Detecting motion trajectories: How do perception and action use visual information?

Marlon Blencowe

October 2020

*Thesis submitted in partial fulfilment of
the Honours degree
in
Psychological Science (Honours)
School of Psychology,
University of Adelaide*

Word Count: 9452

Contents

List of Figures

Abstract

Whenever a person moves to intercept an object, they engage in a complex set of predictions, about the object's trajectory, and about the set of motions required to intercept it. However, the way that people use perceptual information to intercept rapidly moving objects is currently not well understood. This is because the problem is multifaceted, as there are delays in receptor transduction, neural conduction, processing and muscle activation. There is considerable as to how the two systems interact, there is some evidence that they do (Watamaniuk & Heinen, 2003). In order to assess the differences between trajectory prediction for perceptual judgments and pointing movements we examined participants using the same stimulus, a moving random dot cinematogram (Watamaniuk & Heinen, 1999; Williams & Sekuler, 1984), which was manipulated across conditions. We used a within subjects repeated measures design to compare participants' performance on two tasks, a perceptual (two alternative forced-choice) task and a pointing task ($N = 6$). For both tasks we assessed participants' precision in extrapolating the trajectory of the cinematogram, as well as their response latency. If the two systems use the same visual information, we would expect that precision for each task changes similarly across the conditions. We found similar patterns of error for both tasks, with lower durations and higher bandwidth motion signals displaying greater directional error. This provides further insight into how we use visual information to guide movement. In particular, it provides insight as to how differences in motion perception affects interceptive movements.

keywords: motion perception, vision-for-action, predictive mechanisms, sensorimotor integration, goal-directed movement

Declaration

This thesis contains no material which has been accepted for the award of any other degree of diploma in any University, and, to the best of my knowledge, this thesis contains no material previously published except where due reference is made. I give permission for the digital version of this thesis to be made available on the web, via the University of Adelaide's digital thesis repository, the Library Search and through web search engines, unless permission has been granted by the School to restrict access for a period of time.

Signed: .... Date: 20/10/2020

Contribution Statement

In writing this thesis my supervisor and I collaborated to generate research questions of interest to assess previously collected data. My supervisor designed and programmed the experiment in collaboration with Dr. Scott Watamaniuk of Wright State University, and they also wrote the software routines to prepare these data for statistical analysis. I conducted the literature search, statistical analyses in jamovi and generated all graphs in RStudio. The experiments were conducted between my supervisor's lab and Dr. Scott Watamaniuk's lab at Wright State University in the United States. I wrote up all sections of the thesis.

Acknowledgements

1. Introduction

People have amazing precision when intercepting moving targets, which is surprising given the speed of the nervous system (Brenner & Smeets, 2015). Interception of moving objects involves different sources of information that need to be brought together. To determine the future position of an object we must predict its trajectory from its current motion. Similarly, in order to make a reaching movement towards an object we must calculate the current position of our arm, the future position of our arm required to intercept the object, then calculate the muscle expansions and contractions (or muscle torque) need to make the movement. There is currently no complete explanation as to how this process is accomplished. This paper will first look broadly at theories of motion perception and motor control, then more closely at how these systems interact, with a focus on the predictive components of these accounts before discussing experimental findings around trajectory prediction and interception strategies. We then outline the current study which aims to further examine the way that trajectory extrapolation in motion perception interacts with interception strategies.

1.1 Motion perception

1.1.1 *Models of motion perception*

Before intercepting a moving object, a person must first detect that the object is in motion. There are a few different models of motion processing. Most involve the use of a "motion sensor" that detects and tracks the direction of changes in luminance over time. These include models based on Reichardt detectors (e.g. Santen & Sperling, 1985), Adelson and Bergen's (1985) energy model and Grzywacz et al.'s (1995) network model.

The earliest model for a motion detector was the Reichardt detector that was constructed through studying motion perception in flies (Reichardt, 1967). Reichardt detectors use a simple mathematical model to compare incoming retinal signals with

delayed retinal signals and from this can determine whether a tracked object has moved from one location to another. Santen and Sperling (1985) propose an elaborated version that incorporates spatial input filters instead of Reichardt's point-based detector, creating a model for motion detection out of a series of detectors.

Adelson and Bergen's (1985) energy model, rather than using a delay and compare system, uses a measurement of motion energy information. This model has two stages, an initial stage of spatiotemporally oriented linear filters tuned in spatial frequency. Pairs of these filters, 90 degrees out of phase with each other (quadrature pairs), are squared and summed resulting in a measure of motion energy which can account for directional selectivity in a way that a simple Reichardt detector cannot. Their approach can account for the same results of Reichardt detector-based models but posits a qualitatively different way of thinking about motion detection.

How is this simple motion detected represented in the brain? Newsome et al. (1989) looked at motion perception in monkeys, finding that neural performance from single cell recordings showed similar performance to psychophysical thresholds. Using a similar stimulus to the one in the present study (a random dot cinematogram) they varied the amount of signal dots moving coherently (i.e. moving in the same direction) against a field of randomly moving dots. By varying the ratio of signal to noise dots they were able to determine a measure of neuronal activity and a perceptual threshold. Neuronal performance was found to detect the motion as well as the monkeys' psychophysical performance, indicating it is possible that the activity of a small group of neurons is responsible for detecting motion signals.

Building on the results of Watamaniuk et al. (1995), Grzywacz et al. (1995) propose any model based on local motion detectors will not be able to account for the data on our ability to detect motion trajectories in noise. A motion trajectory in this case was the displacement of a dot in a constant direction over successive frames. Watamaniuk et al. (1995) used a random dot cinematogram similar to those explained above, though rather than varying the amount of dots moving coherently they used a single dot against noise dots and varied both the step-size (how far the dots were

displaced frame by frame), the duration, noise density as well as the shape and temporal structure of the trajectory. Grzywacz et al. (1995) constructed a network trajectory model to explain this phenomenon, as other models were unable to account for the results.

