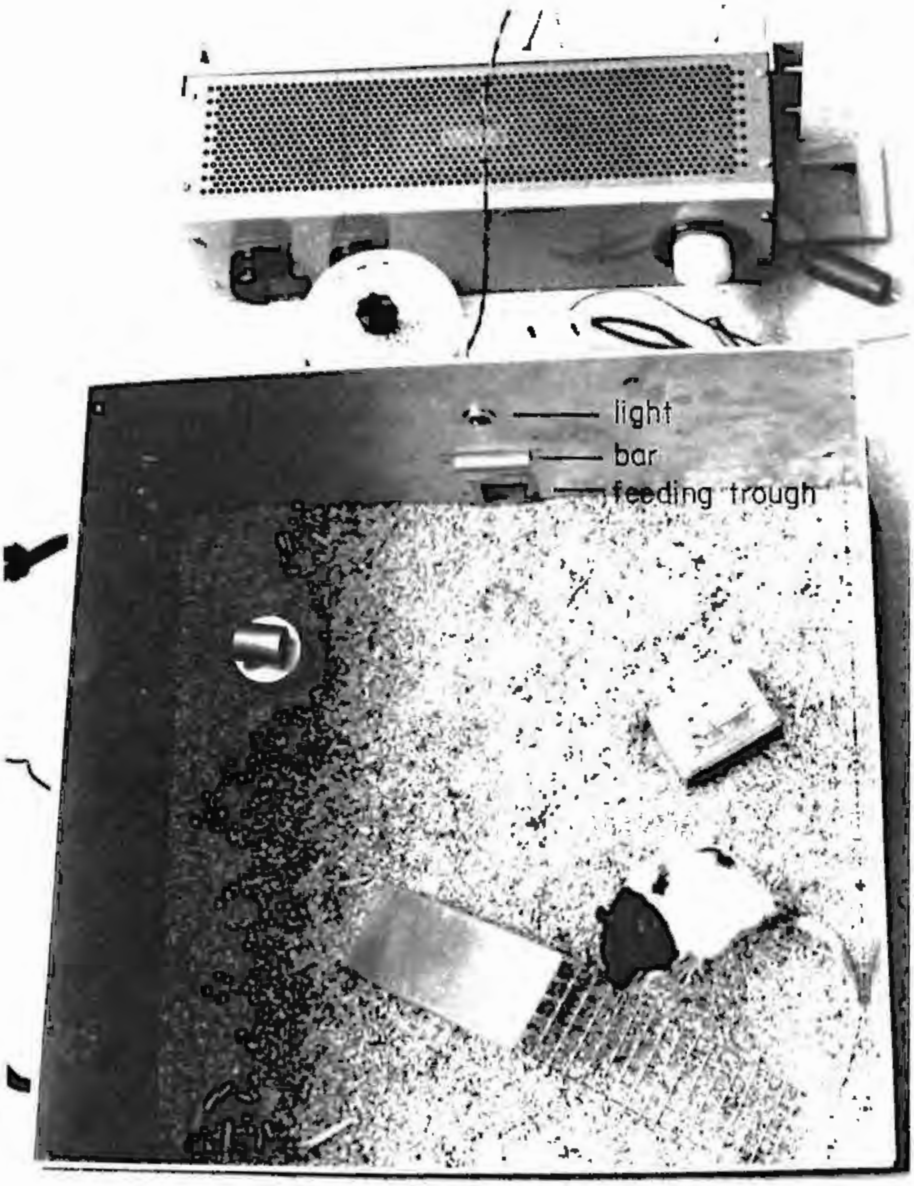


FIGURE 5.1: Experimental testing chamber used in experiment 1.

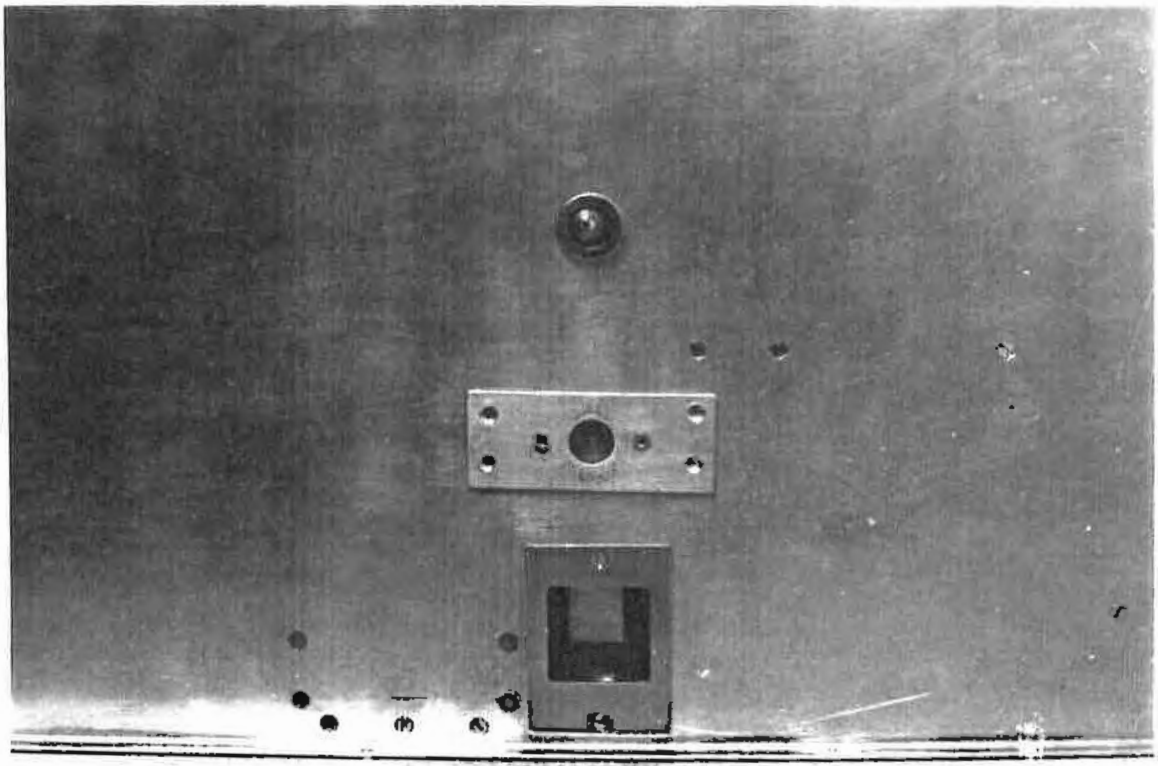


FIGURE 5.2: Partition showing nose-key, light and feeding trough, as employed in Group N.

Located on the outer side of both of the first two of these partitions was a buzzer and pellet dispenser. For Group BAR, reinforcements were delivered by means of a 24V D.C. Power Supply, operated with a hand-held trigger. For Group NOSE-KEY, pellets were dispensed using a *PDP-11* computer programmed for continuous reinforcement. Each time a food pellet was delivered, the buzzer and light were triggered automatically.

The exploration box contained 3 removable objects which were clipped on to the floor (Figure 5.3). (For a list of the names of the objects, see Appendix 1.)

Animals were transported from their home cages to the experimental apparatus by means of a small plastic box containing sawdust. The experimental apparatus was located in a room some distance from the animals' holding room.

Observation equipment

Trials were recorded using a *National WVP 100N* video camera with inbuilt timer, an *Audio 2CH Panasonic* video cassette recorder and *VHS* video tapes. The camera was set up directly above the experimental box. A wooden partition separated the experimental box and camera from a *Sony* video monitor attached to the video cassette recorder.

Recordings of the sessions were later viewed on a *National Panacolour* video monitor and specific behaviours were entered on to *North Star Advantage* computer files by means of an event recording program. Behaviours were entered by means of a box with 4 buttons (Figure 5.4); the depression of one of the buttons recorded the duration and frequency of the particular event under observation.

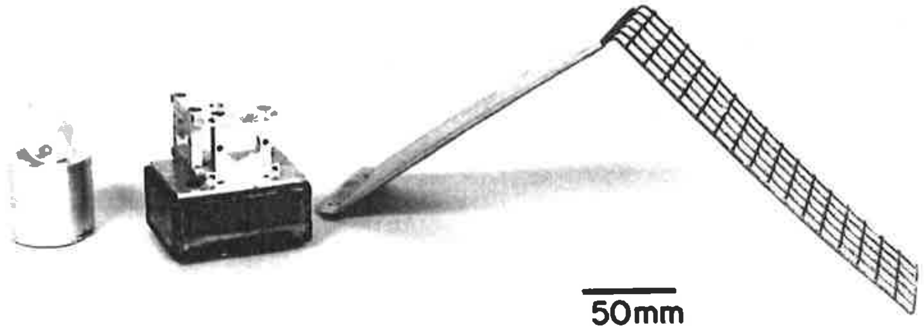


FIGURE 5.3: Experiment 1 novel objects.

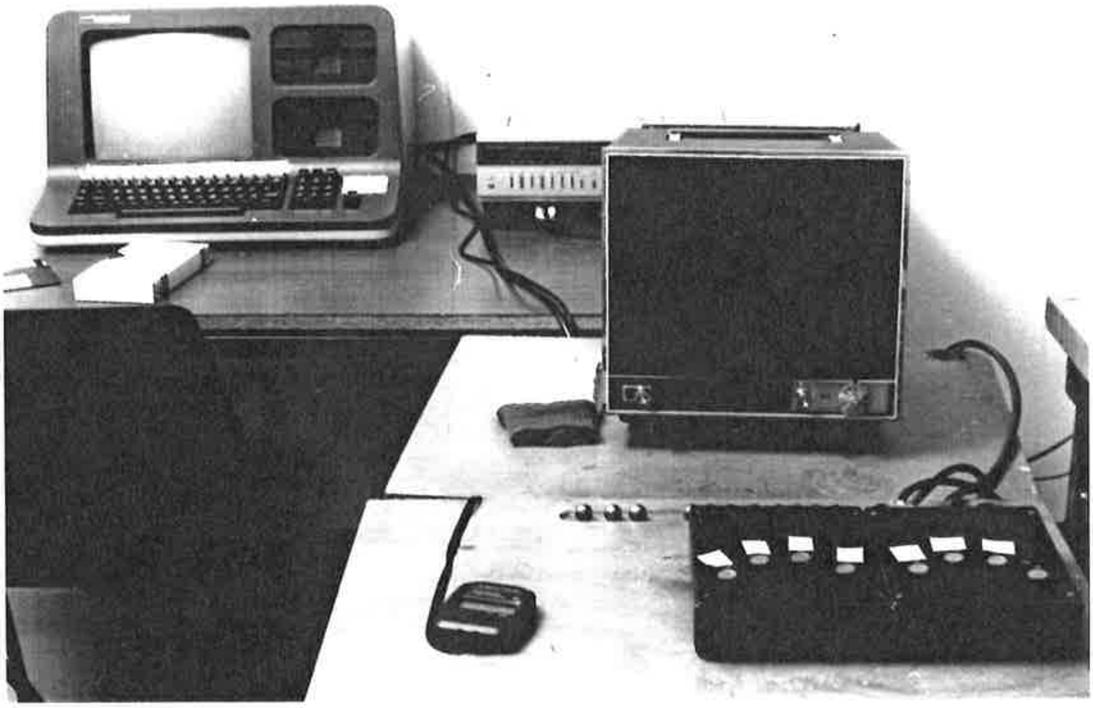


FIGURE 5.4: Event recording apparatus.

Procedure

For each of the three groups of animals (BAR, NOSE-KEY and CONTROL) the experimental design consisted of three parts: firstly, handling; secondly, familiarisation, training to criterion and conditioning; and finally, extinction. Following this, data were recorded by means of an event recording program, and independent judges were employed to undertake reliability tests.

Handling

All rats were handled for the same amount of time prior to the running of the experiment. Handling lasted 5 days and consisted of taking the rat out of its home cage and gently stroking it for 10 minutes. Each time the rats were moved from their home cages to the experimental apparatus (and vice versa) they were picked up by hand and placed in the small transport box. At the beginning of each session, rats were placed in the middle of the experimental box.

Familiarisation, training to criterion and conditioning

Animals in Groups BAR and NOSE-KEY were subjected to the following procedure. With no objects in the box, experimental rats took part in several individual training sessions, in which bar-pressing or key-pushing was shaped. Following this, animals were placed on a schedule of continuous food reinforcement. Each rat experienced from 2-5 training sessions, depending on the amount of training required before a criterion of 100 bar-presses or key-pushes was reached. Training sessions varied in length as a function of progress made in conditioning by each particular rat; the total average training time was 66 minutes.

Throughout this stage of the procedure control rats (Group CONTROL) were placed in the box (without the objects, the bar or the nose-key) for the mean number of sessions and the mean amount of time taken for the experimental rats to be conditioned (i.e., 4 sessions totalling 66 minutes).

The procedure for shaping both the bar-pressing and the key-pushing responses was the same, except that different behaviours were shaped so as to result in the appropriate conditioned responses. During the training sessions a rat was placed in the experimental box fitted with the bar or nose-key, the feeding trough, but no objects. Within the first few seconds of being in the box a free reinforcement was delivered by means of pressing a button attached to the pellet dispenser. Pressing the button also triggered the light and buzzer simultaneously with the delivery of the reinforcement. The conditioning phase of the procedure ended once animals had reached a criterion of 100 responses within the space of 15 minutes.

Extinction

Animals were observed on three separate occasions, each session lasting 15 minutes. During these sessions rats in Groups BAR and NOSE-KEY underwent extinction for bar-pressing and key-pushing respectively, and the sessions for Group CONTROL parallelled those of the experimental groups.

During the extinction sessions the objects were fitted into the experimental box. Exploratory behaviour was recorded under three conditions, each group being subjected to one condition: extinction in the presence of the partition fitted with the bar and feeding trough (Group BAR); extinction in the presence of the nose-key and feeding trough (Group NOSE-KEY); and animals in Group CONTROL were observed with only the plain wall panel, as in the conditioning phase.

Before attaching the bar or nose-key partition to the box (for Groups BAR and NOSE-KEY), all food pellets were removed from the pellet dispenser and the feeding trough was cleaned. The purpose of this was to eliminate any smell of food so that animals on extinction were not reinforced for bar-pressing, key-pushing or approach to the food trough area. In addition, the sawdust on the floor of the box was changed and the objects were wiped clean.

At the beginning of each extinction session the video recorder was set to 'record' and the timer on the camera was started. Following this, a rat was placed in the middle of the exploration box and the transparent plastic cover was closed. For 15 minutes the rat was left alone, while the session was viewed on the video monitor behind the partition in the room. When the timer display shown on the video monitor reached 15 minutes the rat was removed from the box and returned to its home cage.

Event recording and independent judging

Following the completion of the observation sessions, behavioural measurements for each 15-minute session were recorded by means of an event recording program. Conditioned responses and exploratory behaviours were represented by four buttons on the event recording apparatus:

(a) *responses* - either bar-pressing (Group BAR), or key-pushing (Group NOSE-KEY);

(b) *sniffing objects* - in which a rat's snout is oriented towards an object, but without touching it;

(c) *touching objects with nose* - in which a rat's snout touches, pushes or moves an object (this category also included any biting of an object);

(d) *touching objects with paws* - in which a rat touches or manipulates an object with one or more paws, including climbing on or digging around the edge of an object.

The category of *responses* (bar-pressing or key-pushing) applied to animals in Groups BAR and NOSE-KEY respectively. The other three categories - the measures of exploratory behaviour - applied to all animals.

For all of the measures both frequency and duration of behaviours were recorded. Each time the appropriate button was pressed it acted as a frequency measure, and durations of behaviour were recorded from the time the button was pressed until it was released.

Total frequencies and durations were calculated at the end of the recording, and the measures were expressed in the following way. The frequencies were transformed into rates per minute by dividing the frequency of each behaviour by the amount of time available for exploration (i.e., total session length in seconds - duration of time spent bar-pressing). Since both durations were measured in seconds, the total was then multiplied by 60 to obtain a rate per minute. For example, to obtain a measure of the rate of sniffing objects, the transformation formula was as follows:

frequency of sniffing objects /(900 - total duration of bar-pressing) x 60

Such a transformation enabled a meaningful comparison between the experimental groups and the control group. Without this, it would not be possible to compare frequency measures, since the total amount of time available for exploration differed between the groups: the control animals had no bar or nose-key, and hence were free to explore for the full 15 minutes, whereas the experimental groups divided their time between operant responses and exploratory behaviour. A rate score provided the possibility of comparison between all of the groups. Similarly, the duration measures were converted into percentage durations, thus expressing the duration of each activity as a percentage of the time available. For example, to obtain a measure of the percentage duration of sniffing objects, the following formula was used:

duration of sniffing objects /(900 - total duration of bar-pressing) x 100

In summary, the measures obtained in the study (i.e., the dependent variables) were expressed in the form *rate of sniffing objects per minute*, *percentage duration of sniffing objects*, etc., and in addition, two extra variables were included, representing the sum of the exploratory behaviour categories (*sniffing objects, touching objects with nose* and *touching objects with paws*), and these were labelled *rate of object exploration per minute* and *percentage duration of object exploration.*

In order to test for the reliability of the experimenter's measurements and the behavioural criteria used, data obtained from three independent judges and the experimenter were analysed. Each judge viewed two video-taped sessions (a total of 30 minutes), and recorded data by means of the event recording apparatus. Data were then analysed by using Kendall's W coefficient of concordance. A high degree of agreement among all judges was obtained for frequencies ($W = .889, p < .001$) and durations ($W = .904, p < .001$) of all of the variables measured.

RESULTS AND DISCUSSION

Experiment 1 investigated effects of response generalisation and extinction on exploratory behaviour in the laboratory rat *Rattus norvegicus*. Three groups of animals were used: BAR, NOSE-KEY and CONTROL. Each of these groups was subjected to three observation sessions. The multivariate analysis of variance procedure was applied to data obtained from the extinction sessions for all measures of behaviour, and the results were analysed in terms of effects due to *session*, effects due to *group*, and interactions between these.

Relevant to *session* effects was the hypothesis that amounts of exploratory behaviour exhibited by all animals would decrease over time, as a function of a decrease in stimulus novelty. Similarly, it was expected that the rate and percentage duration of responses (for Groups BAR and NOSE-KEY) would decline with time, representing the extinction process taking place.

With respect to *group* effects, it was expected that Groups BAR and NOSE-KEY would display greater amounts of exploratory behaviour than Group CONTROL, supporting the idea that extinction instigates exploratory behaviour. In addition to this general hypothesis, other predictions were made concerning the topologies of exploratory behaviour exhibited by Groups BAR and NOSE-KEY, in accordance with the phenomenon of response generalisation. Specifically, no difference in amounts of sniffing was expected for the Groups BAR and NOSE-KEY, since sniffing was not a differential component of either bar-pressing or key-pushing. However, it was predicted that animals in Group BAR would exhibit the greatest amount of paw-type behaviour, whilst animals in Group NOSE-KEY would exhibit the greatest amount of nose-type behaviour. If this hypothesis held true, it would imply an influence of response generalisation for bar-pressing and key-pushing during extinction for those respective responses.

Figures 5.5(I) and 5.5(II) show the session means of each behavioural measure. Significant declines in rates of bar-pressing and key-pushing were observed

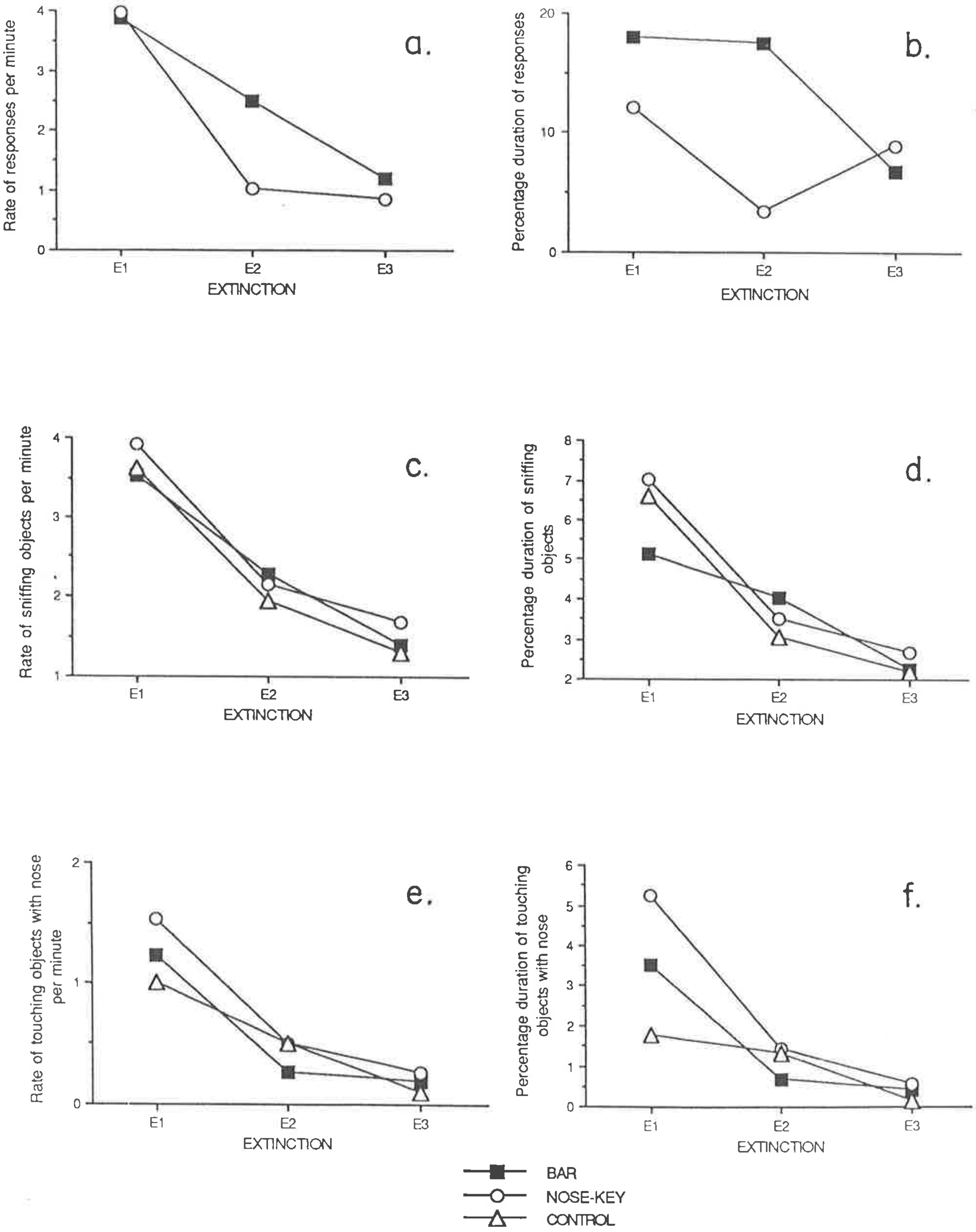


FIGURE 5.5(I): Session means of behavioural measures in experiment 1.

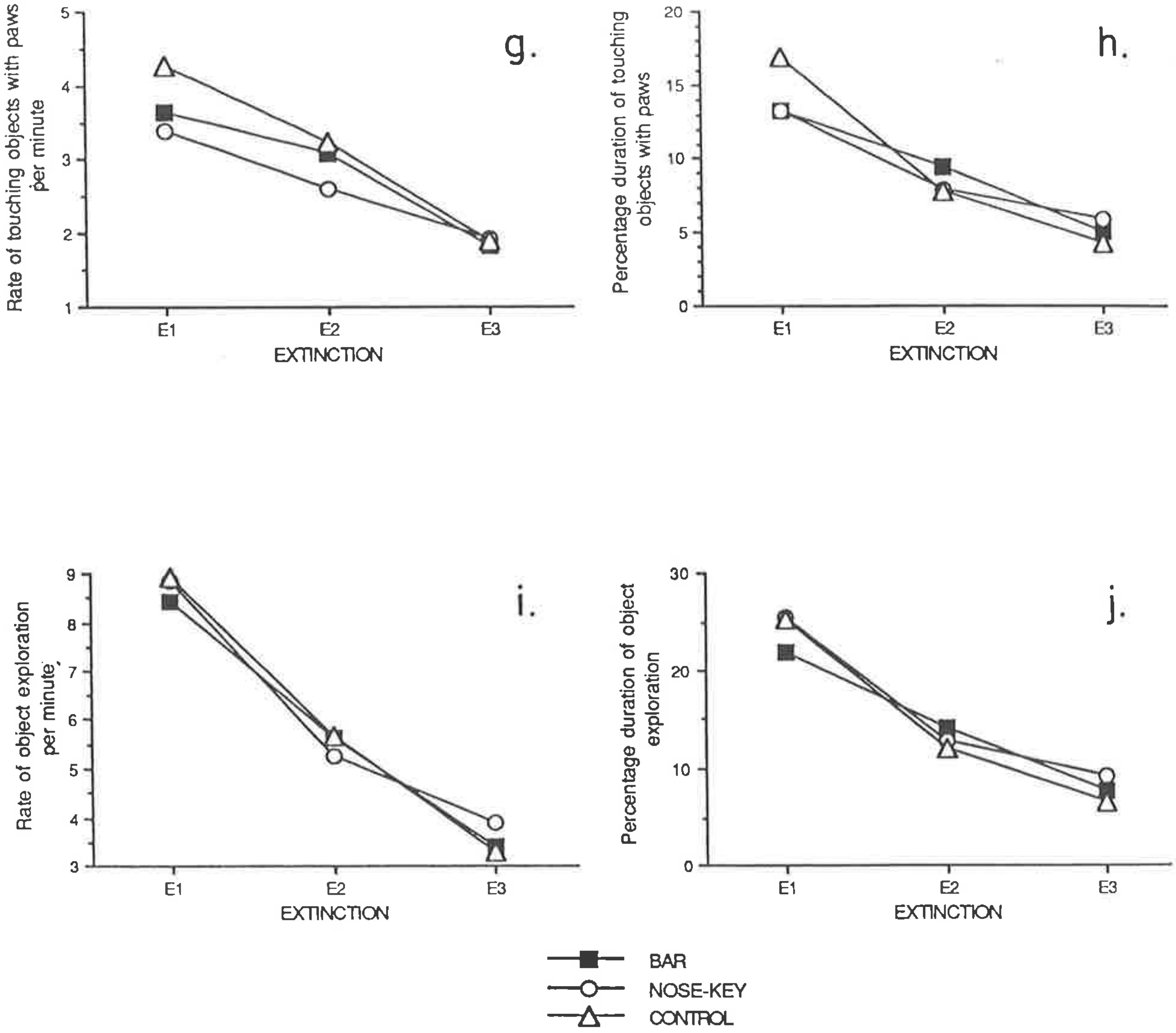


FIGURE 5.5(II): Session means of behavioural measures in experiment 1.

over the course of the three observation sessions (*F*[2,20] = 21.40, *p* < .001), indicating that extinction did in fact take place. High rates of responding were observed during the first session, as would be predicted from accounts of extinction by Thompson and Bloom (1966) and Wong (1978), and these rates gradually declined as time passed.

In addition to the declines in response measures, significant declines for every measure of exploratory behaviour were also observed (Table 5.1). This result can be accounted for by the habituation theory relating to optimal arousal levels (Berlyne, 1950; Dember, Earl, & Paradise, 1957; Montgomery, 1953), and other theories of habituation (e.g., Hutt, 1967b; Ratner, 1970; Ivinskis, 1970; O'Keefe & Nadel, 1978; Ellen & Weston, 1983; Rogers, Sink, & Hambley, 1988). The result is also consistent with Hall (1934a), who found that repeatedly testing rats in an open field sometimes led to a decrement in the amount of locomotor activity displayed. Whimbey and Denenberg (1967) argued that such a decrement in activity may reflect exploratory behaviour as well as emotionality; thus, the habituation of object-directed behaviour observed in the present experiment may have reflected either decreases in locomotor activity, decreases

Table 5.1: Significance levels obtained for measures of exploratory behaviour (*session* effects).

Variable	*F*	Significance level
Rate of sniffing objects	*F*(2,30) = 76.53	*p* < .001
Duration of sniffing objects	*F*(2,30) = 38.90	*p* < .001
Rate of touching objects with nose	*F*(2,30) = 49.95	*p* < .001
Duration of touching objects with nose	*F*(2,30) = 37.13	*p* < .001
Rate of touching objects with paws	*F*(2,30) = 56.65	*p* < .001
Duration of touching objects with paws	*F*(2,30) = 49.26	*p* < .001
Rate of object exploration	*F*(2,30) = 125.60	*p* < .001
Duration of object exploration	*F*(2,30) = 71.35	*p* < .001

in exploration, or both. As noted by Russell and Williams (1973), there is a problem in testing between such alternatives because of the inherent difficulty in distinguishing between activity which is escape directed and that which has an exploratory basis. Finally, some support was found for Renner and Rosenzweig's (1986) idea that habituation on one occasion does not necessarily carry over into the subsequent day's testing, since each extinction session began with an initial bout of exploration, despite the overall declines. This also supports Thor, Harrison, Schneider and Carr (1988) and Poucet, Durup and Thinus-Blanc (1988): a burst of sustained object exploration, followed by attention away from the novel objects.

An analysis of interactions between *session* and *group* showed that *rate* and *percentage duration of responses* did not produce significant effects, and only *percentage duration of touching objects with nose* yielded a statistically significant interaction ($F[4,30] = 4.21, p < .01$). Thus, behaviour occurring during extinction and habituation could not, for the most part, be predicted by knowledge of the group to which the animals belonged: declines in behaviour were observed for all animals, whether they bar-pressed, nose-pushed or were exposed to the objects alone. This indicates that extinction and habituation occurred regardless of the experimental conditions.

Differences between groups were examined, separate comparisons being performed for the response categories and the exploratory behaviour measures. Analysis of variance only yielded statistically significant differences for the object-directed measure *percentage duration of touching objects with nose*, for which trained animals produced higher levels compared to the control group ($F[2,15] = 4.76, p < .05$). This isolated result supported the hypothesis that extinction induces exploratory behaviour. In keeping with the idea that learning activates the learner (Kvist, 1983), it is therefore suggested that increases in exploration may be at their peak during conditioning rather than extinction (and this proposition is examined later in experiment 4, Chapter 7).

Comparisons between individual groups indicated that, overall, Groups BAR and NOSE-KEY were not significantly different from one another in terms of *rate* and *percentage duration of responses*. This shows that the bar-pressing and key-pushing responses were similar. During sessions 1 and 2, however, animals in Group BAR responded for more of the time than animals in Group NOSE-KEY, and statistically significant t ratios were obtained for session 2 (*percentage duration of responses* $t[10] = 4.83, p < .01$). To explain this, it is suggested that bar-pressing (as opposed to key-pushing) inherently results in animals producing longer duration measures. For example, when an animal pressed the bar, it often lingered in that position with its paws remaining on the bar, hence adding to the amount of time a given duration measure was recorded. In contrast to this, animals trained for key-pushing typically would not remain in contact with the nose-key for any longer than required to fully depress the key.

Since the groups did not yield significant main effects, comparisons between groups were made for each separate observation session. In particular, the variables *sniffing objects* and *touching objects with nose* were examined, in order to test the response generalisation hypothesis: that key-pushing would subsequently result in more nosing actions than bar-pressing. Conversely, rats trained to bar-press were expected to explore more using their paws. This effect occurred solely during the first session of extinction: Group NOSE-KEY exhibited a significantly greater amount of time touching objects with the nose than Group CONTROL ($t[10] = 4.16, p < .01$), indicating that the generalisation effect did occur, but was relatively short-lived. The brevity of this effect is consistent with Frick and Miller (1951), who described the disruption in behaviour induced by extinction as being very variable after the first half hour of extinction, such that the gross direction of movements becomes difficult to predict.

Regarding the possibility of response generalisation for the bar-pressing response, statistically significant differences were not obtained, but as can be seen from graphs g and h in Figure 5.5(II), the direction of the results was as predicted. This suggests that *some* degree of response generalisation did indeed take place: animals trained to bar-press subsequently explored objects by touching or manipulating them with their front paws during extinction.

A possible explanation for the general lack of strong differences between the groups could be that bar-pressing and key-pushing are highly similar tasks. For example, it was observed that often when animals key-pushed, they also placed their front paws on either side of the nose-key, hence engaging in paw-type behaviour. Furthermore, animals trained for bar-pressing often touched the bar with their noses as well as their paws. As a result, any subsequent response generalisation directed towards objects in the box would involve both paw-type and nose-type behaviour.

In relation to the idea that the two operant responses were of a similar nature, the results of a short *post hoc* study are relevant. Following the three extinction phases, the conditions under which the experimental animals were trained were reversed. In other words, animals in Group BAR were placed under conditions of continuous reinforcement for key-pushing, and animals in Group NOSE-KEY were placed under conditions of continuous reinforcement for bar-pressing. The two tasks proved to be highly interchangeable: every animal learnt the new task within 1 minute of being in the box, usually less (whereas a naive animal would typically take four 20-minute training sessions in which to learn one of the tasks). This *post hoc* result may explain the lack of any obvious response generalisation effect in the observed exploratory behaviours: the two tasks were similar to begin with.

A further study involving two more overtly diverse tasks (such as bar-pressing versus ladder-climbing) would be useful in determining if this is in fact a valid explanation; however, it may be the case that rats always tend to touch and manipulate with their paws *and* nose, no matter what the task. During the pilot study for the present experiment, some difficulty was experienced in isolating the nose-pushing response from the bar-pressing response. This suggests that bar-pressing and nose-pushing tend to occur together as co-existing units of behaviour, and so it is difficult for an animal to carry out one action without the other. Thus, effects of response generalisation may simply be a question of differences in *degree* of the use of paws or nose, since both occur concurrently as major components of the rat's natural behavioural repertoire.

5.3. CONCLUSION

Experiment 1 examined exploratory behaviour in association with the extinction process, and showed that animals trained to perform an operant task (either bar-pressing or key-pushing) subsequently engaged in more exploration in the form of nose contacts than control animals receiving no training. This result provided some support for the hypothesis that extinction instigates exploration (as implied in the work of Kvist, 1983). However, the effect did not occur for the other measures of exploration (*sniffing objects* or *touching objects with paws*), contradicting previous experiments by Forster (1986) and Litchfield (1987). However, since measurements were only made during extinction, the results do not rule out the possibility that *conditioning* of bar-pressing and nose-pushing may be enriching, leading to increased object contacts. A second observation was that the operant responses and the exploratory behaviour declined over time, reflecting the extinction process and habituation to the objects respectively.

In reference to any *group* effects occurring as a result of the phenomenon of response generalisation, results showed that animals trained to key-push subsequently contacted objects with their noses more than bar-pressing and control animals, although this only occurred during the first session of extinction. No significant effect was observed for the bar-pressing response. Thus, the little response generalisation which did occur in this experiment had a short-lived effect, only being apparent during one 15-minute session of extinction. This result is consistent with Frick and Miller's (1951) description of the rapid disruption of behaviour after the first half hour of extinction. In explaining the relative lack of statistically significant results, it was suggested that paw touches and nose touches function as co-existing smaller units of an animal's larger response repertoire, such that one does not occur without the other.

Experiments 2 and 3, reported next in Chapter 6, provide an alternative context in which to measure exploratory behaviour and its relationship to aspects of the learning process: that of the behaviour systems approach. In a later experiment (reported in Chapter 7), the findings from the present experiment are further expanded and clarified, with comparisons between conditioning and extinction (because if learning activates the learner, it may only be during conditioning), and comparisons between novel and familiar objects.

CHAPTER 6

EXPLORATION IN THE CONTEXT OF THE BEHAVIOUR SYSTEMS APPROACH

6.1. INTRODUCTION

Chapter 6 views exploration in the context of the behaviour systems model, and in particular in relation to the rat's appetitive behaviour. The chapter opens with a discussion of the behaviour systems approach, as put forward by Timberlake (1983a), and this is applied to two experiments using Timberlake's methodology. In experiment 2, rats' exploratory behaviour was examined in a testing chamber modelled on that used by Timberlake, Wahl and King (1982), in which food was signalled by the appearance of a moving ball bearing. The aim of the experiment was to observe exploration in combination with the appetitive behaviour produced. A balanced combination between feeding behaviour and exploration has previously been suggested (e.g., Birke & Archer, 1983; Chapter 2, section 2.4), emphasising the adaptive significance brought about by such a relationship. Experiment 3 extended the findings of experiment 2 by measuring exploratory behaviour in the presence of a series of novel objects, using the same apparatus. The chapter concludes with a summary of the findings of experiments 2 and 3, showing how they fit in with the behaviour systems model, and indicating where results fall short of supporting the model.

6.2. THE BEHAVIOUR SYSTEMS APPROACH

The behaviour systems approach, as expounded by Timberlake (1983a), represents a reaction against the use of arbitrary environments to measure arbitrary behaviour, and instead aims to treat learning as an ecologically functional capacity for adjustment to predictable change in the environment. This view of learning, where the classic laboratory approach is integrated with functional accounts of behaviour, exemplifies the ethoexperimental approach to learning. This section (preceding experiment 6) serves as an outline of the behaviour systems approach, and acts as a summary of Timberlake's (1983a) chapter, *The functional organization of appetitive behavior: Behavior systems and learning.*

It has been argued that learning does not proceed in a random or unpredictable manner (since such a course would probably be maladaptive to an animal, Emlen, 1973), but instead follows a planned course related to the potential demands of a particular environment (Plotkin & Odling-Smee, 1979; Rozin, 1977). Similarly, it has been suggested that behaviour does not consist of random units, but is organised into systems of processes that serve particular survival functions (Baerends, 1976; Hogan & Roper, 1978). Timberlake described such systems as consisting of a set of functional patterns (made of smaller units called 'modules'), with each pattern potentially related to a terminal event; for example, feeding, mating or body care.

For present purposes, the feeding system (the 'appetitive behaviour system') of the rat will be described in detail; Timberlake concentrated on this in his chapter, and it provides the framework for the two experiments reported in this chapter.

The appetitive behaviour system of the rat is said to be made up of a hierarchically-arranged set of modules, beginning with individual foraging and social-approach, in which an animal systematically moves through its environment and interacts with other feeding animals. The next stage of the system consists of investigation (approach, sniff, nose, lick, bite) and predation (dig, pounce, chase, carry, bite), followed by food handling (shell seeds, break grass stems, hold, gnaw). The last modules in the hierarchy are hoarding (transport and store food), ingestion (chew, swallow, nibble), and rejection (drop, spit out). Thus, the system accounts for all of the behaviour associated with feeding, from the very first events to the terminal events. A key point in Timberlake's argument is that learning may occur at one or more points in the behaviour system; it may involve modification in the frequency, order, timing, integration or elicitation of behaviours, modules, or even whole systems.

Having postulated the appetitive behaviour system of the rat, Timberlake (1983a) next set out several hypotheses which were generated from the model; for example, it should be possible to observe the distinct segments of appetitive behaviour in natural situations as well as in artificial learning environments. Following this, Timberlake listed a series of hypotheses concerning the relationship between a terminal event and the conditioned behaviour preceding it. It was predicted that:

> *The module most strongly conditioned by presentation of a terminal event should be the one for which the external stimuli most closely resemble stimuli normally controlling and eliciting behaviors in it. Thus, the delivery of food following presentation of an imitation seed should condition seed-shelling (food-handling) behaviors, but the delivery of food following a small moving stimulus is more likely to condition predatory behaviors* (p. 185).

Such behaviour, however, would not necessarily apply to animals from other species; the conditioned behaviour of individual animals was said to depend upon the organisation of species-specific characteristics (behaviour systems). Finally, Timberlake proposed that it ought to be difficult to condition behaviour within a particular behaviour system by presenting terminal events from another system (but it should be easy to condition modules within the same system).

Experiments investigating autoshaping provide support for Timberlake's model: the phenomenon of autoshaping occurs when an animal produces species-specific behaviour in the absence of any imposed response requirement. For example, it has been shown that if a lighted disc predicts food, pigeons will peck at the disc (Brown & Jenkins, 1968); rats will bite and manipulate a bar that predicts food (Peterson, Ackil, Frommer, & Hearst, 1972); and rats will carry and chew a moving ball bearing that predicts food (Timberlake, Wahl, & King, 1982). Other studies have shown that animals' responses differ as a function of the nature of the terminal event. For example, pigeons peck hard at a key that predicts food (Jenkins & Moore, 1973; Woodruff & Williams, 1976), but peck more softly at a key that signals water (Reberg, Innis, Mann, & Eizenga, 1978). Similarly, rats have been shown to make longer lever presses when responding for food, and shorter responses when responding for water drops (Hull, 1977; Hull, Bartlett, & Hill, 1981).

These findings are related to literature on 'instinctive drift', in which "learned behavior drifts toward instinctive behavior" (Breland & Breland, 1961, p. 684). Breland and Breland formed this principle as a result of attempts to train a raccoon and a pig to pick up coins and drop them into a piggy bank. They found that, some time after successful training, the raccoon would not let go of the coins, but spent a great deal of time rubbing them together (the racoon's instinctive washing behaviour), whilst the pig tended to drop the coins, toss them into the air, root them along the ground, drop them, and toss them again (the pig's instinctive appetitive behaviour). According to Breland and Breland, these animals were trapped by their strong instinctive behaviour, since the observed behavioural patterns appeared to represent a violation of the 'law of least effort', in which an animal will exert the least amount of effort required to receive reinforcement. The drift towards instinctive behaviour is said to be very powerful, to the point where it can delay or even preclude reinforcement.

Timberlake, Wahl and King (1982) conducted a similar experiment, investigating 'misbehaviour' in rats. In their study, a rolling ball bearing predicted the delivery of food, regardless of a response from the animal. It was found that 'misbehaviour' occurred, in that rats engaged in unnecessary species-specific pawing, nosing, carrying, chewing and retrieving of the ball bearing, as well as digging at the entry hole, thus delaying the arrival of food. Timberlake (1983b) conducted a further experiment, testing for differences in ball bearing-directed behaviour when the reinforcement was either food or water (i.e., to discriminate between a stimulus substitution explanation, in which the stimulus is treated like the reward, or the behaviour systems model). Timberlake found support for his model: stimulus substitution did not seem to occur, since rats did not lick the ball bearing, as they would water. In addition, rats did not treat the food-related ball bearing as an item of food, by simply picking it up and chewing it. In fact, each rat:

> *...often dug the bearing out of its entrance hole, seized it in its paws, stuffed it in its mouth, ran to the other end of the apparatus, and then sat and gnawed it with its incisors, turning it in its paws and dropping it and retrieving it* (p. 317).

According to Timberlake, this behaviour was never directed towards a food pellet.

Rather than accounting for the rat's behaviour in terms of stimulus substitution, Timberlake argued that the behaviour is better explained in relation to the rat's predatory behaviour system. The ball bearing-directed responses were comparable to descriptions of predation by rats in the wild; for example, when confronted by an insect, a rat typically responds with a sequence of digging, chasing, seizing, killing and food handling behaviour (Karli, 1956). Consequently, according to Timberlake, the presentation of a small moving stimulus immediately preceding food makes these responses readily available for conditioning. Similarly, King and Norwood (1989) found that squirrel monkeys could easily learn to catch fish, because they are adapted to seizing rapidly moving visual targets (such as flying insects). Thus, although squirrel monkeys do not normally catch fish in their natural aboreal environment, they rapidly learnt to catch them on the first day of presentation.