This model involves three stages, a local stage, similar to the above elaborated Reichardt or motion energy models, followed by a coherence stage and finally an outlier selection stage. As the local stage is akin to the models already discussed we will discuss the latter two stages here, the coherence stage and outlier stage. The coherence stage involves accumulation of rough directional information from adjacent cells over time through a network. The outlier stage, which is a more high-level, potentially cognitively influenced stage, accounts for outliers across multiple coherence stage neighbourhoods. In doing so this model is able to account for extended trajectories in noise that the other models based only on local integration stages or those based on "position cues" (essentially detecting motion as forming a "shape") are unable to account for.

It is important to consider this type of model of motion perception when looking at manual interception, as interacting with moving objects often involves predicting motion over large spatial expanses. While these models only discuss motion perception and the tasks involved do not involve either eye or hand movement, they give us indications as to an important building block in determining how we intercept moving objects.

1.1.2 *Local versus global motion*

Most important to note about the models in these studies is that in order to integrate direction information from across local receptors an integration time of 80-120ms is required (Grzywacz et al., 1995). This gives us a limit on how quickly trajectory information can be determined, which informs the amount of time a motion signal must be present for the perception of direction. When using a RDC there are several ways to manipulate a motion signal to examine integration time. One is to manipulate the

duration of the signal (which is the number of frames shown in succession divided by the frame-rate) (Watamaniuk et al., 1989). Another is to manipulate the directional noise bandwidth, or the distribution of directions. For example, uniform distributions of directions up to 180° around a mean direction have been shown to be produce a percept of motion in the mean direction of the dots (Williams & Sekuler, 1984). These have been shown to decrease direction discrimination thresholds, but only at bandwidths higher than 17° and very low durations (Watamaniuk et al., 1989).

1.1.3 *Motion prediction and ensemble processing*

One way of looking at the integration of motion signals is as an example of a more general strategy that the brain uses, that of ensemble perception (Whitney & Leib, 2017). This theory is used in an attempt to explain findings on demonstrating the limited amount of information available to awareness (Cohen et al., 2016). Whitney and Leib (2017) demonstrate many examples of situations in which visual information is likely represented in the form of a summary statistic. Both motion trajectory extrapolation and ensemble perception involve what can be thought of as predictive components. For example, the averaging process performed in the perception of a random dot cinematogram can be seen as a prediction being made about the direction of any one dot in the signal.

These strategies demonstrate examples of the leveraging of statistical regularities in the environment to encode information more efficiently. This will become important when we later discuss predictive coding and active inference in section 1.4.2.

Having looked at motion and different facets of direction discrimination in vision, the next section will look at theories on the working of the motor system, with an eye to examining the interaction between the two systems.

1.2 Motor control

To understand how the motor system interacts with motion perception, we need to understand the calculations the motor system performs by looking at some mo-

tor control models. First, we need to consider the fact that the eyes, hand, torso and the objects we interact with are all positioned differently. Second, these models need to take into account the "curse of dimensionality" - "vividly illustrated if we consider the 600 or so muscles in the human body as being, for extreme simplicity, either contracted or relaxed. This leads to 2^{600} possible motor activations, more than the number of atoms in the universe." (Wolpert & Ghahramani, 2000, p. 1212). This is further complicated by the fact that motor plans are underconstrained (Sober & Sabes, 2005; Wolpert et al., 2011) meaning that given infinite possible trajectories and infinite possible paths, at each point along that path there are a huge number of possible joint angle combinations (Harris & Wolpert, 1998). In order to do this, we must discuss different reference frames, both for perception-action interaction and for motor control.

1.2.1   Reference FRAME TRANSFORMATIONS for MOVEMENT planning

Where the trajectory extrapolation of a perceived motion signal amounts to a prediction about the future position of the signal, a reaching movement to intercept an object is a prediction about the necessary future position of the hand. A person engaging in manual interception of a moving object is engaging in the estimation of two trajectories (that of the object and that of the hand) (Fiehler et al., 2019). These are potentially encoded in two different reference frames (Goodale & Milner, 1992; Schenk, 2006).

Why two different reference frames? In order to determine the trajectory of a moving object a person needs to perceive that object is in motion (see the above discussion of motion detectors), the coordinate frame that this occurs in is not explicitly relative to the observer, but rather the object is seen relative to its past position (though there are exceptions, for example, objects approaching the observer, for which the rate of expansion would be a more relevant metric, Lee and Reddish, 1981). This reference frame is generally referred to as being allocentric (Crawford et al., 2011). This must then be converted into an egocentric reference frame (one centred on the hand, or the

hand's position relative to that of the eye) where the absolute size and spatial location of the object is relevant. Why is this important? The easiest way of demonstrating the importance of this conversion is to think about how people achieve the correct grip aperture to engage with objects. Relative spatial relationships in retinocentric (or eye-centred) coordinates, while useful for making perceptual judgments of size, shape or direction of motion, are not easily turned into motor commands as motor commands must conform to the exact dimensions of an object. There are several different explanations for how this transformation occurs (see section 1.3).

1.2.2 *Neural underpinnings of reference frame transformations*

There is evidence that movement planning occurs in eye centered coordinates (Batista et al., 1999; Buneo & Andersen, 2006). There are neurons in posterior parietal cortex, specifically the area referred to as the parietal reach region that encode hand position and eye position in eye centered coordinates (Buneo & Andersen, 2006). Buneo and Andersen (2006) refer to this area as "encoding a 'displacement vector in eye coordinates'" (p. 2596). They argue that this displacement is encoded in a way such that systems responsible for moving the eyes and the hand are able to access a single information source that each system decodes relative to itself (because when viewing activations, this relationship goes both ways). There is also evidence that there are neurons in the PPC that encode both hand and eye position and appear to be involved in reference frame transformations (Buneo & Andersen, 2006).

1.3 Vision-for-action and vision-for-perception

One prominent theory as to how visual perception and movement interact suggests that the brain splits visual information across two streams, one for action, one for perceptual judgment. Goodale and Milner (1992) proposed, building on the work of Ungerleider and Mishkin (1982), that there is an anatomical separation between two streams. One being a ventral stream that projects from striate cortex to inferotemporal cortex that facilitates the perceptual identification of objects the other a dorsal

stream from the striate cortex to the posterior parietal cortex that facilitates visually guided movement. These streams are sometimes seen to correspond respectively to the allocentric and egocentric coordinate systems mentioned above (Schenk, 2006).

This theory has come under some scrutiny, with many suggesting the distinction is poorly characterised (Schenk & McIntosh, 2010). One convincing case made by Smeets and Brenner (2010) is that rather than requiring a dorsal visual stream, proprioceptive position information can be combined with allocentric visual information, creating a system that is more robust to errors (as error signals from either modality can apply to the other). This is echoed in the idea that the dorsal stream is better viewed as a centre of multimodal sensory integration, rather than being explicitly "visual" (Jackson, 2010). It also accords more closely with the findings around neural representations of reference frame transformations above.

Having looked at motion perception and some of the interactions between perception and action in the next section we will discuss some models of motor control.

1.3.1 Models of MOTOR control

We will consider two different paradigms of motor control, the presently dominant paradigm, optimal control theory (Friston, 2011), and specifically the use of internal forward models combined with feedback mechanisms (Todorov, 2004; Todorov & Jordan, 2002) and one based on predictive coding (Adams et al., 2013; Friston et al., 2010; Friston et al., 2011). Both accounts are solving some of the same problems, so these will be discussed first.

In addition to the idea that there are different reference frames that must be computed to engage in a reaching movement towards an object, there are also different kinds of information that must be used. A kinematic transformation involves the coding of the current state or placement of the limb in space in terms of joint angles. In order to make a reaching movement, a person must determine where their arm is presently located, this is known as an inverse kinematic transformation. They must then determine the transformation required to perform the reaching movement, this

is known as a forward kinematic transformation. To get there though, this trajectory must be turned into a set of torques and subsequently a set of muscle activations to actuate the movement, this is called a kinetic (or dynamic) transformation. (Sober & Sabes, 2003; Wolpert et al., 2011)

These are also sometimes referenced relative to the reference frames mentioned earlier, with visually based allocentric and egocentric coordinate systems referred to as extrinsic and information based on the proprioceptive system (e.g. muscle lengths, joint angles) as intrinsic (Wolpert et al., 2012).

The dominant theory for understanding motor behaviour currently is optimal control theory (Friston, 2011; Todorov, 2004). This theory is powerful in that unlike other theories of motor control that require more detailed inputs in order to model movement, optimal control theory takes a goal state (e.g. an object that needs to be intercepted through a certain kinematic transformation) as an input and searches for the control strategy that achieves optimal performance (Todorov, 2004). This technique is used in other fields and involves minimising or maximising a predefined performance criterion or mathematical function (Umberger & Miller, 2017). This strategy is useful because it allows systems to "solve a control problem completely rather than complete its solution" (Bernshtein, 1967 in Todorov, 2004, p. 908). In other words, the way that you get to a solution is dynamically controlled rather than having to to calculate each solution individually.

1.4 Prediction across systems

Having discussed some of the more dominant models of motion perception and motor control, it's informative to discuss these in the context of more general theories of how our brains process information. Trajectory prediction and manual interception of moving objects are notable as they constitute a particularly salient instance of prediction. Prediction is thought to be a more general strategy we use to interact with the environment (both because of its efficiency and its ability to account for neural delays). One theory as to how the brain engages in predictions is that of predictive

coding and for motor control, active inference. The following section touches on the basics of predictive coding and active inference and some alternative ways of thinking about the role of prediction in motor control.

1.4.1 Predictive coding

Predictive coding models are a system for looking at cortical architecture in a general sense that offer a somewhat different perspective on perception and in particular on motor control than other systems (Mumford, 1992). While there are many different variations of predictive coding they all possess the following characteristics (Shipp, 2016). They all involve the generation of models refined by sensory data. These models are hierarchical, in that they involve gradual levels of abstraction. They use error signals derived from sensory data in order to refine the model. It is important to note that this prediction is not the prediction of the future state of the system, but rather a prediction about what *is* likely to be happening in adjacent areas of the cortical hierarchy (Hogendoorn & Burkitt, 2019). Rao and Ballard (1999) have used the approach to computationally model vision in a way that accounts for some effects that other models have difficulty accounting for.

1.4.2 Active inference

An alternative viewpoint on motor control derived from predictive coding, is that of active inference (Adams et al., 2013; Friston et al., 2010). Where predictive coding schemes generally minimize errors by using sensory information to change predictions, in active inference the motor system minimizes prediction errors by engaging in actions to produce predicted sensations (Friston, 2011). One advantage of this predictive coding scheme in explaining hand motion is that it does not require an optimality criterion (Adams et al., 2013; Friston, 2011). Adams et al. (2013) posit a theoretical argument about the anatomy of the motor system, arguing that where traditionally we would view motor control as the production of motor "commands" as mentioned above, it would make more sense to think of the motor system as making

and fulfilling sensory "predictions". This method ties into the above ideas around ensemble prediction and trajectory extrapolation. In all cases sensory signals are expressed as top down predictions that are updated through sensory stimuli.

1.5 Manual Interception

Given that manual interception of moving objects is an informative example of humans using prediction, how do we do it? The following section looks at some more experimental findings that are important considering the above discussion of different models of motor planning. There are conflicting ideas on how we are able to engage in accurate manual interception of moving objects. Though this ability does appear to be somewhat task-dependent (Zago et al., 2009).