Another example reporting limited success at conditioning particular behaviours according to whether or not the conditioned responses were species-specific is that of Bolles (1970). Bolles found a relationship between certain species-specific defence reactions and ease of conditioning in rats: by administering aversive stimulation (such as occasional electric shocks), freezing, fleeing and fighting were especially easy to condition. Bolles (1975) later concluded that such effects (as well as 'misbehaviour') make sense when learning is thought of as specialised and selective.

Experiments 2 and 3, reported in the following sections (6.3 and 6.4), were designed to examine exploratory behaviour directed towards objects (as in experiment 1), except the apparatus and procedure were modelled after those employed by Timberlake, Wahl and King in their 1982 experiment. The aims of the experiments were two-fold: to test Timberlake's behaviour systems theory, and to yield information about exploration under a range of learning conditions. As in the experiment by Timberlake *et al.* (1982), the present studies focused on the rat's appetitive behaviour system, using a rolling ball bearing to signal the arrival of food. In addition, various novel objects were included in the testing chamber, thus allowing for the possibility of exploratory behaviour.

6.3. EXPERIMENT 2: EXPLORATION IN THE PRESENCE OF A ROLLING BALL BEARING

In experiment 2, the rat's exploratory and ball bearing-directed behaviour was examined within the context of Timberlake's behaviour systems theory. While experiment 1 only focused on exploration during extinction, the present study was concerned with the effect of both conditioning and extinction on exploration. A relationship in which conditioning and extinction enhance exploratory behaviour would be consistent with Kvist (1983), in which learning activates the learner; and the occurrence of ball bearing-directed 'misbehaviour' would be consistent with Timberlake, Wahl and King (1982). The aim of experiment 2 was to observe the balance between these two predicted tendencies.

Methodologically, the experiment was based on that of Timberlake, Wahl and King (1982). The study was a 2 x 2 design, testing for effects of the presence/absence of a rolling ball bearing and the presence/absence of a set of objects. Thus, there were four groups of animals: Ball Bearing with Objects (BBO), Ball Bearing with No Objects (BBNO), Control with Objects (CO) and Control with No Objects (CNO). Several hypotheses were generated regarding contacts with the objects and contacts with the ball bearing, and these differed according to whether conditioning or extinction was imposed.

Hypotheses regarding *session* effects on object-directed behaviour remained the same as for experiment 1: it was predicted that object interactions would decline over time, reflecting a decrease in stimulus novelty. The same set of objects were used throughout the study (during conditioning and extinction), and therefore it was expected that habituation would occur as novelty decreased (e.g., Hutt, 1967b; Ratner, 1970; Ivinskis, 1970; O'Keefe & Nadel, 1978; Ellen & Weston, 1983; Rogers, Sink, & Hambley, 1988). This account is also consistent with theories of optimal arousal (which were mentioned in Chapter 5).

Secondly, predictions concerning *group* effects on object-directed behaviour were made. The present experiment tested for effects of both conditioning and extinction on exploratory behaviour (whereas experiment 1 only tested for effects of the latter). Consistent with Kvist (1983), who reported that learning activates the learner, it was expected that animals in Group BBO (for which the ball bearing predicted food) would produce more object contacts than animals in Group CO (for which the ball bearing was presented alone). This hypothesis applied to conditioning and extinction sessions, with the additional prediction that an initial burst of exploration would occur in Group BBO during the first session of extinction (but not in Group CO). Such a finding would be consistent with the idea that extinction instigates exploration (Wong, 1977, 1978; Harcourt, 1983; Forster, 1986; Litchfield, 1987), and theories in which a variety of new behaviours are said to arise when the extinction process is imposed (Azrin, 1961; Thompson & Bloom, 1966; Gentry, 1968; Azrin, Hutchinson, & Hake, 1966).

A third set of hypotheses were formed, relating to *session* and *group* effects on ball bearing-directed behaviour. Regarding *session* effects, ball bearing contacts were not expected to decline during conditioning, since the ball bearings predicted the arrival of food for each session. During extinction, however, an initial burst of contact was predicted, followed by declines over time, as would normally be the case for any conditioned response undergoing extinction.

Regarding *group* effects on ball bearing-directed behaviour, the hypotheses were based on those of Timberlake, Wahl and King (1982). Groups BBNO and CNO replicated the groups used by Timberlake *et al*; that is, rolling ball bearings were presented (with no objects in the chamber), and these resulted in the delivery of food in the former group and no food in the latter. Thus, as hypothesised by Timberlake *et al.*, during conditioning the animals in Group BBNO were expected to contact the ball bearing (*paw*, *chew*, *carry*, *nose/dig at entrance hole*), then release it, obtain and eat the food reward; and at the onset of extinction a greater amount of ball bearing contact was predicted, followed by an overall decline. In contrast, for Group CNO less ball bearing contact was expected during conditioning and extinction, since the ball bearings did not predict the arrival of food.

For the groups in which objects were present, it was expected that animals in Group BBO would contact the ball bearings to much the same degree as animals in Group BBNO, since the ball bearings predicted the arrival of food. Group CO was expected to display the least amount of ball bearing-directed behaviour of all the groups, since the ball bearings did not predict the arrival of food, and the objects provided animals with an alternative activity.

METHOD

Subjects

The subjects were 24 male Hooded Wistar rats (*Rattus norvegicus*) obtained at 90 days of age. As before, 2 extra animals took part in a pilot study. Details concerning the housing conditions, temperature, lighting, feeding and preliminary handling sessions were the same as for experiment 1.

The rats were randomly allocated to one of four groups, each group consisting of 6 animals. There were two experimental groups: Ball Bearing with Objects (BBO) and Ball Bearing with No Objects (BBNO); and two control groups: Control with Objects (CO) and Control with No Objects (CNO).

Apparatus

Experimental apparatus

The experimental apparatus consisted of a box measuring 49cm x 49cm x 34cm (Figure 6.1). The box was made of stainless steel, and had a transparent plastic cover. Ball bearings measuring 1.5 cm in diameter were dispensed into the box by means of a tube (angled at 10^0) leading to an entrance hole at floor level. When a ball bearing entered the box, it ran along a *V*-shaped channel for the length of the apparatus to an exit hole, where it subsequently left the apparatus. Once outside the box, the ball

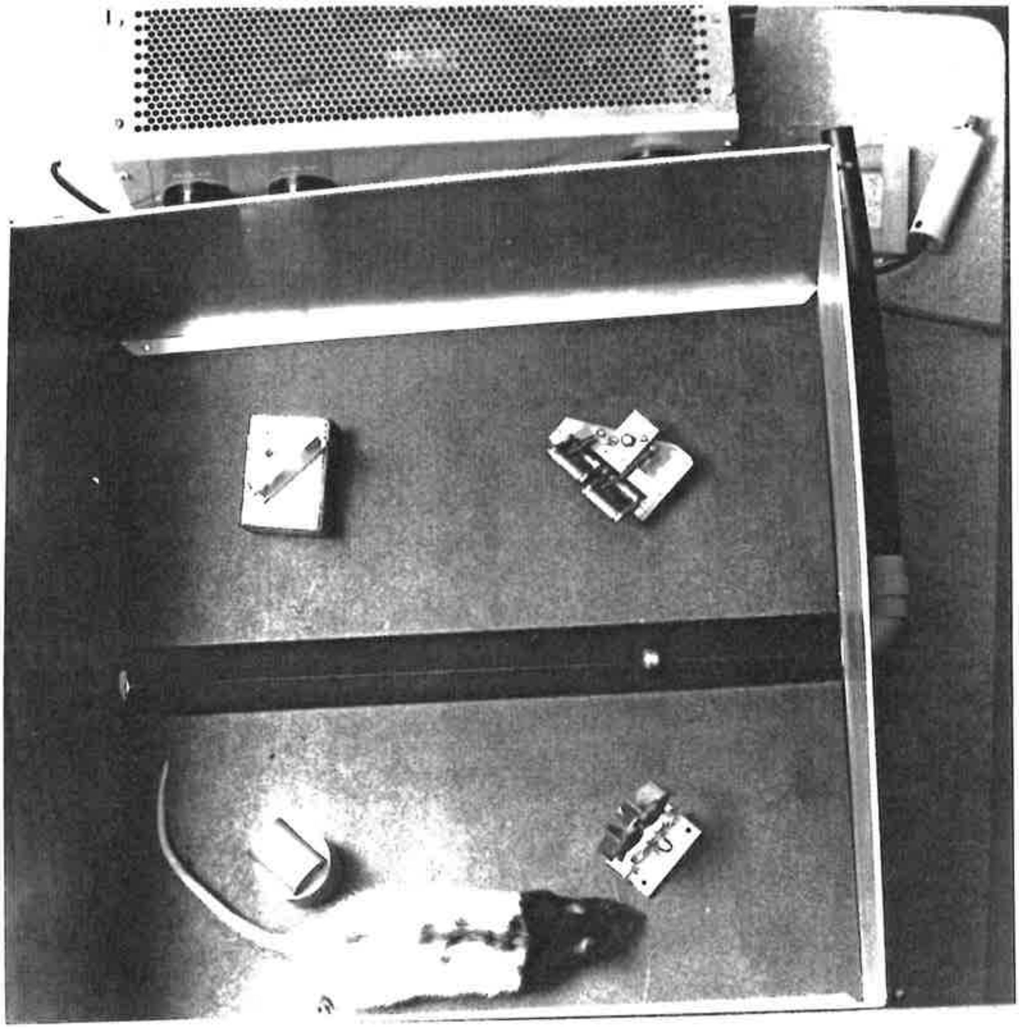


FIGURE 6.1: Experimental testing chamber used in experiment 2, showing rolling ball bearing and four novel objects in place.

bearing rolled along a small channel with a light-sensitive switch to trigger the delivery of a food pellet.

The experimental box was slanted 5^0 downwards from the entrance hole. The floor was slanted inwards from either side, in such a way that if impeded and subsequently released, a ball bearing eventually returned to the channel and left the apparatus. The channel (3cm deep) allowed the ball bearing to roll, unobstructed by the rat. If undisturbed, each ball bearing left the box 1.5 seconds after emerging from the entrance hole.

Food pellets were delivered into a food trough located 4cm to the right of the exit hole in the box. This was done by means of a 24V D.C. Power Supply. Above the food trough was a small light, and this flashed simultaneously with a buzzer outside the box, whenever a food pellet was delivered.

For both of the control groups, in which food was not delivered, a plain wall panel was substituted, housing only an exit hole and a receptacle for collecting the ball bearings once they had left the apparatus.

The experimental box contained 4 removable objects which were clipped on to the floor (Figure 6.2). (For object names, see Appendix 1.)

Observation equipment

This consisted of the same equipment as used in experiment 1: a video camera, a video cassette recorder, video tapes and a video monitor. The experimenter sat behind a partition during experimental trials, and coded ball bearing and object-directed behaviour by means of an event recording program. The event recording apparatus differed from that used in experiment 1 in that a greater number of behavioural events could be recorded: 7 buttons allowed the recording of 7 different behaviours.

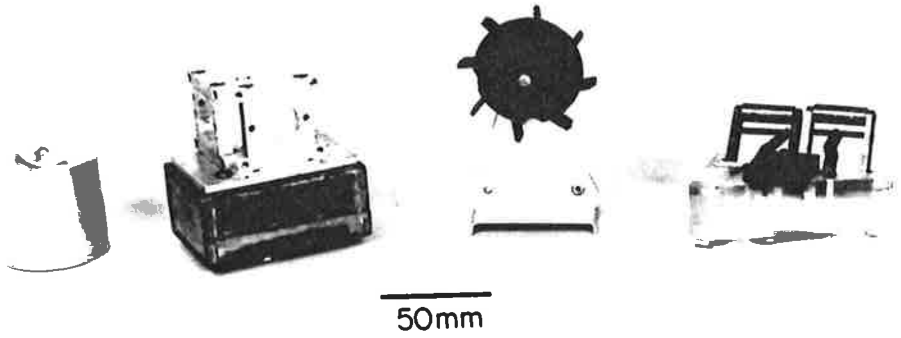


FIGURE 6.2: Experiment 2 novel objects.

Procedure

For each of the four groups of animals (BBO, BBNO, CO and CNO) the experimental design consisted of four parts: handling, familiarisation, conditioning and extinction.

Handling

This procedure was the same as that used in experiment 1; that is, rats were handled 10 minutes each day for 5 days prior to the experimental sessions.

Familiarisation

Animals in the two experimental groups (BBO and BBNO) were exposed to the apparatus (without ball bearings or objects), and trained to approach the food trough and eat food pellets. Training sessions varied, depending on the amount of time required for animals to reach a 'food summoning' stage. This stage was said to be reached when it was possible to summon an animal to the food trough by triggering the light and buzzer together with the delivery of a food pellet. On average, a single session was required, lasting 16 minutes. Animals in the two control groups (CO and CNO) were exposed to the box for the mean amount of time taken for the experimental animals to be trained (i.e., 16 minutes). Between sessions, the floor of the apparatus was wiped clean.

Conditioning

This phase of the procedure consisted of four conditioning sessions. During each session, animals received 10 presentations of the ball bearing. A rat was placed in the centre of the box, the transparent plastic cover closed, and the timer started. 45 seconds later the first of the 10 ball bearings was delivered through the tube. The second ball bearing was delivered 45 seconds after the first one had left the box, and so on until all the ball bearings had been released. This applied to animals in all groups.

The procedure varied as a function of the group being tested. The treatments were as follows:

(a) Ball Bearing with Objects (BBO). The 4 objects were placed in the box, and a food pellet was delivered following each exit of the ball bearing.

(b) Ball Bearing with No Objects (BBNO). With no objects present, a food pellet was delivered following each exit of the ball bearing.

(c) Control with Objects (CO). With the 4 objects in the box, the ball bearings were presented alone (no food was delivered).

(d) Control with No Objects (CNO). The objects were removed, and the ball bearings were presented alone.

Extinction

Extinction sessions parallelled conditioning sessions; that is, there were four sessions, each consisting of 10 presentations of the ball bearing. The distribution of objects in the box remained as for conditioning. The only difference was that no animals received any food pellets following the exit of the ball bearings.

Event recording and independent judging

As in experiment 1, behavioural measurements for each session were recorded by means of an event recording program. During each trial the experimenter coded the animal's activities into one of 7 categories, comprising behaviours directed towards the ball bearing and behaviours directed towards the objects. In this experiment the frequency scores were not transformed into rates (as they were in experiment 1), since the time available for exploration in all groups was the same, and so direct comparisons between the groups' scores were possible. The 7 behavioural categories (each measured in terms of frequencies and durations) were as follows:

(a) *sniffing objects* - in which a rat's snout is oriented towards an object, but without touching it;

(b) *touching objects with paws* - in which a rat touches or manipulates an object with one or more paws, including climbing on or digging around the edge of an object;

(c) *chewing objects* - in which a rat bites, chews, licks or mouths an object;

(d) *touching ball bearing with paws* - in which a rat touches or manipulates a ball bearing with one or more paws (including picking it up, provided the rat does not carry it);

(e) *chewing ball bearing* - in which a rat bites, chews, licks or mouths a ball bearing;

(f) *carrying ball bearing* - in which a rat carries a ball bearing in its mouth (at least one step);

(g) *nosing or digging at entrance hole* - in which a rat pokes its nose into the entrance hole, including sniffing and digging at the hole.

Prior to data analysis, total frequencies and durations were calculated, and the variables were expressed in the form *frequency of sniffing objects*, *duration of sniffing objects*, etc. As in experiment 1, additional variables were included, acting as overall measures of exploration and ball bearing-directed behaviour: *frequency of object exploration* and *duration of object exploration* (calculated by summing the measures *sniffing objects*, *touching objects with paws* and *chewing objects*); and *frequency of ball bearing-directed behaviour* and *duration of ball bearing-directed behaviour* (calculated by summing the measures *touching ball bearing with paws*, *chewing ball bearing*, *carrying ball bearing* and *nosing or digging at entrance hole*). The measures were not transformed into rates per minute or percentage durations (as in experiment 1), since there was no discrepancy in the time available for animals to explore or contact ball bearings: all animals received 10 presentations of the ball bearings.

Three judges viewed three video-taped sessions (a total of 30 minutes) and recorded data by means of the event recording apparatus. The Kendall's W coefficient of concordance procedure was then performed on the data obtained. A high degree of agreement among all judges was obtained for frequencies ($W = .920, p < .001$) and durations ($W = .939, p < .001$) of all of the variables measured.

RESULTS AND DISCUSSION

Experiment 2 acted partially as a replication of Timberlake, Wahl and King's 1982 experiment, testing the hypothesis that ball bearings predicting the delivery of food would be contacted more than ball bearings presented alone. The second aim of the experiment was to expand the findings from experiment 1: to test not only whether extinction enhances exploratory behaviour, but also to examine exploration during conditioning. Four groups of animals participated in the experiment: Ball Bearing with Objects (BBO), Ball Bearing with No Objects (BBNO), Control with Objects (CO) and Control with No Objects (CNO). Behaviour directed towards a series of objects and ball bearings was observed under each experimental condition. As in experiment 1, the results were analysed in terms of effects due to *session*, effects due to *group*, and interactions between these. The multivariate analysis of variance procedure was applied separately to data obtained from conditioning and extinction sessions for all measures of behaviour.

A series of predictions were made regarding object-directed and ball bearing-directed behaviour, and these hypotheses were tested separately. Predictions concerning effects of *session* on exploration (time-related effects) remained the same as for experiment 1: it was expected that object interactions would decline over time, reflecting a decrease in stimulus novelty (since the same objects were used in every conditioning and extinction session).

Secondly, predictions were made concerning effects of conditioning and extinction on exploratory behaviour. Experiment 1 tested for effects of extinction on exploration, and produced a limited effect, in that more nose contacts were made by animals undergoing extinction compared to untrained animals. In experiment 2, more sessions were conducted, and observations were recorded during conditioning as well as extinction, with the aim of testing Kvist's (1983) hypothesis that learning activates the learner. It was hypothesised that the group for which the ball bearings predicted the delivery of food (Group BBO) would produce more object interactions than the control group (Group CO), and this effect was expected to occur during both conditioning and extinction. Furthermore, during the first session of extinction the experimental group was expected to show a higher initial amount of exploration, consistent with accounts in which extinction instigates exploration (e.g., Wong, 1977, 1978; Harcourt, 1983; Forster, 1986; Litchfield, 1987).

The third set of hypotheses was concerned with ball bearing-directed behaviour. The contacts with the ball bearings were expected to remain constant during conditioning, but to decline after an initial burst during extinction, as would any conditioned response subjected to extinction. The main predicted *group* effect was that the experimental groups (BBO and BBNO) would contact the ball bearing, then release it and eat the food pellet, whereas the control groups (CO and CNO) would contact the ball bearing to a lesser degree. This hypothesis follows directly from the experiment by Timberlake, Wahl and King (1982). It was also predicted that the groups for which the objects were present would contact the ball bearing less than their object-absent counterparts, since the objects may provide a competing response.

Figures 6.3(I), 6.3(II), 6.3(III) and 6.3(IV) show the session means of each behavioural measure. The analysis of the results begins with *session* effects, and then goes on to discuss *group* effects and interactions between these (as in Chapter 5).

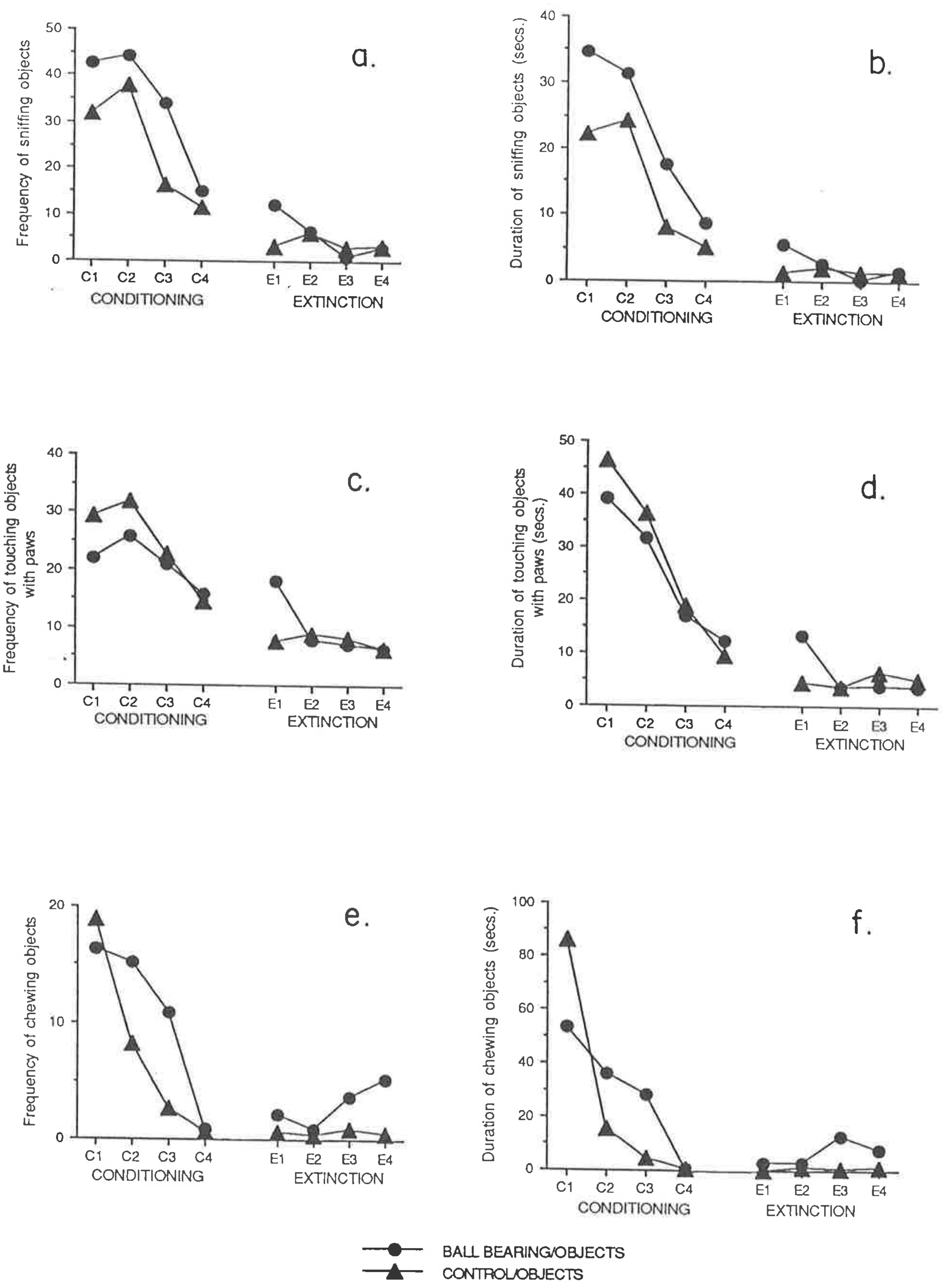


FIGURE 6.3(I): Session means of object-directed behaviours in experiment 2.

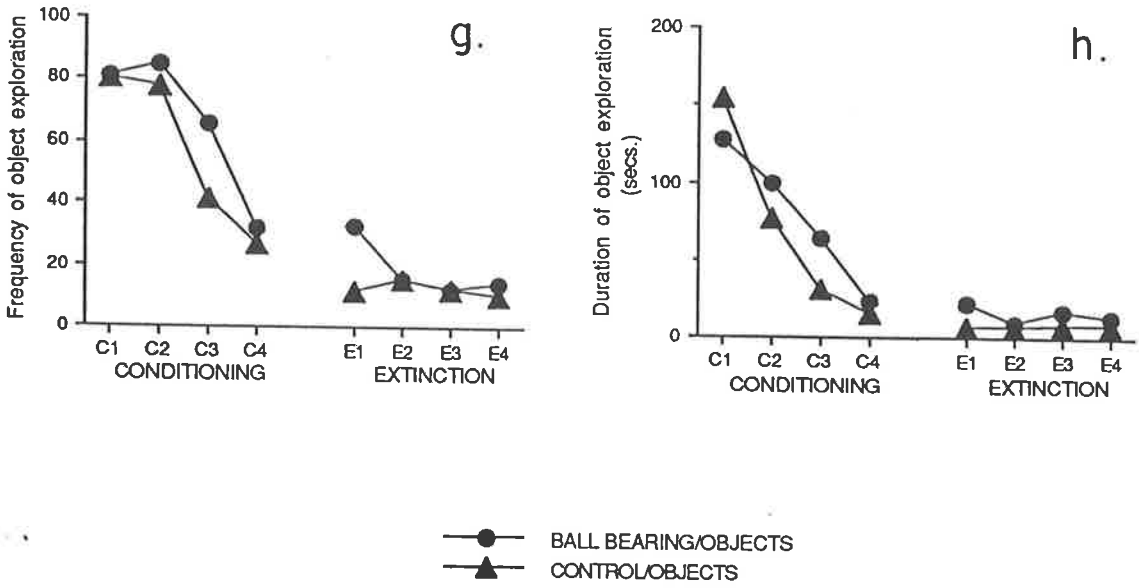


FIGURE 6.3(II): Session means of object-directed behaviours in experiment 2.

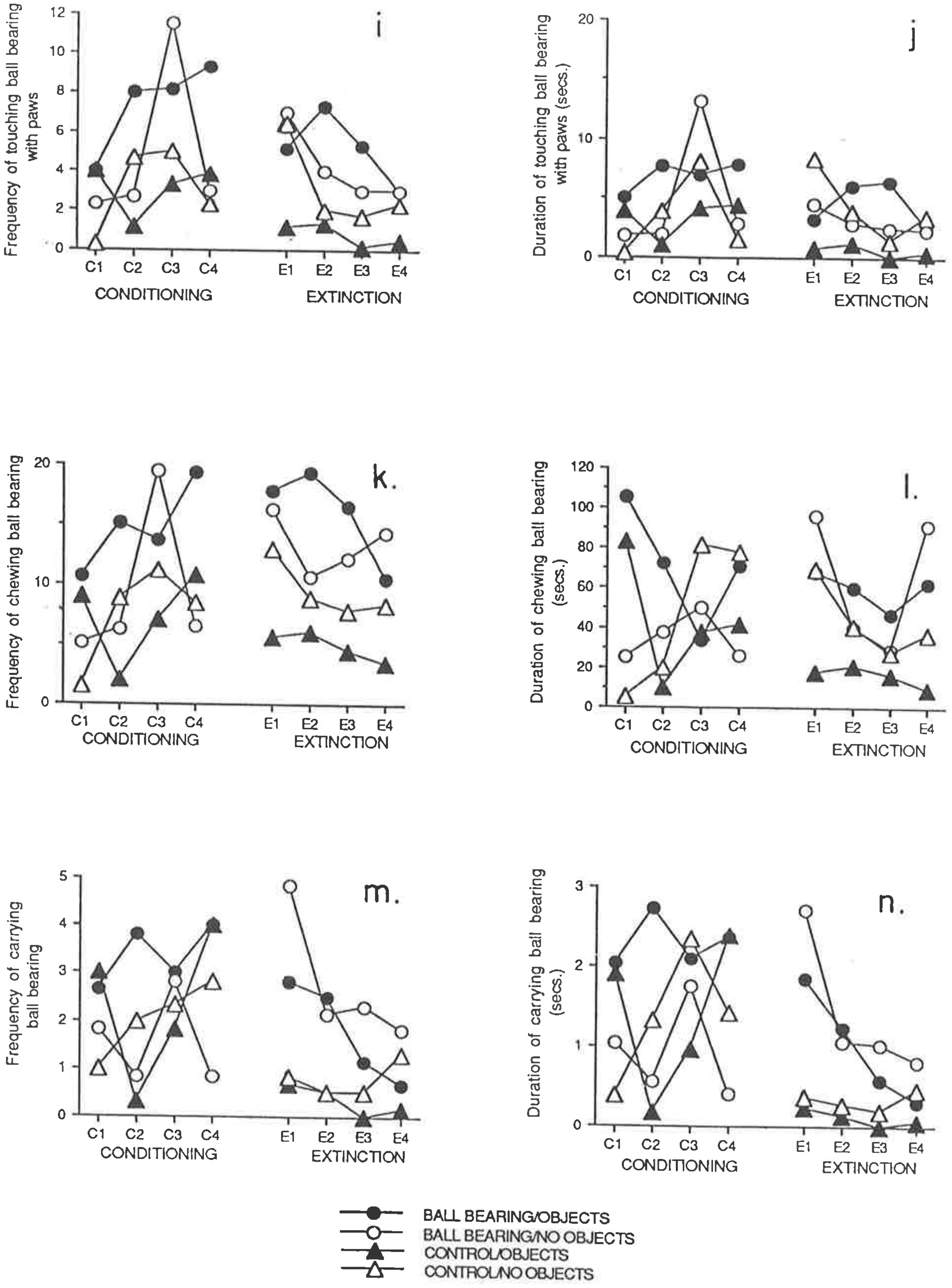


FIGURE 6.3(III): Session means of ball bearing-directed behaviours in experiment 2.

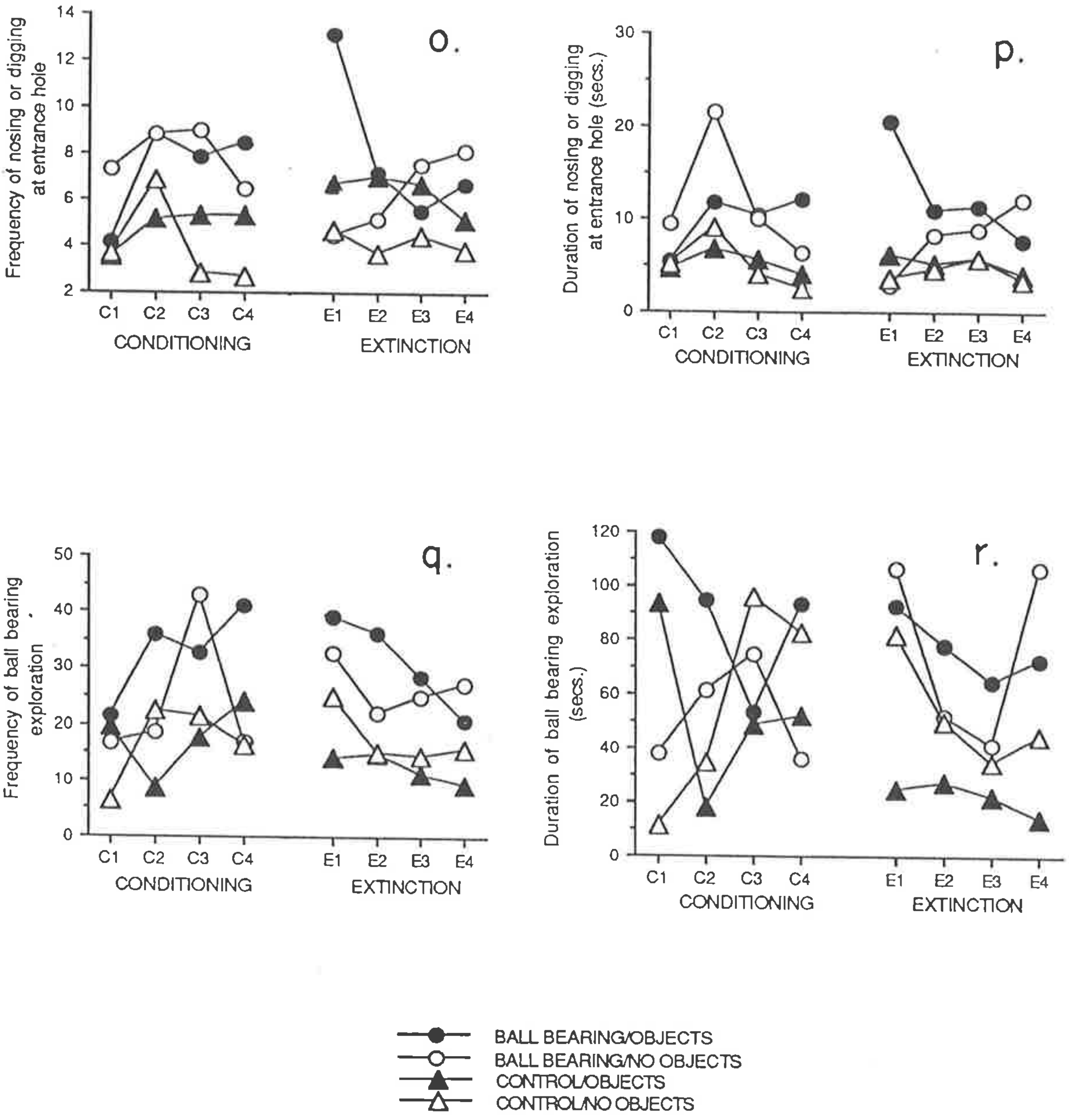


FIGURE 6.3(IV): Session means of ball bearing-directed behaviours in experiment 2.

During conditioning, all exploratory behaviour measures declined over time (Table 6.1), reflecting the decline in object novelty, and hence a decline in interest in the objects (habituation). In contrast to this, analysis of variance examining behaviour directed towards the ball bearing yielded no significant *F* ratios, indicating that ball bearing contacts remained constant during conditioning.

Table 6.1: Significance levels obtained for measures of exploratory behaviour during conditioning (*session* effects).

Variable	*F*	Significance level
Frequency of sniffing objects	$F(3,30) = 19.34$	$p < .001$
Duration of sniffing objects	$F(3,30) = 28.74$	$p < .001$
Frequency of touching objects with paws	$F(3,30) = 8.42$	$p < .001$
Duration of touching objects with paws	$F(3,30) = 11.87$	$p < .001$
Frequency of chewing objects	$F(3,30) = 13.86$	$p < .001$
Duration of chewing objects	$F(3,30) = 12.54$	$p < .001$
Frequency of object exploration	$F(3,30) = 31.80$	$p < .001$
Duration of object exploration	$F(3,30) = 27.87$	$p < .001$

Thus, familiarity with the ball bearing did not result in a loss of interest in it: ball bearing habituation did not occur for experimental or control animals. This result fits in well with Karli's (1956) description of the rat's species-specific responses to insects, suggesting that behaviour directed towards a small moving object (in this case: *touching ball bearing with paws*, *chewing ball bearing*, *carrying ball bearing* and *nosing or digging at the entrance hole*) form part of the rat's predatory behaviour system (Timberlake, 1983b).

During extinction, most of the object-directed behaviours declined over time (Table 6.2), indicating the continuing effect of habituation. In addition, there was an

Table 6.2: Significance levels obtained for measures of exploratory behaviour during extinction (*session* effects).

Variable	*F*	Significance level
Frequency of sniffing objects	$F(3,30) = 5.91$	$p < .01$
Duration of sniffing objects	$F(3,30) = 4.37$	$p < .05$
Frequency of touching objects with paws	$F(3,30) = 5.16$	$p < .01$
Duration of touching objects with paws	$F(3,30) = 3.98$	$p < .05$
Frequency of chewing objects	$F(3,30) = .80$	N.S.
Duration of chewing objects	$F(3,30) = .86$	N.S.
Frequency of object exploration	$F(3,30) = 6.21$	$p < .01$
Duration of object exploration	$F(3,30) = .72$	N.S.

interaction between *session* and *group* for *frequency of object exploration* at the onset of extinction compared to the last session of conditioning ($F[1,10] = 5.36, p < .05$). As can be seen from Figures 6.3(I) and (II), graphs *c* to *h*, the trained animals explored objects more at the onset of extinction, while control animals generally explored less and less over time. This lends support to the idea that extinction enhances exploratory behaviour, even although by this time the objects were highly familiar to the rats. The sudden rise in object contacts at the onset of extinction is consistent with reports by Wong (1977, 1978), Harcourt (1983), Forster (1986) and Litchfield (1987), as well as the idea that extinction can induce a variety of new behaviours (e.g., Azrin, 1961; Thompson & Bloom, 1966; Gentry, 1968; Azrin, Hutchinson, & Hake, 1966).

As was the case during conditioning, this effect did not occur for the measures of ball bearing-directed behaviour. This suggests that the extinction effect applies only to object exploration rather than general activity (an hypothesis tested later, in Chapters 7 and 8). The higher level of exploration in the first session of extinction and the subsequent reduction in object contacts showed up as a significant interaction between *session* and *group* over the four extinction sessions (*frequency of object exploration*

$F[3,30] = 7.18$, $p < .01$) and this was also the case for the variables *sniffing objects* and *touching objects with paws*. No interaction effects of this kind occurred for the ball bearing-directed behaviour during conditioning or extinction. In other words, the extinction-induced activity only manifested itself in the form of object contacts, and did not generalise to ball bearing contacts. This strongly suggests that extinction induces object-directed exploratory behaviour rather than increases in general activity.

To test the hypothesis that the animals for which ball bearings predicted the delivery of food would display greater amounts of exploratory behaviour than control animals, analysis of variance was conducted testing for *group* effects. During conditioning, analysis of the data obtained for the measures *frequency* and *duration of sniffing objects* supported the view that learning produces an increase in exploration (*frequency of sniffing objects* $F[1,10] = 5.65$, $p < .05$; *duration of sniffing objects* $F[1,10] = 6.26$, $p < .05$). The other measures did not yield significant F ratios, but, as can be seen from Figure 6.3(II), graphs g and h, results were in the predicted direction. During extinction, the groups were not significantly different from one another, except during session 1 of extinction, where exploration was higher for animals in Group BO (consistent with the interaction effects reported above).

Analysis pertaining to Timberlake, Wahl and King's (1982) hypotheses (i.e., 'misbehaviour' directed towards the ball bearing) showed that significant increases in ball bearing contacts by experimental animals occurred during extinction but not during conditioning. Table 6.3 shows the significance levels obtained from analysis of variance testing for *group* effects on ball bearing-directed behaviours. In many cases where main effects did not occur, planned comparisons between Groups BBO and CO indicated significant differences, with experimental animals contacting the ball bearing more (*frequency of touching ball bearing with paws* $t = 2.85$, $p < .01$; *duration of touching ball bearing with paws* $t = 2.49$, $p < .05$; *frequency of chewing ball bearing* $t = 3.05$, $p < .01$; *frequency of ball bearing-directed behaviour* $t = 2.54$, $p < .05$).

Table 6.3: Significance levels obtained for measures of ball bearing-directed behaviour during extinction (*group* effects).

Variable	F	Significance level
Frequency of touching ball bearing with paws	$F(3,20) = 3.30$	$p < .05$
Duration of touching ball bearing with paws	$F(3,20) = 2.60$	N.S.
Frequency of chewing ball bearing	$F(3,20) = 3.54$	$p < .05$
Duration of chewing ball bearing	$F(3,20) = .84$	N.S.
Frequency of carrying ball bearing	$F(3,20) = 2.93$	$p < .05$
Duration of carrying ball bearing	$F(3,20) = 3.16$	$p < .05$
Frequency of nosing or digging at entrance hole	$F(3,20) = .57$	N.S.
Duration of nosing or digging at entrance hole	$F(3,20) = 1.25$	N.S.
Frequency of ball bearing-directed behaviour	$F(3,20) = 2.68$	N.S.
Duration of ball bearing-directed behaviour	$F(3,20) = 1.10$	N.S.

Thus, for the groups in which objects were present, the hypotheses of Timberlake *et al.* (1982) were supported.

In summary, experiment 2 viewed exploration in the context of the behaviour systems approach; that is, in relation to systems of processes which serve particular survival functions. In the experiment, the rats' appetitive behaviour system was the particular system evoked, and behaviour directed towards a rolling ball bearing and a set of objects was observed.

Results concerning exploratory behaviour showed that animals in the experimental group engaged in more object interactions than the control group, supporting the idea that learning enhances exploration. Particularly notable were the increases in object contacts at the onset of extinction, compared to a general decline in exploration in the control group. Since experimental animals did not engage in significantly more ball bearing contacts during conditioning, it could be argued that learning does not enhance activity in general, but object contacts in particular.

Concerning the hypotheses generated by Timberlake, Wahl and King (1982), results from experiment 2 were consistent with the idea that the rat's appetitive behaviour system is evoked (and easily conditioned) when a rolling ball bearing predicts the delivery of food. As can be seen from the graphs displaying frequencies and durations of ball bearing contacts, experimental animals did indeed contact the ball bearing more often and for a longer time than control animals. This was especially evident during extinction. The groups for which the objects were present (Groups BBO and CO) displayed the predicted effect more strongly than the groups which replicated the study by Timberlake, Wahl and King (Groups BBNO and CNO).

Following from the findings from experiment 2, a third experiment was conducted in which variations in object novelty were included. Experiment 3, then, assessed effects of novelty on the present results.

6.4. EXPERIMENT 3: EFFECTS OF OBJECT NOVELTY ON EXPLORATION IN THE PRESENCE OF A ROLLING BALL BEARING

Experiment 3 served as a second replication of Timberlake, Wahl and King's (1982) experiment, and added to the findings of experiment 2 by including 32 novel objects. A new set of objects was used for each session, with the aim of countering the effect of habituation on exploratory behaviour.

Predictions regarding ball bearing contacts remained the same as in the previous experiment: during conditioning the animals in Group BBNO were expected to contact the ball bearing and then release it to obtain the food reward; at the onset of extinction an immediate rise in ball bearing-directed behaviour was predicted, followed by a gradual decline over time. Group CNO, the group replicating Timberlake, Wahl and King's control group, was expected to display less ball bearing contact during conditioning and extinction, since the ball bearings were independent of the arrival of food. For the groups in which objects were present (BBO and CO), less ball bearing-directed behaviour was expected, since the novel objects ought to generate exploration (thus competing with behaviour directed towards the ball bearings).

As discussed in Chapter 4, novelty (defined as 'change', Welker, 1971) has been shown to result in marked increases in exploratory behaviour (e.g., White, 1961; Schneider & Gross, 1965; Glickman & Sroges, 1966; Taylor, 1974; Rogers, Sink, & Hambley, 1988; Thor, Harrison, Schneider, & Carr, 1988; Paquette & Prescott, 1988). However, it has been shown that habituation to novelty can occur rapidly, especially in species which are highly exploratory by nature (Poucet, Durup, & Thinus-Blanc, 1988). This effect can easily be countered, though, by making regular changes to the environment, even if such changes are small; for example, changes in colour (Welker, 1956; Corman & Shafer, 1968), or changes in the spatial relationships between objects (Poucet, Chapuis, Durup, & Thinus-Blanc, 1986; Thinus-Blanc, Bouzouba, Chaix, Chapuis, Durup, & Poucet, 1987).

In the present experiment, regular changes to the environment were made by using a new set of objects for each session. As a result, hypotheses concerning behaviour directed towards objects were different from those of experiment 2. It was predicted that continued novelty would result in continued interest in the objects, and hence sustained levels of exploration throughout both conditioning and extinction (in contrast to the levels of object-directed behaviour observed in experiment 2). In other words, since object novelty did not decline, no habituation was expected (other than habituation within each session).