Having looked at theories of motion perception, motor control, as well as some theories as to how the two interact we will discuss closer to the present study. An important consideration in much of the experimental literature on interception is whether people predominantly use online (sometimes referred to as continuous) control in which sensory signals constantly update movements or pre-programmed (or model based) control in order to guide their movements, in which more of the movement is planned in advance (Brenner & Smeets, 2018; Zhao & Warren, 2015). What is considered in these types of studies is how rapidly visual information is acted upon to guide movement. This is difficult to study because the outcome of either method might be similar. There is conflicting evidence as to whether this is possible. There are some findings suggesting that we mainly use model-based control for example when intercepting falling objects that had their trajectories occluded, participants were no less accurate (Scaleia et al., 2015). Some suggest that the use of model-based control might predominate for certain tasks (for example, hitting a ball, e.g. Tresilian, 2005). Others suggest that online control is essential particularly as people seem to keep their eyes on objects until just before their interaction with it is complete (Brenner & Smeets, 2018; Land, 2009). Brenner and Smeets (2017) suggest that we combine both model-based and online control, using a model that we continuously update.

Work on interception in natural environments has shown varying results, and the methods used are increasingly considered to be task dependent (Zago et al., 2009). While there is evidence that the last portion of visual information about a trajectory is not used (Bosco et al., 2015; Zago et al., 2008, 2009), there is also evidence that depending on the task it is possible to intercept very briefly presented targets (Mrotek et al., 2004). There is also evidence that predictive information could be different for eye movement and manual interception (Bosco et al., 2015; Eggert et al., 2005; Wexler & Klam, 2001). Our experience with gravity might also have an effect (Brenner et al., 2016). These findings indicate task-dependent use of visual information. This makes sense if we think of seeing as a way of acting within an environment (Gibson, 1979; O'Regan & Noë, 2001). The next section will discuss the current study into how visual information and motion trajectory extrapolation differs across modalities.

1.6 The present study

Previous studies using a similar stimulus to the one used in the current study have shown that when looking at the difference between perceptual thresholds and smooth pursuit eye movements there is a similar amount of internal noise between the perceptual and oculomotor systems (Watamaniuk & Heinen, 1999). Contrary to the above suggestions around differences between vision-for-perception and vision-for-action this would suggest that the same information is being used by each system, at least in this circumstance. There is also evidence that the quality of visual information at the outset and throughout a reach is a more important predictor than motor noise as to the precision of a movement (Ma-Wyatt & McKee, 2006, 2007).

The present study aims to investigate the way that we extrapolate trajectories from motion information by varying the motion signal in a similar manner to that done in Watamaniuk and Heinen's earlier experiments on oculomotor performance. To accomplish this we conducted an experiment involving two tasks, a perceptual task and a reaching task using the same stimulus (a random dot cinematogram). We compared visual thresholds with hand direction error and precision to determine whether

changes in the quality of the visual information were reflected similarly in the precision of psychophysical judgments and reaching performance. Previous experiments suggest the quality of the visual information should be the limiting factor on motor performance. As an additional parameter we looked at two different interception points (in the form of circles at which the imagined stimulus trajectory had to be extrapolated to). We also investigated the extent to which degraded visual information affected the timing of movements, in order to determine whether the timescale of reaching (in movement latency and time) was affected by the quality of the visual information. Especially whether the time required for integrating signals with a large amount of directional noise resulted in an increase in movement time or latency.

Based on previous findings, we expect that shorter durations and increased directional noise will result in decreases in precision for both the perceptual and reaching task and that these two parameters will interact. We also expect that directional noise will result in longer movement latencies and movement times for the reaching task, as the motion signal will take longer to integrate. In addition, participants should show less precision in the 25° circle than the 12° circle as there is a wider area extrapolated across.

2. Method

2.1 Participants

A total of six participants completed both the perceptual task and the touch task, one of whom was involved in programming the experiment, the remainder of whom were naïve to the purposes of the experiment. All participants were right-handed and had normal or corrected to normal vision, no participants had motor deficits.

The study received ethics approval from the University of Adelaide School of Psychology Ethics Committee, and the Institutional Review Board of Wright State University (USA) which is the American equivalent of an Australian ethics committee. Participants could withdraw their consent at any point during the experiment without penalty.

2.2 Apparatus

The experiments were run on a computer with an Intel(R) i7 processor running at 3.07 GHz, with 12 GB RAM, running Windows XP, using custom software written in Matlab with extensions from the Psychophysics toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). Stimuli were displayed on and touch responses collected using a 17" ELO screen with a 1024 x 768 resolution and a 75Hz refresh rate with an overlaid touch responsive layer. A keyboard was used to collect responses for the perceptual task. A chin rest was secured to the table, to allow the participant to comfortably rest their chin while completing the experiment at a viewing distance of 40cm. A computer mouse was secured to the desk with Velcro, directly in front of the chin rest and in line with the participant's midline.

2.3 Stimulus

The stimuli used were random dot cinematograms that measured 12 degrees of visual angle in diameter. This consisted of a field of dots that moved from frame to frame. See figure 1.

Figure 1
The Stimulus

12° circle   *25° circle*
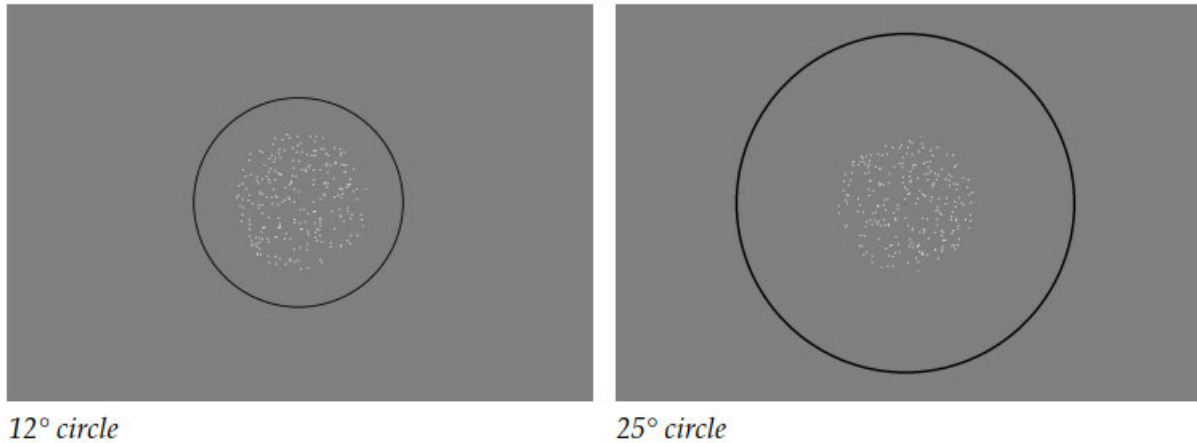
*Note.*White dots in the center are the random dot cinematogram. The outer circle is the circle that the signal was the signal to be intercepted in the reaching task. A mark was placed on the out circle for the perceptual task.

Four parameters were manipulated for each of the two tasks. These were the number of frames displayed (i.e. the duration of the stimulus - 4, 6 or 12 frames, corresponding to 50, 80, 160ms), the directional noise bandwidth (0° or 160°), the direction of the motion signal (180°, 225°, 270°, 315°, 360° (referred to throughout as 0°) and the diameter of the surrounding circle (12° or 25°).

2.3.1 Directional Noise

Directional noise was added by varying the direction of the dots around a mean direction. Two noise bandwidths were used, a 0° bandwidth, in which all of the dots moved in the same direction and 160° bandwidth in which the dots varied their directions randomly from frame to frame within a 160° range, again with the same mean direction.

2.4 Procedure

A within subjects, repeated measures design was used. Each participant completed both the perceptual and pointing tasks. Participants completed two blocks for each pointing condition, which was equivalent to 20 repeats of each condition at

each of the 5 directions. The order of tasks and conditions was not identical across participants. Data were collected at the University of Adelaide and Wright State University (USA) on comparable equipment, across separate sessions between 2016 and 2019. Data in Adelaide were collected in the same period across the end of 2016 and early 2017. Data from Wright State were collected in 2017. The tasks are described below.

2.4.1 Perceptual Task

The perceptual task used a method of single stimuli paradigm. Thresholds measured with this task have been just as effective as those measured using a comparison interval (Morgan et al., 2000). Each trial involved the participant beginning the trial by hitting the space-bar, which would initiate the stimulus. The motion stimulus was shown, and then a target dot was shown on the circumference of the circle. The participant then pressed a key corresponding to the direction (clockwise or counter-clockwise) in which they perceived the dots were deviating from the target dot. Proportion clockwise was then collated across blocks and trials to calculate a psychophysical threshold for each condition. 5 blocks of each condition were used to calculate perceptual thresholds.

2.4.2 Reaching Task

The pointing task involved the same stimuli as the perceptual task. Participants sat in front of the touchscreen monitor with their hand on the computer mouse secured to the desk and and in line with the participant's mid-line. The participant pressed the mouse button to begin each trial once a tone was sounded to indicate the onset of the trial. The onset of this tone was randomised from trial to trial. Upon the release of the button the stimulus was presented on the screen. The participant reached and touched the screen at the point at which they believed the array of dots would intersect the circle had they continued to be visible. They were given feedback to indicate if their response was more than 2 degrees from the target direction, or too

slow (more than 1 sec for movement time). Previous work from Ma-Wyatt's lab has shown that a fast reach over 40cm will usually be in the range of 400-500ms, so this feedback was provided as a guide. As we were interested in the pattern of errors, all data were included in analyses. Data were then collated across conditions and the following measures calculated: movement latency (the time between when the stimulus appeared and the participant released their hand from the mouse button), movement time (the time from the release of the mouse button to the touch response on the screen), directional error (the direction that the participant indicated the target moved in) and the pointing precision (the variable error associated with this direction judgement).

3. Results

3.1 Data collation and processing

For the perceptual task, data were collated across all repeats of each condition, for each participant, and psychometric curves were then fitted to these data. Step sizes were consistent across all direction conditions for a given block of trials. Most direction conditions resulted in data that could be fitted with a psychometric curve. However, there were a few instances in which it was not possible to fit psychometric functions to 1 or more of the 60 conditions in a block. In those cases, the threshold estimate was removed from further analyses. This criterion resulted in the removal of 65 thresholds out of a total of 360. No more than 22 were removed from any one participant. To quantify the perceptual judgement, we converted the proportion correct to Z scores. We then took the difference between the 75 point and the 50 percent point. We used this estimate, equivalent to a d' of 1 given the psychometric curve (Ma-Wyatt & McKee, 2006) as an estimate of precision for the perceptual judgement. This fitting was carried out in Excel.

For the reaching data, we quantified movement latency as the time between the cue to start the trial and when the participant released the mouse button. Movement time was defined as the time between the release of the mouse button and the participant's finger hitting the touchscreen. The location of the touch was registered by the screen. We calculated the difference between this touch and the true location for each trial. As we were interested in how participants predicted the trajectory of the motion signal, we calculated this distance by rotating all direction locations to one axis and then calculate the distance of the deviation from that "true" direction. We included all data for analyses since as it was believed that any directional error or differences in movement latency would be informative. From this, we were able to collate the reach errors for each condition. All data processing for the reach was conducted using custom written software in Matlab.

3.2 Statistical model

All analyses were performed using a linear mixed model (LMM) conducted using the gamlj package in jamovi (Galluci, 2019; jamovi project, 2019). The fixed effects examined by each model were the duration of the signal (4, 6 or 12 frames at 75Hz), the circle circumference (12° or 25°), the direction (180°, 225°, 270°, 315°, 0) and the directional noise bandwidth (either 0° or 160°). From these models we were able to determine the amount of the variance explained by the fixed effects, expressed as the marginal R^2 value ($R^2_{GLMM(m)}$) as well as the amount of variance explained by the fixed and random effects combined, expressed as the conditional R^2 value ($R^2_{GLMM(c)}$)(Nakagawa & Schielzeth, 2013). The random effect for each of the models was to vary the intercept for each participant. The significant main effects were then further examined using post-hoc *t*-tests with a Bonferroni correction for multiple comparisons.