Experiment 3 also tested for effects of conditioning and extinction on exploratory behaviour. To be consistent with experiment 2, more object contacts would be expected for the experimental group (BBO) compared to the control group (CO). However, combined with the predicted effect of sustained object novelty (as above), it may be the case that the effect of novelty on exploration outweighs the effect of learning. Experiment 3 provided a test for such a possibility: should object novelty outweigh the learning effect, the groups would exhibit similar amounts of exploratory behaviour; but if the reverse occurred, Group BBO would display more object interactions than Group CO.

METHOD

Subjects

The subjects were 24 male Hooded Wistar rats (*Rattus norvegicus*) obtained at 90 days of age. As before, 2 extra animals took part in a pilot study. Details concerning the housing conditions, temperature, lighting, feeding and preliminary handling sessions were the same as for experiments 1 and 2.

The grouping of animals was the same as for experiment 2; that is, there were four groups, each consisting of 6 animals: Ball Bearing with Objects (BBO), Ball Bearing with No Objects (BBNO), Control with Objects (CO) and Control with No Objects (CNO).

Apparatus

Experimental apparatus

The apparatus was the same experimental box as that used in experiment 2 (refer to Figure 6.1). To ensure novelty throughout the conditioning and extinction sessions, a total of 32 objects were employed. Objects were divided into 8 groups (4 for conditioning and 4 for extinction). Each group consisted of 4 objects: two with movable parts and two without (Figures 6.4 and 6.5). (Object names are given in Appendix 1.) The reason for varying object manipulability followed from a study by Renner and Rosenzweig (1986), who found differences in exploration by rats depending on whether objects were movable or not. By including equal numbers of each, this effect was controlled.

Observation equipment

This consisted of the same equipment as that used in experiment 2, including the event recording apparatus with 7 buttons to record 7 different behaviours.

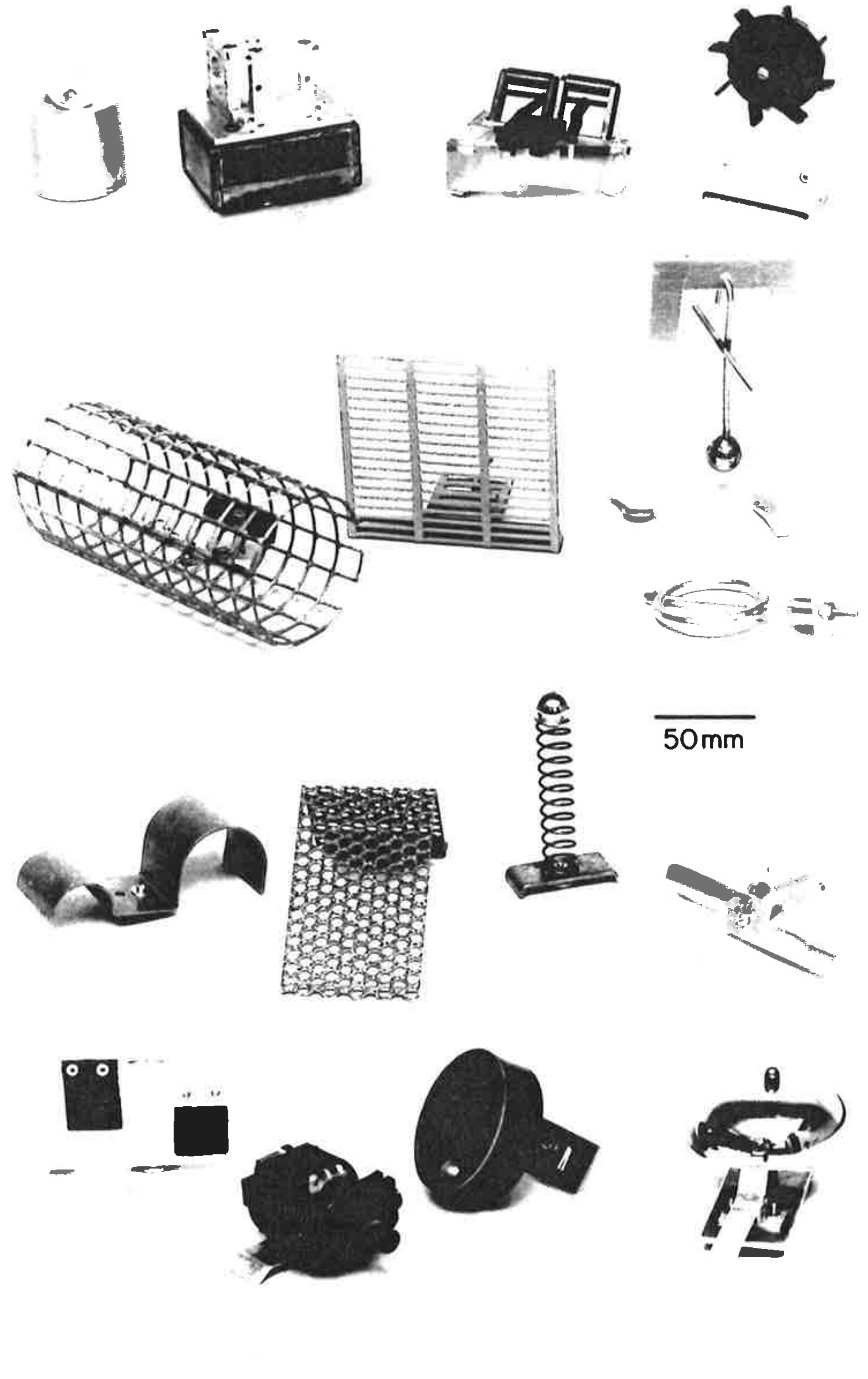


FIGURE 6.4: Experiment 3 novel objects used during conditioning.

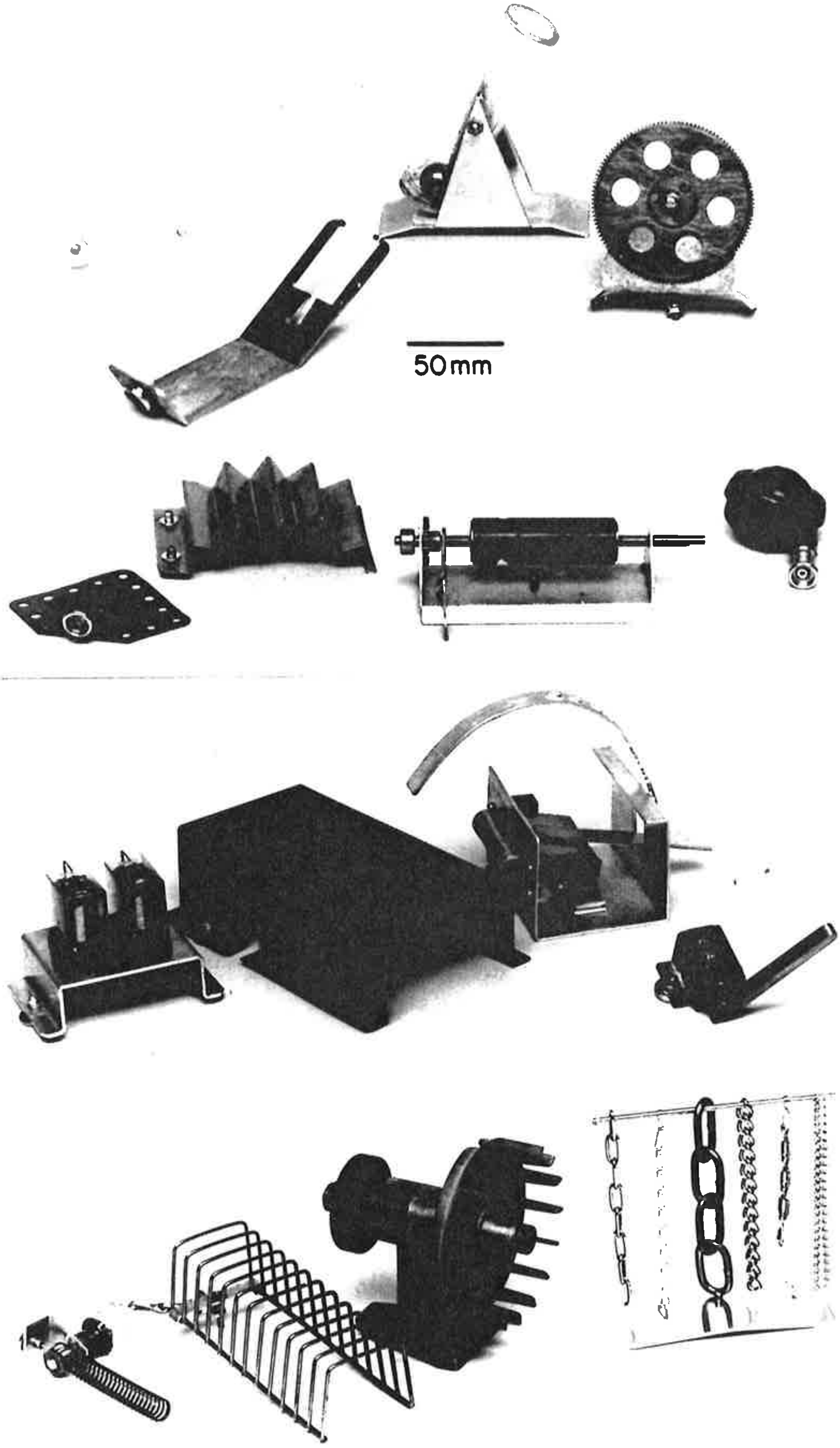


FIGURE 6.5: Experiment 3 novel objects used during extinction.

Procedure

The procedure was the same as that of experiment 2 (handling, familiarisation, conditioning and extinction), with the exception of the objects used over the course of the eight sessions. There was a total of 32 objects, divided into 8 groups of 4. On any given session (for Groups BO and CO), the experimental box contained two objects with movable parts and two without. A new set of objects was placed in the box before the commencement of each session.

Event recording and independent judging

The behavioural measurements taken in experiment 3 were the same as those of experiment 2: behaviours directed towards the objects and behaviours directed towards the ball bearing. The same 7 categories were employed, each expressed as frequencies and durations. As before, the exploratory behaviour categories were summed and the ball bearing-directed behaviours were summed, producing four additional variables: *frequency of object exploration*, *duration of object exploration*, *frequency of ball bearing-directed behaviour* and *duration of ball bearing-directed behaviour.*

The Kendall's W coefficient of concordance procedure was performed on data obtained from three independent judges' scoring of three video-taped sessions, as in experiment 2. A high degree of agreement among all judges was obtained for frequencies ($W = .912, p < .001$) and durations ($W = .920, p < .001$) of all of the variables measured.

RESULTS AND DISCUSSION

In experiment 3 a new set of objects was used for each of the conditioning and extinction sessions, thus maintaining novelty for the duration of the study. Apart from this, the experiment followed the procedure of experiment 2. It could be argued, then, that the occurrence of any differences in the results could be attributed to the independent variable of object novelty.

It was predicted that continued object novelty would result in sustained exploration over time in both of the groups for which objects were present (BBO and CO), countering the effect of habituation (which occurred in experiments 1 and 2). The experiment also provided a means for discriminating between the relative strength of the learning effect observed in experiment 2 and the effect of object novelty: if the effect of learning outweighed that of novelty, this would imply more object contacts by animals in Group BBO compared to Group CO, whereas a greater novelty effect would suggest similar amounts of exploration by both groups. The other two groups (BBNO and CNO) provided a second replication of the study by Timberlake, Wahl and King (1982), with the expectation that more ball bearing-directed behaviour would be produced by the group for which ball bearings predicted the delivery of food (BBNO).

Figures 6.6(I), 6.6(II), 6.6(III) and 6.6(IV) show the session means of each behavioural measure. Analysis of variance showed that object novelty had a marked effect on the distribution of exploration over time. In experiment 2 object exploration declined during conditioning and again during extinction, but in experiment 3 behaviour directed towards objects was much more variable: during both conditioning and extinction there were fluctuations in the amounts of exploration observed (Figures 6.6(I) and (II), graphs *a* to *h*). This variability may have reflected the rats' preferences for particular objects, since where one individual object was favoured, it was favoured by animals in all groups. In other words, some novel objects seemed to be more interesting to the animals than others.

The significance of object characteristics was emphasised by Renner and Rosenzweig (1986), who reported that rats' exploration is affected particularly by object manipulability. Renner and Rosenzweig explained this in terms of an increase in sensory feedback provided by manipulable objects compared to those which are non-manipulable. Similarly, Renner (1987) found that the larger an object was, the more rats interacted with it. In a study of chimpanzees (reported in Chapter 4, section 4.3.1), Welker (1956) found that the animals preferred objects which were more movable, larger, brighter, more heterogeneous, and which incorporated changing

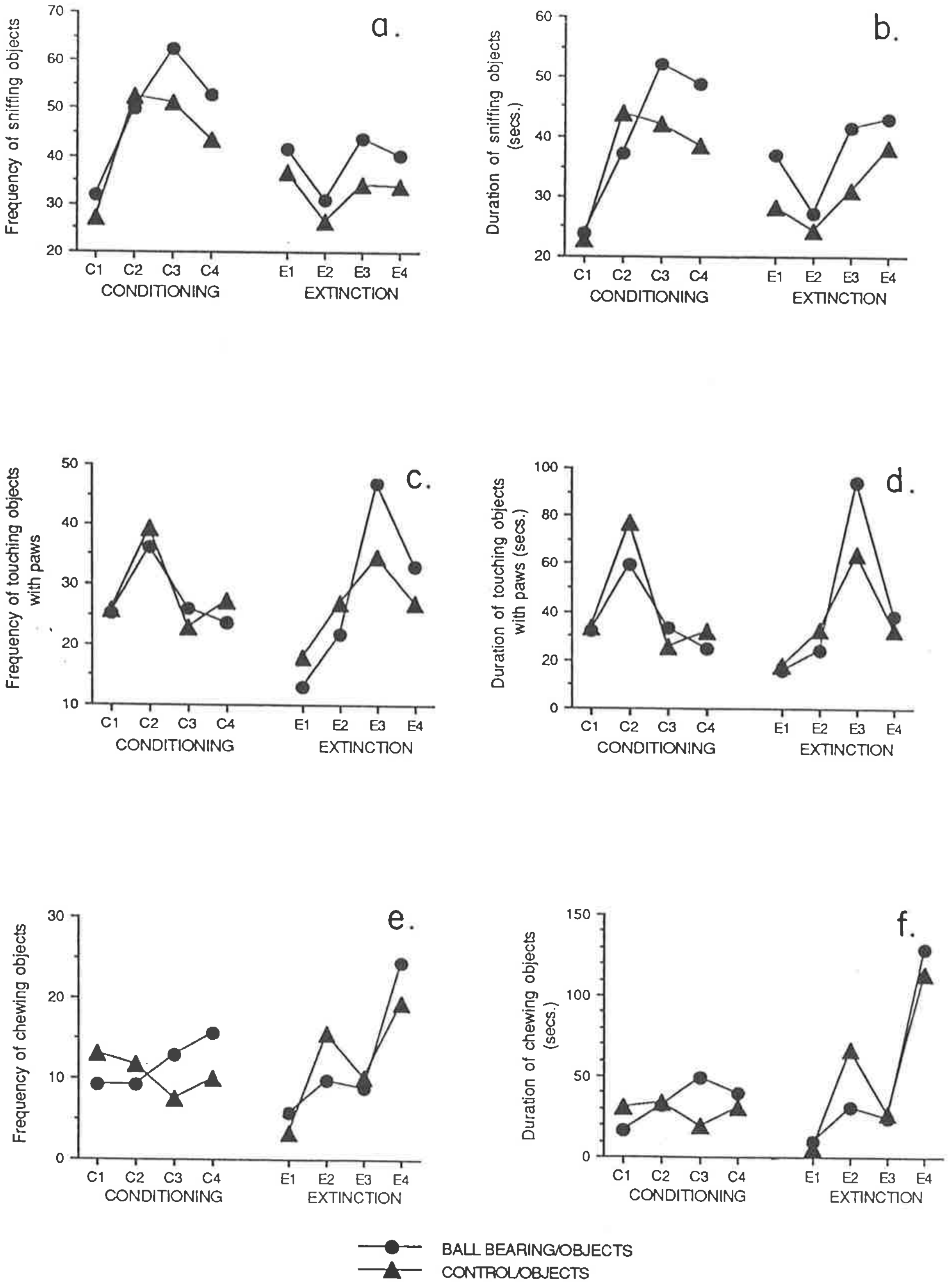


FIGURE 6.6(I): Session means of object-directed behaviours in experiment 3.

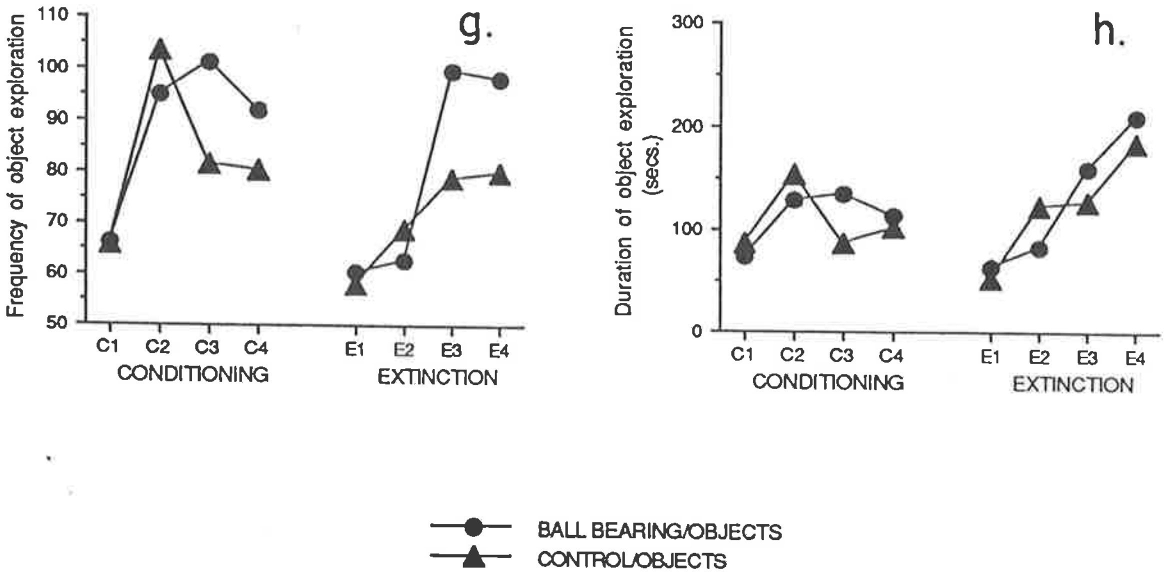


FIGURE 6.6(II): Session means of object-directed behaviours in experiment 3.

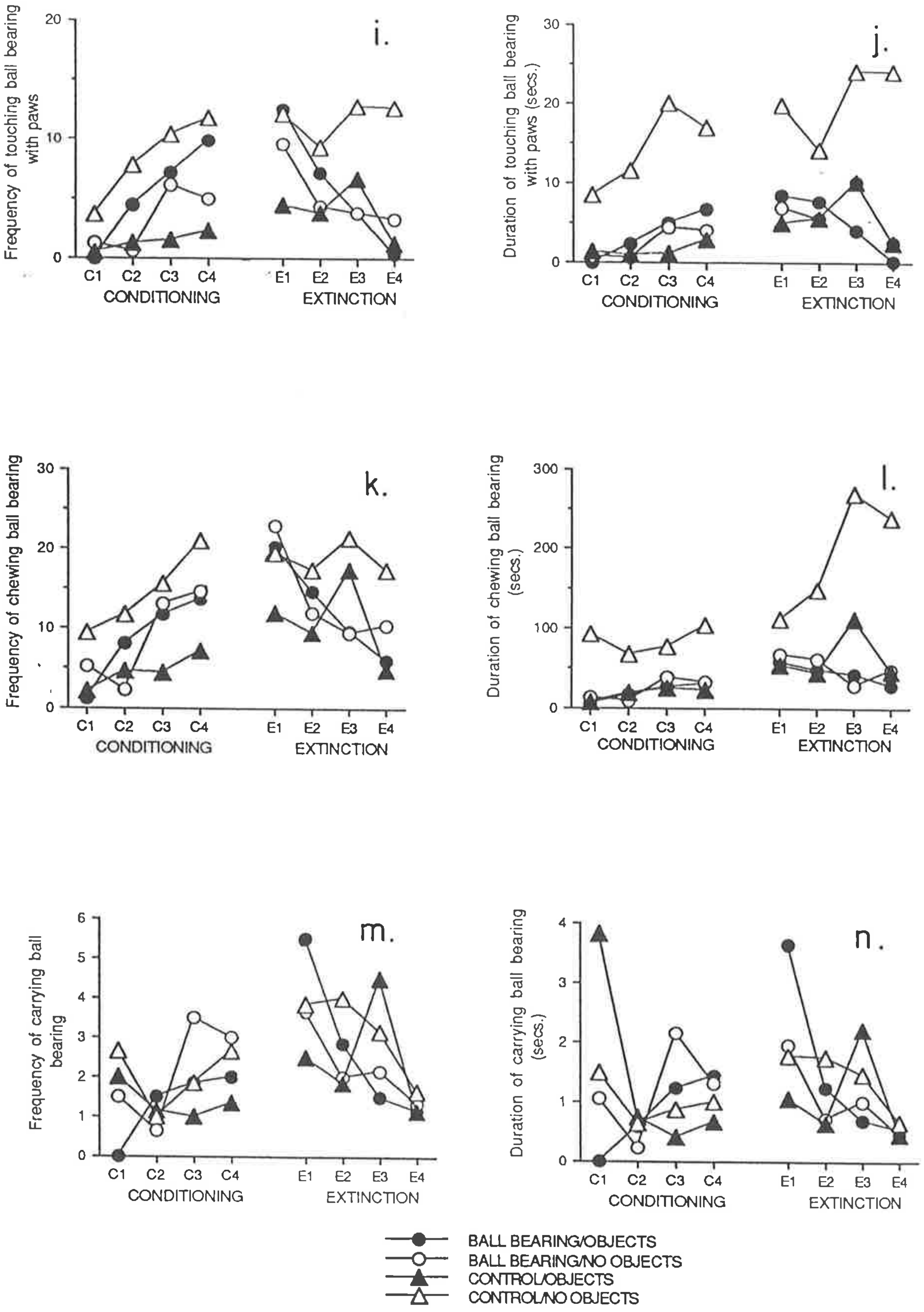


FIGURE 6.6(III): Session means of ball bearing-directed behaviours in experiment 3.

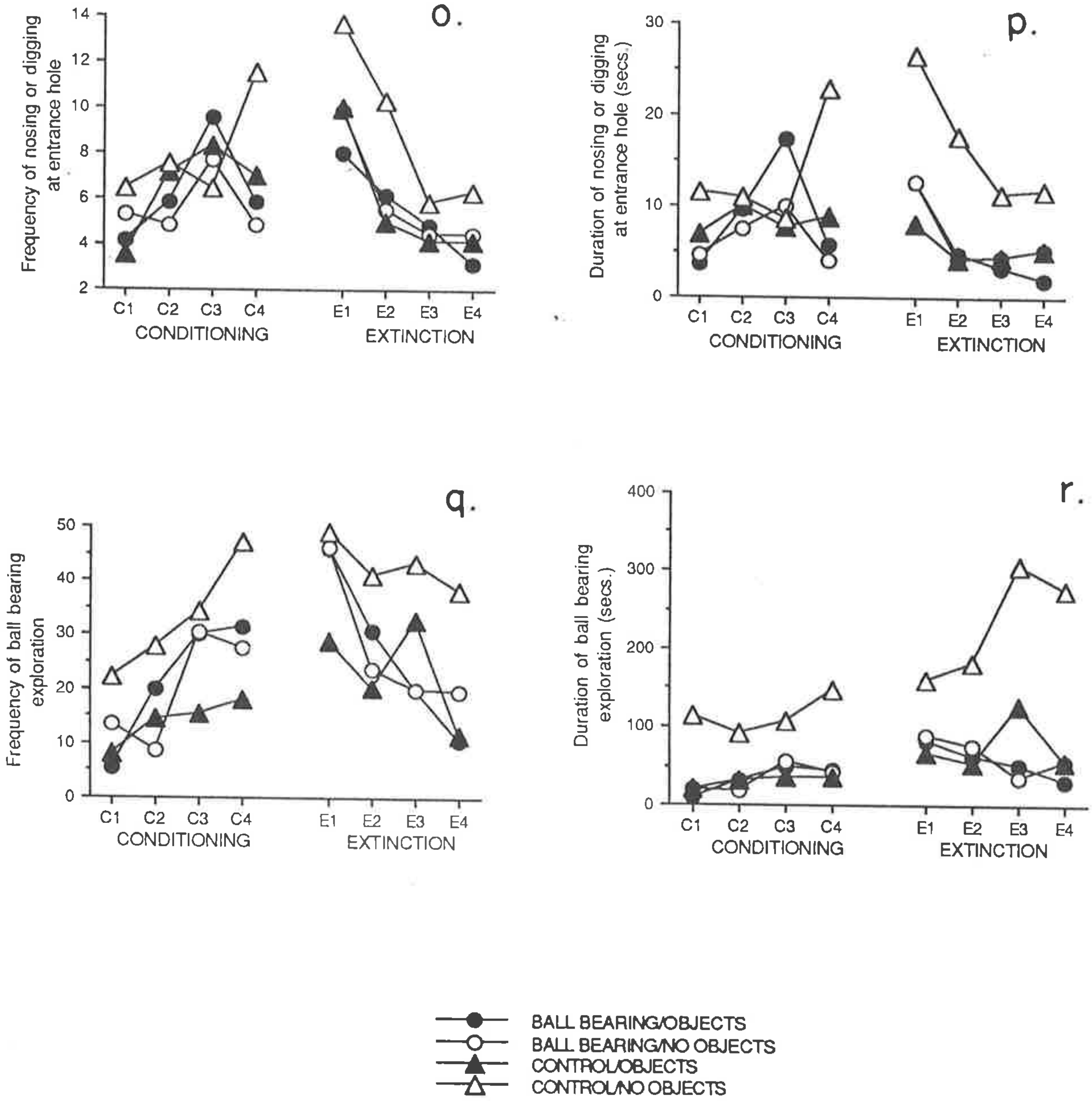


FIGURE 6.6(IV): Session means of ball bearing-directed behaviours in experiment 3.

auditory and visual stimulus configurations. Such characteristics seem to apply equally well to rats: in the present study, objects in group 8 (see Appendix 1) were explored most of all, and in this group there was an object which consisted of swinging chains suspended from a bar. The suspended chains were the most movable and noisy of all the objects used in the study, and this seems to account for the large amount attention directed towards them. In general, objects in groups 2, 3, 7 and 8 were explored more than the others (see Figure 6.6(II), graphs *g* and *h*).

Continued object novelty and variability in object preferences account for the finding that no statistically significant declines in exploration occurred during conditioning or extinction. In fact, significant increases were observed for most of the exploratory behaviours during extinction (Table 6.4).

Table 6.4: Significance levels obtained for measures of exploratory behaviour during extinction (*session* effects).

Variable	*F*	Significance level
Frequency of sniffing objects	$F(3,30) = 2.43$	N.S.
Duration of sniffing objects	$F(3,30) = 3.57$	$p < .05$
Frequency of touching objects with paws	$F(3,30) = 28.57$	$p < .001$
Duration of touching objects with paws	$F(3,30) = 34.44$	$p < .001$
Frequency of chewing objects	$F(3,30) = 22.26$	$p < .001$
Duration of chewing objects	$F(3,30) = 23.83$	$p < .001$
Frequency of object exploration	$F(3,30) = 12.31$	$p < .001$
Duration of object exploration	$F(3,30) = 26.25$	$p < .001$

In contrast to this, the *frequency of ball bearing-directed behaviour* tended to increase during conditioning ($F[3,60] = 4.42, p < .01$) and decrease during extinction (Table 6.5).

Table 6.5: Significance levels obtained for measures of ball bearing-directed behaviour during extinction (*session* effects).

Variable	*F*	Significance level
Frequency of touching ball bearing with paws	$F(3,60) = 3.11$	$p < .05$
Duration of touching ball bearing with paws	$F(3,60) = .59$	N.S.
Frequency of chewing ball bearing	$F(3,60) = 3.84$	$p < .05$
Duration of chewing ball bearing	$F(3,60) = 1.59$	N.S.
Frequency of carrying ball bearing	$F(3,60) = 3.64$	$p <.05$
Duration of carrying ball bearing	$F(3,60) = 5.56$	$p < .01$
Frequency of nosing or digging at entrance hole	$F(3,60) = 16.16$	$p < .001$
Duration of nosing or digging at entrance hole	$F(3,60) = 8.33$	$p < .001$
Frequency of ball bearing-directed behaviour	$F(3,60) = 6.02$	$p < .01$
Duration of ball bearing-directed behaviour	$F(3,60) = 1.01$	N.S.

To sum up the *session* effects for exploratory and ball bearing-directed behaviour, there were no main effects for the variables of exploratory behaviour during conditioning (but animals appeared to prefer certain individual objects), whereas ball bearing contacts increased over time. The occurrence of ball bearing 'misbehaviour' is consistent with Timberlake, Wahl and King's (1982) model, and the sustained exploration suggests that interest in sets of novel objects can be maintained concurrently with such 'misbehaviour'. During extinction, the combination of an increase in object contacts and a decrease in ball bearing-directed behaviour suggests that, as predicted, extinction induced more exploration, and further, that the exploratory behaviour was favoured over continued ball bearing contacts since the ball bearings no longer predicted the delivery of food.

In testing for an initial enhancement of exploration at the onset of extinction, *session* x *group* interactions were examined. No interaction effects were statistically significant, suggesting that the already high level of exploration induced by the novel objects over-shadowed any additional increase corresponding to the onset of extinction.

Finally, analysis of variance was conducted to assess the effect of *group* on object contacts and ball bearing-directed behaviour. For both conditioning and extinction sessions there was little evidence of any interaction between *session* and *group*, implying that novelty had a greater influence on object and ball bearing contacts than did learning (as suggested above). This was further supported in analysis of variance testing for *group* effects and planned comparisons between groups. No significant *group* effects were obtained for measures of object exploration; thus, exploratory behaviour was similar in all groups, regardless of whether the ball bearing predicted the delivery of food or not. The fact that the patterns of exploration displayed by the experimental animals were so similar to those produced by the control animals (Figures 6.6(I) and (II), graphs *a* to *h*) strongly suggests that most animals preferred the same particular objects (the objects in groups 2, 3, 7 and 8 were explored more than the others).

Furthermore, few *group* effects were obtained for the ball bearing-directed behaviours. Where planned comparisons yielded significant *t* ratios, they generally occurred for comparisons between Groups BBNO and CNO (Tables 6.6 and 6.7).

Table 6.6: Significance levels obtained for measures of ball bearing-directed behaviour during conditioning (planned comparisons between Groups BBNO and CNO).

Variable	*t*	Significance level
Duration of touching ball bearing with paws	$t = -2.60$	$p < .05$
Duration of chewing ball bearing	$t = -2.24$	$p < .05$
Duration of nosing or digging at entrance hole	$t = -2.74$	$p < .05$
Duration of ball bearing-directed behaviour	$t = -2.56$	$p < .05$

Table 6.7: Significance levels obtained for measures of ball bearing-directed behaviour during extinction (planned comparisons between Groups BBNO and CNO).

Variable	*t*	Significance level
Duration of touching ball bearing with paws	$t = -2.02$	$p < .05$
Duration of chewing ball bearing	$t = -2.18$	$p < .05$
Duration of nosing or digging at entrance hole	$t = -2.22$	$p < .05$
Duration of ball bearing-directed behaviour	$t = -2.24$	$p < .05$

In each case, the control animals contacted the ball bearing more than the animals in the experimental group. One control animal in particular often held on to each ball bearing for several minutes at a time, and this explains the higher means for the group as a whole.

In summary, the lack of significant *group* effects indicates a lack of support for predictions consistent with Timberlake, Wahl and King (1982). Group BBNO generally contacted the ball bearings more than Group CO, although differences were not statistically significant.

The results concerning exploratory behaviour directed towards the novel objects showed that, firstly, animals in experiment 3 engaged in far more object contacts than animals in experiment 2, suggesting that continued environmental variation enhances exploratory behaviour. Secondly, the declines over time which had previously been observed in experiment 2 did not occur in experiment 3, indicating a lack of habituation. This effect is evident from comparing the graphs in Figure 6.3(III) and (IV) with those in Figure 6.6(III) and (IV).

Another contrast to the results of experiment 2 was that differences between the experimental and control groups' exploration were not so apparent: animals receiving food following the exit of the ball bearing did not produce more exploratory behaviour than controls in the presence of the ball bearing alone. A possible explanation for this is that the effect of object novelty outweighed or over-shadowed that of the learning effect. Given that the experimental animals in experiment 2 did explore more than their controls, it seems likely that effects of learning can only be seen when objects are not continually changed over each session; in other words, when the environment is not constantly changing. In experiment 3, where objects were always novel, the effect of learning on exploration was not evident.

Moreover, the predicted effect of extinction on exploration did not occur (as it had done in experiment 2): at the onset of extinction no increase in exploratory behaviour was observed. Again, it seems that continuous novelty overrode the extinction effect by inducing large quantities of exploration regardless of other experimental manipulations.

A practical implication of these findings is that in order for a captive animal to maintain interest in its surroundings, keeping its enclosure novel is effective - more effective than learning. Results from experiment 2 suggested that in the absence of continual object novelty, learning does indeed improve the quantity of exploration produced, but experiment 3 showed that much more exploration can be produced by maintaining a novel environment, with or without learning.

6.5. CONCLUSION

Experiments 2 and 3, in viewing exploration in the context of the behaviour systems approach, provided data relevant to the issue of which types of learning may enrich exploration and the comparative importance of object novelty under these circumstances. Experiment 2 suggested that the learning situation previously designed by Timberlake, Wahl and King (1982) was indeed conducive to increases in behaviour directed towards a rolling ball bearing, as well as increases in object-directed activities. Experiment 3, however, indicated that the variable of object novelty over-shadowed any possible enhancement in exploration resulting from learning.

Given that the aim of enrichment research is to assess ways of improving the favourable and constructive behaviours of captive animals, experiment 3 suggests that novelty alone is equally or more effective in enhancing exploration, compared to the implementation of a simple learning procedure.

In light of the findings from experiments 2 and 3, two further experiments were conducted using two different species. The aim of these experiments was to examine species differences in exploratory behaviour, and to evaluate effects of object novelty and learning using the simple bar-pressing task which was used in experiment 1.

CHAPTER 7

COMPARATIVE STUDIES

7.1. INTRODUCTION

In Chapter 2 two approaches in the study of exploration were suggested, one involving single species studies of cause-effect relationships, and a second involving cross-species comparisons in an ethological framework. Taken together, experiments 4 and 5 can be viewed as a larger comparative study, in which exploration is examined in the rat and the common marmoset.

Since the 1950s animal studies within the field of experimental psychology have mostly focused on the behaviour of the laboratory rat (Figure 7.1), and some have used other rodents, birds and primates (Russell, 1983). Concentration on a narrow range of animals has been particularly associated with the arbitrary approach to animal behaviour (as described in Chapter 1), since such an approach aims to deduce laws of behaviour which are largely independent from external factors (Seligman, 1970), and thus treats animals as laboratory 'preparations' which display behavioural phenomena of theoretical interest (Russell, 1983).

Certain physiological and behavioural characteristics of particular animals have been seen as desirable for laboratory experimentation. The choice of the rat, according to Deutsch (1963), arose from such characteristics as its large litter sizes and shortness of pregnancy (21 days), its small size (not only so that a number can be kept in one cage, but also because large numbers can be used, thus fulfilling conditions necessary for statistical procedures), the fact that it is ready for experimentation at 3 months old, its cheapness to buy and maintain, and its temperament ("lively, inquisitive and highly adaptable", p. 267). Similar arguments have been used for pigeons and small primates (e.g., Bachrach, 1962).

FIGURE 7.1: The laboratory rat, *Rattus norvegicus*.

Researchers with a more ethologically oriented approach, however, tend to emphasise the need for cross-species studies, and later in this chapter (section 7.3) attention will be directed towards the marmoset as a laboratory subject.

Chapter 7 begins with experiment 4: a discussion of exploration in the rat (*Rattus norvegicus*) during conditioning and extinction. Section 7.3 introduces the marmoset, placing the animal into the context of experimental research, and lastly experiment 5 is described: exploration in the common marmoset (*Callithrix jacchus jacchus*) during conditioning and extinction. The chapter concludes with a summary of the findings of experiments 4 and 5, indicating similarities and differences found between the two species studied.

7.2. EXPERIMENT 4: EXPLORATION IN THE RAT *(RATTUS NORVEGICUS)* DURING CONDITIONING AND EXTINCTION

Experiment 4 examined the exploratory behaviour of the rat during operant conditioning and extinction. Behaviour directed towards a series of objects was measured, using the testing chamber previously used in experiment 1. The aim of the experiment was to compare behaviour observed during conditioning with that observed during extinction, as well as studying differences in behaviour directed towards either familiar or novel objects. Thus, the study was a 2 x 2 design, testing for effects of learning/no learning and the presence of familiar/novel objects on exploratory behaviour. The four groups of animals were as follows: Bar/Familiar Objects (BF), Bar/Novel Objects (BN), Control/Familiar Objects (CF) and Control/Novel Objects (CN).

Firstly, the experiment sought to make a comparison between amounts of exploratory behaviour produced by animals which learnt a bar-pressing task and animals for which no learning took place. As in the previous studies, experimental animals were expected to produce more exploration than control animals during the conditioning phase (consistent with Kvist, 1983), and a sudden increase in object contacts at the onset of extinction (Wong, 1977, 1978; Harcourt, 1983; Forster, 1986;

Litchfield, 1987). These predictions were the same as those in experiments 2 and 3, the only difference being the kind of learning task (bar-pressing instead of associating a moving ball bearing with food).

The main difference between experiment 4 and the previous experiments was that exploration was observed in the presence of either familiar or novel objects. It was expected that the novel objects would arouse more exploratory behaviour than the familiar objects, in accordance with the theories of novelty reported in Chapter 4, section 4.3 (e.g., Glickman & Sroges, 1966; Fowler, 1971; Poucet, Durup, & Thinus-Blanc, 1988; Rogers, Sink, & Hambley, 1988), stating that most mammals display increased activity and exploratory reactions (approach, investigation and manipulation) when placed in a novel environment. The prediction was also made in accordance with reports dealing with animals' responses to novel objects in particular (e.g., Berlyne, 1955; Welker, 1956; Jowaisas, 1969; Leyland, Robbins, & Iverson, 1976; Forster, 1986, 1990; Millar, Evans, & Chamove, 1988; Litchfield, 1991a, 1991b, 1991c). Furthermore, habituation was expected to occur more rapidly for the familiar objects group rather than the novel objects group, since habituation is said to rely on repeated exposure to the same stimuli (Berlyne, 1950; Dember, Earl, & Paradise, 1957; Montgomery, 1953).

It follows from these two sets of hypotheses that the group trained to bar-press in the presence of the novel objects (BN) would produce the most exploratory behaviour of all the groups, indicating an interaction between novelty and learning.

METHOD

Subjects

The subjects were 32 male Hooded Wistar rats (*Rattus norvegicus*) obtained at 150 days of age. 3 extra animals were kept on stand-by throughout the study. Details concerning the housing conditions, temperature, lighting, feeding and preliminary handling sessions were the same as for the previous experiments.

The rats were randomly allocated to one of four groups, each group consisting of 8 animals. There were two experimental groups: Bar/Familiar Objects (BF) and Bar/Novel Objects (BN); and two control groups: Control/Familiar Objects (CF) and Control/Novel Objects (CN).

Apparatus

Experimental apparatus

The apparatus was the experimental box previously employed in experiment 1 (refer to Figure 5.1). Two removable partitions were used for the experimental and control conditions respectively:

(a) a partition fitted with a bar (50mm x 12.5mm), feeding trough and light (Groups BF and BN);

(b) a plain wall panel (Groups CF and CN).

A total of 24 objects were available in the study (Figures 7.2 and 7.3; see also Appendix 1). In Groups BN and CN all of the objects were used, such that stimuli were continuously novel throughout the conditioning and extinction sessions. Objects were divided into 8 groups (4 for conditioning and 4 for extinction); each group consisted of 3 objects, one with movable parts and two without. In Groups BF and CF (the groups for which objects remained familiar), a single set of 3 objects was used for all sessions.

Observation equipment

This consisted of the same equipment as that used in experiment 1, including the event recording apparatus with 4 different buttons to record 4 different behaviours.

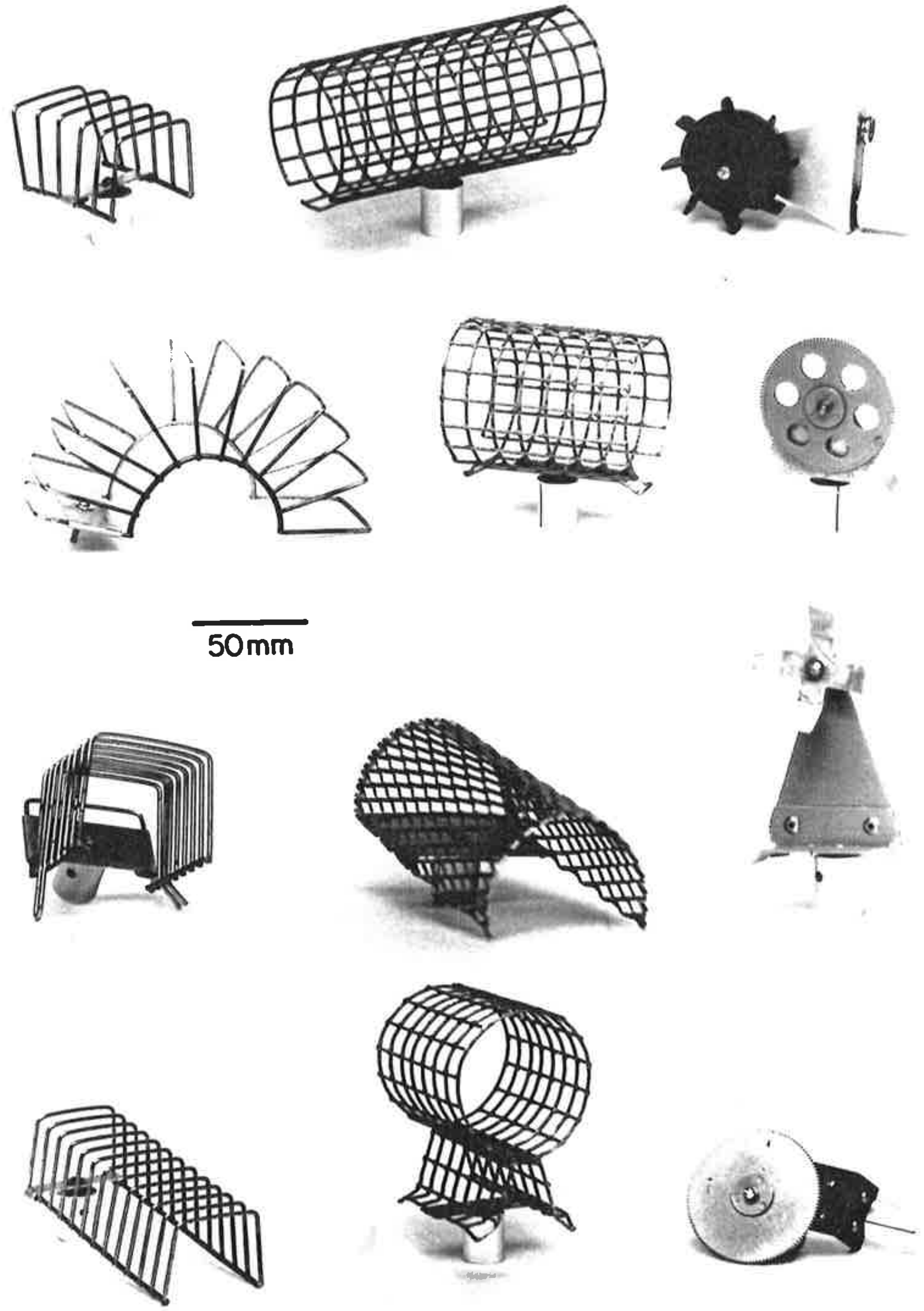


FIGURE 7.2: Experiment 4 novel objects used during conditioning.