As there is not agreed upon way of measuring effect size for linear mixed models (see Snijders, Bosker et al., 1999, and no agreed upon method for conducting power analyses for models with fixed and random effects these were not included (Brysbaert & Stevens, 2018).

3.3 Reaching Task

3.3.1 Movement latency

First we looked at movement latency. More of the variance was explained by combining the fixed and random effects (R-squared conditional) (71% of the variance, $R^2_{GLMM(c)} = .71$) than was explained by the fixed effects alone (R-squared marginal) (6.58% of the variance, ($R^2_{GLMM(m)} = .06$)). There were significant main effects for duration ($F(2, 525) = 7.32, p < .001$), directional noise bandwidth ($F(1, 525) = 66.68, p < .001$) and circle size ($F(1, 525) = 10.55, p = .001$). There was no significant main effect of direction ($F(4, 525) = 0.63, p = .63$). Significant interaction effects were also found between the effect of duration and circle size ($F(2, 525) = 3.4, p = .034$)

Figure 2

Mean Movement Latency by Bandwidth and Circle Size Collapsed Across Directions and Participants
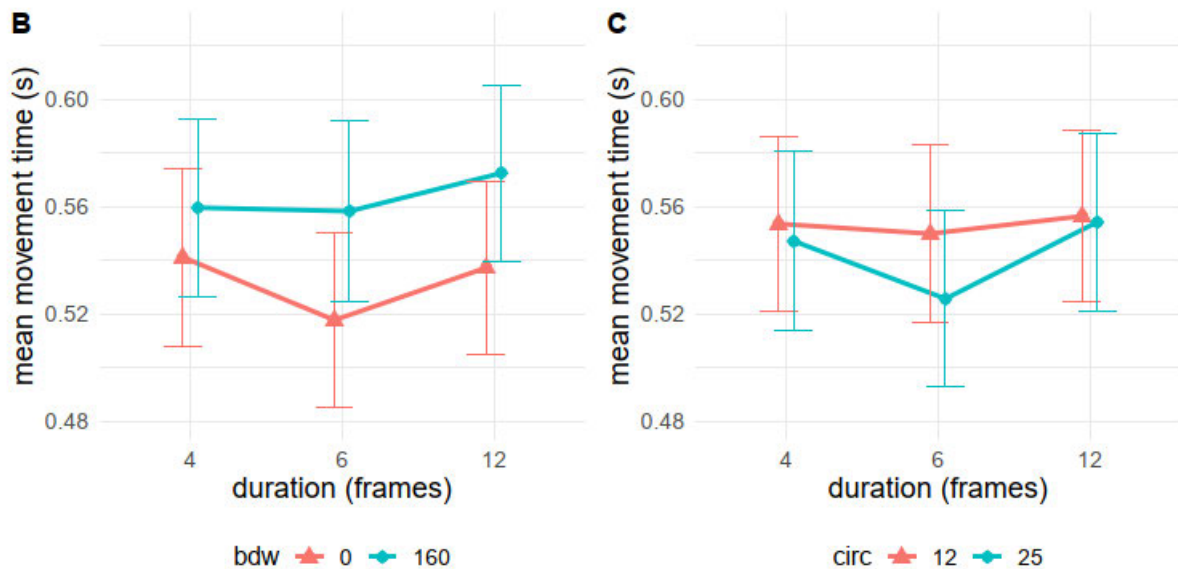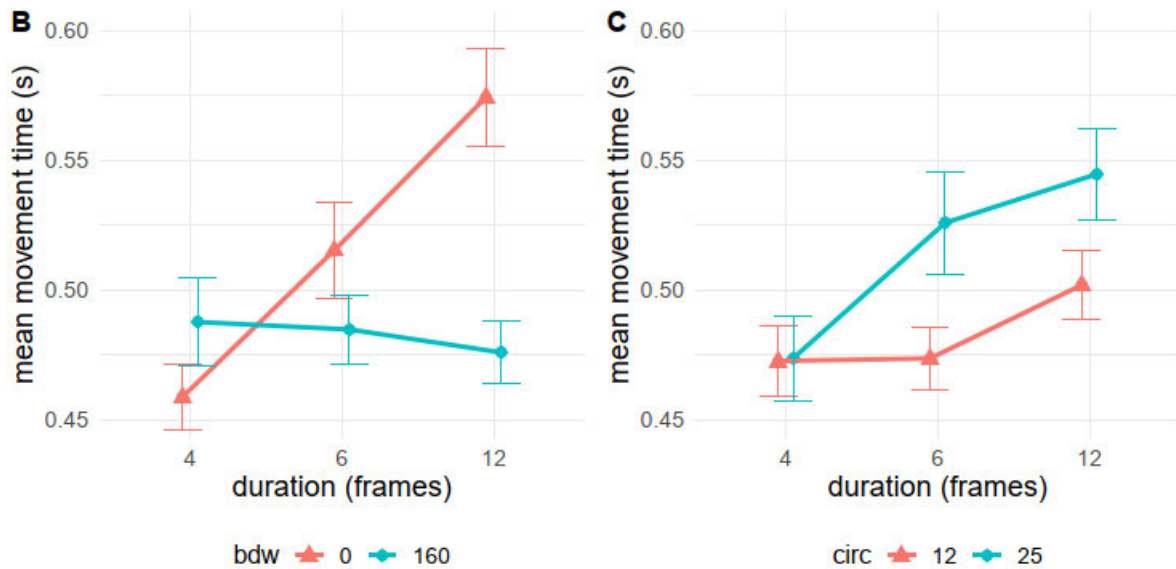

Note. **B** shows the by directional noise bandwidth (bdw). **C** shows the circle sizes (circ). Movement latency is in seconds. Error bars represent standard error of the mean.

and duration and bandwidth ($F(2, 525) = 3.33, p = .036$).