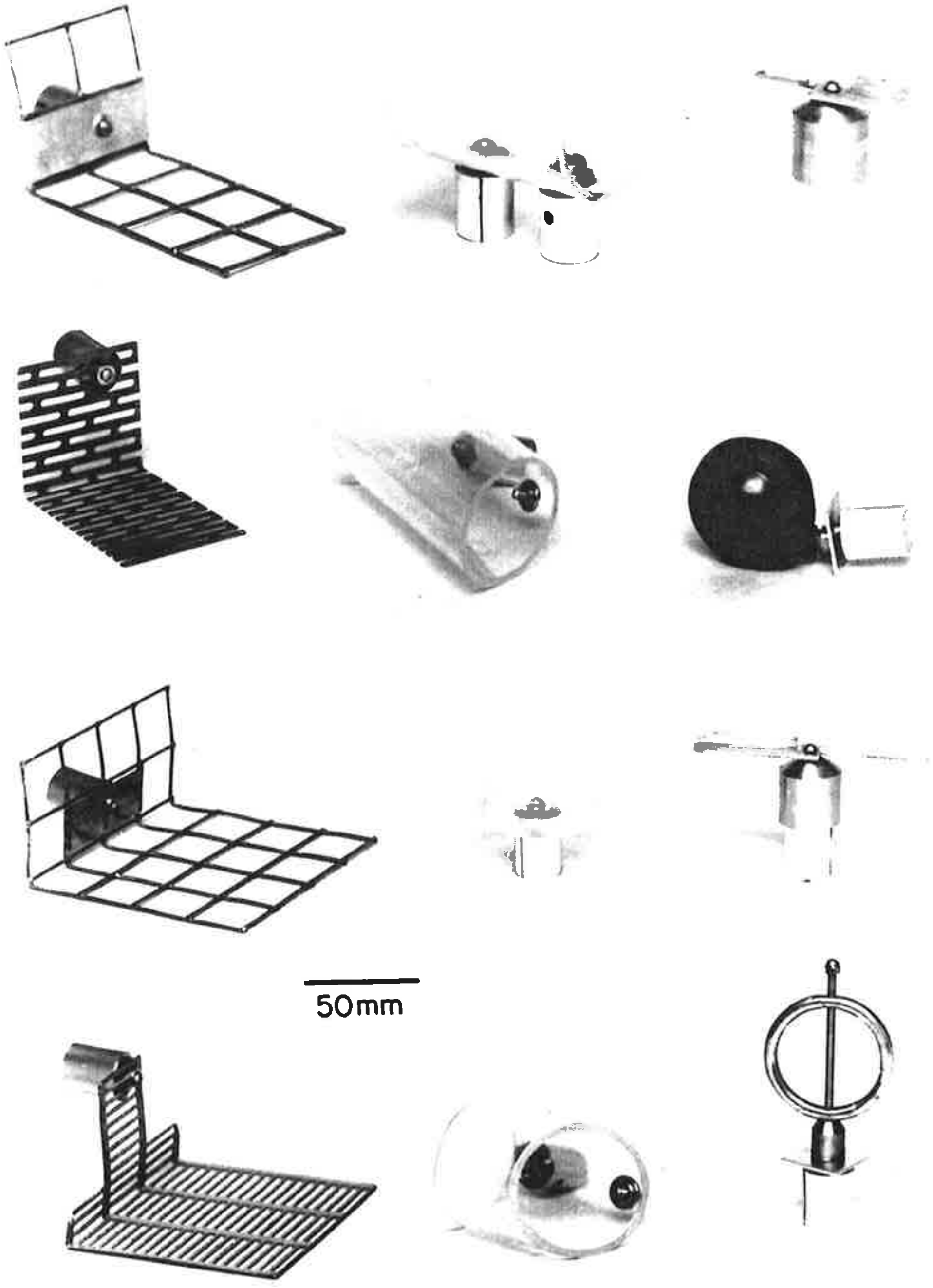


FIGURE 7.3: Experiment 4 novel objects used during extinction.

Procedure

For each of the four groups of animals (BF, BN, CF and CN) the experimental design consisted of four parts: firstly, handling; secondly, familiarisation and training to criterion; thirdly, conditioning; and finally, extinction. Following this, data were recorded by means of an event recording program, and independent judges were employed to undertake reliability tests.

Handling

This procedure was the same as that used in the previous experiments; that is, rats were handled 10 minutes each day for 5 days prior to the experimental sessions.

Familiarisation and training to criterion

Animals in Groups BF and BN were subjected to a similar familiarisation and training procedure to that used in experiment 1; that is, with no objects placed in the box, experimental rats took part in several individual training sessions, in which bar-pressing was shaped. Following this, animals were placed on a schedule of continuous food reinforcement. Each rat experienced from 3-7 training sessions, depending on the amount of training required before a criterion of 100 bar-presses was reached. Training sessions varied in length as a function of progress made in conditioning by each particular rat; the total average training time was 63 minutes.

Throughout this stage of the procedure control rats (Groups CF and CN) were placed in the box (without the objects or the bar) for the mean number of sessions and the mean amount of time taken for the experimental rats to be conditioned (i.e., 5 sessions totalling 63 minutes).

Conditioning

Animals were observed on four separate occasions, each lasting 15 minutes. The treatments for each group were as follows:

(a) Bar/Familiar Objects (BF). Animals were placed on a schedule of continuous reinforcement for bar-pressing in the presence of 3 objects. The same 3 objects were used in all four sessions (Group 1 objects).

(b) Bar/Novel Objects (BN). Animals were placed on a schedule of continuous reinforcement for bar-pressing in the presence of 3 objects. A different set of objects was used for each of the four sessions (Group 1 objects, followed by Group 2 objects, etc.).

(c) Control/Familiar Objects (CF). The plain wall panel was used. Animals were placed in the box for four 15-minute sessions in the presence of 3 objects. The same 3 objects were used in all four sessions (Group 1 objects).

(d) Control/Novel objects (CN). Also using the plain wall panel, animals were observed in the presence of the novel objects (changed over each session).

Extinction

Animals were observed on four separate occasions, each session lasting 15 minutes. The treatments for each group were the same as in the conditioning sessions except that no pellets were delivered to the experimental animals.

Event recording and independent judging

During each 15-minute session the experimenter viewed the video monitor and coded each animal's activities into particular categories, obtaining several behavioural measures. These were the same as the measures employed in experiment 1, and, as before, the frequency and duration measures were transformed into rates per minute and percentage durations respectively, so that the experimental groups (for which less time was available for exploring) could be meaningfully compared to the control groups (for which no bar was present). Thus, the dependent variables were as follows:

(a) *responses* - bar-pressing (Groups BF and BN);

(b) *sniffing objects* - in which a rat's snout is oriented towards an object, but without touching it;

(c) *touching objects with nose* - in which a rat's snout touches, pushes or moves an object (this category also included any biting of an object);

(d) *touching objects with paws* - in which a rat touches or manipulates an object with one or more paws, including climbing on or digging around the edge of an object.

The category of *responses* applied to animals in Groups BF and BN. The other categories - the measures of exploratory behaviour - applied to all animals. As for the previous experiments, the exploratory behaviour categories (*sniffing objects*, *touching objects with nose* and *touching objects with paws*) were added together, producing two extra variables, *rate of object exploration* and *percentage duration of object exploration.*

The Kendall's W coefficient of concordance procedure was performed on data obtained from three independent judges' scoring of two 15-minute video-taped sessions. A high degree of agreement among all judges was obtained for frequencies ($W = .985, p < .001$) and durations ($W = .934, p < .001$) of all of the variables measured.

RESULTS AND DISCUSSION

The aim of experiment 4 was to compare exploratory behaviour directed towards either familiar or novel objects, and to observe effects of learning on such behaviour. Four groups of animals participated in the experiment: Bar/Familiar Objects (BF), Bar/Novel Objects (BN), Control/Familiar Objects (CF) and Control/Novel Objects (CN). As in experiment 1, bar-pressing behaviour was observed as well as exploration directed towards the familiar or novel objects. As before, the multivariate analysis of variance procedure was used separately in the conditioning and extinction sessions, to analyse results in terms of effects due to *session*, effects due to *group*, and interactions between these.

In general, the experimental animals were expected to produce more exploratory behaviour than the controls (consistent with Kvist, 1983), including a sudden increase in object-directed activity at the onset of extinction (Wong, 1977, 1978; Harcourt, 1983; Forster, 1986; Litchfield, 1987). Furthermore, it was expected that the novel objects would arouse more exploratory behaviour than the familiar ones (Berlyne, 1955; Welker, 1956; Jowaisas, 1969; Leyland, Robbins, & Iverson, 1976; Forster, 1986, 1990; Millar, Evans, & Chamove, 1988), and that habituation would occur more rapidly in the familiar objects group (Berlyne, 1950; Dember, Earl, & Paradise, 1957; Montgomery, 1953). These predictions imply that the most exploration of all ought to occur in Group BN, the group in which animals learnt the bar-pressing task and the objects were novel.

Figures 7.4(I) and 7.4(II) show the session means of each behavioural measure. Analysis of variance showed that the rate of bar-pressing remained approximately constant during conditioning, but decreased significantly over the four extinction sessions ($F[3,42] = 50.88, p < .001$). *Percentage duration of responses* increased during conditioning ($F[3,42] = 12.49, p < .001$) and declined during extinction ($F[3,42] = 35.38, p < .001$). Thus, after a high rate of bar-pressing during conditioning, this response declined during extinction.

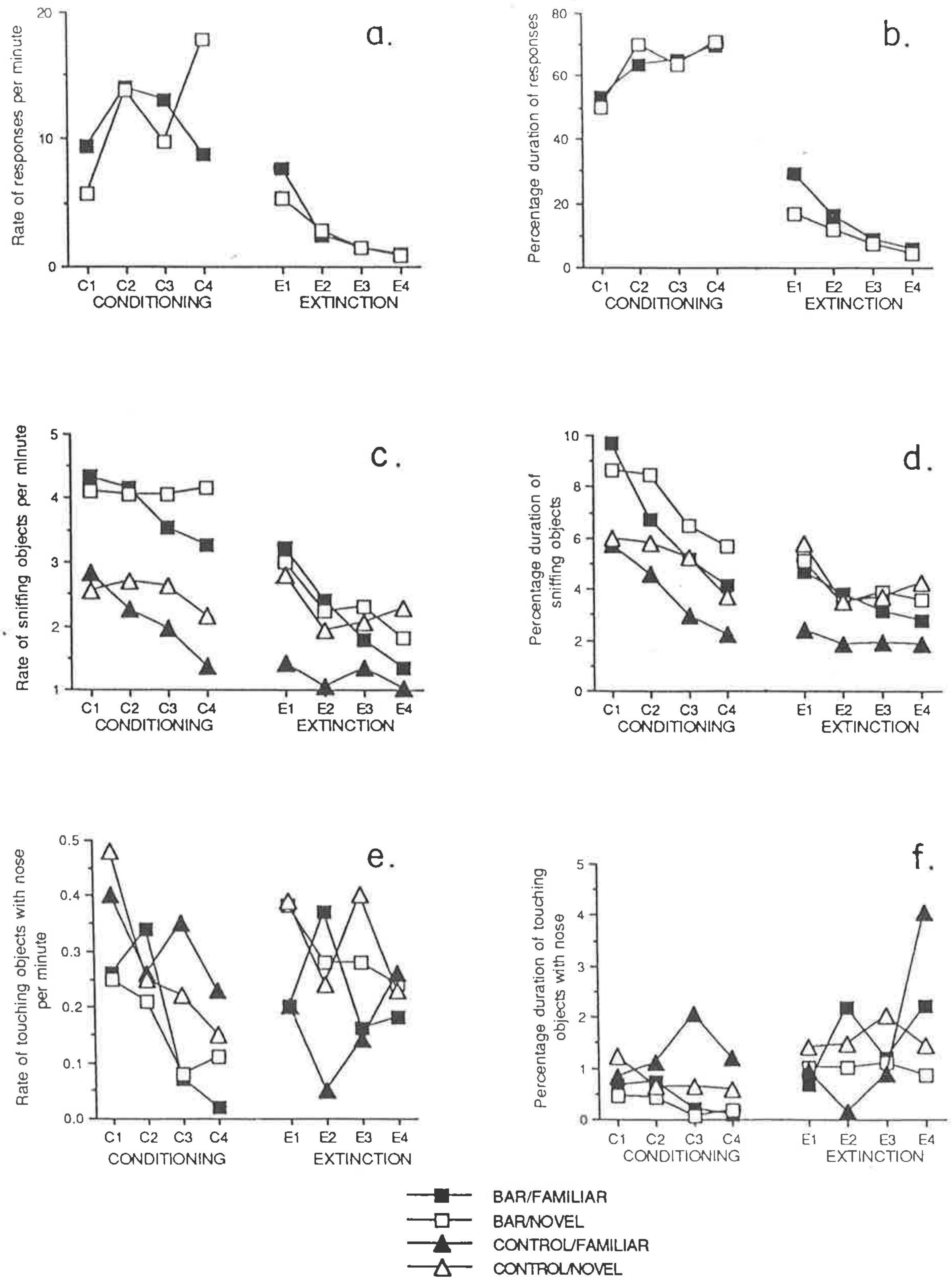


FIGURE 7.4(I): Session means of behavioural measures in experiment 4.

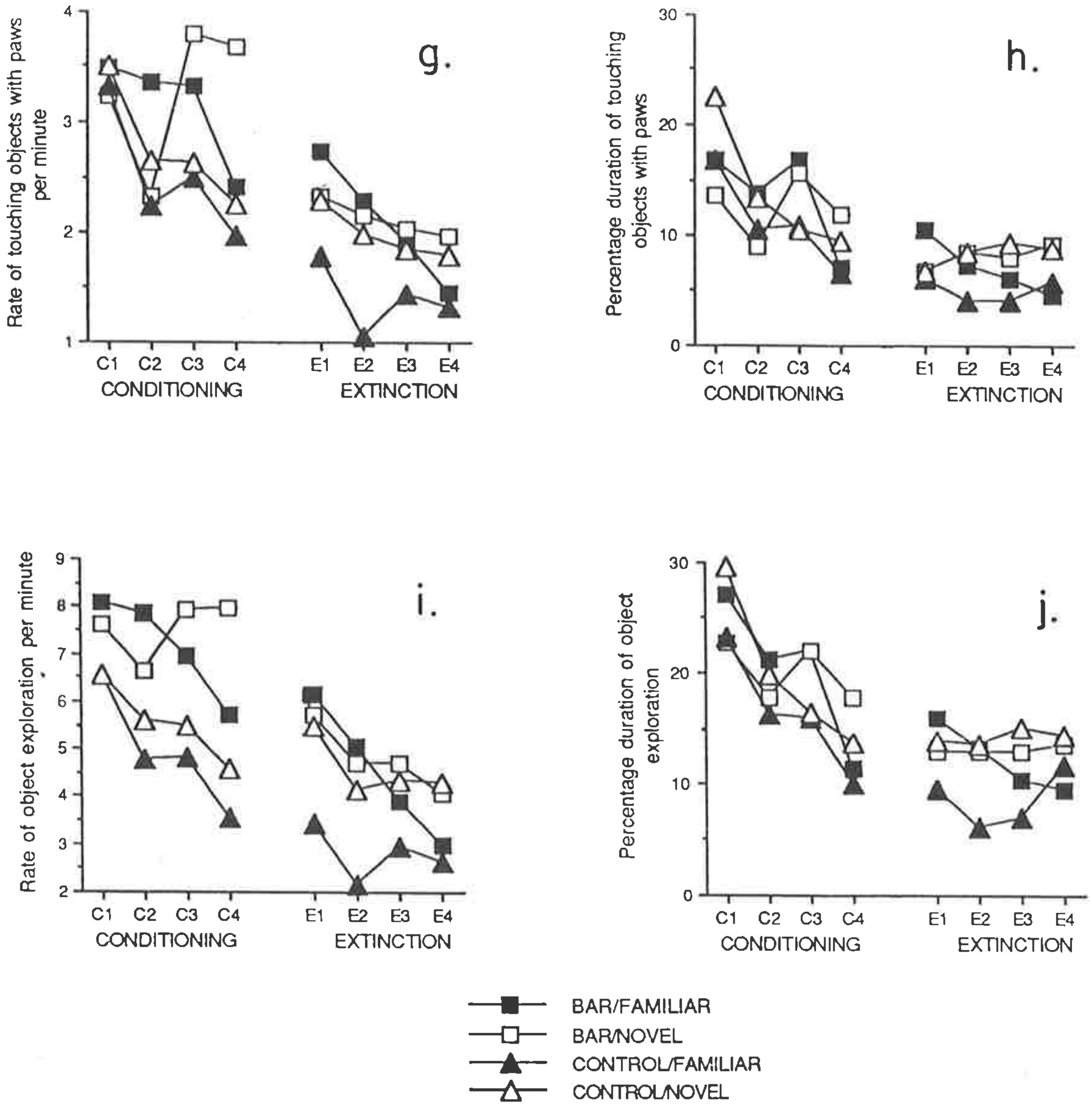


FIGURE 7.4(II): Session means of behavioural measures in experiment 4.

All measures of exploratory behaviour except one (*percentage duration of touching objects with nose*) exhibited significant declines during conditioning (Table 7.1), and furthermore there were interaction effects between *session* and *group* for the overall measures of object exploration (*rate of object exploration* $F[9,84] = 2.46, p < .05$; *percentage duration of object exploration* $F[9,84] = 2.02, p < .05$).

Table 7.1: Significance levels obtained for measures of exploratory behaviour during conditioning (*session* effects).

Variable	*F*	Significance level
Rate of sniffing objects	$F(3,84) = 4.66$	$p < .01$
Duration of sniffing objects	$F(3,84) = 19.69$	$p < .001$
Rate of touching objects with nose	$F(3,84) = 4.25$	$p < .01$
Duration of touching objects with nose	$F(3,84) = .21$	N.S.
Rate of touching objects with paws	$F(3,84) = 7.18$	$p < .001$
Duration of touching objects with paws	$F(3,84) = 21.87$	$p < .001$
Rate of object exploration	$F(3,84) = 9.04$	$p < .001$
Duration of object exploration	$F(3,84) = 25.86$	$p < .001$

Thus, despite a general trend in which animals became habituated towards the objects, the interaction effects showed that the trained animals (and in particular those for which objects were novel) tended to explore more than the control animals, which contacted objects less and less over time. This supports the idea that learning increases object-directed behaviour.

Tests for differences between the experimental and control groups showed that the trained animals contacted objects at a higher rate than the control animals during conditioning (Table 7.2), however, this effect did not occur for the percentage duration scores.

Table 7.2: Significance levels obtained for measures of exploratory behaviour during conditioning (*group* effects).

Variable	*F*	Significance level
Rate of sniffing objects	$F(1,28) = 85.67$	$p < .001$
Rate of touching objects with nose	$F(1,28) = 4.51$	$p < .05$
Rate of touching objects with paws	$F(1,28) = 4.52$	$p < .05$
Rate of object exploration	$F(1,28) = 35.16$	$p < .001$

During extinction the effects of novelty became much more pronounced and the groups could be distinguished from one another according to whether objects were novel or familiar (Table 7.3) rather than on the basis of learning versus no learning. An interaction between *session* and *group* occurred for object exploration during extinction (*rate of object exploration* $F[9,84] = 2.75, p < .01$; *percentage duration of object exploration* $F[9,84] = 1.94, p < .05$), again showing that the novel objects remained interesting to the animals in Groups BN and CN. In contrast, the extinction-induced exploration in Group BF declined, as did the object contacts of animals in Group CF.

Table 7.3: Significance levels obtained for measures of exploratory behaviour during extinction (*group* effects).

Variable	*F*	Significance level
Rate of sniffing objects	$F(1,28) = 15.44$	$p < .01$
Duration of sniffing objects	$F(1,28) = 14.17$	$p < .01$
Rate of touching objects with nose	$F(1,28) = 4.05$	$p < .05$
Duration of touching objects with paws	$F(1,28) = 4.83$	$p < .05$
Rate of object exploration	$F(1,28) = 11.38$	$p < .01$
Duration of object exploration	$F(1,28) = 4.82$	$p < .05$

To test the prediction that more exploratory behaviour would be produced by experimental animals at the onset of extinction, the measurements taken at session 4 of conditioning and session 1 of extinction were compared by means of analysis of variance. The majority of variables did produce a statistically significant interaction between *session* and *group*, supporting this hypothesis (Table 7.4). The effect was particularly pronounced where objects were familiar (Group BF). A possible explanation for the lesser effect in Group BN is that fluctuations in contacts with the novel objects may have been partly due to the animals' individual object preferences, thus obscuring the initial effect of the onset of extinction.

Table 7.4: Significance levels obtained for measures of exploratory behaviour during session 4 of conditioning and session 1 of extinction (*session* x *group* effects).

Variable	*F*	Significance level
Rate of sniffing objects	$F(3,28) = 4.50$	$p < .05$
Duration of sniffing objects	$F(3,28) = 3.41$	$p < .05$
Rate of touching objects with nose	$F(3,28) = 1.77$	N.S.
Duration of touching objects with nose	$F(3,28) = 1.62$	N.S.
Rate of touching objects with paws	$F(3,28) = 4.36$	$p < .01$
Duration of touching objects with paws	$F(3,28) = 4.60$	$p < .05$
Rate of object exploration	$F(3,28) = 4.90$	$p < .01$
Duration of object exploration	$F(3,28) = 2.93$	$p < .05$

In summary, the results from experiment 4 indicated that the two experimental treatments of learning and novelty interacted with the schedule of reinforcement. During the conditioning phase of the experiment the animals trained to bar-press (BF and BN) explored more than the animals which did not learn the task, and this occurred irrespective of whether objects were familiar or novel. In contrast to this, during the extinction phase the animals exposed to the novel objects (BN and CN) explored more than the animals for which objects were familiar, irrespective of the learning/no learning distinction. This result suggests that a schedule of continuous reinforcement is equally effective in producing an enhancement in exploratory behaviour, but that in the absence of such reinforcement, a supply of novel objects is effective in maintaining a high level of exploration.

In adaptive terms, the findings from experiment 4 can be explained in the following way. The conditioning phase of the experiment can be likened to a situation in which an animal is behaving successfully in its environment, such as finding an adequate supply of food. In such a situation, the animal is continually reinforced for carrying out a particular piece of behaviour, and it may be argued that in this case the familiarity or novelty of the surrounding environment is of little import and the animal need not carry out further exploration. The extinction phase of the experiment, however, may be likened to a situation in which food is not readily available. In this situation, an animal would be expected to explore a novel environment more than a familiar one, in order to increase its chance of finding food. This is consistent with reports of increased activity in combination with restricted resources (e.g., Davies & Houston, 1981; Timberlake & White, 1990; see Chapter 2, section 2.4) and increased activity in response to novelty (e.g., Berlyne, 1955; Poucet, Durup, & Thinus-Blanc, 1988; Rogers, Sink, & Hambley, 1988; see Chapter 4, section 4.3.1)

The results from experiment 4 were also consistent with those obtained in Chapter 6, in that the enhancement of exploration observed in the novel objects groups continued throughout the latter sessions of the experiment, showing no significant declines in the final four sessions. However, where experiments 2 and 3 indicated that novelty alone was more effective in maintaining a high level of exploration compared to the pairing of a ball bearing with food, experiment 4 showed that the bar-pressing task induced object exploration during conditioning, and the presence of novel objects maintained a high level of exploration during extinction.

It may be concluded that the use of learning procedures and novel objects is effective in enhancing exploratory activity, but that these have different effects according to the nature of the schedule of reinforcement in place at the time. Thus, although the intuitive solution to improving the variety of behaviours of captive animals may be a combination of learning and novelty, this is not necessarily the case. In fact, comparable levels of exploration can be achieved by the use of either one of these manipulations, provided the schedule of reinforcement is appropriate. In practical terms, this means that behavioural enrichment for animals in captivity may be achieved by either the implementation of a learning program (as suggested in Chapter 4), or by the maintenance of novelty in the animals' surroundings.

7.3. THE MARMOSET AS A LABORATORY ANIMAL

As stated at the beginning of this chapter, animal studies in experimental psychology have mostly concentrated on a narrow range of species, and in particular the laboratory rat. Several factors were suggested to account for the choice of the rat, such as its reproductive characteristics, small size, cheapness to buy and docile temperament. The present section serves as an introduction to the marmoset, a small South American primate (Figure 7.5), arguing not only in favour of its value for comparative studies, but also that it too can adapt to the laboratory routine.

By the early 1970s, the marmoset had assumed some importance as an experimental animal (e.g., Stellar, 1960; Hampton, Hampton, & Landwehr, 1966; Kingston, 1969; Epple, 1968, 1970; Poswillo & Richards, 1972), and since then marmosets have been used on an increasing scale in many branches of laboratory research, such as anatomical, physiological, reproductive, genetic and behavioural studies (e.g., Hearn, Lunn, Burden, & Pilcher, 1975; Ingram, 1975; Stevenson & Poole, 1976; Stevenson, 1978; Snowdon & Pola, 1978; Abbott, 1978; Box, 1978; Menzel & Menzel, 1979; Millar, Evans, & Chamove, 1988; Kidman, 1990). As noted by Ingram (1975) and Hearn, Lunn, Burden and Pilcher (1975), the importance of setting up and maintaining laboratories containing captive-bred marmosets became a far greater priority in the 1970s due to the rapidly decreasing numbers of many species in their natural habitats, as well as the poor condition of animals imported from the wild.

FIGURE 7.5: The common marmoset, *Callithrix jacchus jacchus*.

Since then, the establishment of laboratory and zoo-bred marmosets has remained a priority.

The aim of this introductory section is firstly to describe the marmoset in terms of its requirements in the laboratory, and secondly to provide some general observations of the behaviour of captive marmosets. Following this, experiment 5 will be described: exploration in the common marmoset (*Callithrix jacchus jacchus*) during conditioning and extinction.

7.3.1. The marmoset's requirements in the laboratory

As early as 1953, according to Stellar (1960), an attempt was made to adapt the marmoset to the laboratory and to investigate its behaviour. This attempt was described as being fraught with obstacles, mainly due to the marmoset's susceptibility to respiratory infections, parasites, dietary deficiencies and other common laboratory diseases. However, by the time of Stellar's article (1960), the marmoset was being described as:

> *...a most attractive animal for comparative behavioral studies, fitting as it does somewhere between such well-studied animals as the rat, cat, and dog on the one hand and the cebus and rhesus monkey on the other. In addition, its small size (300 to 500 gm. at full maturity), its docility, its tremendous emotional range, its capacity for social organization, and its relatively short reproductive cycle all suggest that it might be an ideal animal for the experimental investigation of behavior in its own right* (p. 1).

Such a description is consistent with a later article on marmoset management by Hearn, Lunn, Burden and Pilcher (1975), in which the animal is recommended for laboratory use (relative to other primates) because it is small, easy to handle and inexpensive to house and feed.

Despite such glowing descriptions, laboratory maintenance of marmosets requires careful management of a variety of aspects of the animals' environment; in particular, diet, temperature and humidity, and cage design.

Stellar (1960) argued that the most critical factor in the successful maintenance of marmosets in captivity is diet. Marmosets eat a variety of fruits, and are carnivorous to a great extent: in the wild they feed on fruit, flowers, plant exudate, insects, spiders, lizards, snails, frogs, and probably fledgling birds and birds' eggs (Stevenson & Rylands, 1988). In the laboratory, Epple (1970) was in favour of feeding marmosets on a mixture of fruit, vegetables, dairy products, cereals, seafish, frogs, mice, and a large variety of insects (e.g., mealworms, crickets, locusts and caterpillars). In addition, a certain amount of indigestible material was suggested, such as feathers or hair. To this list, Kidman (1990) added plant exudates (gum and sap), since these are often eaten in the wild. Finally, marmosets require a source of vitamin D, and this can be provided by means of daily exposure to ultra-violet lamps.

Stellar (1960) also stressed the importance of maintaining appropriate temperature and humidity levels for marmosets held in laboratories. Ideally, according to Stellar, the room temperature needs to be kept between 24^0 and 27^0C, and humidity should be kept above a minimum of 50%. Such variation is comparable to the range observed by Hubrecht (1983, 1984) in studies of the marmoset's natural habitat in north-eastern Brazil, where temperatures range from 21-31^0C and humidity is 77-99%.

On the topic of cage design, Stellar provided a basic minimum guideline for the individual marmoset: a metal cage measuring 18 x 18 x 36 inches, including a solid wall and back to reduce drafts, a 9 inch-wide wooden shelf across the back wall and a wooden dowel perch. When not involved in an experiment, however, Stellar suggested that family groups should be housed together in larger breeding cages. Papers by Hearn, Lunn, Burden and Pilcher (1975), Ingram (1975) and Poole and Evans (1982) give details concerning the maintenance of successful breeding colonies of marmosets, in which animals are kept in breeding groups consisting of an adult pair and their offspring.

A regime fulfilling all of these criteria, according to Stellar, reduces the probability of diseases (such as the common respiratory infections), and allows the possibility of maintaining marmosets for their full life span (10-15 years). However, other researchers (e.g., Hearn, Lunn, Burden, & Pilcher, 1975) have stressed the danger of boredom in the management of marmosets, arguing that laboratory attendants ought to hand feed and talk to their animals as often as possible. As will be seen later in this chapter (section 7.4), the marmoset, like the rat, can benefit from the inclusion of novel objects its cage, as well as the implementation of learning procedures.

7.3.2. Observations of marmoset behaviour in captivity

A major source of information about the behaviour of marmosets in captivity has come from Stellar (1960), as well as a sequence of papers by Epple which offer a complete guide to the maintenance, breeding and development of marmoset monkeys in captivity (1970). For the present purposes, this section will consist of a brief summary of Stellar's general observations, with additional observations from some more recent experimental and field studies.

Stellar described the captive marmoset as being an active, alert and visually oriented animal, following all activity outside its cage with its eyes. When left undisturbed, the marmoset actively explores its cage, feeds, drinks, grooms and examines the outside surroundings.

If a marmoset is disturbed, however (e.g., by experimenter handling or by the presence of an experimenter who has previously restrained or injected the animal), the behaviour changes markedly, as Stellar (1960, p. 4) described:

> *Upon any disturbance, it runs actively about its cage, retreating to the rear and coming forward to look out of its cage, in rapid succession. In addition to the typical mammalian signs of piloerection, pupillary dilation, and rapid breathing, the emotionally disturbed marmoset characteristically licks its nose in quick darts of its long tongue. Also, it chatters and chirps noisily in a characteristic vocal pattern that is different for each strain of marmoset. Upon handling, the marmoset reacts to restraint by vocalizing and struggling wildly, and unlike the rhesus monkey, may continue this emotional display to the point of physical exhaustion. This is true even of animals sufficiently tamed to perch on the O's shoulder and feed.*

Some additional distress reactions have been noted by Hampton, Hampton and Landwehr (1966), who observed a group of marmosets in the first author's back yard. When approached by a stranger, the marmosets faced forward and shifted their heads from side to side in quick jerking motions. It was suggested that this 'owl-like cocking of the head' (or 'headcock stare', Menzel, 1980; Stevenson & Rylands, 1988; Millar, Evans, & Chamove, 1988) provides the animals with a three-dimensional view, making up for the fact that marmosets have limited eye movement. The distressed marmosets observed by Hampton *et al.* also typically held their mouths open, sometimes vocalising, and hid in their nest boxes whenever a bird or aeroplane flew overhead. Such behaviour is consistent with the behaviour of wild marmosets, which have been observed giving alarm calls, moving behind branches, and freezing whenever large birds fly overhead (Stevenson & Rylands, 1988).

In view of all of these reactions, and given that captive marmosets readily use nest boxes for protection, Epple (1970) suggested that marmosets be transported inside their boxes, thereby avoiding being handled by the experimenter.

A final point made by Stellar concerns the observation of captive marmosets in simple learning situations. Examples of marmoset learning experiments include two-choice object discrimination, training in a Skinner box or shuttle box, and avoidance conditioning. However, the only information given by Stellar is that marmosets are predominantly right-handed (since they usually reach for objects with their right hands in discrimination studies), and that they can be motivated for food reward by feeding once daily.

Other researchers have provided more detailed information about marmoset behaviour in experimental situations, and of particular relevance to the experiment reported in section 7.4 is the reaction of the captive marmoset to new objects in its environment. In the words of Epple (1970, p. 57):

> *Alterations of the environment stimulate the activity of the animals and frequently result in intensive exploratory behavior, play and scent marking responses.*

In an experiment by Millar, Evans and Chamove (1988, described in Chapter 4), marmosets presented with a set of novel objects reacted to them with a wide range of behaviours: vocalising, headcock stares, piloerection, threatening aggressive displays, tail-raised presenting, followed by approaching, sniffing and manipulating the objects. The duration of the object contacts, however, was not very long: an average of 7.5

minutes in each 30-minute session, and furthermore, interest in the objects decreased with repeated presentations.

On the whole, general observations such as those discussed in this section suggest that the captive marmoset, like the laboratory rat, may benefit from the implementation of learning procedures and the addition of novel objects in their cages. The following experiment was designed in order to investigate the exploratory behaviour of captive marmosets in connection with operant conditioning and extinction, as well as the presence of familiar or novel objects.

7.4. EXPERIMENT 5: EXPLORATION IN THE COMMON MARMOSET *(CALLITHRIX JACCHUS JACCHUS)* DURING CONDITIONING AND EXTINCTION

Experiment 5 replicated experiment 4 as closely as possible, but used marmosets as subjects instead of rats. Some changes to the procedure were necessary as a result of differences in caging and feeding, and these differences are discussed in the sections describing the apparatus and procedure.

The main experimental hypothesis in experiment 5 was based on the findings of experiment 4, one of the aims being to obtain comparative data in order to determine differences and similarities between the rat and the marmoset. Consistent with the interactions between schedule of reinforcement and novelty obtained in experiment 4, it was expected that the trained marmosets (Groups BF and BN) would explore objects more than the control animals during conditioning, but that animals for which objects were novel (Groups BN and CN) would explore more than the familiar objects groups during extinction. As suggested by the data from the previous experiment, this prediction implies that learning is an effective means of enhancing exploratory behaviour provided the schedule is one of continuous reinforcement, whereas object novelty is effective when no food is available.

In addition, a series of non-object-directed measures were taken, the intention of which was to determine whether effects of learning and object novelty extended to other behaviours, such as vocalising, general locomotion, grooming or chewing the perch.

METHOD

Subjects

The subjects were 8 male common marmosets (*Callithrix jacchus jacchus*). Their ages at the commencement of the experiment varied from 17 months to 24 months.

Each marmoset was housed individually in a cage (66cm high x 35cm wide x 45cm deep) in an animal holding room at the Queen Elizabeth Hospital Animal House, Adelaide, South Australia. The cages were furnished with 2 wooden perches, a metal nest box (which animals used for overnight sleeping), a drinking bottle for *ad libitum* supplies of water, and an empty yoghurt container (for play). Food was supplied by means of ceramic bowls, which were placed in the animals' cages at feeding time (daily each morning), and removed and washed the following morning.

The temperature of the animal holding room was kept constant at 25^0C, and lighting followed a 12/12 light-dark cycle (lights on 7.00am, off 7.00pm). The last half hour of lighting was ultra-violet light.

The marmosets' feeding regime was as follows: each animal received a handful of food pellets, 4 slices of banana, and 4 one-eighth sections of either apple or orange (given on alternate days). Once a week, 3 small pieces of bread soaked in a vitamin supplement solution (*Penta Vite*) were included, as well as either sultanas or pieces of hard-boiled egg. The normal feeding routine for the marmosets prior to the experiment was the presentation of food at 10.30am each day; during the study feeding time was changed to 5.00pm; that is, animals received their usual amounts of food at the end of each day's experimental sessions.

Preliminary handling sessions were carried out in order to familiarise the animals with the experimenter and the procedure of being removed from their home cages. Handling consisted of taking a marmoset out of its home cage (using two pairs of leather gloves), gently stroking it for 10 minutes, and then returning it to its cage.

The marmosets were randomly allocated to one of four groups, each group consisting of a pair of animals. There were two experimental groups: Bar/Familiar Objects (BF) and Bar/Novel Objects (BN); and two control groups: Control/Familiar Objects (CF) and Control/Novel Objects (CN).

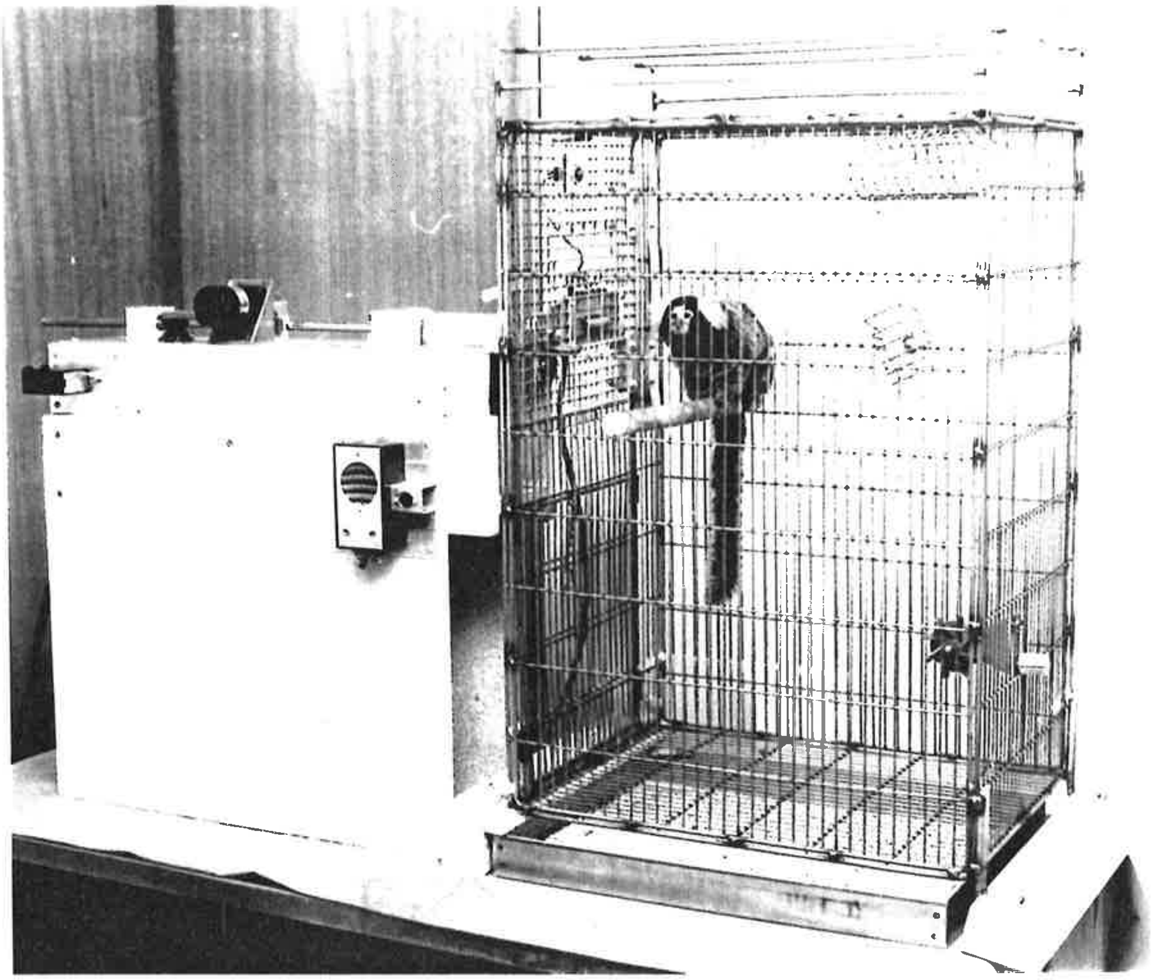
Apparatus

Experimental apparatus

The experimental apparatus consisted of a modified version of the animals' home cages. A spare home cage (including the two perches, but without the nest box, the drinking bottle or the empty yoghurt container) was fitted with a grid-door housing a bar, light, buzzer and feeder (Figures 7.6 and 7.7). For conditions not requiring the bar and feeder, the normal cage door was closed and the extra grid-door was removed.

The feeder consisted of a syringe (25.4mm in diameter, 130mm long), the end of which protruded through the grid-door immediately below the bar (Figure 7.8). Small amounts of banana were dispensed from the syringe by means of a 24V DC Power Supply, powering a plunger to move through the syringe at small regular intervals. A bar-press triggered the plunger movement, and hence provided the animal with a small amount of banana. Reinforcements could also be released manually by the experimenter (for the response shaping procedure).

As in experiment 4, a set of 32 objects was used throughout the study, in groups of 3 for any one session (refer to Figures 7.2 and 7.3, and Appendix 1). Objects were changed over each session for conditions requiring object novelty, and kept constant for conditions requiring object familiarity.



<u>FIGURE 7.6</u>: Experimental testing cage used in experiment 5.

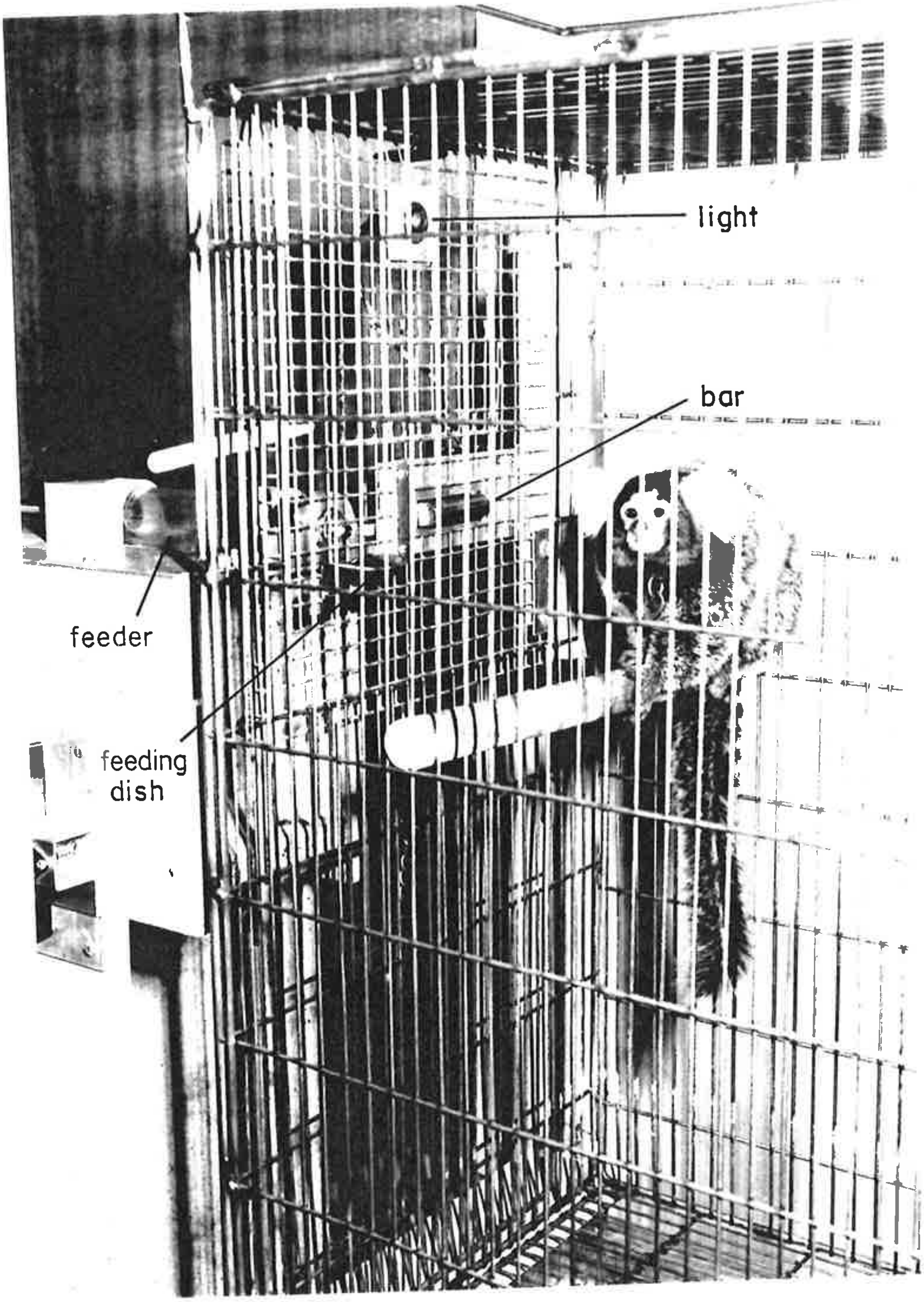


FIGURE 7.7: Close-up of marmoset in testing cage, showing bar, feeder and light.

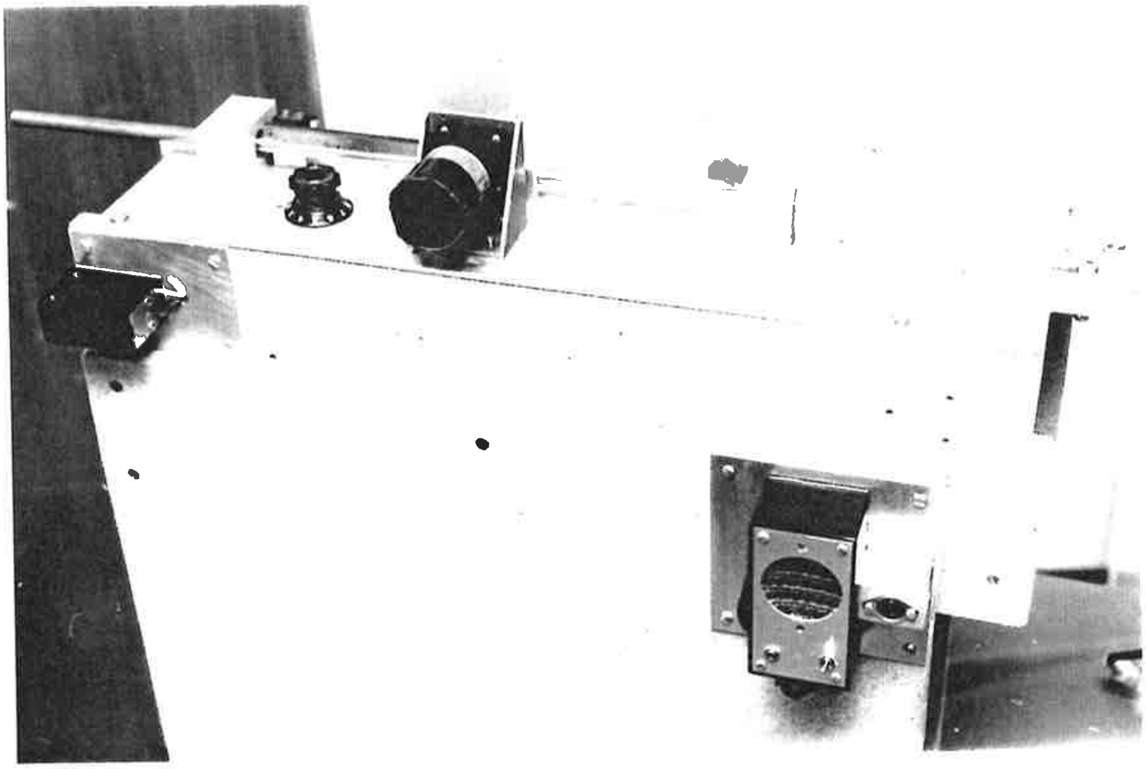


FIGURE 7.8: Banana feeder used in experiment 5.

In order to transport animals from their home cages to the experimental apparatus, the marmosets were carried inside their own nest boxes (these could be closed with a lid fitting on the entrance of each box), thus reducing effects of handling stress. During the experiment (including the familiarisation and initial training sessions) the experimenter sat behind a wooden screen, minimising disturbances to the animals, since any movement or sound tended to arouse their attention. (The importance of a hide in observing marmosets has been pointed out by Ingram, 1975.) The experimental apparatus was located in a room some distance from the animals' holding room.

Observation equipment

Recordings were made using a *National VCT-800* video camera with inbuilt timer, a *National NV-100* video cassette recorder and *VHS* video tapes. The camera was set up adjacent to the experimental cage, such that the grid-door with the bar and feeder was visible to the far left of view.

Recordings of the sessions were later viewed on a *Panasonic Quintrix* video monitor and specific behaviours were entered on to *North Star Advantage* computer files by means of an event recording table with 9 buttons (8 behaviours, 1 stop button).

Procedure

For each of the four groups of animals (BF, BN, CF and CN) the experimental design consisted of five parts: handling, familiarisation, training to criterion, conditioning and extinction. Following this, data were recorded by means of an event recording program, and independent judges were employed to undertake reliability tests.

Since marmosets are prone to sound disturbance, especially from uncontrollable outside stimulation such as the opening and closing of doors (Kish, 1966), throughout all phases of the procedure an attempt was made to keep the environment as quiet as possible.

Handling

Preliminary handling of the marmosets was carried out using two pairs of thick gloves (as suggested by Ingram, 1975), and initially in the presence of a person familiar to them (their feeder). Unlike rats, marmosets can be difficult to handle: as Stellar (1960) noted, they may in fact struggle until they become exhausted. For this reason, rather than carrying the animals from the holding room to the experimental room, the marmosets were transported inside their own nest boxes, a method recommended by Hampton, Hampton and Landwehr (1966) and Epple (1970), thus reducing the stressful reactions associated with handling.

Once in the experimental room the nest box was placed inside the experimental cage and the lid removed. After the animal had emerged, the nest box was taken out (usually immediately the lid was opened).

Following each experimental session, the same method was used to transport the marmoset back to its home cage; that is, the nest box was placed in the experimental cage, and the lid was closed once the animal was inside. The nest box was then carried back to the home cage, where it was hooked to the top of the cage, and the lid was removed.

Familiarisation

All animals were subjected to one 60-minute familiarisation session in the experimental cage, in order to become familiar with the cage and the room in which the experimental sessions took place. For experimental animals (Groups BF and BN) the bar, light and feeder were present, but no food was delivered. For control animals (Groups CF and CN) the plain grid-door was used.

Training to criterion

The experimental animals (Groups BF and BN) participated in several training sessions (without any objects), in which the bar-pressing response was acquired through shaping. Initially, some banana was dispensed into the feeding dish after the animal had eaten this, more banana was dispensed using the manual control of the feeder. The experimenter observed the marmoset via the video monitor behind the wooden screen, and reinforced successive approximations to bar-pressing. Training sessions varied in length and number as a function of varying progress made by each particular marmoset: on average, there were 18 training sessions, and the total average training time was 293 minutes (4 hours, 53 minutes). (This was much longer than the time required to train the rats in all of the previous experiments.) Criterion was reached when animals pressed the bar 15 times within the space of a 30-minute session.

Throughout this stage of the procedure control marmosets (Groups CF and CN) were placed in the experimental cage (without the objects or the bar) for the mean number of sessions and the mean amount of time taken for the experimental marmosets to be conditioned (i.e., 18 sessions totalling 293 minutes).

Conditioning

Animals were observed on four separate occasions, each lasting 30 minutes. The treatments for each group were as follows:

(a) Bar/Familiar Objects (BF). Animals were placed on a schedule of continuous reinforcement for bar-pressing in the presence of 3 objects. The same 3 objects were used in all four sessions (Group 1 objects).

(b) Bar/Novel Objects (BN). Animals were placed on a schedule of continuous reinforcement for bar-pressing in the presence of 3 objects. A different set of objects was used for each of the four sessions (Group 1 objects, followed by Group 2 objects, etc.).

(c) Control/Familiar Objects (CF). The plain grid-door was used. Animals were placed in the experimental cage for four 30-minute sessions in the presence of 3 objects. The same 3 objects were used in all four sessions (Group 1 objects).

(d) Control/Novel Objects (CN). Also using the plain grid-door, animals were observed in the presence of the novel objects (changed over each session).

Extinction

Animals were observed on four separate occasions, each session lasting 30 minutes. The treatments for each group were the same as in the conditioning sessions, except that no banana reinforcements were delivered to the experimental animals.

Event recording and independent judging

Following the completion of the conditioning and extinction sessions the experimenter viewed the video monitor and coded each animal's activities into particular categories, obtaining several behavioural measures. As before, the frequency and duration measures were transformed into rates per minute and percentage durations respectively, so that the experimental groups could be meaningfully compared to the control groups.

Some of the behavioural measures chosen for the experiment 5 originated from Stevenson and Poole's (1976) ethogram of the common marmoset. They described a general behavioural repertoire, categorising marmoset behaviour into sitting and resting postures, locomotory patterns, body gestures, facial expressions and head movements, scent-marking, interaction with objects (e.g., biting, gnawing, licking, muzzle rubbing, handling and sniffing), social acts involving contact, grooming, startle responses, tail positions and vocalisations. Other categories were derived from Epple (1968), Roder, Timmermans and Vossen (1989), Lacher, da Fonseca, Alves and Magalhaes-Castro (1981) and Kidman (1990).

Firstly, a category of *staring at objects* was used, since marmosets are markedly visual in their orientation to the environment (in contrast to rats). This category was partly derived from Stevenson and Poole's description of facial expressions and head movements: marmosets stare at objects with their eyes wide open, often moving their heads from side to side (the 'headcock stare', an observational technique which allows the marmoset to obtain a three-dimensional image of an object, Menzel, 1980). The 'headcock stare' has been observed in all callitrichids (Stevenson & Rylands, 1988), and Stevenson and Poole (1976) have also observed that marmosets often flatten their ear tufts when approaching a strange object. These facial characteristics were useful in determining whether the marmosets in the present experiment were staring at objects.

Touching objects with nose and *handling objects* were also derived from Stevenson and Poole (1976). These both came under their general category of 'interaction with objects', thus providing a measure of object-directed exploratory behaviour which could be compared with that of the rats in the previous experiments.

The category of *vocalisation* was included in order to test for a possible relationship between learning, the introduction of novel objects, and the amount of vocalisation produced. According to Epple (1968), vocal repertoires of marmosets may be classified on the basis of the situations that elicit them. For example, contact calls consist of a wide variety of monosyllabic and rhythmical vocalisations (twitters, trills and other sound sequences), whilst warning signals, given to flying objects and predators appearing suddenly on the ground, are short, high-pitched and very sharp whistles. Stevenson and Rylands (1988), in their detailed analysis of marmoset vocalisations, described sixteen different calls according to their sound, the context in which they are normally heard, and their possible function. For example, 'loud shrill', a loud 2-second call with the mouth open, is heard when animals are out of visual contact, thus serving to maintain contact throughout the group; whereas 'chirping' occurs in rapid series (like the chirping of birds), and is given when resting in close body contact or at the sight of an infant, suggesting that it is an amicable response associated with close contact with group members. The present study did not distinguish between these different kinds of calls, but aimed instead to obtain an overall measure of vocalisation during the experimental sessions.

Locomotion was included as a measure of non-object-directed behaviour. Following Roder, Timmermans and Vossen (1989), who measured locomotion in cynomolgus monkeys, this measure was broadly defined as 'any change in location', whether it be by walking, running, jumping or climbing. This measure provided a contrast to the measures of object-directed behaviour, addressing the issue of whether learning and novelty lead to increases in object exploration only, or a combination of object contacts and a general increase in activity.

Another category used in the present study was *grooming*, a behaviour which plays a major role in the marmoset's repertoire, mostly occurring between pairs of individuals. Stevenson and Rylands (1988, p. 185) described allogrooming in the following manner: "the groomer parts the fur of the groomee, who lies in a relaxed posture, and removes particles with the mouth." Since the marmosets in the present study were observed alone, only self-grooming was included in the list of behavioural categories.

Finally, the category of *chewing perch* was derived from Lacher, da Fonseca, Alves and Magalhaes-Castro (1981), who related such behaviour back to wild marmosets, whose dentition is designed for gnawing tree bark. Plant exudates (sap, gum, resin and latex) form a significant part of the wild marmoset's diet; to obtain these, marmosets typically anchor their upper incisors in a fixed position on the tree bark and use their lower, cup-shaped dentition to scoop out the bark (Stevenson & Rylands, 1988). Following this 'gouging' behaviour, marmosets frequently scent-mark the holes (Coimbra-Filho & Mittermeier, 1976). Kidman (1990) has shown that the introduction of gum tree branches into a marmoset zoo enclosure stimulates immediate gnawing and scent-marking. Thus, the behaviour is included in the present study as a possible reaction to novelty.

In summary, the dependent variables for experiment 5 were as follows:

(a) *responses* - bar-pressing (Groups BF and BN);

(b) *staring at objects* - in which a marmoset stares at an object with its gaze remaining fixed, including 'headcock stares';

(c) *touching objects with nose* - in which a marmoset's nose touches, pushes or moves an object (this category also included any biting of an object);

(d) *handling objects* - in which a marmoset touches or manipulates an object with one or both hands, including climbing on an object;

(e) *vocalisation* - any vocal sound emitted by a marmoset (all types);

(f) *locomotion* - in which a marmoset moves about its cage, including walking, running, jumping and climbing;

(g) *grooming* - in which a marmoset scratches or licks itself;

(h) *chewing perch* - in which a marmoset chews the wooden perch, including biting and teeth-grinding against the perch.

The category of *responses* applied to animals in Groups BF and BN. The other categories - the measures of exploratory and non-object-directed behaviour - applied to all animals. As for the previous experiments, the exploratory behaviour categories (*staring at objects*, *touching objects with nose* and *handling objects*) were added together, producing two extra variables, *rate of object exploration* and *percentage duration of object exploration.*

The Kendall's W coefficient of concordance procedure was performed on data obtained from three independent judges' scoring of two 15-minute portions of the video-taped sessions. A high degree of agreement among all judges was obtained for frequencies ($W = .948, p < .001$) and durations ($W = .897, p < .001$) of all of the variables measured.

RESULTS AND DISCUSSION

Experiment 5 provided a comparison to experiment 4, assessing effects of learning and novelty on the exploratory behaviour of the common marmoset. As in the previous experiments, the multivariate analysis of variance procedure was used to analyse the data; however, it should be noted at the outset that the sample of animals was small (a total of 8 marmosets), and consequently the data were intended to be analysed primarily by description rather than by means of statistical testing.

The principle experimental hypothesis of the present experiment was based upon the findings from experiment 4, taking into account the interaction effects of schedule of reinforcement and novelty. It was predicted that the trained marmosets (Groups BF and BN) would explore objects more than the control animals during conditioning, but that animals for which objects were novel (Groups BN and CN) would explore more than the familiar objects groups during extinction. Such a result would strengthen the idea that learning is an effective means for enhancing exploratory behaviour provided the schedule is one of continuous reinforcement, and that object novelty is effective when no food is available.

A difference between the present experiment and experiment 4 was the inclusion of the non-object-directed categories of behaviour. *Vocalisation*, *locomotion*, *grooming* and *chewing perch* were activities not specifically directed towards objects and hence not regarded as 'exploratory'. These categories were included to provide a contrast to the object-directed activities, thus providing data concerning the generalisability of the learning and novelty effects. For example, the experiment could determine whether an increase in object contacts also resulted in a simultaneous increase in general activity.

Figures 7.9(I), 7.9(II) and 7.9(III) show the session means of each behavioural measure. Analysis of variance showed that *rate of responses* and the rates of exploratory and non-object-directed behaviours remained at a constant level throughout conditioning (no overall increases or decreases were observed), although there was a decrease in *percentage duration of object exploration* ($F[3,12] = 7.63, p < .01$).

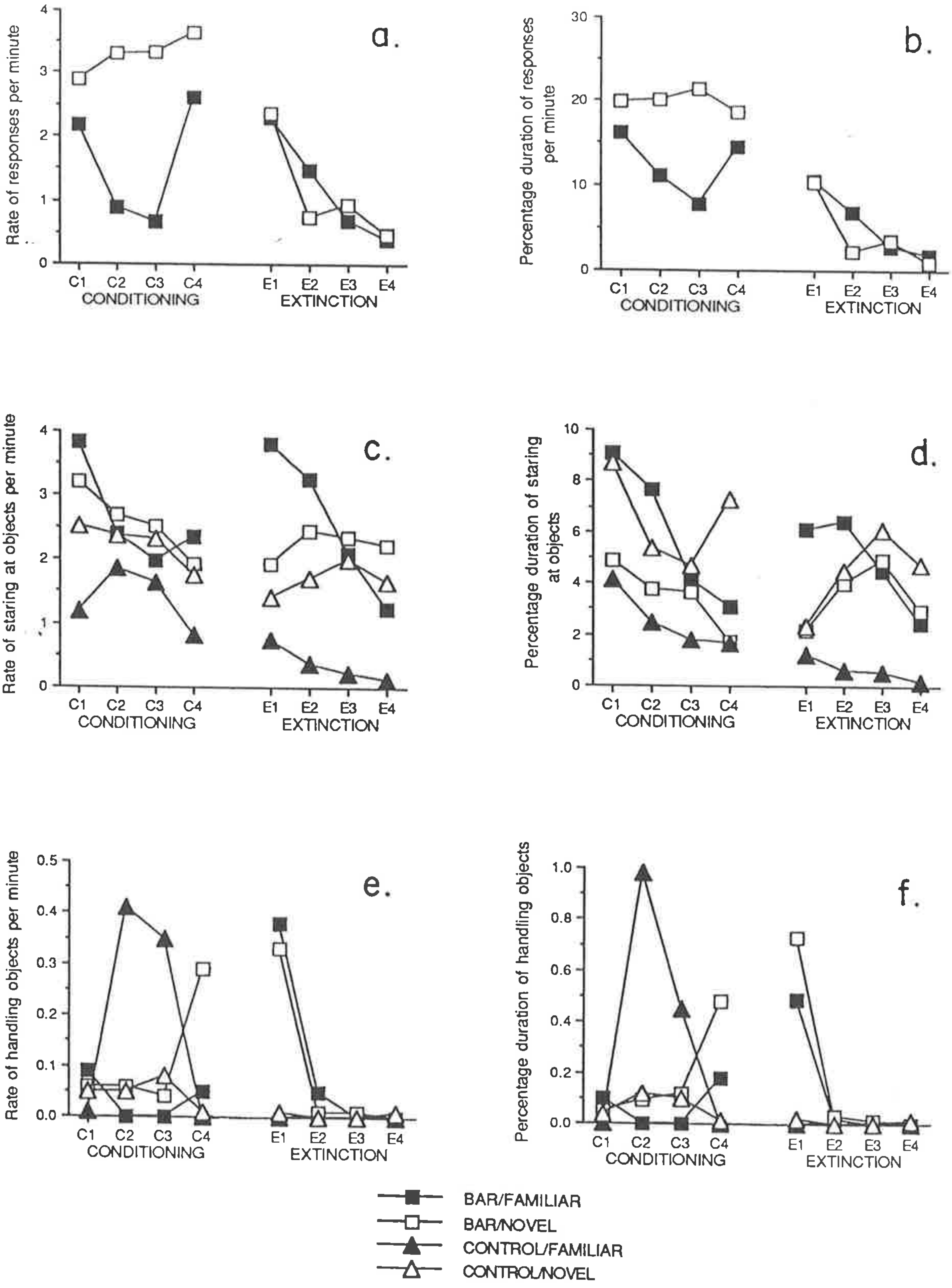


FIGURE 7.9(I): Session means of responses and object-directed behaviours in experiment 5.

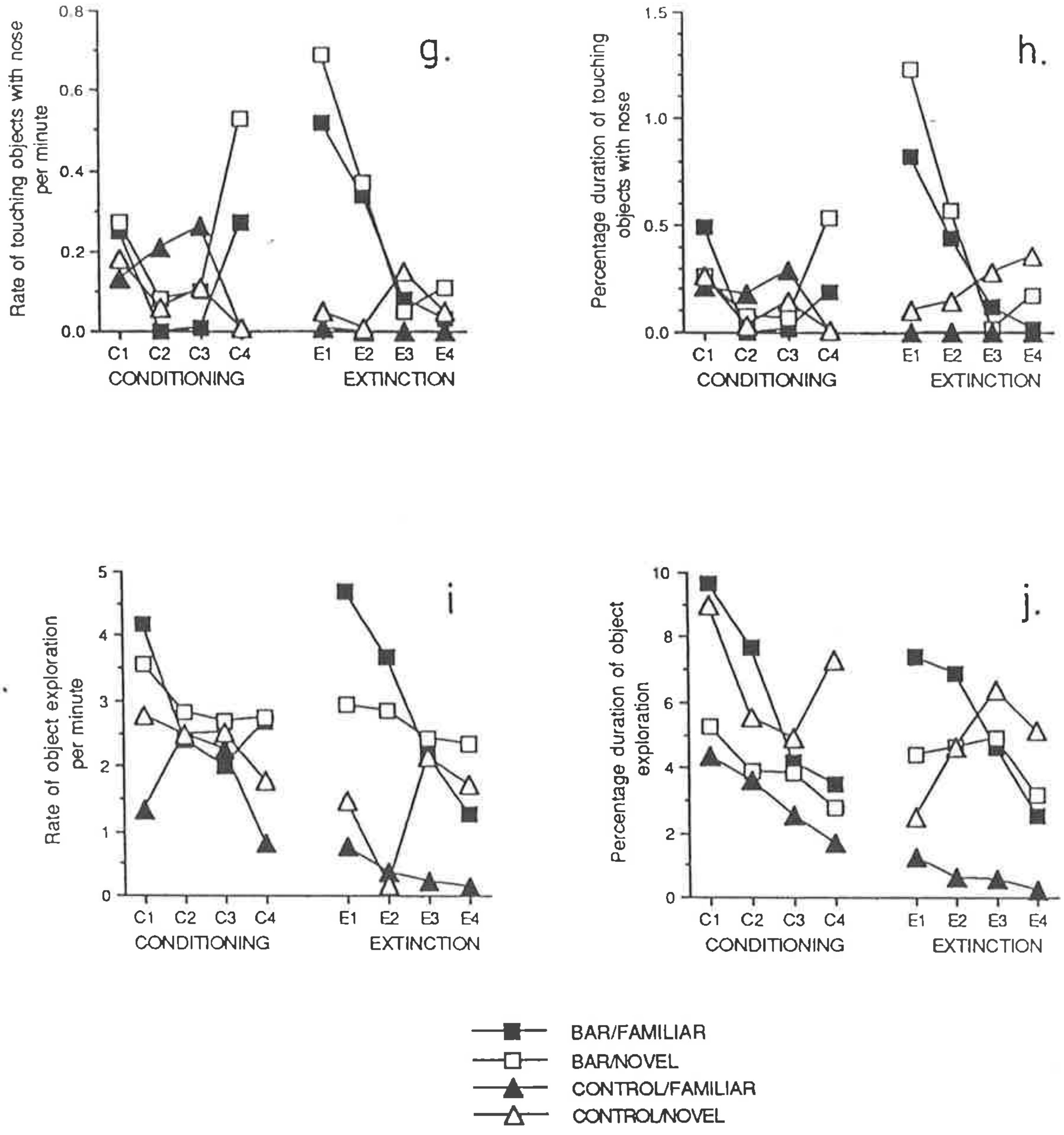


FIGURE 7.9(II): Session means of object-directed behaviours in experiment 5.

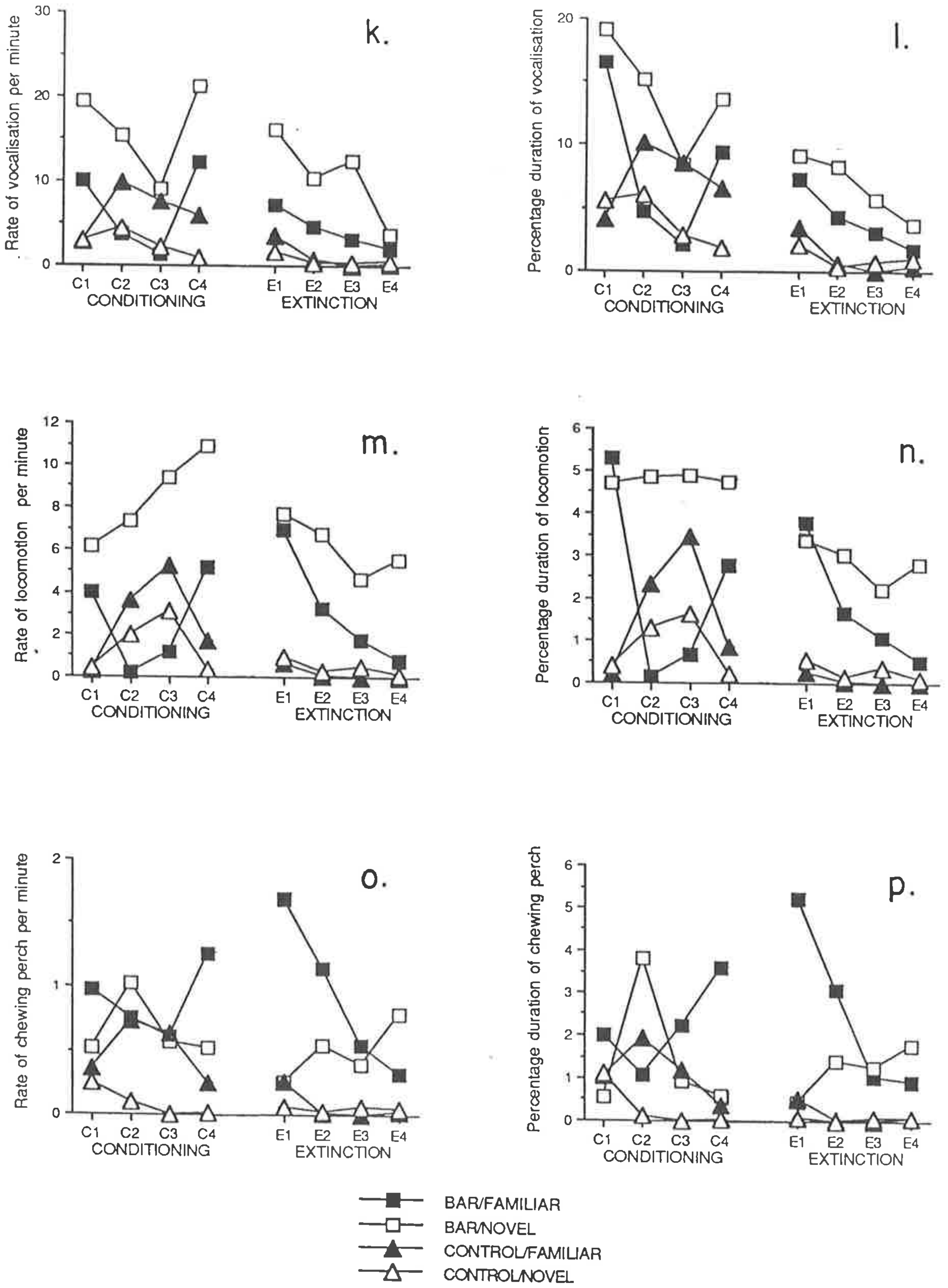


FIGURE 7.9(III): Session means of non-object-directed behaviours in experiment 5.

In contrast, *rate of responses* and all of the measures of object exploration declined significantly during extinction (Table 7.5), as did *vocalisation* and *locomotion* (Table 7.6). *Grooming* and *chewing perch* were the only behaviours to remain constant.

Table 7.5: Significance levels obtained for responses and measures of exploratory behaviour during extinction (*session* effects).

Variable	F	Significance level
Rate of responses	$F(3,6) = 6.09$	$p < .05$
Rate of staring at objects	$F(3,12) = 7.56$	$p < .01$
Duration of staring at objects	$F(3,12) = 8.22$	$p < .01$
Rate of touching objects with nose	$F(3,12) = 27.41$	$p < .001$
Duration of touching objects with nose	$F(3,12) = 4.68$	$p < .05$
Rate of handling objects	$F(3,12) = 11.59$	$p < .01$
Duration of handling objects	$F(3,12) = 53.83$	$p < .001$
Rate of object exploration	$F(3,12) = 12.00$	$p < .01$
Duration of object exploration	$F(3,12) = 5.72$	$p < .05$

Table 7.6: Significance levels obtained for measures of non-object-directed behaviour during extinction (*session* effects).

Variable	F	Significance level
Rate of vocalisation	$F(3,12) = 4.16$	$p < .05$
Duration of vocalisation	$F(3,12) = 9.15$	$p < .01$
Rate of locomotion	$F(3,12) = 8.28$	$p < .01$
Duration of locomotion	$F(3,12) = 6.77$	$p < .01$
Rate of grooming	$F(3,12) = 1.09$	N.S.
Duration of grooming	$F(3,12) = 1.12$	N.S.
Rate of chewing perch	$F(3,12) = 2.46$	N.S.
Duration of chewing perch	$F(3,12) = 2.54$	N.S.

These results are comparable with those obtained using rats as subjects (experiment 4): the marmosets maintained a steady level of interest in the objects during the first four sessions, but after this, overall declines in activity and object exploration occurred. The fact that *grooming* and *chewing perch* remained constant suggests that these activities were not affected by repeated exposure to the environment. Thus, the marmosets tended to groom themselves and chew the perch throughout the experimental procedure.

Analysis of variance testing for differences between groups showed that learning and novelty did not significantly enhance exploration during conditioning, although examination of Figures 7.9(I) and (II), graphs *c* to *j* suggests that some effect was present. In particular, when objects were familiar the experimental marmosets spent more time exploring them compared to controls (graph *j*). In addition, examination of Figure 7.9(III), graphs *k* to *n* shows that the experimental animals which were given access to the novel objects exhibited more vocalisation and locomotion than controls. *Chewing perch*, however, remained constant during conditioning.

During extinction, significant increases for the bar-pressing groups (BF and BN) were obtained for the measures *rate of staring at objects*, *rate of touching objects with nose*, *percentage duration of handling objects* and *rate of object exploration* (Table 7.7). This result indicates that extinction for bar-pressing enhanced object-directed exploratory behaviour.

Table 7.7: Significance levels obtained for measures of exploratory behaviour during extinction (*group* effects).

Variable	*F*	Significance level
Rate of staring at objects	$F(3,4) = 10.90$	$p < .05$
Duration of staring at objects	$F(3,4) = 5.23$	N.S.
Rate of touching objects with nose	$F(3,4) = 31.75$	$p < .01$
Duration of touching objects with nose	$F(3,4) = 1.29$	N.S.
Rate of handling objects	$F(3,4) = 6.01$	$p < .05$
Duration of handling objects	$F(3,4) = 30.58$	$p < .01$
Rate of object exploration	$F(3,4) = 13.20$	$p < .05$
Duration of object exploration	$F(3,4) = 4.41$	N.S.

In support of this finding, two further analyses were carried out, both on the data obtained during extinction. Firstly, planned comparisons between groups showed that for all measures of exploratory behaviour (except *percentage duration of touching objects with nose*), Group BF exhibited more object exploration than its control counterpart, Group CF (Table 7.8). This applied to the non-object-directed categories

Table 7.8: Significance levels obtained for measures of exploratory behaviour during extinction (planned comparisons between Groups BF and CF).

Variable	*t*	Significance level
Rate of staring at objects	$t = 5.32$	$p < .01$
Duration of staring at objects	$t = 3.60$	$p < .05$
Rate of touching objects with nose	$t = 6.65$	$p < .01$
Rate of handling objects	$t = 3.37$	$p < .05$
Duration of handling objects	$t = 5.42$	$p < .01$
Rate of object exploration	$t = 5.74$	$p < .01$
Duration of object exploration	$t = -3.32$	$p < .05$

as well, although without the support of statistical significance. Secondly, an analysis was carried out in which the two experimental groups were compared with the two control groups, and the measures *rate of staring at objects*, *rate of touching objects with nose*, *rate of handling objects*, *percentage duration of handling objects*, *rate of object exploration*, *percentage duration of vocalisation*, *rate of chewing perch* and *percentage duration of chewing perch* showed enhancements for the bar-pressing groups and diminution for the control groups (Table 7.9). These results further support the idea that extinction instigates exploratory behaviours, as well as several of the non-object-directed behaviours.

Table 7.9: Significance levels obtained for measures of exploratory and non-object-directed behaviour during extinction (*group* effects comparing experimental groups with control groups).

Variable	*F*	Significance level
Rate of staring at objects	$F(1,4) = 21.84$	$p < .01$
Rate of touching objects with nose	$F(1,4) = 89.18$	$p < .01$
Rate of handling objects	$F(1,4) = 17.68$	$p < .05$
Duration of handling objects	$F(1,4) = 85.07$	$p < .01$
Rate of object exploration	$F(1,4) = 29.35$	$p < .01$
Duration of vocalisation	$F(1,4) = 7.65$	$p < .05$
Rate of chewing perch	$F(1,4) = 154.61$	$p < .001$
Duration of chewing perch	$F(1,4) = 85.51$	$p < .01$

In addition, significant interaction effects (*session* x *group*) were observed for the object-directed activities during extinction (Table 7.10): at the beginning of extinction, the experimental groups (BF and BN) explored more than the control groups (CF and CN), but by the end of extinction, the groups for which objects were novel (BN and CN) displayed more exploration than the familiar objects groups (BF and CF).

Table 7.10: Significance levels obtained for measures of exploratory behaviour during extinction (*session* x *group* effects).

Variable	*F*	Significance level
Rate of staring at objects	$F(9,12) = 7.71$	$p < .01$
Duration of staring at objects	$F(9,12) = 7.71$	$p < .01$
Rate of touching objects with nose	$F(9,12) = 11.74$	$p < .001$
Duration of touching objects with nose	$F(9,12) = 2.81$	$p < .05$
Rate of handling objects	$F(9,12) = 3.71$	$p < .05$
Duration of handling objects	$F(9,12) = 18.00$	$p < .001$
Rate of object exploration	$F(9,12) = 7.23$	$p < .01$
Duration of object exploration	$F(9,12) = 7.16$	$p < .01$

This result seems to correspond to the interaction effects obtained in experiment 4, although in this case the effect did not occur until after extinction had begun. In the previous experiment, learning affected exploratory behaviour during conditioning and novelty produced enhanced exploration during extinction; in the present experiment, the enhancements associated with the learning process continued until the penultimate session of extinction, and only then did the effects of novelty become dominant. These results indicate a parallel with the previous study, however they suggest that extinction has a more pronounced (i.e., longer lasting) effect for marmosets than it does for rats. Notably, there were no interaction effects for the non-object-directed measures of behaviour.

Another instance of a difference between the exploratory and non-object-directed activities was that the former rose significantly at the onset of extinction (*rate of object exploration* $F[3,4] = 10.91, p < .05$; *percentage duration of object exploration* $F[3,4] = 9.39, p < .05$), whilst *vocalisation*, *locomotion* and *chewing perch* did not produce this effect. Apart from giving support to the findings of experiment 4 (that extinction induces an immediate increase in object contacts), this result suggests that *locomotion* need not necessarily be exploratory; that is, an increase in exploration is not always accompanied by an increase in movement around the living space. This supports Halliday (1968), Fowler (1965), Sheldon (1968a), Corman and Shafer (1968) and Leyland, Robbins and Iverson (1976), who argued that novelty may induce object investigation, but no corresponding increase in ambulation.

In summary, the results from experiment 5 provided additional support for the idea that learning instigates exploratory behaviour: like the rats in experiment 4, the trained marmosets directed much of their attention towards the objects, and in particular, exploration rates were high at the beginning of conditioning and the beginning of extinction. As before, the control animals exhibited the least exploratory behaviour.

However, experiment 5 produced one main discrepancy with the results of experiment 4. In contrast to the previous study, object novelty did not immediately become a differentiating factor between the groups during extinction: marmosets trained to bar-press tended to continue exploring familiar objects more than control animals. The cross-over effect observed in the rat study occurred for the marmosets only in the penultimate extinction session, when the novel objects were preferred over the familiar objects. This suggests that extinction has a more pronounced effect for marmosets than it does for rats.

One of the aims of experiment 5 was to determine whether learning and object novelty lead to increases in object exploration only, or to a combination of object contacts and non-object-directed activities, such as vocalisation, grooming, chewing the perch and locomotory activity. It was found that marmosets which were exposed to the novel objects vocalised more than controls, indicating a relationship between vocalisation and the changing aspects of the marmosets' environment. In contrast, all marmosets groomed themselves and chewed the perch throughout the experiment, suggesting that these forms of behaviour are not influenced by repeated exposure to an environment, learning or object novelty. The measure *locomotion* seemed to be related to object exploration, insofar as the trained animals moved about more than the control animals; however, the experimental marmosets did not walk, run, jump or climb more than controls at the onset of extinction. This result highlights one of the problems in using locomotion as a measure of exploratory behaviour: under certain conditions object exploration and ambulation seem to be measuring the same thing, but at the onset of extinction this did not seem to be the case.

7.5. CONCLUSION

Experiments 4 and 5 suggested that both the rat and the marmoset react to the combination of learning and novel objects in similar ways: both species' exploratory behaviour was enhanced when given the opportunity to learn a bar-pressing task and when provided with either familiar or novel objects. In particular, extinction gave rise to an immediate increase in object contacts, and novelty tended to be less salient to the animals during conditioning than it was during extinction. Both experiments point to the conclusion that the enhancement effects of learning procedures and novel objects differ according to the schedule of reinforcement in use, responding for food being more powerful in inducing exploration during conditioning and at the onset of extinction, and the inclusion of novel objects giving rise to enhanced exploration towards the end of the experimental sessions.

These findings have practical implications for the design of cages or enclosures for captive animals. In order to achieve a degree of behavioural enrichment, the opportunity to learn need not be simultaneous with the introduction of novel objects; rather, one or other of these procedures can achieve a similar result, provided the schedule of reinforcement is appropriate. For example, the implementation of an operant reward system could be used during feeding time (providing animals with continuous reinforcement and hence inducing increased exploration between reinforcements), and at other times animals could be allowed access to a series of objects, provided the stimuli are changed over regularly enough to maintain novelty.

One of the problems with experiment 5 was that the marmosets were fearful of the experimental apparatus, probably in part due to the stress of being moved and released into a completely new environment. As a consequence, the marmosets' training times were long (e.g., up to 5 hours of training, compared to 1 hour for the rats), and the exploratory behaviour was probably also affected. The experiment reported next in Chapter 8 represented an attempt to observe marmosets without the intervening and unsettling variables associated with moving from one cage to another and from one room to another. The study was conducted in the marmosets' holding room, with the least conceivable experimenter interference, thus observing the animals in their normal captive condition in the Animal House. It was hoped that testing the marmosets in their home cages would not only generate results which could be directly applied to the particular colony of animals used in the study, but also to achieve the greatest possible beneficial effects of learning and object novelty.

CHAPTER 8

HOME CAGE EXPLORATION

8.1. INTRODUCTION

As emphasised in Chapter 3, details of handling, animal transport and placement in cage are not only seldom reported in animal experiments, but these can have significant consequences on open-field behaviour. The ethoexperimental interpretation of open-field behaviour put forward by Gallup and Suarez (1980) and Suarez and Gallup (1981a, 1981b, 1983) stated that removal from the home cage and experimental testing procedures usually involve sudden social separation from conspecifics and a simulated predatory encounter. The conditions in which marmosets were observed in experiment 5 were consistent with such an interpretation: animals were taken away from a group of conspecifics in their holding room, they were constrained and then transported by the experimenter to an isolated room. According to Gallup and Suarez, such experimental testing puts animals into a stressful situation, resulting in effects on the subsequent open-field behaviour: the animals react to the stress of moving as well as the controlled experimental variables.

In particular, handling and transport have been shown to have adverse effects on marmosets. For example, Stellar (1960) described the marmoset's reaction to being touched and picked up by an experimenter as extremely stressful, resulting in excessive struggling. (Adverse reactions to transport have also been observed in other species; for example, Bramblett, 1989, reported that vervet monkeys show fear at the mere sight of the net used for capturing them). As a result, many marmoset researchers have favoured less distressing methods of transport; for example, a box (Nielson, 1971; Tighe, 1965; Epple, 1970), a tube (Dixon & DeFries, 1968b), or a transport cup (Hofer, 1970). It has also been suggested that animals be habituated to the transport container and the carrying procedure prior to testing (e.g., Nielson, 1970, in using white rats).

These methods may reduce the stress of transport, but they do not address the problem of separation from conspecifics: in experiment 5 the marmosets were moved inside their own nest boxes, but this still involved separating them from the other members of their holding room. Experiment 6, therefore, was conducted entirely in the marmosets' holding room; animals were neither handled nor moved into a separate testing chamber, and experimental manipulations were kept to a minimum. Such a use of unobtrusive measures has been recommended for researchers favouring an ethoexperimental approach to the study of behaviour (e.g., Zayan, 1989), thus allowing for control without the effects of invasive experimental manipulations. As summed up by Snowdon and Soini (1988, p. 288), in reporting that tamarins learn better in their home cages:

> *It is likely that testing animals in natural social groups in their home environment is much less stressful and more natural than testing animals in isolation in strange testing environments.*

Another difference between experiment 6 and the previous marmoset study was that some animals were socially reinforced rather than rewarded with food. Since marmosets rely heavily on their sense of vision for information, it would seem logical that the opportunity to see neighbouring marmosets should serve as a reinforcer. A second reason for using a social reward was so that animals did not have to be deprived of food prior to the experiment, thus keeping conditions as close to the usual laboratory routine as possible. Experiment 6, then, was designed to examine differences between food and social reward on the exploratory behaviour of marmosets, with as little experimenter interference as possible.