   Post-hoc tests. The effect of duration, bandwidth and circle size on movement latency are shown in figure 2. Interestingly there was no significant difference between 4 frames ($M = 550ms, SD = 63.6ms$) and 12 frames ($M = 555ms, SD = 80.3ms$) for mean movement latency. However, participants were significantly faster for the 6 frame condition ($M = 537ms, SD = 92.3ms$) than for either the 4 frame condition ($t(525) = 2.5, p = 0.038$) or the 12 frame condition ($t(525) = -3.76, p < .001$). Participants showed significantly faster movement latencies for the 0° condition ($M = 532ms, SD = 75.4ms$) than the 160° condition ($M = 564ms, SD = 80.9ms$). There were also significant differences for circle size, with slightly longer movement latencies for the 12° circle ($M = 553ms, SD = 70.3ms$) than for the 25° circle ($M = 542ms, SD = 87.7ms$).

Figure 3

Mean Movement Time by Bandwidth and Circle Size Collapsed Across Participants and Directions


Note. **B** shows the by directional noise bandwidth (bdw). **C** shows the circle sizes (circ). Movement time is in seconds. Error bars represent standard error of the mean.

3.3.2 Movement time

We next looked at movement time. For mean movement time the fixed effects explained only 9.5% of the variance $(R^2_{GLMM(m)} = .095)$ where the fixed and random effects combined explained 75% of the variance $(R^2_{GLMM(c)} = .75)$, indicating that most of the variation in movement time was explained by differences between the participants, rather than by the manipulations. However, there were a number of significant main effects that explain this small variance, including duration $(F(2, 525) = 20.54, p < .001)$, directional noise bandwidth $(F(1, 525) = 29.38, p < .001)$, circle size $(F(1, 525) = 28.09, p < .001)$ and direction $(F(4, 525) = 3.18, p = .013)$. There were significant interaction effects between duration and circle size $(F(2, 525) = 7.23, p < .001)$, duration and bandwidth $(F(2, 525) = 32.23, p < .001)$ and circle size and bandwidth $(F(1, 525) = 8.35, p = .004)$

Post-hoc tests. The results for movement time for across duration, bandwidth and circle size are displayed in figure 3. We observed significantly lower movement

20

Figure 4

Reaching Accuracy by Circle Size Collapsed Across Durations and Bandwidths
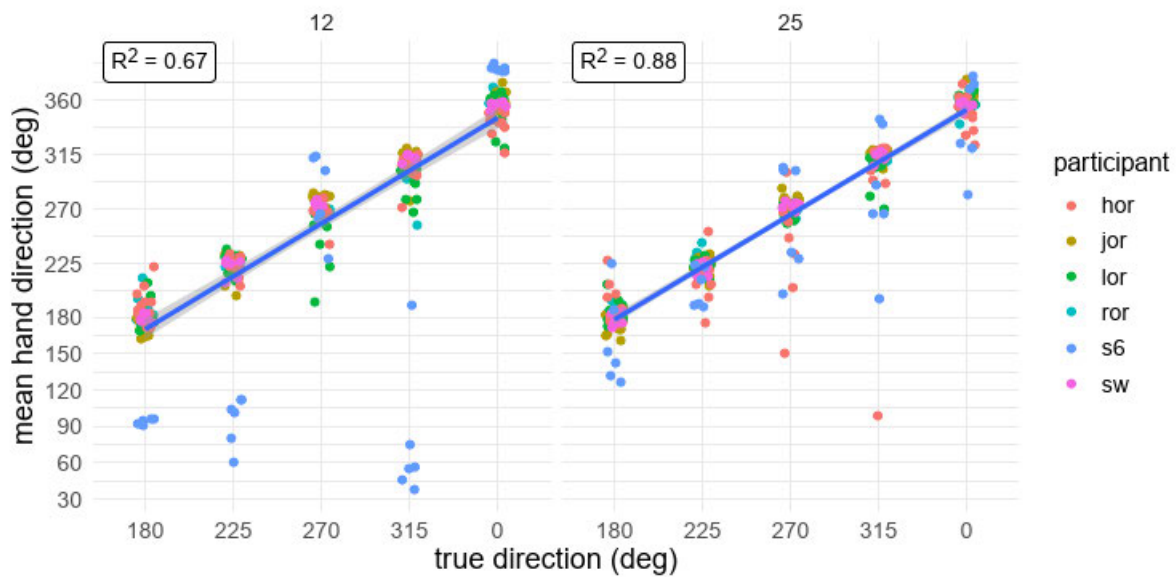
Note. The mean hand direction in degrees as a function of the actual mean direction in degrees. Colours represent individual participants' scores. 12 and 25 refer to the 12° and 25° circle conditions.

times for 4 frames ($M = 473ms$, $SD = 111ms$) than for 6 frames ($M = 500ms$, $SD = 148ms$) ($t(525) = -2.91$, $p = .011$) as well as for 6 frames compared to 12 frames ($M = 524ms$, $SD = 178ms$) ($t(525) = -3.47$, $p = .002$). There were significantly longer movement times for the 0° noise bandwidth condition ($M = 525ms$, $SD = 169ms$) than for the 160° condition ($M = 483ms$, $SD = 124ms$) ($t(525) = 5.42$, $p < .001$). There were also significantly shorter movement times for the 12° circle size ($M = 483ms$, $SD = 124ms$) than the 25° circle ($M = 515ms$, $SD = 168ms$).

3.3.3 Reaching accuracy

We conducted a simple analysis to examine the relationship between where participants touched the screen and the true direction of the target. A simple linear regression was used to determine participants' accuracy by predicting the true direction of the stimulus against participants' direction for hand direction distance, finding a significant relationship ($R^2 = 0.76$, $F(1, 588) = 1960$, $p < .001$). As demonstrated in

figure 4 accuracy was lower for the 12° circle $(R^2 = 0.67, F(1, 288) = 611, p < .001)$ than for the 25° circle $(R^2 = 0.88, F(1, 298) = 2383, p < .001)$.