8.2. EXPERIMENT 6: EFFECTS OF FOOD REWARD AND SOCIAL REWARD ON MARMOSETS' EXPLORATION IN THEIR HOME CAGES

Experiment 6 differed from all of the other experiments described in this thesis in that it took place in the animals' holding room. Marmosets were observed in their home cages, with the aim of examining exploration under various conditions of reinforcement, as well as unobtrusively observing their reactions to a collection of novel objects.

Some of the benefits of non-invasive home cage testing on marmosets and tamarins have been outlined by Snowdon and Savage (1989); for example, learning is faster and subsequent performance at acquired tasks is better, and the information gathered from home cage studies can be used to complement data from the wild (where animals are not handled or moved). According to Moser, Moser, Wultz and Sagvolden (1988), an animal's behaviour in its home cage need not relate to or predict its behaviour in the open-field, the former representing a free exploration test, and the latter representing a forced exploration test. In a forced test, an animal's behaviour may be interpreted as a reflection of fear an exploration (e.g., Welker, 1957; Hayes, 1960; see Chapter 3). The free test, however, may lessen or eliminate fear, and has the advantage of approximating conditions in the wild more accurately, thus providing a more ecologically-relevant measure of behaviour (Moser, Moser, Wultz, & Sagvolden, 1988). Moser *et al.* argued that rats exhibit a greater frequency of rearing and exploration when given access to an open field connected to their home cages, compared to rats forced to explore an unconnected novel field. The marmosets in experiment 6, therefore, were expected to engage in more activity and object-directed exploration than the marmosets in experiment 5.

A second purpose of experiment 6 was to distinguish between two forms of reinforcement: food and social. In experiments using rats as subjects, it has been shown that animals behave differently in an open field according to whether or not they have been deprived of food or water (e.g., Bolles, 1965; Draper, 1967), with the former being more active than the latter. Other researchers (e.g., Hull, 1977; Timberlake, 1983b) have observed that response topographies differ in rats depending on whether they are responding for food or water, with the topography resembling either consummatory or predatory behaviour. Given these findings, it is reasonable to expect that an animal such as the marmoset may behave differently under different learning conditions. In the present experiment, social reinforcement was chosen as a contrast to food reinforcement for the reasons outlined below.

Firstly, the inclusion of a socially rewarded task meant that marmosets could be observed without being deprived of food, more in keeping with an ethoexperimental approach to the study of the behaviour of laboratory animals. In experiment 5 (and in all of the previous experiments) exploration was observed only when animals were hungry. Experiment 6, however, provided measures of exploratory behaviour in the context of the marmosets' ordinary eating habits, without changing the usual laboratory routine.

Secondly, the choice of a social reward followed from other studies in which vision has successfully been used as a reinforcing stimulus. Barnes and Baron (1961), for example, reported that mice found a complex visual stimulus pattern more reinforcing when it incorporated illumination changes compared to when the stimulus was unchanging. Stahl, O'Brien and Hanford (1973) found that pigeons which had been placed in an isolation chamber could be trained to peck a key in order to open a shutter for 10 seconds, allowing visual access to the room in which the pigeon colony was located.

For primates, animals which are "strongly social creatures and much dependent on vision" (Mason, 1968a, p. 200), sensory stimulation has often been used as reinforcement. Butler (1953), for example, demonstrated that rhesus monkeys could learn an object discrimination task with visual exploration as the reward, explaining his result by suggesting that primates have a strong motive towards visual exploration in their environment. Later, Butler (1957, 1958, 1965) was able to train rhesus monkeys to press a lever in order to open a window, thus obtaining a view of the environment outside the experimental box. Butler and Woolpy (1963), in comparing monkeys' preferences for various types of visual display, reported that their subjects spent more time looking at moving or coloured pictures (rather than still or monochromatic ones), that they preferred pictures which were in focus, fairly bright, and right side up; that is, the more lifelike the pictures, the more the monkeys preferred them. Other studies focusing on visual learning in primates include those of Cooper (1978), Schrier and Povar (1978), Snyder, Birchette and Achenbach (1978) and Jarvis and Ettlinger (1978). Given that marmosets are highly visual in their orientation to the environment (Stellar, 1960), a door-opening task similar to Butler's was employed in experiment 6: by jumping on to a wire grid, a sliding door opened allowing marmosets to view the neighbouring cage.

Unlike the views of the environment or visual displays used by Butler, the nature of the visual reward associated with the door-opening task in experiment 6 was social, in that marmosets were able to see their immediate neighbour through the door. This followed partly from studies of learning, locomotion and exploration facilitation due to the presence of another animal (e.g., Simmel & McGee, 1966; Hughes, 1969), but was chosen primarily because of the importance of social contact in marmosets. As emphasised by Stellar (1960), Hearn, Lunn, Burden and Pilcher (1975), Ingram (1975) and Poole and Evans (1982), marmosets are highly social animals, and need to be housed in groups in order to be maintained successfully.

In summary, experiment 6 sought to determine differences in novel object exploration by marmosets which learnt a food-rewarded task (Group FOOD) and animals which learnt a socially-rewarded task (Group DOOR). In addition two control groups (Groups DEPRIVATION and NO DEPRIVATION) were included in order to examine possible effects of hunger on home cage exploration, and to provide controls for the experimental groups. It was expected that marmosets in Groups FOOD and DOOR would explore novel objects more than control groups (there were no familiar objects), consistent with the model of learning-induced activity tested throughout this thesis. It was suggested in experiments 4 and 5 that object novelty is more salient to rats and marmosets during extinction, when no food is available. However, the animals in these earlier experiments were all deprived of food. The present experiment allowed for the possibility that increases in exploration may increase during the extinction of a socially-rewarded task, even when food is available.

A modified list of non-object-directed activities was also used in experiment 6, allowing for the measurement of some of the behaviours which only occurred in the home cages, due to the inclusion of a food bowl, a drinking bottle and a nest box. The particular non-object-behaviours measured were *eating &/or drinking*, *locomotion*, *grooming*, *chewing perch* and *entries into nest box*. As before, these were included in order to determine whether effects of learning and object novelty were restricted to interactions with objects, or whether effects extended to other activities.

METHOD

Subjects

The subjects were 8 female common marmosets (*Callithrix jacchus jacchus*). Their ages at the commencement of the experiment varied from 13 months to 35 months. Details concerning the housing conditions, temperature and lighting remained the same as for experiment 5, but no preliminary handling sessions were carried out.

The marmosets were randomly allocated to one of four groups, each group consisting of a pair of animals. There were two experimental groups: FOOD, DOOR; and two control groups: DEPRIVATION and NO DEPRIVATION.

The feeding regime for the marmosets in Groups FOOD and DEPRIVATION remained the same as in experiment 5: during the study animals received their usual amounts of food at the end of each day's experimental testing sessions (5.00pm). Groups DOOR and NO DEPRIVATION, however, were fed at the beginning of the day (10.30am), which was the normal feeding time in the Animal House.

Apparatus

Experimental apparatus

Each marmoset was viewed in its own home cage (66cm x 35cm x 45cm), housed with two wooden perches, a nest box and a drinking bottle. During the running of the experimental sessions additions were included in some of the cages, in accordance with the particular experimental treatment.

The marmosets in Group FOOD were supplied with a yoghurt feeder and a feeding dish (Figure 8.1). The feeder consisted of a syringe (14mm in diameter, 67mm long), the end of which protruded through the roof of the cage (Figure 8.2). Yoghurt was dispensed in drops from the syringe by means of a 24V DC Power Supply. The syringe was activated by closing a micro-switch, achieved when the marmoset jumped on to a wire grid (13cm x 15cm) on the inside of the cage. Reinforcements could also be released manually by the experimenter.

For animals rewarded by the opening of a door (Group DOOR), a metal cover was designed to fit over the animal's home cage. A rectangular window (5cm x 8cm) was located in the upper central region of one of the walls of the cage. This was covered by a sliding door (Figure 8.3), which could be opened by triggering the micro-switch on the grid inside the cage. Each time a marmoset jumped on to the grid, the door opened for 2 seconds, during which time the marmoset was able to view the animal in the neighbouring cage.

The marmosets in Group NO DEPRIVATION were observed in their home cages, under usual living conditions; the ceramic food bowls were present and contained the usual supply of food throughout the experimental sessions. Animals in Group DEPRIVATION, however, had their food bowls removed until the end of each day.

A new set of 32 objects was constructed for experiment 6, used in groups of 3 as in the previous experiment (Figures 8.4 and 8.5; see also Appendix 1). Within each group, one object was made of wood and the other two were made of stainless steel. Each object was suspended from the marmoset's cage by a short chain, allowing for more manipulability than in the previous experiments. In each group the objects were changed over after each session, so that conditions of novelty were maintained for all animals.

FIGURE 8.1: Marmoset home cage, with yoghurt feeder attached to roof.

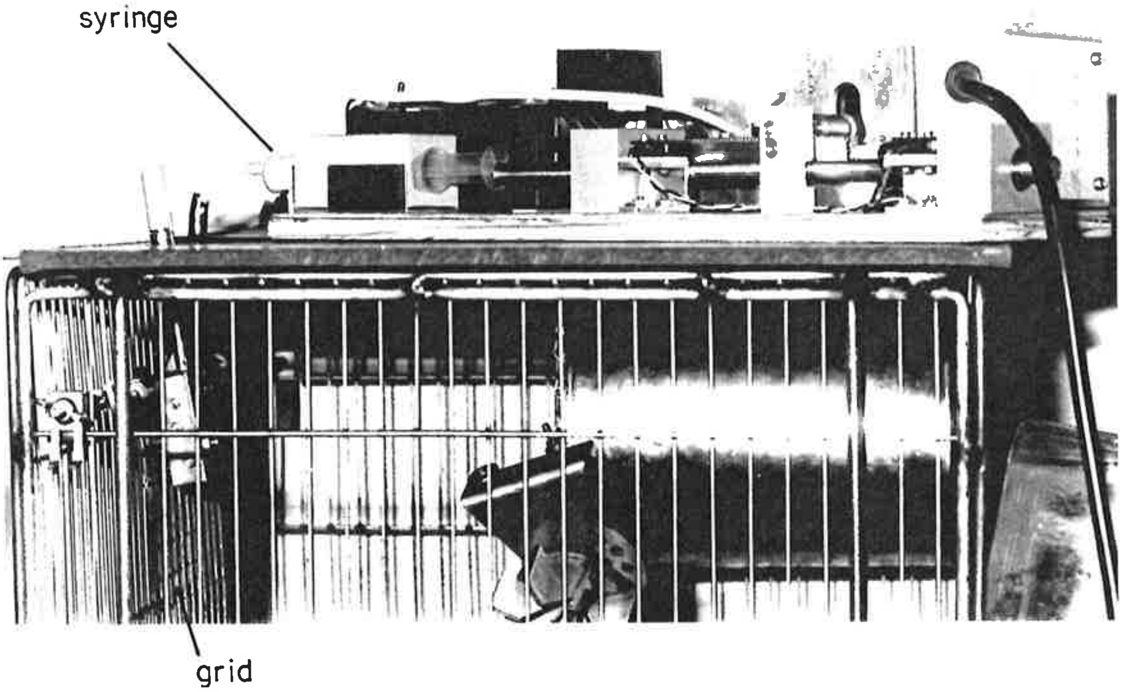


FIGURE 8.2: Close-up of yoghurt feeder, showing syringe and grid for conditioned responses.

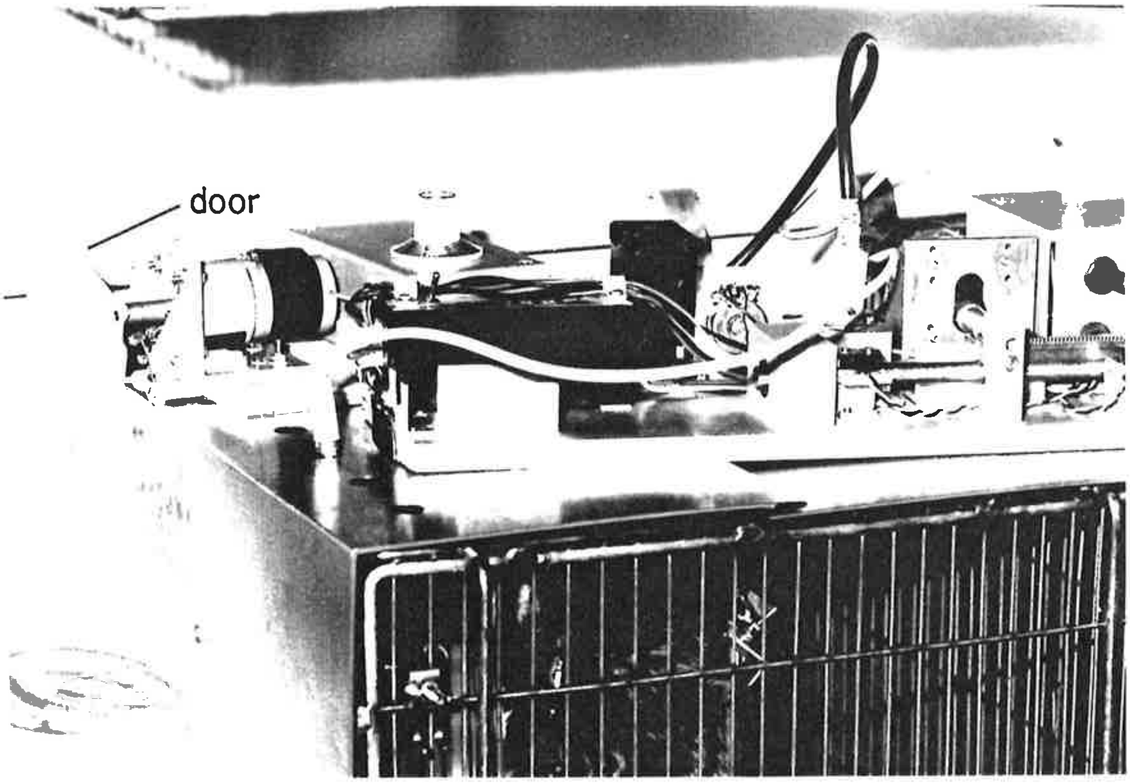


FIGURE 8.3: Close-up of door in the open position.

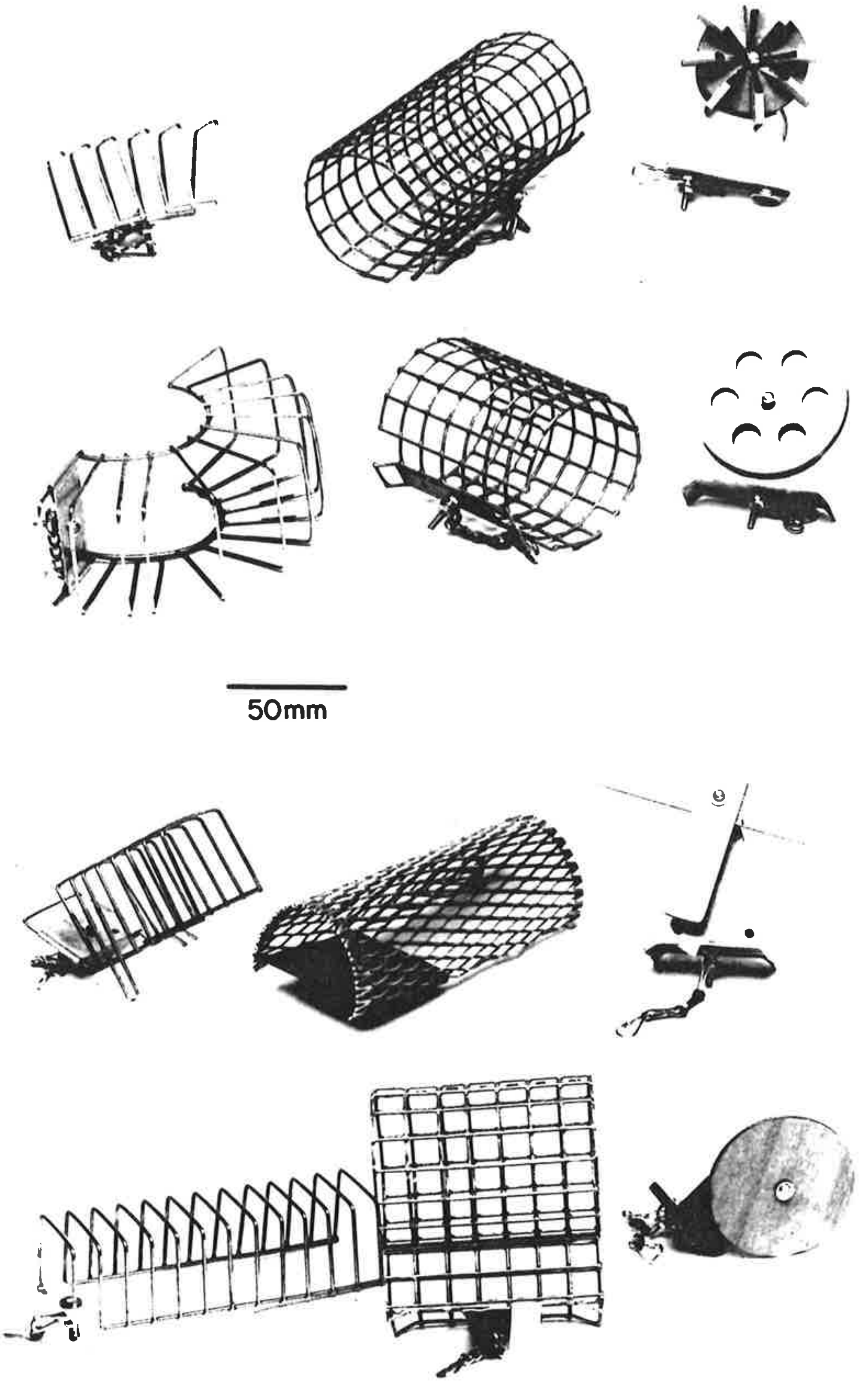


FIGURE 8.4: Experiment 6 novel objects used during conditioning.

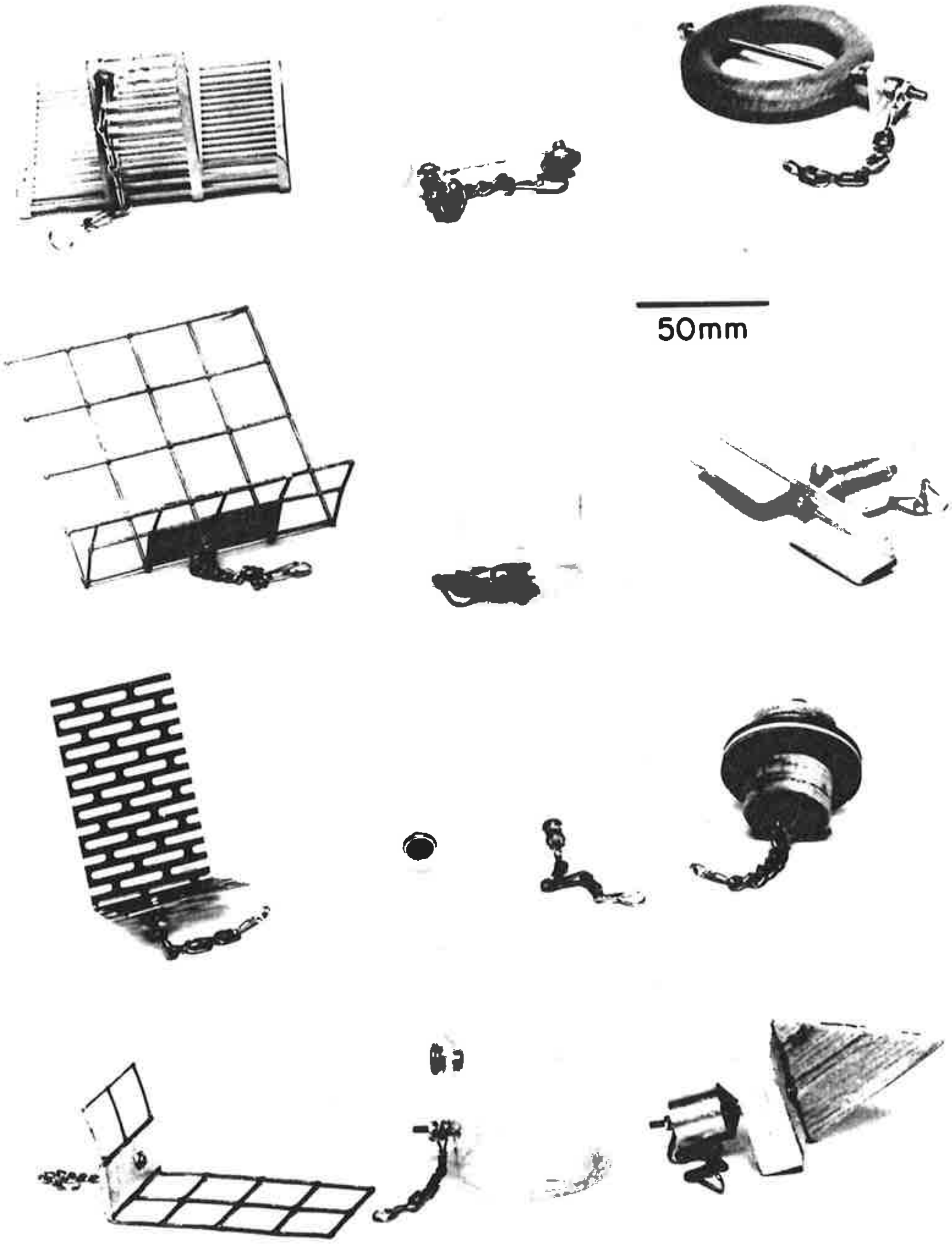


FIGURE 8.5: Experiment 6 novel objects used during extinction.

During the initial training sessions the experimenter sat in the animal holding room behind a wooden screen, minimising disturbances to the animals. However, once the experiment proper began, the experimenter left the room at the beginning of each session, after the equipment was in place and the video recording started.

Observation equipment

This consisted of the same equipment as that used in experiment 5, including the event recording table. In this experiment 11 buttons of the table were used (10 behaviours, 1 stop button).

Procedure

For each of the four groups of animals (FOOD, DOOR, DEPRIVATION and NO DEPRIVATION) the experimental design consisted of three parts: training to criterion, conditioning and extinction. Following this, data were recorded by means of an event recording program, and independent judges were employed to undertake reliability tests.

Training to criterion

The experimental animals (Groups FOOD and DOOR) participated in several training sessions (without any objects), in which jumping on the wire grid was acquired through shaping. For animals in Group FOOD the yoghurt dispenser was used, releasing a drop of yoghurt into the feeding dish after each response. For animals in group DOOR the cage cover and sliding door were put in place; each time the marmoset jumped on to the grid, the door swung open for 2 seconds. The experimenter sat behind a wooden screen, observing each marmoset via the video monitor, supplying yoghurt or door-opening reinforcements as necessary. On average, 3 training sessions were necessary before a criterion of 50 responses within the space of 15 minutes was reached, the total average training time being only 43 minutes (compared to 293 minutes in the previous experiment).

For Group NO DEPRIVATION no experimental treatment was carried out, and for Group DEPRIVATION the marmosets' feeding time was changed to evenings instead of mornings.

Conditioning

Animals were observed on four separate occasions, each lasting 30 minutes. The treatments for each group were as follows:

(a) FOOD. Animals were observed prior to their evening feeding time, and placed on a schedule of continuous reinforcement for jumping on the grid to receive rewards of yoghurt. A different set of objects was used for each of the four sessions (Group 1 objects, followed by Group 2 objects, etc.).

(b) DOOR. With the food bowls present, the cages were covered and animals were placed on a schedule of continuous reinforcement for jumping on the grid to receive rewards in the form of the opening of the sliding door for 2 seconds. The objects were changed over each session.

(c) DEPRIVATION. Animals were observed prior to their evening feeding time, in the presence of the novel objects (changed over each session).

(d) NO DEPRIVATION. With food available, animals were observed in the presence of the novel objects.

Extinction

Animals were observed on four separate occasions, each session lasting 30 minutes. The treatments for each group were the same as in the conditioning sessions, except that no yoghurt or door-opening reinforcements occurred for the experimental animals.

Event recording and independent judging

Following the completion of the conditioning and extinction sessions the experimenter viewed the video monitor and coded each animal's activities into particular categories, obtaining several behavioural measures. As before, the frequency and duration measures were transformed into rates per minute and percentage durations respectively, so that the experimental groups could be meaningfully compared to the control groups.

Most of the behavioural measures used in experiment 6 were the same as those of experiment 5 (*responses, staring at objects, touching objects with nose, handling objects, locomotion, grooming, chewing perch*). *Vocalisation* was omitted from the list due to the fact that the study took place in the animal holding room, where several marmosets often vocalised at once, making discrimination between individuals difficult. In addition, some extra measures were included in the study. *Biting objects* was included because each set of objects contained one wooden object, allowing the opportunity to chew and bite something other than the wooden perches. *Eating &/or drinking* was included because the food bowl was present in Groups DOOR and NO DEPRIVATION, and water was available in all groups. Finally, the presence of the nest box in the marmosets' cages provided an escape or retreat from the learning tasks, the novel objects, and from other animals. Therefore, the variable *entries into nest box* was intended to provide a measure of fear or unwillingness to explore.

In summary, the dependent variables for experiment 6 were as follows:

(a) *responses* - jumping on the grid to receive either yoghurt (Group FOOD) or opening the door (Group DOOR);

(b) *staring at objects* - in which a marmoset stares at an object with its gaze remaining fixed, including 'headcock stares';

(c) *touching objects with nose* - in which a marmoset's nose touches, pushes or moves an object;

(d) *handling objects* - in which a marmoset touches or manipulates an object with one or both hands, including climbing on an object;

(e) *biting objects* - in which a marmoset bites, chews, licks or mouths an object;

(f) *eating &/or drinking* - in which a marmoset picks up and ingests food from its food bowl (Groups DOOR and NO DEPRIVATION) or drinks from its water bottle (all groups);

(g) *locomotion* - in which a marmoset moves about its cage, including walking, running, jumping and climbing;

(h) *grooming* - in which a marmoset scratches or licks itself;

(i) *chewing perch* - in which a marmoset chews the wooden perch, including biting and teeth-grinding against the perch;

(j) *entries into nest box* - in which a marmoset enters its nest box and either sits or lies down inside it.

Except where indicated, these measures applied to all animals. As for the previous experiments, the exploratory behaviour categories (in this case, *staring at objects*, *touching objects with nose*, *handling objects* and *biting objects*) were added together, providing two extra variables, *rate of object exploration* and *percentage duration of object exploration.*

The Kendall's W coefficient of concordance procedure was performed on data obtained from three independent judges' scoring of two 15-minute portions of the video-taped sessions. A high degree of agreement among all judges was obtained for frequencies ($W = .939, p < .001$) and durations ($W = .924, p < .001$) of all of the variables measured.

RESULTS AND DISCUSSION

Experiment 6 was designed to observe marmosets' exploration with as little experimenter interference as possible, in keeping with an ethoexperimental approach to the study of behaviour, and providing data relevant to the maintenance of marmosets in captivity. As in the previous experiment, the multivariate analysis of variance procedure was used to analyse the data; however, since the sample of animals consisted of only 8 marmosets, analysis was primarily intended to be descriptive.

In the study, exploration was viewed in connection with food and social rewards, one of the aims being to suggest ways of enriching the behaviour of captive marmosets. For example, if effects of novelty and learning enhance exploratory behaviour in marmosets' home cages, this has implications for the preservation of a wide range of natural behaviours of marmosets held in zoos or laboratories.

The experimental hypotheses were based on those of experiments 4 and 5, testing whether the trends observed previously also occurred in the marmosets' home cages. Group FOOD was a replication of Group Bar/Novel Objects in experiments 4 and 5, except that behaviour was observed in the home cages; thus, any differences in exploratory behaviour between these groups could be interpreted as the result of a lack of experimenter manipulations for the marmosets filmed in the animal holding room. In accordance with Moser, Moser, Wultz and Sagvolden (1988), it was expected that by observing marmosets in their home cages, fear would be reduced and consequently more exploration would be produced by all animals (compared to amounts produced in experiment 5).

Group DOOR was included in order to determine whether enhancements of exploration would occur not only when animals learnt a task involving food deprivation, but when *any* learning takes place (such as a door-opening task resulting in visual access to neighbouring marmosets). Response topographies have been reported to differ according to the nature of the reinforcement (e.g., food or water: Bolles, 1965; Draper, 1967; Hull, 1977; Timberlake, 1983b); in the present study, enhancements in exploration were predicted for Groups FOOD and DOOR compared to the control groups, but no predictions were made concerning possible differences between the two experimental groups.

Finally, experiment 6 allowed for the testing of effects of food deprivation on marmoset exploration. Groups DEPRIVATION and NO DEPRIVATION served as controls for the experimental groups, providing baseline measures of object-directed and non-object-directed behaviours. In addition, the conditions under which these groups were observed corresponded to the conditions in which the marmosets were normally maintained (before and after feeding time respectively), the only difference being the presence of the sets of novel objects.

Figures 8.6(I), 8.6(II), 8.6(III) and 8.6(IV) show the session means of each behavioural measure. In analysing the results, an initial observation was made of the differences in response rates and activity levels of the marmosets in experiment 6 compared to the marmosets in the previous experiment. A comparison of Figures 7.9(I) and 8.6(I), graphs *a*, shows that marmosets responded at higher rates in their home cages compared to the marmosets tested in the experimental cage: the average response rate during conditioning for marmosets in Group FOOD (experiment 6) was 10 to 12 responses per minute, whilst the same measure for animals in Group Bar/Novel Objects (experiment 5) was only 3 or 4 responses per minute. The time required for training was similarly affected: the marmosets trained in their home cages took only a couple of minutes to learn the grid-jumping task (and 3 short sessions to reach the criterion of 50 responses within the space of 15 minutes), whereas the marmosets trained in the experimental cage typically required 4-5 hours (18 sessions) of training over a period of several weeks in order to reach a lower criterion. This effect is consistent with Snowdon and Savage (1989), who reported very rapid rates of learning (as well as improved long-term performance) by marmosets and tamarins tested in groups in their home cages.

The marmosets observed in their home cages also displayed more object exploration than the animals in the previous experiment (compare graph *l* in Figure 8.6(II) with graph *j* in Figure 7.9(II)). These findings may be attributed to the lack of experimenter interference in experiment 6, and are consistent with Moser, Moser, Wultz and Sagvolden (1988), who suggested that home cage exploration is the least fear-provoking and hence most preferred form of exploration. The trend is also consistent with Hughes (1969), who reported that locomotion and exploration are facilitated by the presence of another animal (i.e., social facilitation), since the animals which were observed in their home cages were surrounded by other marmosets, whereas the animals in experiment 5 were observed alone in an isolated room.

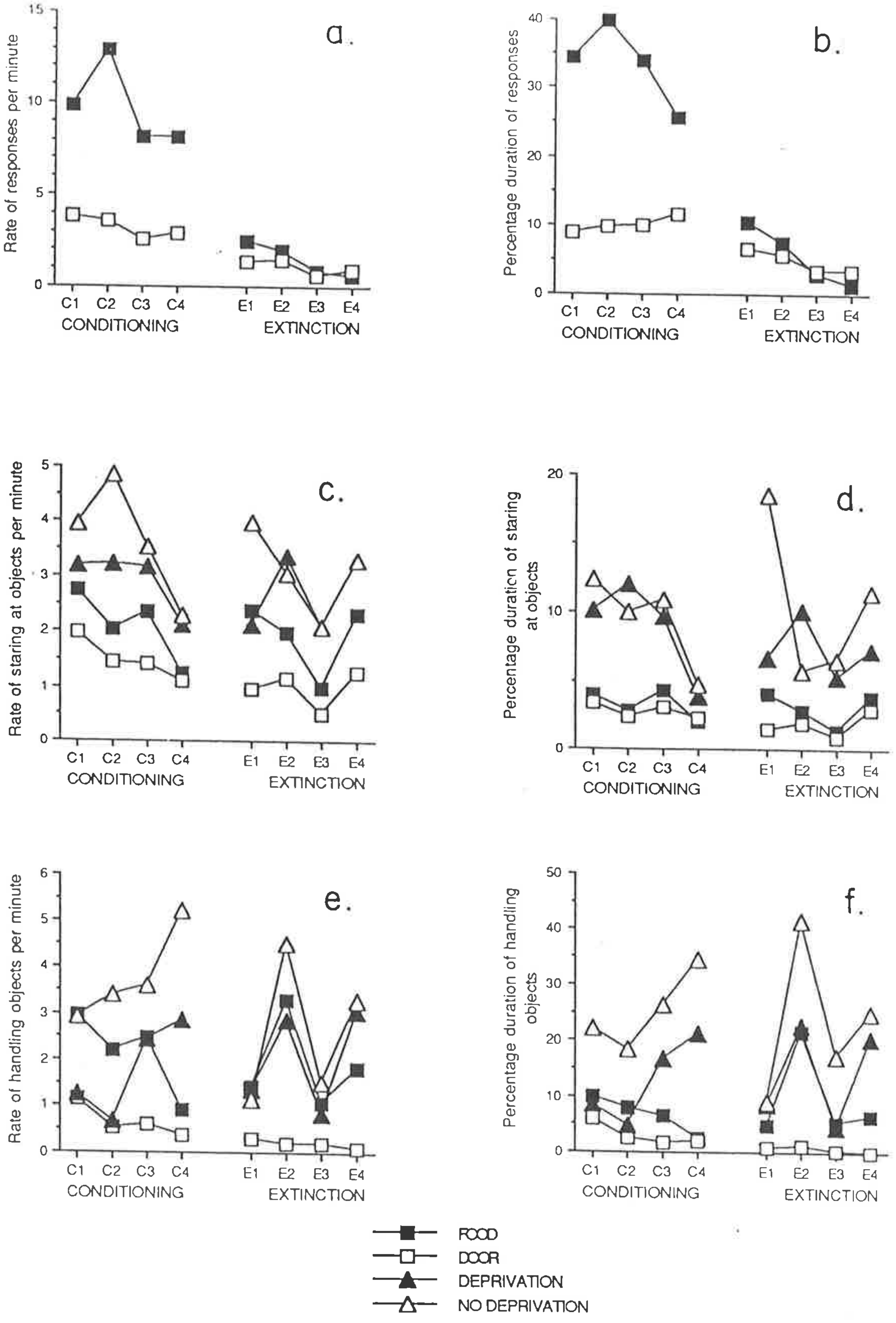


FIGURE 8.6(I): Session means of responses and object-directed behaviours in experiment 6.

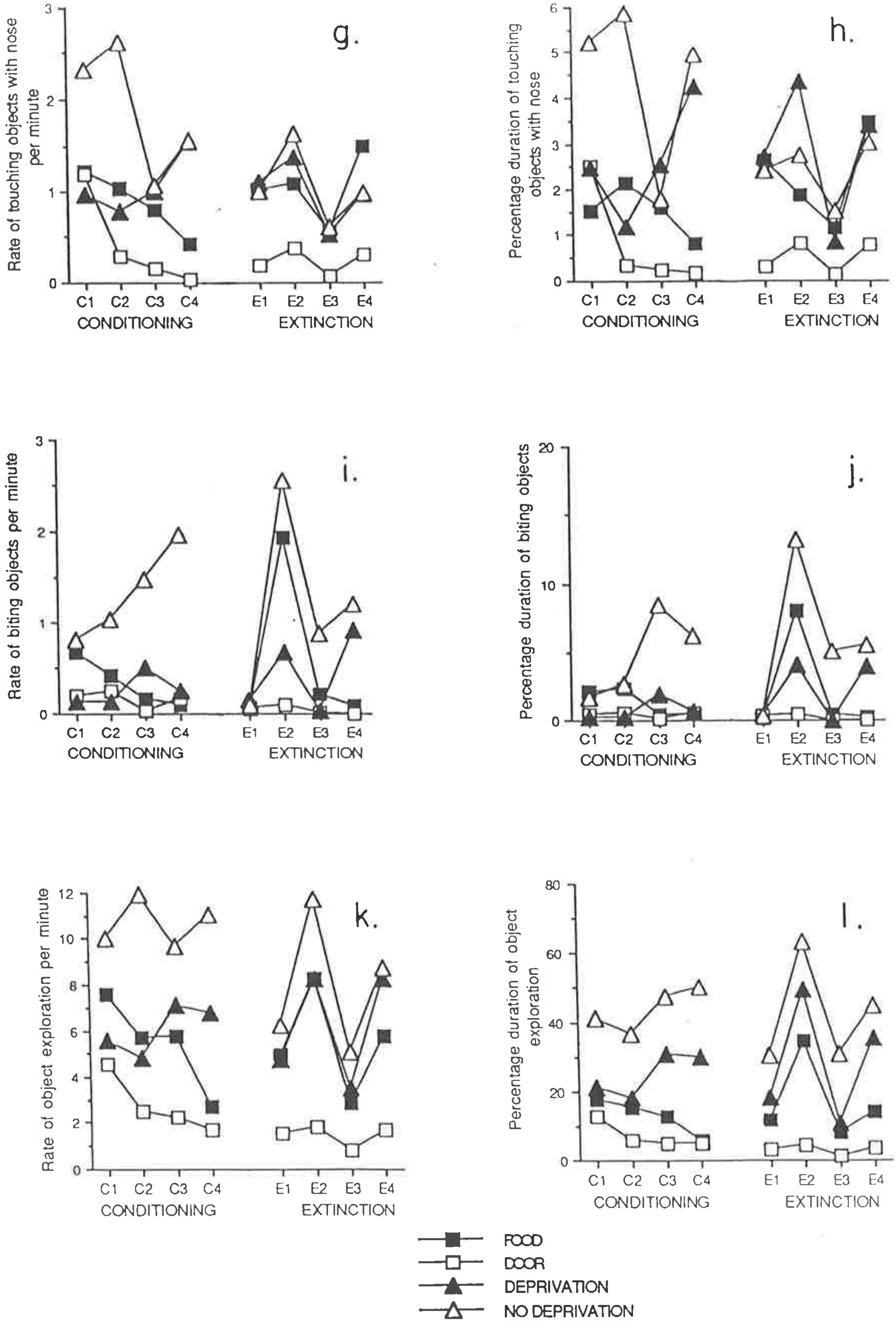


FIGURE 8.6(II): Session means of object-directed behaviours in experiment 6.

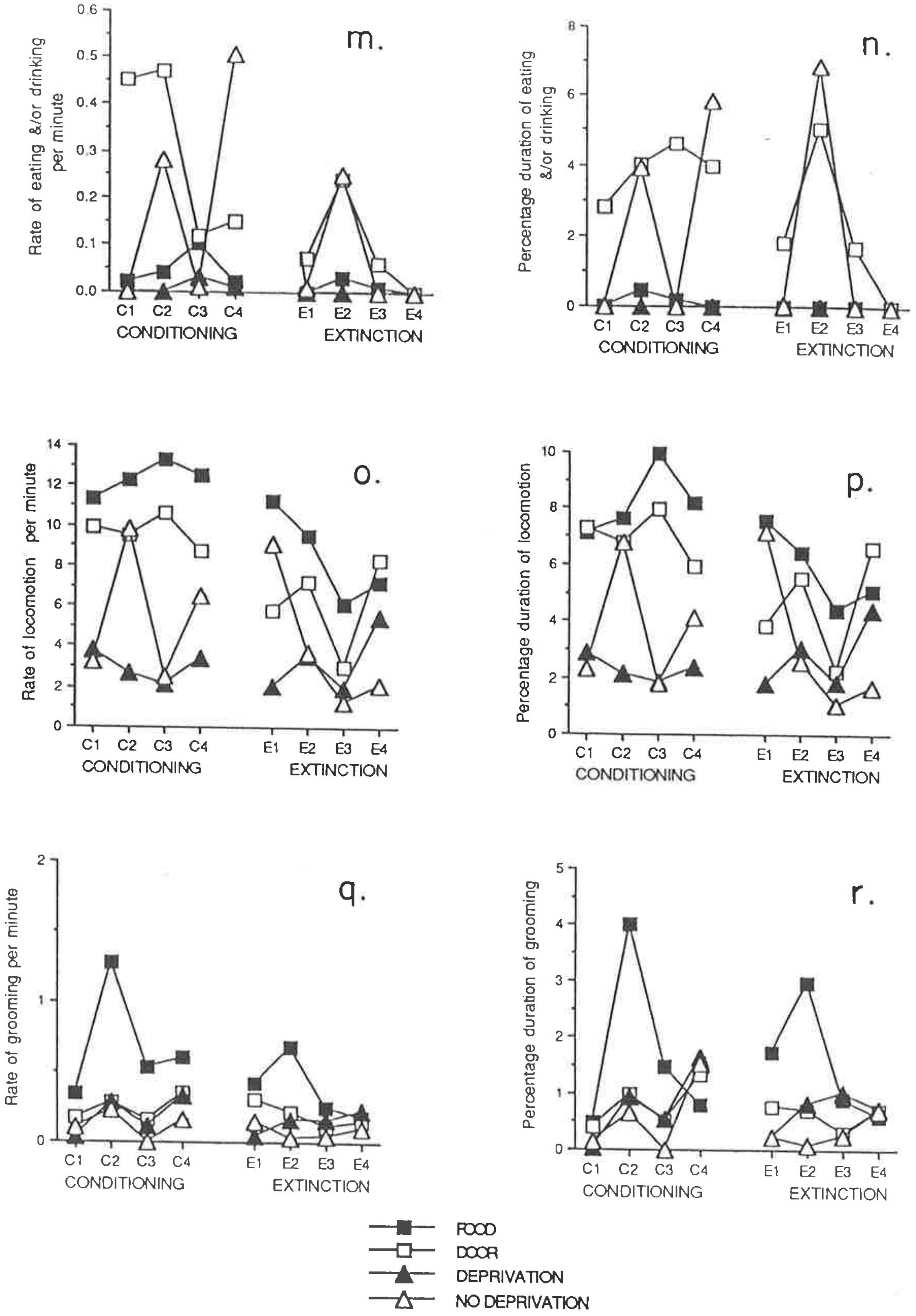


FIGURE 8.6(III): Session means of non-object-directed behaviours in experiment 6.

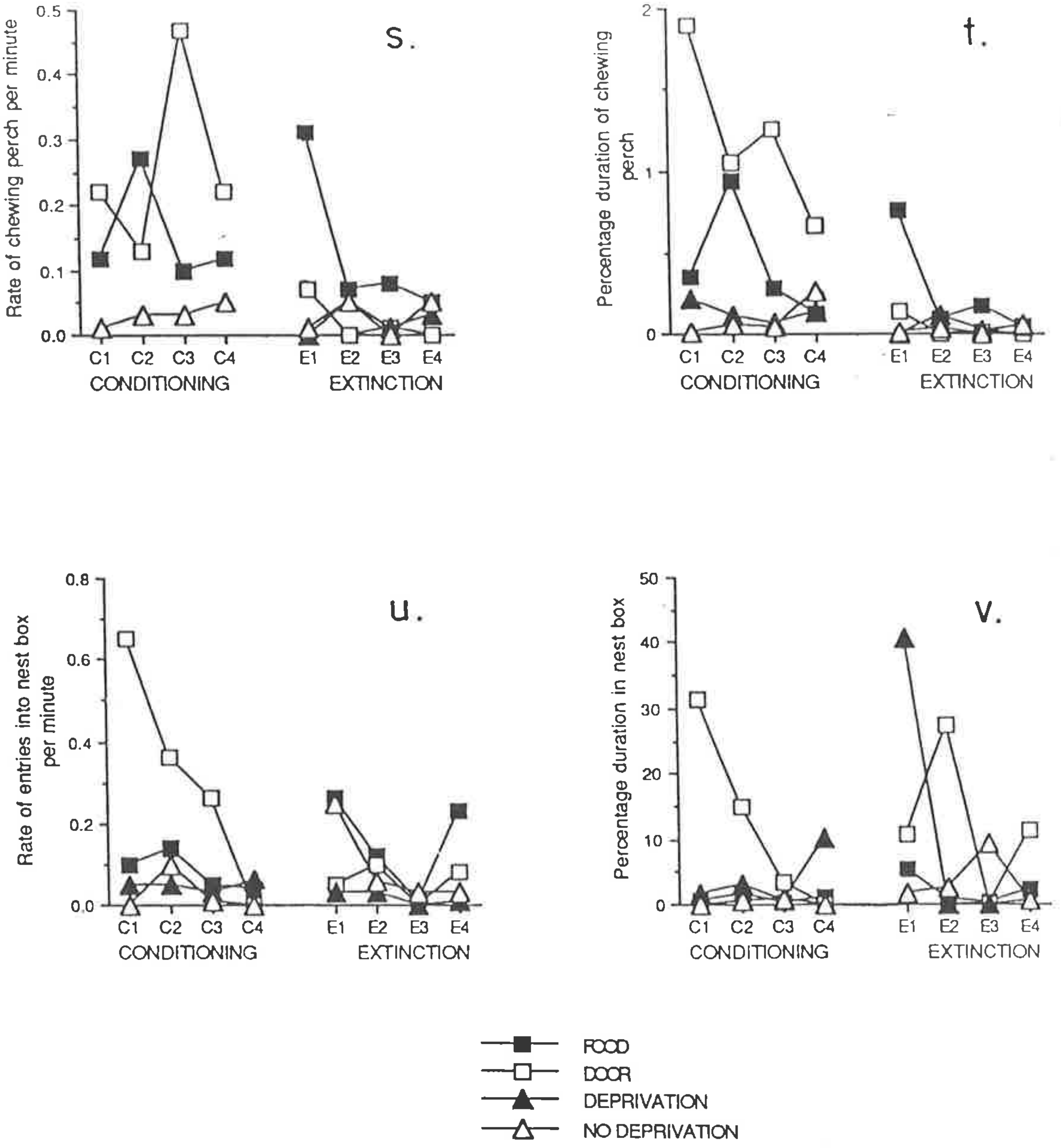


FIGURE 8.6(IV): Session means of non-object-directed behaviours in experiment 6.

Analysis of *session* effects for marmosets in experiment 6 showed that, for the most part, measures of exploration and non-object-directed activities remained constant during conditioning and decreased during extinction, as they had done in experiment 5 (Table 8.1). In contrast, the non-object-directed activities remained constant over time.

Table 8.1: Significance levels obtained for measures of exploratory behaviour during extinction (*session* effects).

Variable	*F*	Significance level
Rate of staring at objects	$F(3,12) = 3.20$	N.S.
Duration of staring at objects	$F(3,12) = 1.06$	N.S.
Rate of touching objects with nose	$F(3,12) = 3.94$	$p < .05$
Duration of touching objects with nose	$F(3,12) = 2.91$	N.S.
Rate of handling objects	$F(3,12) = 6.00$	$p < .05$
Duration of handling objects	$F(3,12) = 11.35$	$p < .01$
Rate of biting objects	$F(3,12) = 11.26$	$p < .01$
Duration of biting objects	$F(3,12) = 8.65$	$p < .01$
Rate of object exploration	$F(3,12) = 7.39$	$p < .01$
Duration of object exploration	$F(3,12) = 6.08$	$p < .01$

Interactions between *session* and *group* did not occur, with the exception of *chewing perch* during extinction (*rate of chewing perch* $F[9,12] = 3.37$, $p < .05$, *percentage duration of chewing perch* $F[9,12] = 7.08$, $p < .01$) which showed that yoghurt-trained animals chewed the perch more than door-trained and control animals at the onset of extinction (Figure 8.6(IV), graphs *s* and *t*). This suggests that chewing the perch is associated with the marmoset's feeding repertoire, since marmosets in Group DOOR did not exhibit the effect at the onset of extinction, and it also shows that chewing the perch is affected by the learning process; in particular, the learning of a food-rewarded task.

Before looking at differences in exploratory behaviour between groups, it should be noted that there were statistically significant differences during conditioning in the amount of time spent responding for food rewards compared to opening the door (*percentage duration of responses* $F[1,2] = 26.25, p < .05$). Animals spent more time responding for yoghurt than they did opening the door, perhaps reflecting a relative priority of food (under conditions of deprivation) over social contact in the marmoset.

Analysis of variance testing for *group* effects during conditioning revealed significant probability levels for all but one measure of exploratory behaviour (Table 8.2) and when both experimental groups together were compared with both control groups, again all but one yielded significant differences (Table 8.3) showing that control animals had higher rates and percentage durations of exploratory behaviour than experimental animals. This result was in direct contrast to any of the results from the previous experiments, showing the marked effect of home cage observation instead of testing in an experimental cage. It is suggested that the high quantity of exploration exhibited by the control groups reflected the fact that these animals were the least fearful, as a direct consequence of the lack of experimental manipulations.

Table 8.2: Significance levels obtained for measures of exploratory behaviour during conditioning (*group* effects).

Variable	*F*	Significance level
Rate of staring at objects	$F(3,4) = 4.40$	N.S.
Duration of staring at objects	$F(3,4) = 12.94$	$p < .05$
Rate of touching objects with nose	$F(3,4) = 34.89$	$p < .01$
Duration of touching objects with nose	$F(3,4) = 6.62$	$p < .05$
Rate of handling objects	$F(3,4) = 7.61$	$p < .05$
Duration of handling objects	$F(3,4) = 10.05$	$p < .05$
Rate of biting objects	$F(3,4) = 12.92$	$p < .05$
Duration of biting objects	$F(3,4) = 7.52$	$p < .05$
Rate of object exploration	$F(3,4) = 10.80$	$p < .05$
Duration of object exploration	$F(3,4) = 16.04$	$p < .05$

Table 8.3: Significance levels obtained for measures of exploratory behaviour during conditioning (*group* effects comparing experimental groups with control groups).

Variable	F	Significance level
Rate of staring at objects	$F(1,4) = 11.02$	$p < .05$
Duration of staring at objects	$F(1,4) = 38.51$	$p < .01$
Rate of touching objects with nose	$F(1,4) = 64.17$	$p < .01$
Duration of touching objects with nose	$F(1,4) = 14.73$	$p < .05$
Rate of handling objects	$F(1,4) = 8.91$	$p < .05$
Duration of handling objects	$F(1,4) = 21.18$	$p < .05$
Rate of biting objects	$F(1,4) = 12.56$	$p < .05$
Duration of biting objects	$F(1,4) = 6.44$	N.S.
Rate of object exploration	$F(1,4) = 18.18$	$p < .05$
Duration of object exploration	$F(1,4) = 36.33$	$p < .01$

In examining differences between experimental and control groups further, planned comparisons pointed to the greatest contrast as being between Group DOOR and the non-deprived control group (Table 8.4). This result can be explained in terms of the covering of the cages for the marmosets trained to open the door. Animals in this group explored least of all, perhaps due to their isolation from the surrounding marmosets (and hence lack of social facilitation, Hughes, 1969). As well as this possibility, Halliday (1968) reported that a methodological difficulty arises when a door is opened for a fixed period after a response, because the experimenter does not know how much of this period the animal is in fact looking out. Thus, the marmosets in Group DOOR may not only have been socially isolated due to the cage cover, but if they were not oriented towards the door when responding, they also may not have received much social reinforcement from the grid-jumping task.

Table 8.4: Significance levels obtained for measures of exploratory behaviour during conditioning (planned comparisons between Groups DOOR and NO DEPRIVATION).

Variable	t	Significance level
Rate of staring at objects	$t = -3.38$	$p < .05$
Duration of staring at objects	$t = -4.78$	$p < .01$
Rate of touching objects with nose	$t = -9.98$	$p < .001$
Duration of touching objects with nose	$t = -4.17$	$p < .05$
Rate of handling objects	$t = -4.72$	$p < .01$
Duration of handling objects	$t = -5.11$	$p < .01$
Rate of biting objects	$t = -5.45$	$p < .01$
Duration of biting objects	$t = -4.22$	$p < .05$
Rate of object exploration	$t = -5.59$	$p < .01$
Duration of object exploration	$t = -6.40$	$p < .01$

Marmosets in Group NO DEPRIVATION, however, explored more than any other group. Since these animals did not have their cages covered, were not hungry, and were submitted to the least amount of experimenter interference, it may be argued that their full attention could be directed towards the novel objects throughout all eight observation sessions. Video tapes showed these marmosets to be the most creative with their exploration too, frequently hanging upside-down from objects and investigating them from all angles.

The enhancements exhibited by Group NO DEPRIVATION were also present during extinction, although the effect was not so pronounced, occurring only for the measures *rate of handling objects* and *rate of object exploration*. The effect was stronger when comparing both experimental groups together with the two control groups, with more exploration produced by the latter groups (*rate of object exploration* $F[1,4] = 22.61, p < .01$; *percentage duration of object exploration* $F[1,4] = 9.83], p < .05$). Many of the planned comparisons between Groups DOOR and NO

DEPRIVATION also showed that the isolated (covered) animals explored less than the uncovered non-deprived animals (Table 8.5), supporting the claim that the presence of other animals facilitates exploration.

Table 8.5: Significance levels obtained for measures of exploratory behaviour during extinction (planned comparisons between Groups DOOR and NO DEPRIVATION).

Variable	*t*	Significance level
Rate of touching objects with nose	$t = -2.70$	$p < .05$
Rate of handling objects	$t = -4.46$	$p < .05$
Rate of biting objects	$t = -2.66$	$p < .05$
Rate of object exploration	$t = -6.03$	$p < .01$
Duration of object exploration	$t = -3.58$	$p < .05$

Despite greater overall amounts of exploration exhibited by the control marmosets, comparison of session 4 of conditioning with session 1 of extinction showed that there was an immediate increase in exploration at the onset of extinction by animals in Group FOOD (Figures 8.6(I) and (II)). Thus, as predicted, a rise in object-directed exploration was observed at the beginning of the extinction sessions. However, this did not occur in Group DOOR, suggesting that the extinction-induced exploratory behaviour was related specifically to the sudden withdrawal of food, rather than an outcome of extinction for any response. Alternatively, the lack of a clear effect in Group DOOR may have been due to the general depression of activity associated with the covering of the cages. In this case, the visual isolation experienced by the marmosets in Group DOOR may have outweighed a possible extinction effect.

Analysis of the data concerning non-object-directed behaviours revealed effects which were notably different from those reported in the object exploration categories, particularly during conditioning. The general trend was that the experimental animals exhibited higher rates and longer durations of *eating &/or drinking*, *locomotion*, *grooming*, *chewing perch* and *entries into nest box* than the controls (Figures 8.6(III) and (IV)). Some of the *group* effects were statistically significant; for example, *rate of locomotion* ($F[3,4] = 9.77, p < .05$) and *percentage duration of locomotion* ($F[3,4] = 9.37, p < .05$), and the effect was highly significant when the experimental groups were combined and compared to both of the control groups; for example, *rate of locomotion* ($F[1,4] = 25.53, p < .01$), *percentage duration of locomotion* ($F[1,4] = 25.89, p < .01$) and *rate entries into nest box* ($F[1,4] = 8.10, p < .05$). In addition, planned comparisons for *locomotion* scores showed that the deprived animals (Group DEPRIVATION) moved around significantly less than the marmosets in Group FOOD: *rate of locomotion* ($t = 4.94, p < .05$), *percentage duration of locomotion* ($t = 4.64, p < .05$).

Taken together, these results indicate that the trained marmosets engaged in more activity (including eating and drinking, walking, running, jumping and climbing around the cage, grooming, chewing their perches and entering their nest boxes) than the untrained marmosets. In spite of this, they did not contact objects more than the control animals. This supports the claim that increased activity does not necessarily imply increased exploration of objects (e.g., Foshee, Vierck, Meier, & Federspiel, 1965; Halliday, 1968; Leyland, Robbins, & Iverson, 1976; File, 1978).

During extinction, there were fewer *group* effects for the non-object-directed measures, but those that were statistically significant showed that the experimental animals were more active than the controls: *rate of locomotion* ($F[1,4] = 10.22, p < .05$), *rate of grooming* ($F[1,4] = 7.09, p < .05$). Planned comparisons showed that the marmosets in Group FOOD were more active than the marmosets in Group DEPRIVATION: *rate of locomotion* ($t = 3.26, p < .05$), *rate of chewing perch* ($t = 3.39, p < .05$), and *percentage duration of chewing perch* ($t = 3.30, p < .05$). These results are consistent with the idea that extinction induces increased activity, although as was the case during conditioning, this effect was not associated with a corresponding increase in object contacts.

In summary, the results from experiment 6, like those of the previous experiments, suggest that there is a relationship between learning and exploration. The marmosets in Group FOOD displayed a sudden increase in object contacts at the onset of extinction, and throughout the sessions the experimental animals tended to engage in more eating, drinking, locomotion, grooming, chewing the perch and entering the nest box compared to the control animals. These observations suggest that whilst object exploration only increases following the learning of a food-reinforced task, overall activity levels are enhanced following the learning of both food-reinforced and socially-reinforced tasks. The non-object-directed behaviours did not increase at the onset of extinction, however, and this was also the case in experiment 5. Thus, as in the previous experiment, learning appeared to be related to both object exploration and general activity levels, but the two types of measures were not interchangeable, and consequently could not be said to measuring the same thing.

Comparisons between the two control groups showed that the non-deprived marmosets explored more than those which were fed after the observation sessions, consistent with observations of rats by Zimbardo and Montgomery (1957b), but inconsistent with reports of exploration enhancement due to hunger (e.g., Glickman & Jensen, 1961; Bolles, 1967) or reports of no effects of hunger (e.g., Hughes, 1965b). It would seem from this result that the differences in amounts of exploratory behaviour exhibited by Groups FOOD and DOOR cannot be explained in terms hunger because the former group were deprived but explored more than the latter. A more likely explanation is that the cage cover used for Group DOOR was responsible for the depressed exploration of this group: the animals were suddenly isolated from their neighbours, putting them in an 'impoverished' condition, which, according to File (1978), leads to reductions in exploration and orienting responses. In addition, the marmosets in Group DOOR spent more time in their nest boxes than the animals in Group FOOD, indicating withdrawal from their surroundings and from the novel objects.

The most striking difference between experiment 6 and all of the previous experiments was that the control animals contacted the novel objects at a higher rate and for longer amounts of time than the experimental animals. Since Group DEPRIVATION in experiment 6 was a replication of Group Control/Novel Objects in experiments 4 and 5, it seems reasonable to conclude that the difference was due to the fact that the marmosets in experiment 6 were observed in their home cages. Thus, in a familiar environment marmosets are highly responsive to small changes (such as the addition of novel objects), and interest in these objects remains high over time.

8.3. CONCLUSION

Experiment 6 provided new information about conditions under which exploration is enhanced, and highlighted the contrast between measures of object-directed activity and other activities. The lack of any experimenter interference (handling or transport of the marmosets) had a strong effect on the subsequent behaviour produced: the marmosets in experiment 6 were less fearful of the experimental apparatus and more active than the marmosets in experiment 5.

The mere addition of novel objects into the marmosets' home cages (without any learning task) induced high levels of object-directed exploratory behaviour, but did not involve a corresponding rise in eating, drinking, locomotion, grooming, chewing the perch or entering the nest box. The trained marmosets, however, did produce higher levels of these non-object-directed activities compared to the control animals, although these were not associated with a rise in object contacts.

In a practical context, the results from experiment 6 suggest that the exploratory behaviour of captive marmosets may be effectively enhanced by the inclusion of novel objects in their home cages, whilst their overall activity levels may be increased by providing them with a learning task (with either food or social reinforcement). Throughout the experiment interest in the novel objects remained fairly constant for the control groups, but the learning-enhanced activities tended to decline with time. For this reason, it may be suggested that the best method for preventing boredom and maintaining marmosets in the laboratory is to provide them with a source of novel stimulation in the form of sets of manipulable objects (the more preferred objects usually being those made of wood, with moveable parts). However, given that one of the aims of research concerned with the enrichment of the behaviour of captive animals is to preserve the widest possible range of natural behaviours, it must also be said that the inclusion of a learning task is a valuable method, since learning has been shown to enhance behaviours not enhanced by novel objects alone.

CHAPTER 9

GENERAL DISCUSSION

The initial concept motivating the research presented in this thesis was that learning and novelty can enrich behaviour, and in particular, exploratory behaviour. To this end, six ethoexperimental studies were designed, each involving the observation of exploratory behaviour directed towards sets of objects in an open field, under varying learning conditions. In this closing chapter, the six studies will be discussed within the context of enrichment, viewing the results not so much in terms of their theoretical interest, but as having practical value for the maintenance of animals in captivity. The aim of the chapter is threefold: to provide a rationale for attempts to enrich the behaviour of captive animals, to review some of the problems associated with captivity, and to interpret the findings of the present studies as possible solutions to these problems.

On a very general level, one may argue that the rationale for enrichment is that animals have intrinsic value and should therefore be treated well, keeping their interests in mind. At the level of the individual, Salzen (1989, p. 134) argued that:

> *Experimental subjects are...no longer code numbers but are named individuals, known and cared for as infants, with a history and personality and often with specific interaction patterns with the individual human caregiver and experimenter.*

At the level of the species, Kelly (1989 p. 147), referred to animals as "ambassadors for those that remain, however precariously, in the wild", thereby justifying the holding of animals in captivity. The reference to animals as ambassadors is a reminder of the importance of biodiversity and conservation: that the loss of a species would mean a reduction in biodiversity, and consequently a loss of potential instrumental value. This argument has been employed in accounts of ecological sustainability, in which the maintenance of essential ecological processes, the preservation of genetic diversity and the sustainable utilisation of ecosystems are advocated (e.g., Endangered Species Advisory Committee, 1989).

Some of the more commonly reported reasons for keeping animals in captivity are as follows: to re-introduce them into the wild at some later point in time (e.g., Kleiman, Beck, Dietz, Dietz, Ballou, & Coimbra-Filho, 1986), to assist animals in the wild by applying knowledge learned from laboratory animals (i.e., to use captive animals as an insurance policy for wild stocks, Kelly, 1989), or to carry out research so that species with decreasing numbers in the wild can be bred from existing animals in captivity (e.g., Ingram, 1975). Whatever the reason, the successful maintenance of animals in laboratories and zoos requires attention to the many problems often associated with captivity.

The fact that captive animals are usually given predictable and plentiful supplies of food which are easy to find is one of the most frequently discussed problems associated with captivity (e.g., Hediger, 1955; Washburn & Hamburg, 1965; Loizos, 1967; Molzen & French, 1989). Erwin and Deni (1979) have also suggested that *ad libitum* supplies of water cause problems in captivity. Combined with protection from predators, the free supply of food and water creates a situation which is very different from the problems and opportunities encountered in the wild, where many animals must spend the greater part of their day locating and appraising hidden foods and water, avoiding non-edible foods, and identifying and dealing with an abundance of predators and competitors. Molzen and French (1989), for example, described their main concerns for the well-being of the captive golden lion tamarin in terms of behavioural capacities related to foraging. In captivity, according to Molzen and French, these animals do not fulfil their capacities for acquiring, preparing and consuming food items, they do not learn how to construct or use tools, how to extract food, to recognise toxic plants, or to avoid predators. Further, they do not learn when to forage or how to forage, since they are provided with unrestricted food. In other words, the environment in the wild is very complex compared to the environment of a laboratory cage or zoo enclosure. Molzen and French went on to suggest that this is a problem for all callitrichids: the standard husbandry involves a readily accessible, large food supply, given in one location once or twice daily; whereas wild callitrichids spend up to 60% of their daily available time foraging for food.

The significant reduction in foraging time and a general lack of complex stimulation in captive animals have often been blamed for the prevalence of boredom, stress, abnormal behaviours and breeding problems in captivity. In the first category, an animal which does not have to search for food and which is subjected to perceptual deprivation due to restricted living conditions may become bored (Loizos, 1967) or even experience disappointment and annoyance (Griffin, 1984), sometimes leading to health problems (Hearn, Lunn, Burden, & Pilcher, 1975). Similarly, stress responses have been reported as a result of overcrowding (Elton, 1979) or spatial restriction (Chamove & Anderson, 1989).

Lacking behavioural alternatives, then, an animal deprived of its foraging time and deprived of a complex environment may fill its free time by engaging in pathological patterns of social and individual behaviour (Eibl-Eibesfeldt, 1970; Erwin & Deni, 1979; Bramblett, 1989). Abnormal primate behaviours induced by a lack of novel stimulation were described in Chapter 4 (e.g., floating limb, self-biting, self-clasping, self-grasping, saluting, stereotyped pacing, head tossing, bouncing in place, somersaulting, rocking, appetitive disorders and sexual disorders). Similar displays can occur in a variety of captive animals, especially in mammals which are normally quite active. For example, racoons may engage in exaggerated food-washing (Morris, 1964), rats may drink excessive amounts of water (i.e., exhibit the phenomenon of polydipsia, Falk, 1971), mongooses may exhibit infanticide (Rasa, 1979) and parrots may engage in feather-plucking (Stevenson, 1983).

Finally, captivity has been shown to induce problems related to breeding. A general poorness in reproduction and parenting skills has been associated with captivity (e.g., in marmosets and tamarins, Epple, 1970; Snowdon, 1983; in gorillas, cheetahs and giant pandas, Stevenson, 1983). In particular, cage size has been correlated with reproductive failure (Erwin & Deni, 1979), along with related variables such as overcrowding and group size (Chamove, 1989b).

In a nutshell, all of these problems (boredom, stress, abnormal behaviours and breeding problems) may be seen as arising from the nature of containment; that is, "caged animals cannot or do not carry out their normal range of behaviour" (Chamove, 1989b, p. 156). Chamove and Anderson (1989, p. 185) pointed out that:

> *Commonly, enclosures are designed by architects whose primary considerations are engineering, maintenance, cost, and human comfort and convenience...Bare, flat, smooth walls are easy to build and to clean, but most animals cannot make use of them...*

In the six experiments reported in this thesis, laboratory rats and marmosets were observed under varying environmental conditions, one of the aims being to attempt to enrich their exploratory behaviour. The studies may therefore be viewed as possible solutions to some of the problems associated with captivity, insofar as learning and novelty can induce enriched exploration. The purpose of the remainder of this chapter is to interpret the six experiments in this light, discussing the variables of learning and novelty separately, and providing additional support from research in the field of environmental enrichment in captivity.

According to Chamove (1989b, p. 155), enrichment is "an attempt to ameliorate problems caused by containment", thereby altering an animal's behaviour so that it is within its normal repertoire. A good captive environment, then, may be described as "one where animals can acquire and retain the behavioral skills they would need to cope successfully with their natural environment were they ever to be released to the wild" (Snowdon & Savage, 1989, p. 77). In this chapter, it will be argued that such an environment can be created in captivity by providing animals with learning tasks and novel objects, both of which can be used to aid the development of behavioural competence.

The conditions of the learning tasks employed in experiments 1, 4, 5 and 6 required the animals to carry out a particular piece of behaviour in order to obtain a reward in the form of a small amount of food. Such a procedure is analogous to the 'work therapy' programs (a label used by Eibl-Eibesfeldt, 1970), which have been designed in attempts to solve the problem of plentiful food supplies for zoo animals.

Snowdon and Savage (1989) have provided many instances of the use of 'foraging analogues' in primate enclosures: techniques which ensure that animals work for their food. Examples described by Snowdon and Savage include complex feeding boxes, hidden food in hanging baskets, food-reinforced video games and puzzles, diving for raisins, and simulated termite foraging. Similarly, Chamove and Anderson (1989) used woodchip litter to cover the floor of the enclosures of eight different primate species, and King and Norwood (1989) encouraged fishing by allowing squirrel monkeys access to a pool containing goldfish.

In an experiment by Mineka, Gunnar and Champoux (1986), rhesus monkeys which worked for their food engaged in more exploratory behaviour than monkeys which received rewards independent of their behaviour. Molzen and French (1989), the designers of the raisin-diving device, found that golden lion tamarins' exploration and foraging times increased when offered the challenge to master the device. In their description, mastery of the device was said to involve time, concentration and skill, all desirable features reflecting behavioural enrichment. In experiments 1, 4, 5 and 6 of this thesis, exploratory behaviour increased when animals were required to work for food. (Increases in exploration were not observed for marmosets which were reinforced by the opening of a door, but this was thought to be a consequence of the isolation of these animals.) Experiments 2 and 3 showed that increases in exploration (as well as ball bearing-directed behaviour) were associated with a learning task which did not involve an operant response from the animals. Thus, behavioural enrichment was achieved not only when animals were required to work for food, but also when they were trained to merely associate a rolling ball bearing with the arrival of food. Experiments 4 and 5 in particular suggested that the enrichment effect is at its strongest during conditioning rather than extinction, and that the result applies to both rats and marmosets (despite differences in training times for the two species).

The results of the present experiments support the idea of 'work therapy': that animals which are given the opportunity to work usually show marked improvements in their general behaviour. A rationale for such an effect is that the chance to work gives animals *control* over their environment (Snowdon & Savage, 1989; Novak & Drewsen, 1989). It should be noted that animals may be given control of alternative aspects of their environment apart from their feeding routines. For example, Novak and Drewsen (1989) and Markowitz and Line (1989) trained rhesus monkeys to press a lever to control the playing of music in their enclosures. Both groups of researchers found that the monkeys spent considerable amounts of time playing the music, and suggested that this provided them with a positive source of stimulation.

Relevant to the issue of problems in captivity, Snowdon and Savage (1989) argued that animals which can act effectively on their environment and receive valuable consequences may be better able to withstand stress and adapt more readily to environmental changes, compared to animals which do not have control over their surroundings. In the present experiments, then, the bar-pressing, key-pushing and grid-jumping tasks could be said to have given the rats and marmosets control over their feeding routines, thereby improving their well-being.

The fact that rats and marmosets both exhibited increases in exploratory behaviour in association with bar-pressing, key-pushing and grid-jumping suggests, in accordance with Bramblett (1989, p. 1), that learning has a beneficial effect, irrespective of species differences:

> *The biological importance of learning does not diminish in proportion to the facility to learn; a snail's learning ability may be as important to its survival as memory is to a human.*

There are plenty of examples of successful work programs which have been employed with a variety of species: Markowitz (1979) devised training programs for captive gibbons and mandrills, where brachiation and leaping (in the former) and visual reaction time (in the latter) were rewarded; Maple (1979) taught a gorilla to play tug-of-war with members of the zoo public (which not only gave the gorilla exercise, but also exposed the public directly to the strength of a gorilla); Bloomsmith (1989) used a food puzzle device for chimpanzees, in which peanuts, sunflower seeds and popcorn could be manipulated to the bottom of the puzzle.

In summary, the use of learning tasks in the present experiments can be seen as analogous to programs of work therapy, allowing animals a degree of control over their environment, and therefore enriching their behaviour. Adding to the argument that learning has beneficial effects on animal behaviour, Markowitz (1979, p. 222) has noted the degree to which animals are willing workers, in that they actually *prefer* to work for their food:

> *It is now fairly well accepted that many animals, given a choice between freely available identical food and working in simple ways for the food, opt for the latter.*

Establishing work programs in laboratories and zoos can therefore provide one answer to the problem of captivity: animals which learn to forage, hunt, learn prescribed tasks, and solve problems and puzzles are healthier psychologically, physiologically and behaviourally, compared to animals denied such possibilities (Novak & Drewsen, 1989). It only remains to take care that animals which are given control are not denied it later; Snowdon and Savage (1989) have argued that to lose control over an environment after having had it may be worse than never having had it at all.

The use of novel objects to promote play and exploratory behaviour has been another common practice in enrichment studies (e.g., Candland, Weldon, Lorinc, & O'Connor, 1978; Bramblett, 1989; O'Neill, 1989). Numerous experiments have pointed to the significance of novelty in ensuring the well-being and behavioural diversity of animals kept in captivity, since animals reared in environments containing objects have been found to be superior on subsequent learning tasks and more active in an open field than animals reared in comparatively impoverished environments (e.g., Greenough, Fulcher, Yuwiler, & Geller, 1970; Manosevitz, 1970; Rosenzweig, 1971; Greenough, Wood, & Madden, 1972; Huck & Price, 1975). An explanation for such an effect is that in responding to novelty, animals learn necessary adaptive skills (Fragaszy, 1979, p. 172):

> *The most general function of behavior is to allow effective adjustment to environmental change. Response to novelty is therefore an important dimension of the behavioral organization reflected in a species' general lifestyle.*

Novelty has been shown to have beneficial effects on many aspects of the behaviour of captive animals, and in particular has been seen as a valuable solution to the some of the problems of captivity. For example, Hearn, Lunn, Burden and Pilcher (1975) argued that talking to, hand feeding and generally distracting marmosets as much as possible (thereby ensuring a continuously changing environment) results not only in less boredom, but also improves health and breeding performance; O'Neill (1989) found that piped classical music reduced distress and stereotyped behaviour in rhesus monkeys; and Blackmore (1989) allowed macaques periodic access to an exercise cage containing objects (e.g., soccer balls, soft children's toys, a trapeze, a hammock and a mirror), as well as a radio which played classical music and a television which showed children's programs, and this resulted in a lower noise level from the monkeys and a lack of aggression. Mineka, Gunnar and Champoux (1986) have also argued that novel objects promote adaptive behaviour, another improvement in the well-being of captive animals.

Various sets of objects were employed in each of the six experiments discussed in this thesis, and an overall trend was that novel objects were preferred over familiar ones, in the sense that more time was spent investigating them. For example, a comparison between the *percentage duration of object exploration* of the animals in experiment 1 (Group CONTROL, for which objects were familiar, see Figure 5.5(II), graph *j*) and that of the animals in experiment 4 (Group Control/Novel Objects, see Figure 7.4(II), graph *j*) shows that by the end of the experimental sessions the former spent 5% of their available time contacting the objects, while the latter spent 15% of their available time exploring.

Experiments 2 and 3 indicated that the variable of object novelty produced a greater effect on exploratory behaviour than the learning procedure: exploration was enhanced for the groups of rats which were exposed to the novel objects, whether learning took place or not. In experiments 4 and 5, the objects enhanced the rats' and the marmosets' exploration particularly towards the end of the experimental sessions, suggesting that novelty is more salient when food is not available. When in their home cages (in experiment 6) novelty had its most powerful effect, especially when no other manipulation was carried out (i.e., Group NO DEPRIVATION, see Figure 8.6(II), graph *l*): the marmosets in this group spent up to 65% of their time contacting the novel objects. As an additional observation, the high levels of object-directed behaviour were not accompanied by a corresponding rise in eating, drinking, locomotion, grooming, chewing the perch or entering the nest box; thus, the enrichment effects of the novel objects were confined to exploratory activities only.

The experiment carried out in the marmosets' home cages most closely resembled studies of enrichment reported by primate researchers such as those collected in Segal's (1989) *Housing, Care and Psychological Wellbeing of Captive and Laboratory Primates* (e.g., Chamove & Anderson; Salzen; Fouts, Abshire, Bodamer, & Fouts; O'Neill). A common theme in this book is that for novelty to achieve its fullest benefit, objects (or other forms of novelty, such as food) ought to be changed periodically, hence maintaining change over time. In the words of Salzen (1989, p. 123), for example, "A flavour a day keeps monotony at bay." (Salzen provided his squirrel monkeys with a different flavour of food each day.) Earlier, Maple (1979, p. 248) gave the same advice, except for objects rather than food:

> *...where any objects are introduced for play, it is helpful to substitute novel objects periodically. As has been previously emphasized, a changing environment is to be preferred over a static one.*

Similarly, Chamove (1989a) suggested small, regular changes in the positions of branches in enclosures. The effect of such changes, according to Snowdon and Savage (1989) is that behavioural stereotypies are reduced, because animals must frequently adjust their routes to get from one place to another within the cage.

One of the outcomes of experiment 6, therefore, is the suggestion that the addition of novel objects into home cages be a continuing routine for marmosets held in captivity. To avoid having to manufacture a vast number of objects, it is suggested that a single set of complex objects be rotated from cage to cage; this follows from Welker's (1956) finding that chimpanzees regained their interest in a set of novel objects after periods of object absence. (These suggestions have been taken up and are being carried out at the Queen Elizabeth Hospital Animal House where the present study took place). Alternatively, the animals themselves (or their cages) could be rotated to various positions in the holding room, as suggested by O'Neill (1989), who regularly moved monkeys to a 'cage with a view', so that they were able to obtain a view from the only window in the room. O'Neill reported that less disturbed behaviour occurred once this became a policy of the laboratory staff.

In summary, in addition to the implementation of learning procedures, object novelty can be used to combat the problems of captivity. In fact, the combination of learning and novelty, rather than one or the other, has been advocated by Snowdon and Savage (1989). These researchers argued that giving animals new objects or exposing them to music or video screens alone does not give animals control over the environment; they suggested instead that animals be given control (in the form of work) so that they can operate effectively on their environment and seek new ways to control it when challenged with novel situations. The results of experiments 4 and 5 suggested that the use of an operant reward system is most effective during feeding time, and that novel objects are more likely to result in increased exploratory behaviour at other times.

It is possible to view the interpretation discussed here as a bid to make the conditions of laboratories and zoos more natural, or more like the conditions each particular animal would encounter in the wild. Pereira, Macedonia, Haring and Simons (1989) favoured such a move, arguing that animal research could greatly benefit by establishing housing conditions which resemble the subjects' natural physical and social environments. For example, primate enclosures ought to contain branches rather than shelves, the cages of scent-marking animals should not be washed too frequently, and social animals should be housed in groups. Similarly, Snowdon and Savage (1989) suggested a high density of branches and ropes (in order to give claws a good grip) placed one meter or more above ground level (to simulate an arboreal environment), and Bayne (1989) suggested that primates be given exercise areas, visual privacy barriers, play objects and puzzle feeders.

In other words, the creation of a natural environment can be achieved by providing an animal with novel objects and situations in which learning can take place, as well as the presence of items which resemble those found in that animal's natural habitat. In this way, the present studies can be interpreted as having relevance to the problems of captivity.

The marmosets in experiment 6 were tested in their home cages, novel objects and learning tasks were provided, and these manipulations involved very little experimenter manipulation or interference. Of all the animals observed in the present studies, the marmosets which were subjected to the least manipulations were the most active and learned the fastest. These results show how beneficial learning and novelty can be for confined laboratory animals: specifically, learning (of the yoghurt-reinforced task in particular) led to increased activity levels, and the novel objects (especially the wooden ones with moveable parts) gave rise to high levels of exploratory behaviour. The failure of marmosets in the socially-reinforced group to engage in as much exploration as the food-reinforced group was attributed to the fact that these animals' cages were covered; therefore the possibility that socially rewarded tasks can be enriching was not ruled out. It was concluded that each of the methods were valuable since they all resulted in different kinds of behaviour, thereby preserving a wide range of the animals' natural repertoire. Experiment 6, then, provided an example of the effectiveness of a naturalistic technique, in that these animals were less fearful and consequently more responsive to changes in their surroundings.

The establishment of naturalistic environments has certain advantages apart from ensuring the well-being of captive animals. If, for example, a researcher wanted to design an experiment to study the processes underlying behaviour acquisition in normal circumstances, it would be appropriate to use a naturalistic and non-invasive research technique in order to yield data relevant to problems encountered by animals in the wild. That is, the use of naturalistic environments in the laboratory corresponds to the ethoexperimental approach to the study of behaviour (as argued in Chapter 1), in which questions about behaviour in the wild can only be answered if testing situations resemble conditions in the wild. Furthermore, it may be argued that there is no point in using naturalistic settings in which to *test* behaviour unless the captive animals are *kept* in naturalistic settings in the first place.

Finally, animals which are able to learn and explore, as they would in the wild, may make better subjects, as suggested by Markowitz and Line (1989, p. 203):

> *Animals that are active, exert some control over their daily schedules, are challenged to solve problems, and have daily positive interactions with humans are almost always better research subjects than those that have lived under typical behaviorally-impoverished caging conditions.*

The present studies advocated the use of challenging learning procedures and attention to novelty, always with the aim of increasing animals' behavioural variability. This aim remains, whether such variables are employed in order to create better subjects, to provide diversions from laboratory or zoo routines (thereby improving the welfare of captive animals), to answer particular sorts of questions about the way an animal behaves in the wild, or to answer questions purely out of theoretical interest.

LIST OF APPENDICES

APPENDIX 1

Names of objects used in experiments 1 to 6.

The novel objects used in the studies reported in this thesis were constructed specifically for the present experiments; they were designed and made in the workshop of the Department of Psychology, University of Adelaide. For the most part, objects were made of stainless steel or wood, although some included parts made of plastic. The following is a list of names for the objects used in each experiment, indicating where applicable the experimental group to which they belonged.

Experiment 1

tunnel, house, slide.

Experiment 2

tunnel, house, windmill, spring lever.

Experiment 3

Group 1 objects: tunnel, house, spring lever, red windmill.
Group 2 objects: grid tunnel, grid wall, suspended ball bearing, gyroscope.
Group 3 objects: semi-circular tunnels, ladder, spring and ball bearing, propeller.
Group 4 objects: mirrored wall, generator, roulette ball bearing, bell.
Group 5 objects: short transparent tunnel, prongs, telescope ball bearing, serrated wheel with holes.
Group 6 objects: mechano, zig-zag ladder, bar and roller, castor wheel.
Group 7 objects: batteries, square tunnel, bar and arc, lever.
Group 8 objects: spring, radiator bars, spiked wheel, suspended chains.

APPENDIX 2 (continued)

Experiments 4 and 5

Group 1 objects: short toast rack, long grid tunnel, red windmill.

Group 2 objects: curved toast rack, short grid tunnel, serrated wheel with holes.

Group 3 objects: raised toast rack, diamond grid tunnel, cross windmill.

Group 4 objects: long toast rack, raised grid tunnel, solid serrated wheel.

Group 5 objects: thin grid wall, wide transparent tunnel, short propeller.

Group 6 objects: thin barred wall, long transparent tunnel, castor wheel.

Group 7 objects: wide grid wall, vertical transparent tunnel, long propeller.

Group 8 objects: wide barred wall, short transparent tunnel, gyroscope.

Experiment 6

Group 1 objects: short toast rack, long grid tunnel, wooden windmill.

Group 2 objects: curved toast rack, short grid tunnel, wooden wheel with holes.

Group 3 objects: raised toast rack, diamond grid tunnel, wooden cross windmill.

Group 4 objects: long toast rack, raised grid tunnel, solid wooden wheel.

Group 5 objects: wide barred wall, short transparent tunnel, wooden gyroscope.

Group 6 objects: wide grid wall, vertical transparent tunnel, long wooden propeller.

Group 7 objects: thin barred wall, long transparent tunnel, wooden castor wheel.

Group 8 objects: thin grid wall, wide transparent tunnel, wooden triangle.

APPENDIX 2

Analysis of Variance tables showing effects of *session* and *group* on object exploration measures in experiments 1 to 6.

The material included in Appendix 2 consists of a selection of Analysis of Variance tables, chosen to represent effects of *session* and *group* on the overall measures of object-directed exploration only (rather than displaying the tables for each individual variable of exploration, as measured by paw contacts, nose contacts, etc.). Two tables are included for each of the six experiments, with divisions between conditioning and extinction (except for Experiment 1, in which exploratory behaviour was measured during extinction only).

Source of Variation	Sum of Squares	DF	Mean Square	*F*	Signif. of *F*
Experiment 1: Rate of object exploration					
Main Effects					
Group	.28	2	.14	.04	.965
Session	246.68	2	123.34	125.60	.000
2-Way Interactions					
Group by Session	2.39	4	.60	.61	.660
Experiment 2: Frequency of object exploration (conditioning)					
Main Effects					
Group	1036.02	1	1036.02	1.05	.330
Session	22315.56	3	7438.52	31.80	.000
2-Way Interactions					
Group by Session	947.23	3	315.74	1.35	.277

APPENDIX 2 (continued)

Source of Variation	Sum of Squares	DF	Mean Square	*F*	Signif. of *F*
Experiment 2: Frequency of object exploration (extinction)					
Main Effects					
Group	462.52	1	462.52	1.28	.248
Session	793.73	3	264.58	6.21	.002
2-Way Interactions					
Group by Session	917.23	3	305.74	7.18	.001
Experiment 3: Frequency of object exploration (conditioning)					
Main Effects					
Group	408.33	1	408.33	.25	.626
Session	7194.25	3	2398.08	21.70	.000
2-Way Interactions					
Group by Session	1330.00	3	443.33	4.01	.016
Experiment 3: Frequency of object exploration (extinction)					
Main Effects					
Group	910.02	1	910.02	.58	.464
Session	8766.73	3	2922.24	12.31	.000
2-Way Interactions					
Group by Session	1476.56	3	492.19	2.07	.125

APPENDIX 2 (continued)

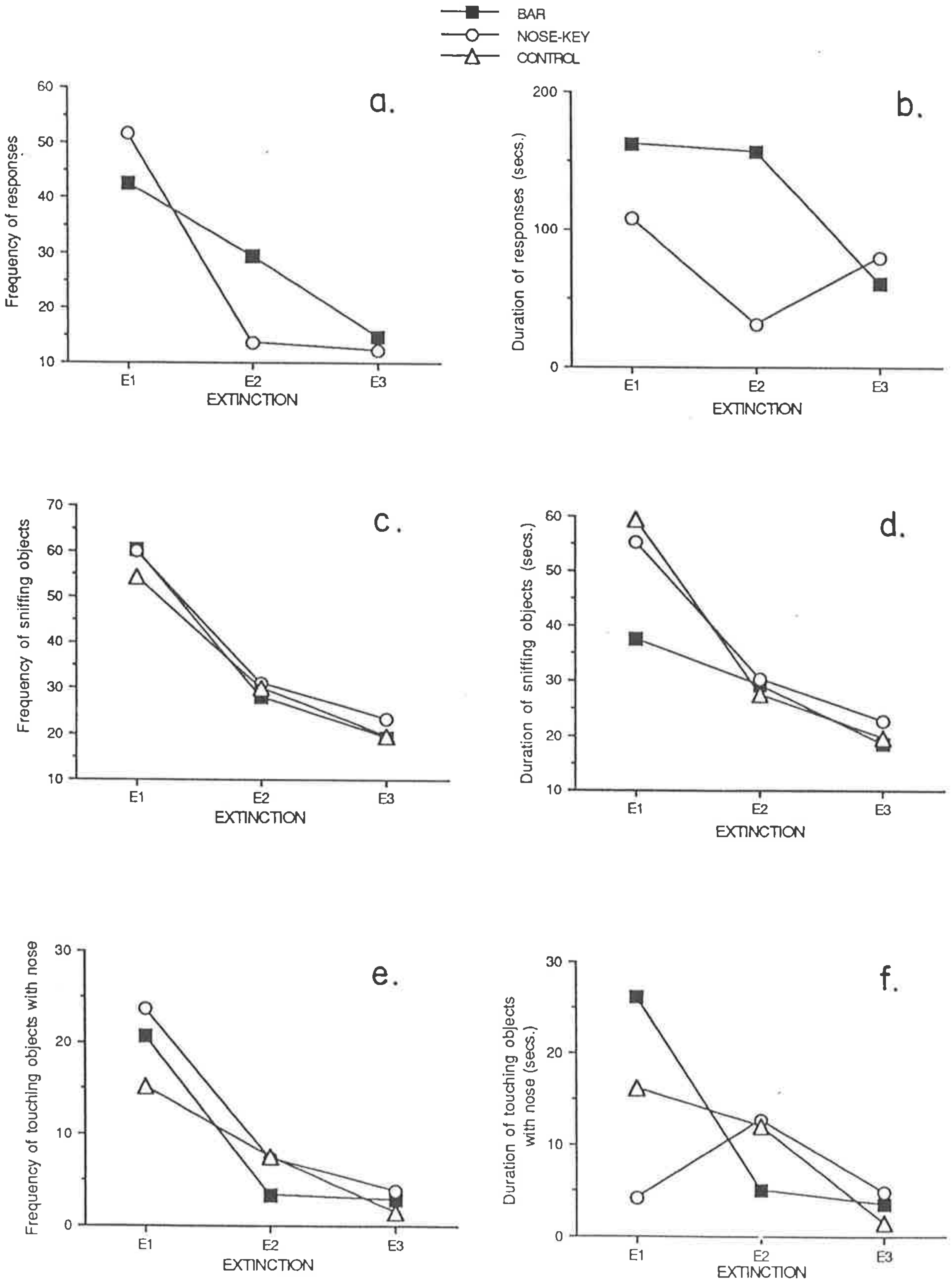
Source of Variation	Sum of Squares	DF	Mean Square	*F*	Signif. of *F*
Experiment 4: Rate of object exploration (conditioning)					
Main Effects					
Group	150.38	3	50.13	12.44	.000
Session	49.41	3	16.47	9.04	.000
2-Way Interactions					
Group by Session	40.26	9	4.47	2.46	.015
Experiment 4: Rate of object exploration (extinction)					
Main Effects					
Group	81.95	3	27.32	9.45	.000
Session	50.47	3	16.82	18.70	.000
2-Way Interactions					
Group by Session	22.29	9	2.48	2.75	.007
Experiment 5: Rate of object exploration (conditioning)					
Main Effects					
Group	32.04	3	10.68	13.20	.015
Session	5.53	3	1.84	12.00	.001
2-Way Interactions					
Group by Session	9.99	9	1.11	7.23	.001

APPENDIX 2 (continued)

Source of Variation	Sum of Squares	DF	Mean Square	*F*	Signif. of *F*
Experiment 5: Rate of object exploration (extinction)					
Main Effects					
Group	7.29	3	2.43	1.07	.465
Session	3.73	3	1.24	1.66	.229
2-Way Interactions					
Group by Session	7.41	9	.82	1.10	.431
Experiment 6: Rate of object exploration (conditioning)					
Main Effects					
Group	259.68	3	86.56	10.80	.022
Session	7.68	3	2.56	.52	.678
2-Way Interactions					
Group by Session	39.34	9	4.37	.88	.565
Experiment 6: Rate of object exploration (extinction)					
Main Effects					
Group	180.61	3	60.20	12.98	.016
Session	92.46	3	30.82	7.39	.005
2-Way Interactions					
Group by Session	27.12	9	3.01	.72	.682

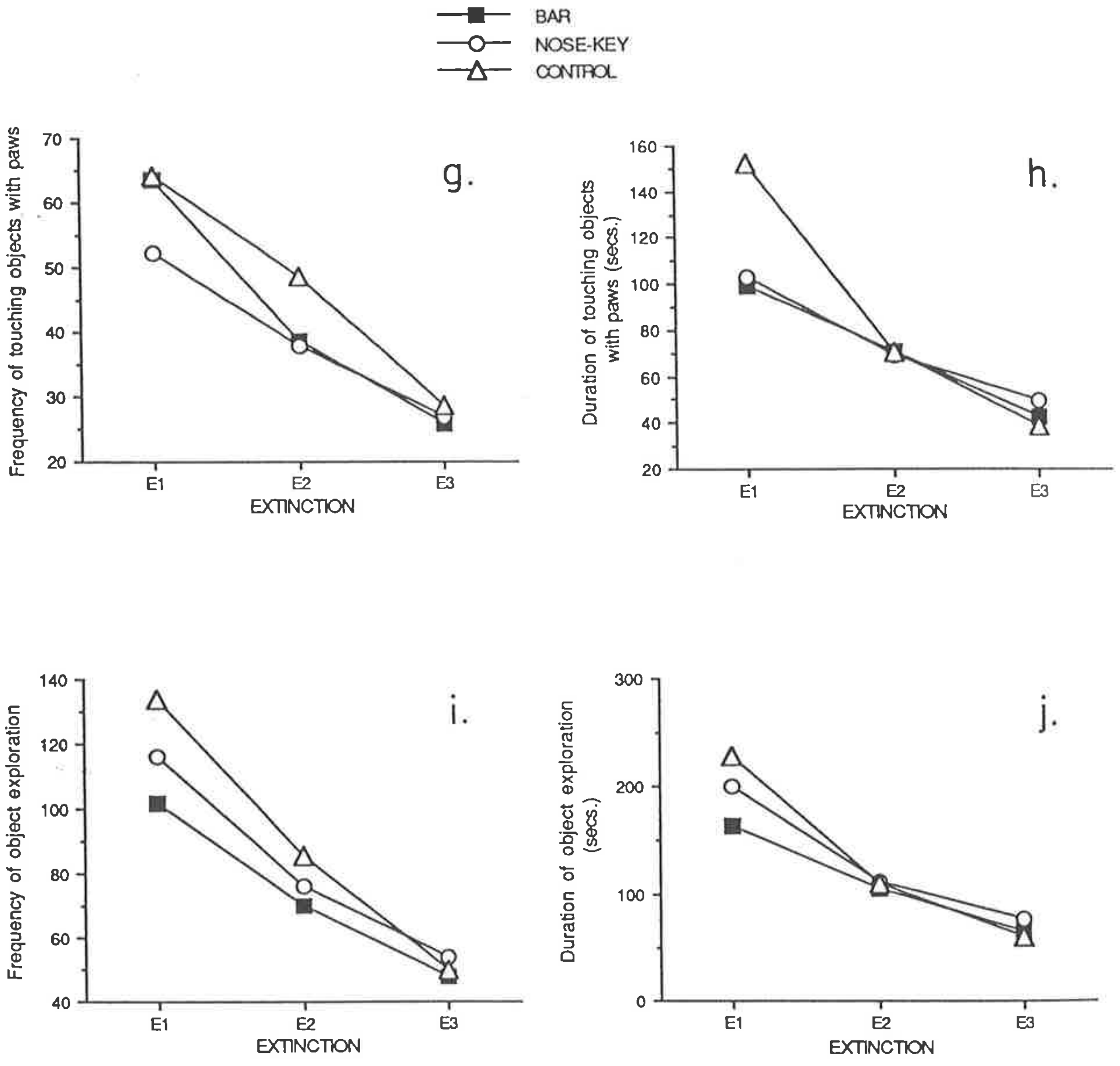
APPENDIX 5.1(I)

Frequencies and durations of behavioural measures in experiment 1.



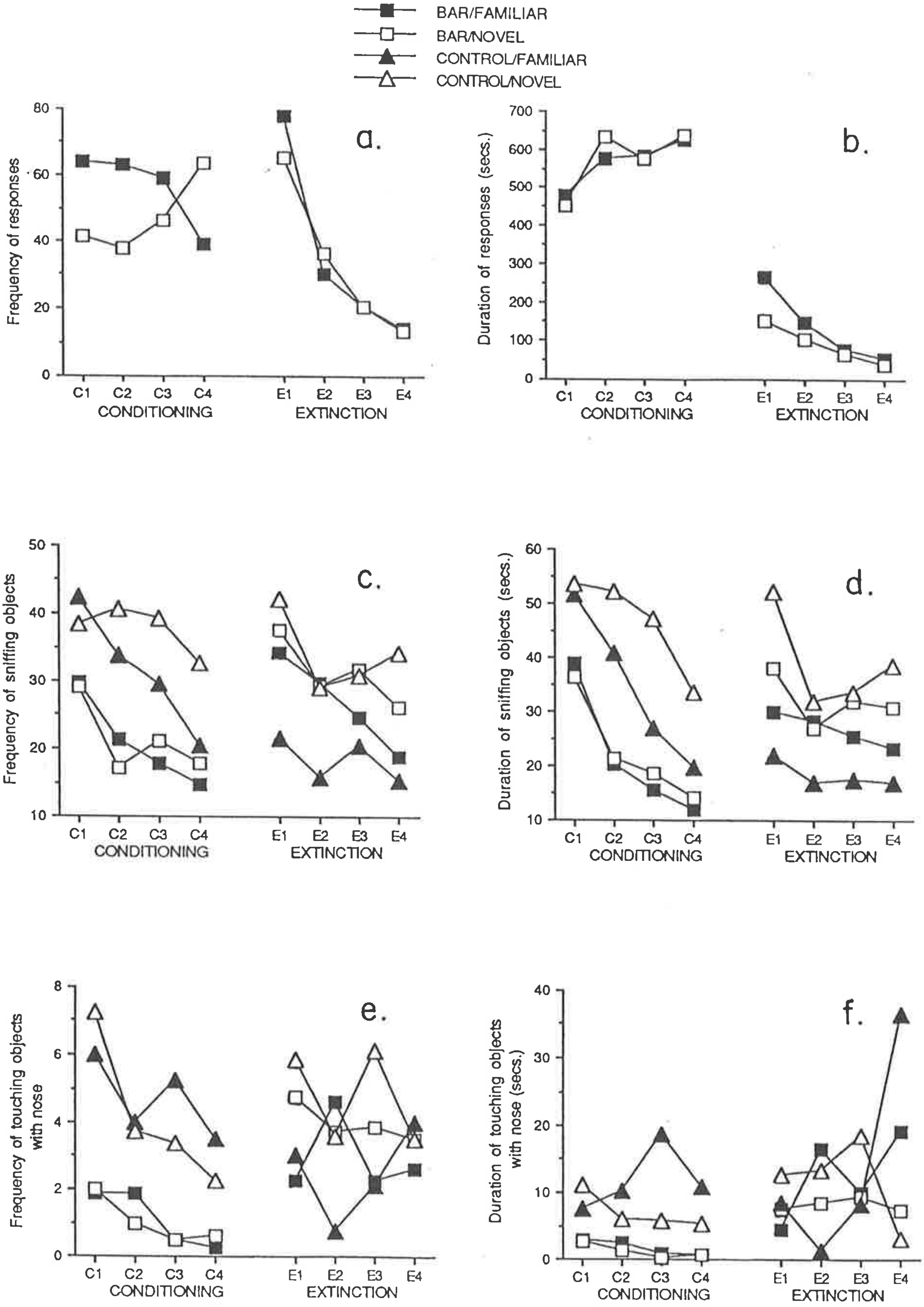
APPENDIX 5.1(II)

Frequencies and durations of behavioural measures in experiment 1.



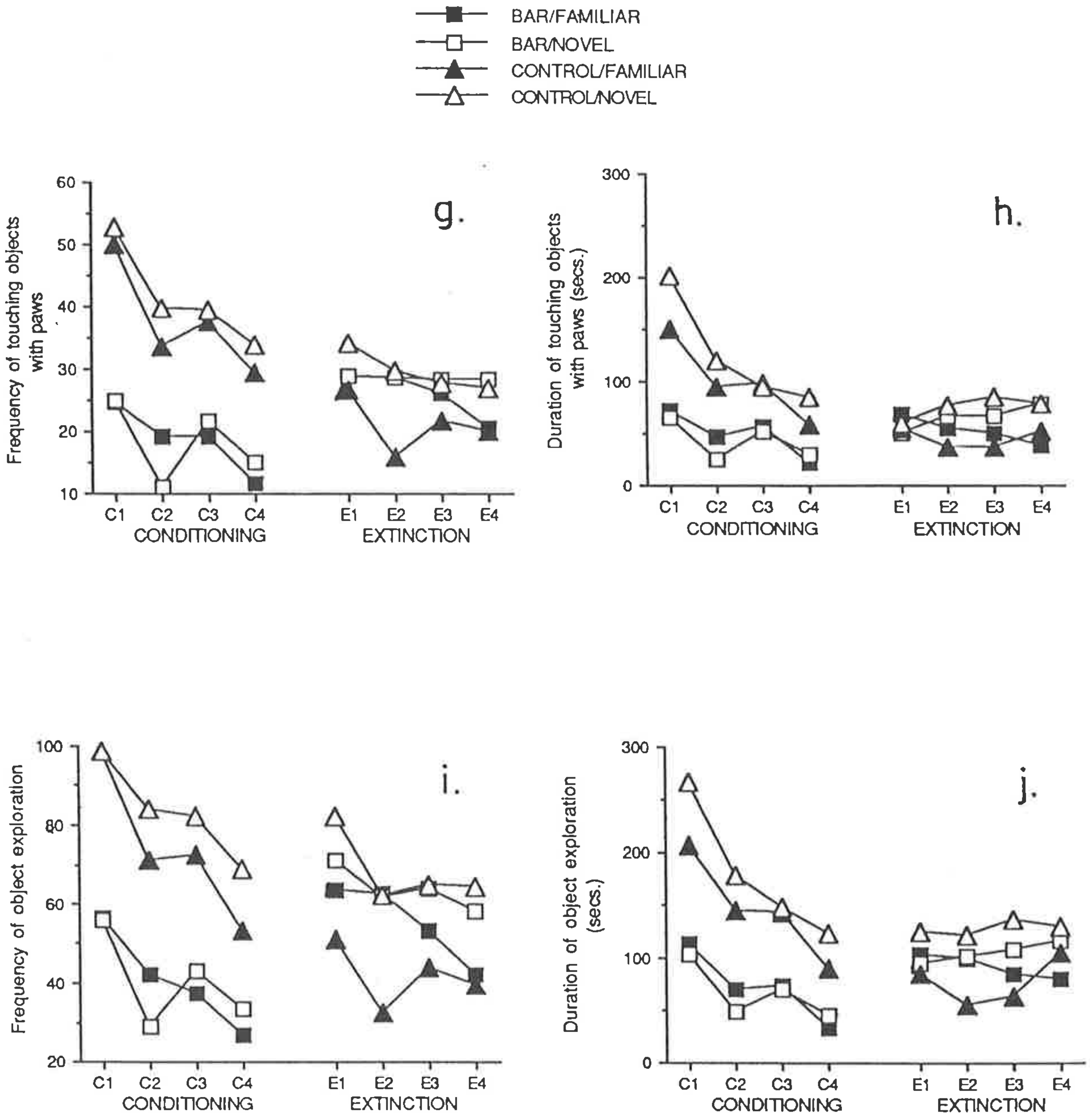
APPENDIX 7.1(I)

Frequencies and durations of behavioural measures in experiment 4.



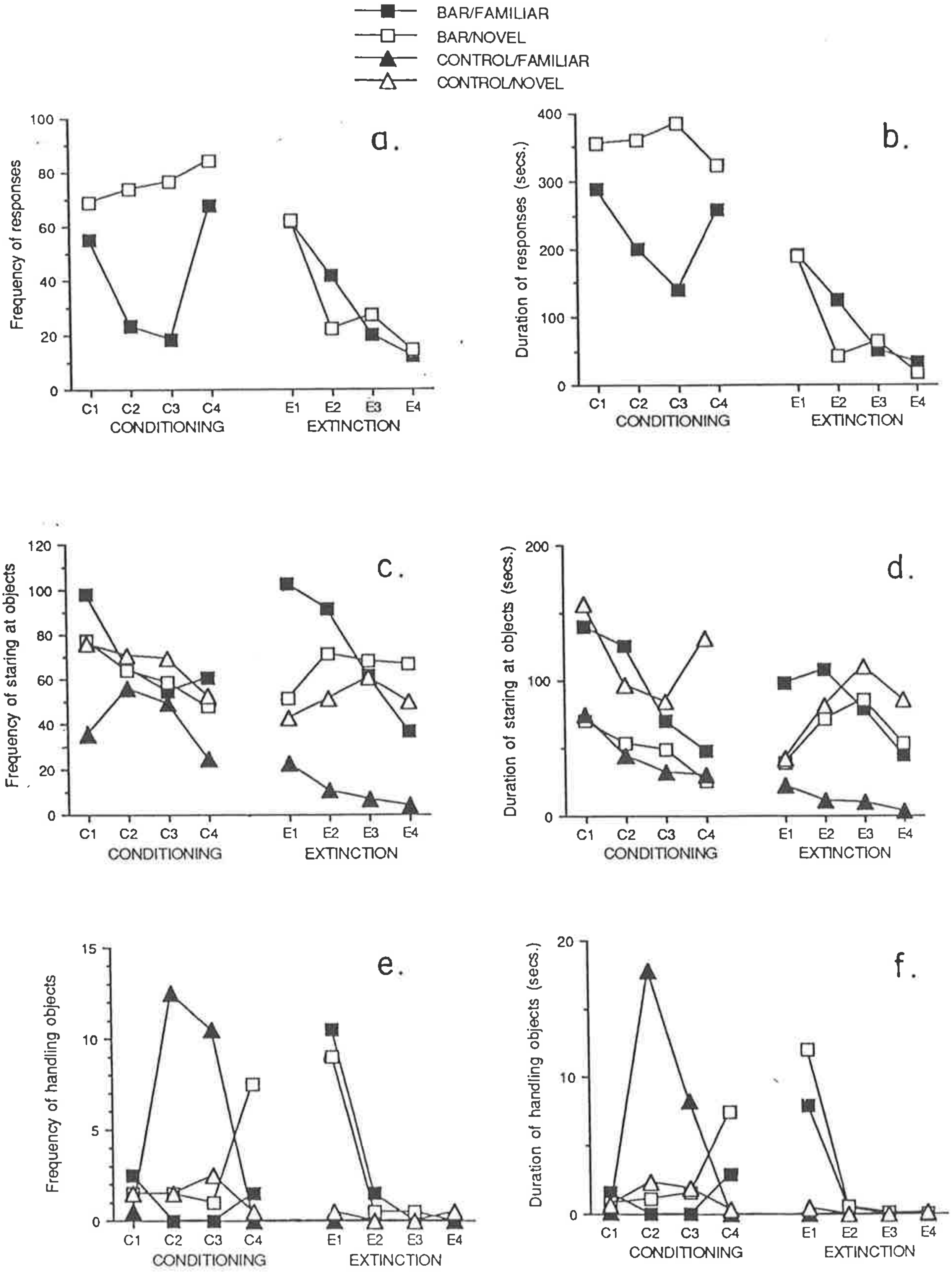
APPENDIX 7.1(II)

Frequencies and durations of behavioural measures in experiment 4.



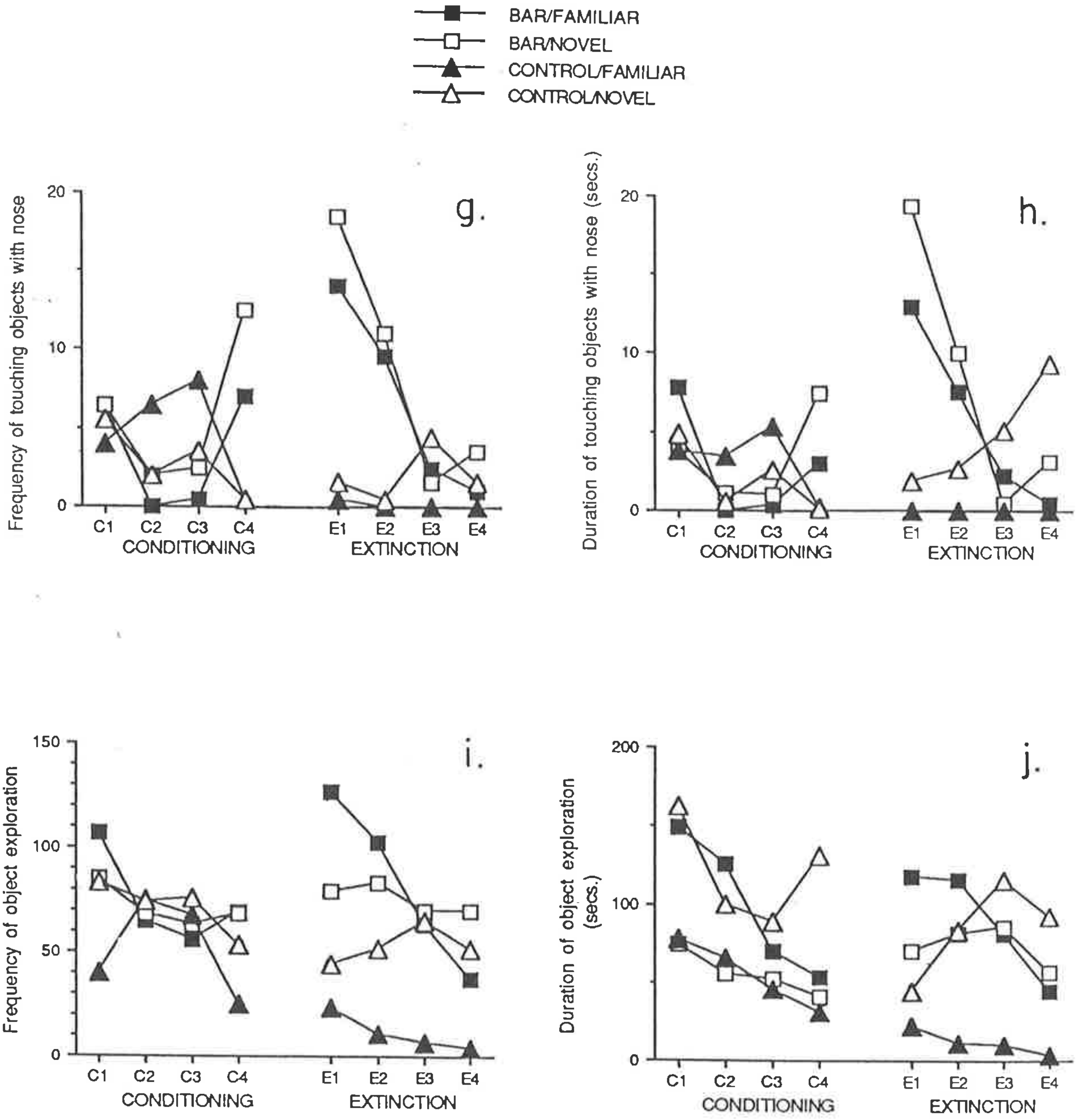
APPENDIX 7.2(I)

Frequencies and durations of responses and object-directed behaviours in experiment 5.



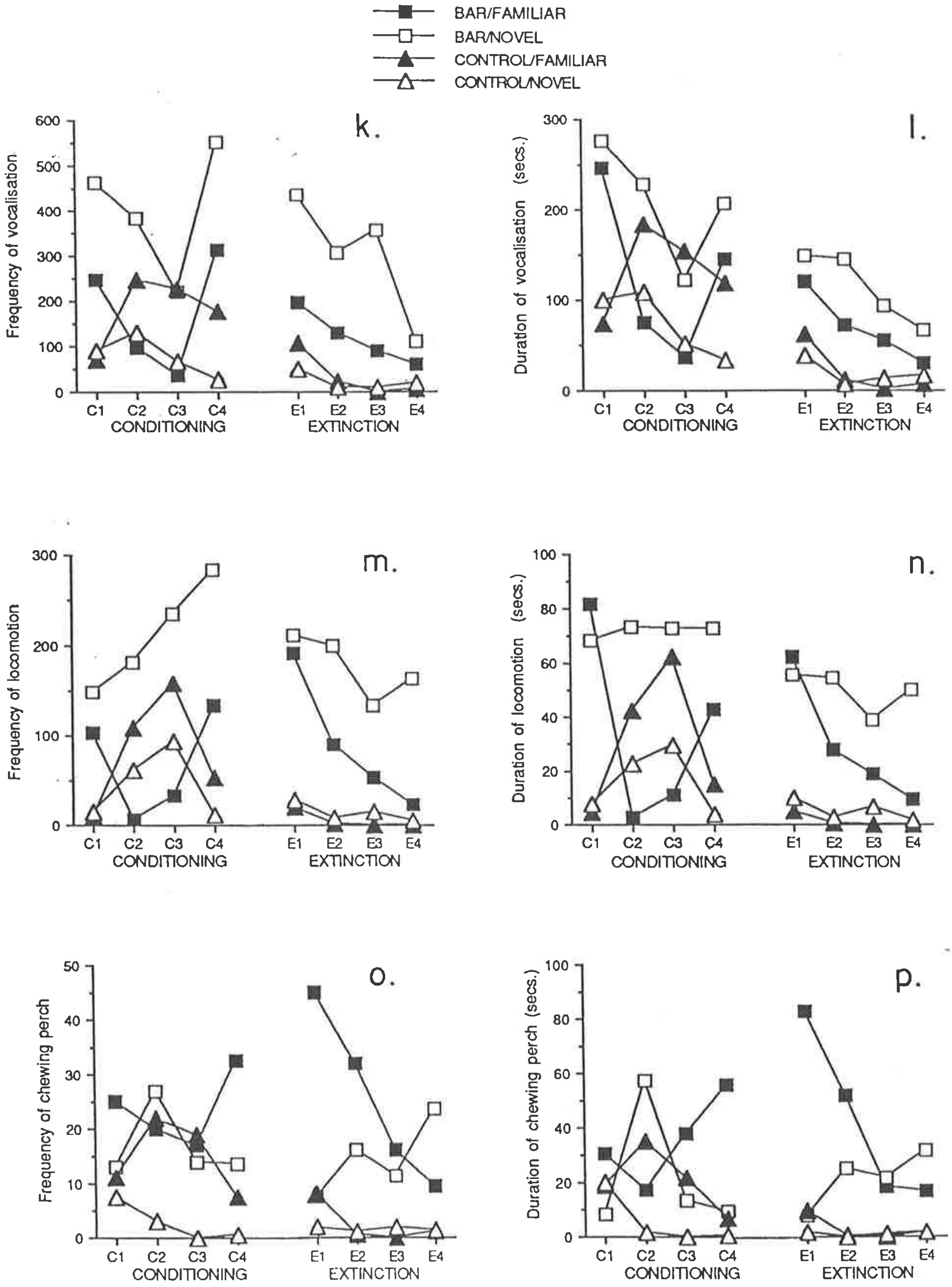
APPENDIX 7.2(II)

Frequencies and durations of object-directed behaviours in experiment 5.



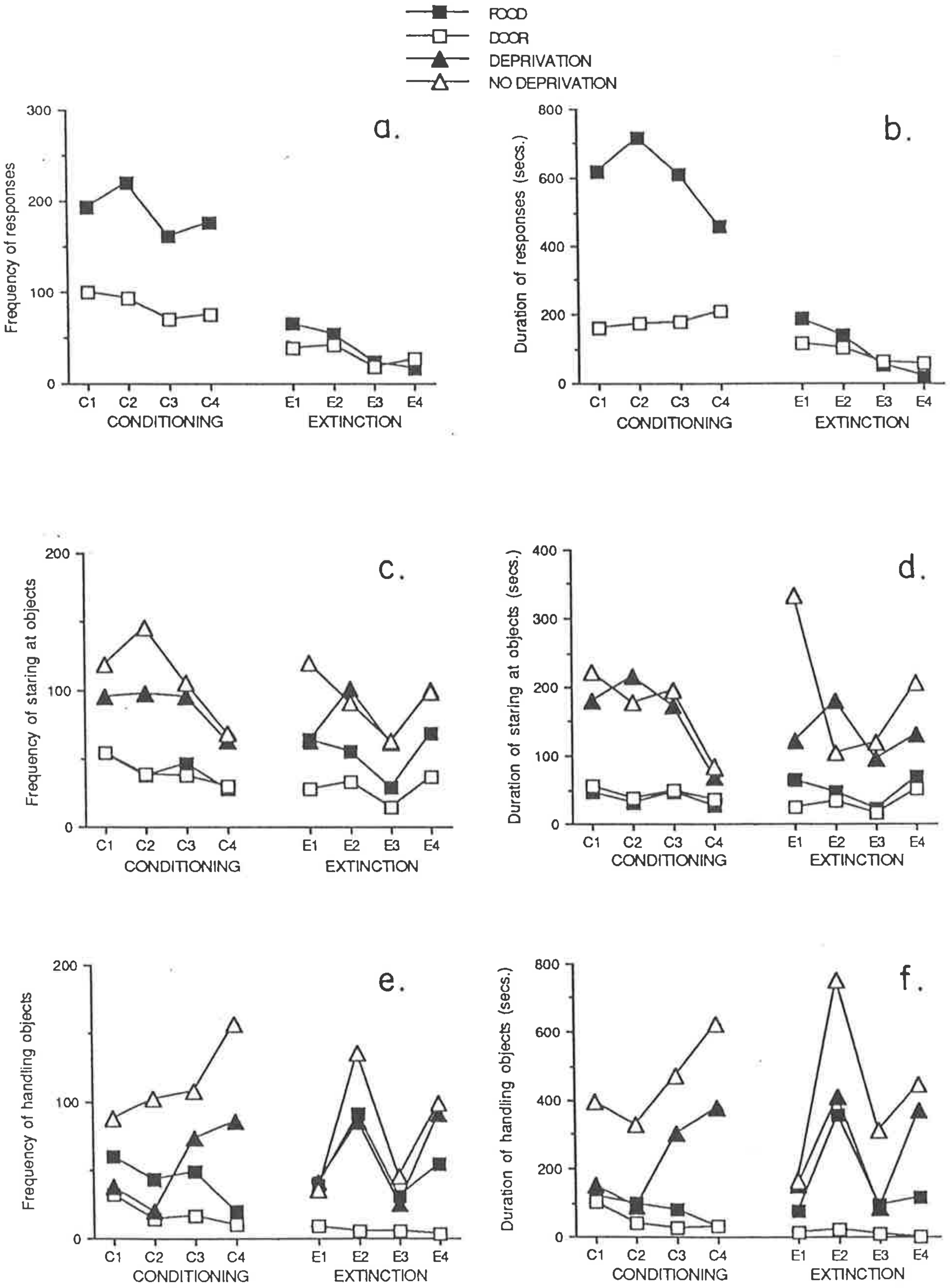
APPENDIX 7.2(III)

Frequencies and durations of non-object-directed behaviours in experiment 5.



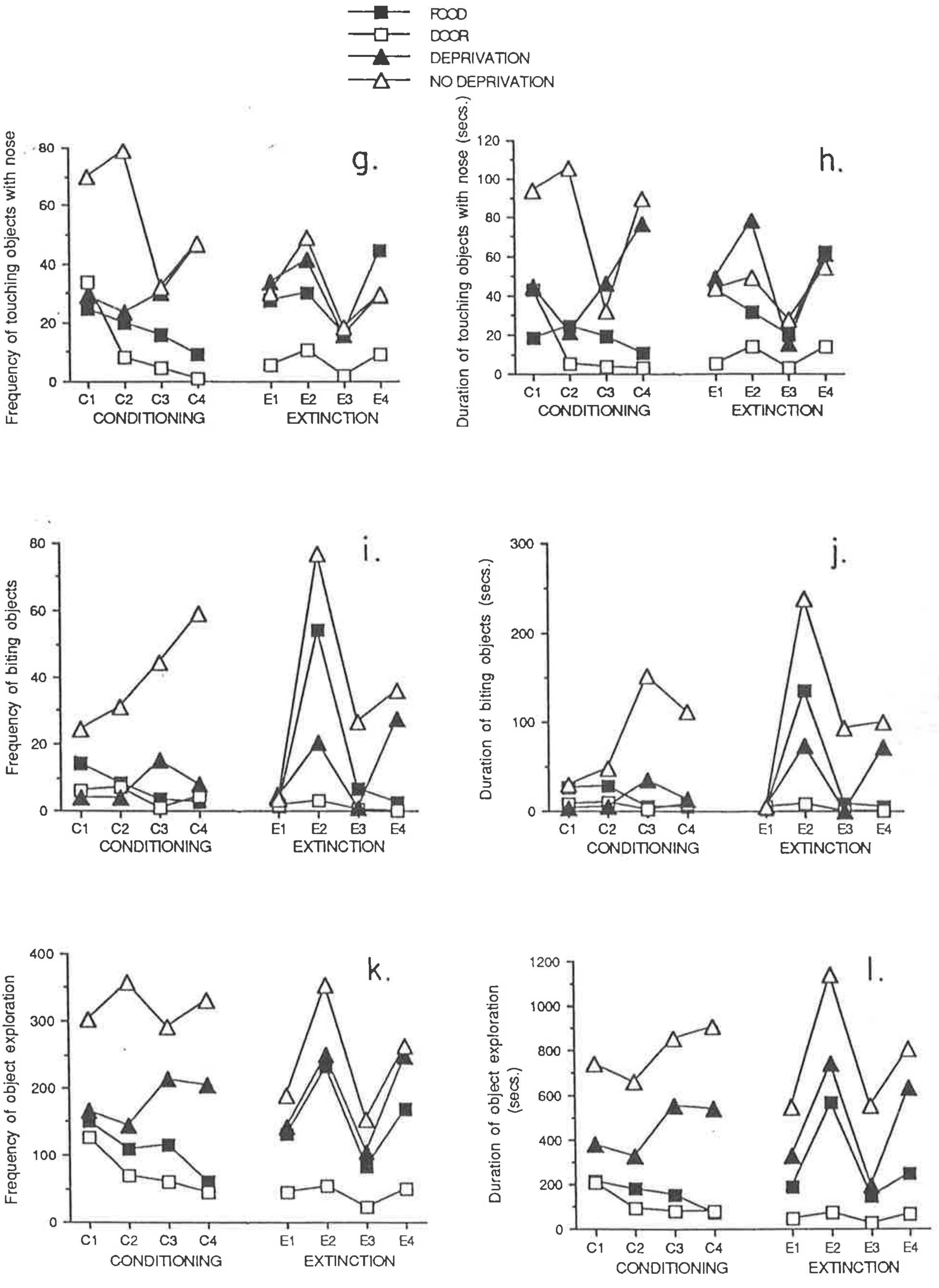
APPENDIX 8.1(I)

Frequencies and durations of responses and object-directed behaviours in experiment 6.



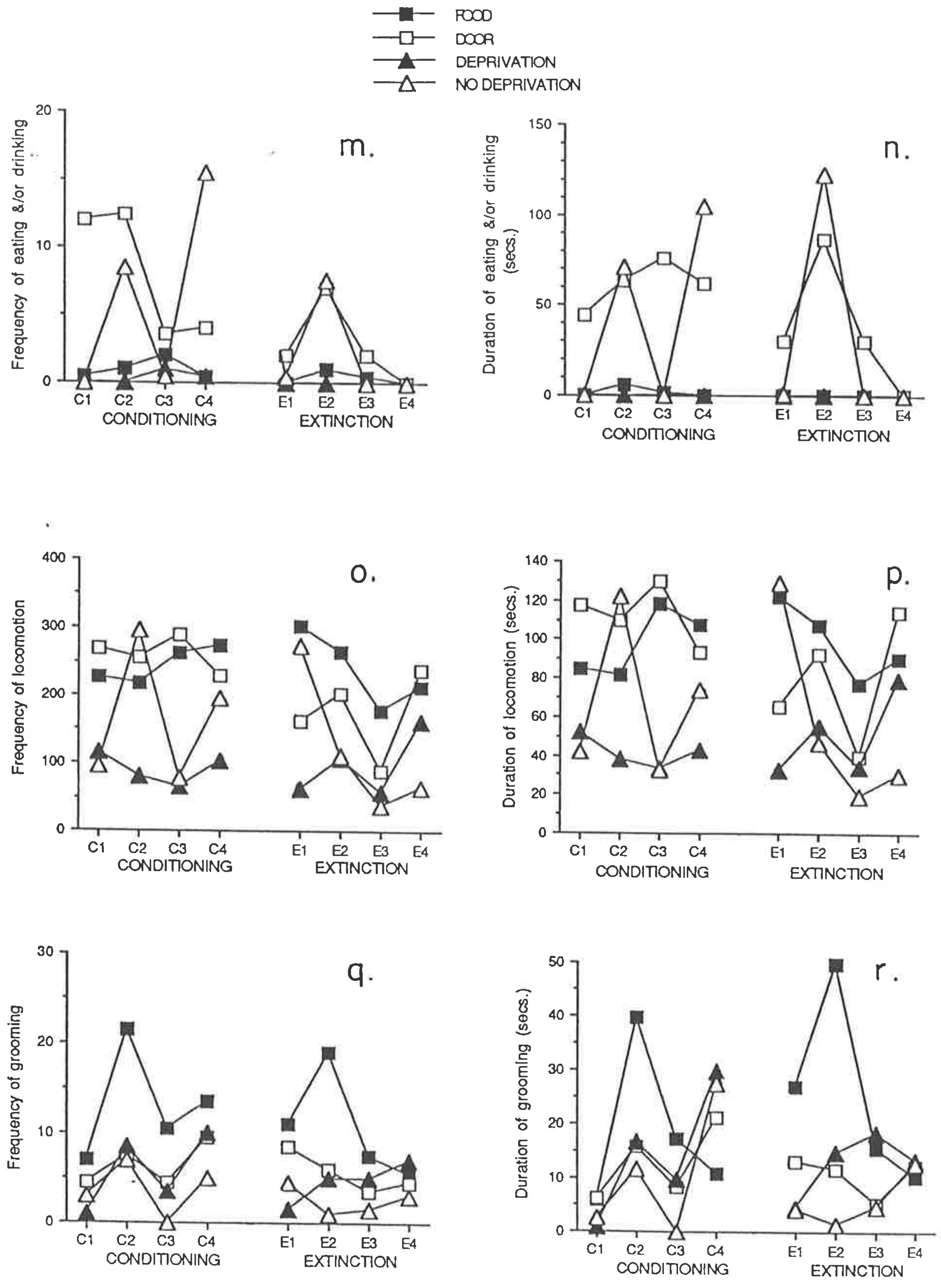
APPENDIX 8.1(II)

Frequencies and durations of object-directed behaviours in experiment 6.



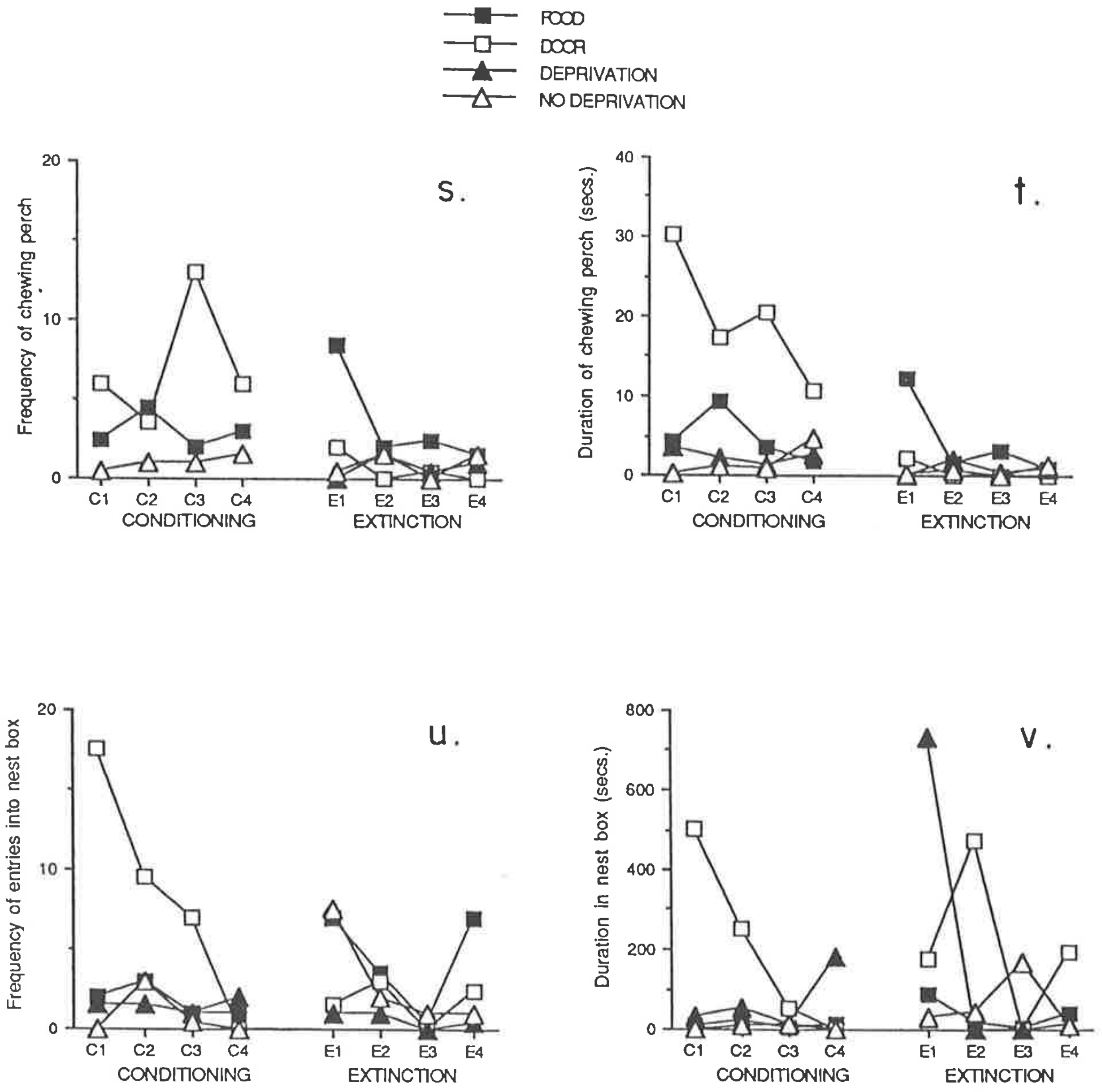
APPENDIX 8.1(III)

Frequencies and durations of non-object-directed behaviours in experiment 6.



APPENDIX 8.1(IV)

Frequencies and durations of non-object-directed behaviours in experiment 6.



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