3.3.4 Reaching precision

For directional error in the reaching task the fixed effects explained only 13% of the variance $(R^2_{GLMM(m)} = .13)$ while the fixed and random effects combined explained 52% of the variance $(R^2_{GLMM(c)} = .52)$. There were significant main effects of duration $(F(2, 525) = 21.183, p < .001)$, directional noise bandwidth $(F(2, 525) = 32.881, p < .001)$, and direction $(F(4, 525) = 5.265, p < .001)$. Interestingly, there was also a significant main effect of circle size $(F(1, 525) = 4.403, p = 0.036)$. There were also significant interaction effects between duration and bandwidth $(F(2, 525) = 3.47, p = .032)$, circle size and direction $(F(4, 525) = 2.87, p = .023)$, and bandwidth and direction $(F(4, 525) = 6.76, p < .001)$.

Post-hoc tests. There was a significantly greater directional error for the 4 frame condition $(M = 36.5, SD = 32.4)$ than for the 6 frame condition $(M = 22.9, SD = 23.6)$ $(t(525) = 5.83, p < .001)$. There was no significant difference in precision between the 6 frame and 12 frame condition $(M = 24.0, SD = 29.7)$ $(t(525) = -1.04, p = 1.0)$. There was a significantly greater directional error for the 160 ° bandwidth condition $(M = 33.4, SD = 31.0)$ than for the 0° condition $(M = 22.3, SD = 26.7)$ $(t(525) = -5.73, p < .001)$. These effects are shown in figure 5.

Interestingly there was also a significant difference in precision present between the two circle sizes for the reaching task. The directional error was significantly greater for the 12° circle $(M = 30.0, SD = 32.0)$ than the 25° circle $(M = 25.8, SD = 26.6)$ $(t(525) = 2.10, p = .036)$. The possible reasons for this will be elaborated upon in the discussion. The difference for each bandwidth and duration between the two circle sizes are shown in figure 6. Directional error for each bandwidth, duration and circle size is shown in figure 7.

Figure 5

Mean Effect of Bandwidth and Duration Precision for Each Task Collapsed Across, Circle Size, Directions and Participants
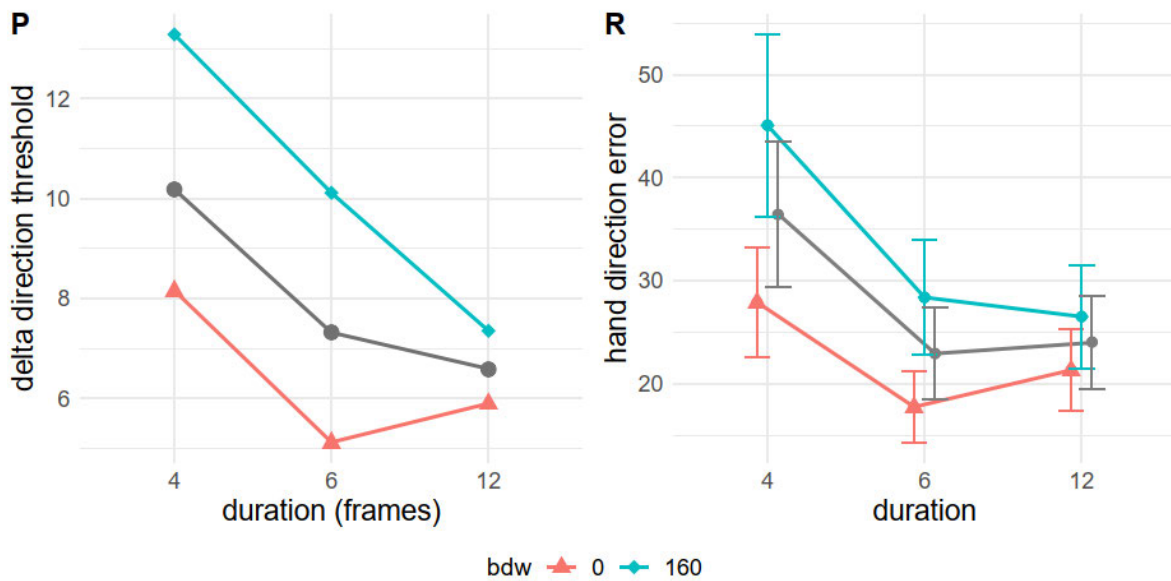
Note. bdw refers to the directional noise bandwidth (0° or 160°), duration refers to the number of frames (4, 6 or 12 frames). **P** refers to the perceptual task and **R** refers to the reaching (or pointing) task. The coloured lines are the different bandwidths and the grey lines are the means for each task. Error bars represent standard error of the mean.

3.4 Perceptual Task

3.4.1 Delta direction threshold

Precision performance on the perceptual task was analysed using the same linear mixed model outlined above. The fixed effects explained a moderate 37.2% of the variance ($R^2_{GLMM(m)}$ = .37) and the random and fixed effects together explained 44.1% of the variance ($R^2_{GLMM(c)}$ = 0.44). As expected from previous research there were significant main effects of duration ($F(2, 233)$ = 22.83, p < .001), directional noise bandwidth ($F(1, 234)$ = 72.98, p < .001) and direction ($F(4, 233)$ = 8.86, p < .001). In contrast to the effect of circle size found for reaching precision, there was no significant main effect of circle size ($F(1, 233)$ = 1.56, p = .21). Significant interaction effects were found between duration and bandwidth ($F(2, 233)$ = 9.15, p < .001) and bandwidth and direction ($F(4, 232)$ = 2.82, p = .026).

Figure 6

Mean Directional Error for the Perceptual and Reaching Task by Duration, Bandwidth and Circle Size Collapsed Across Directions and Participants
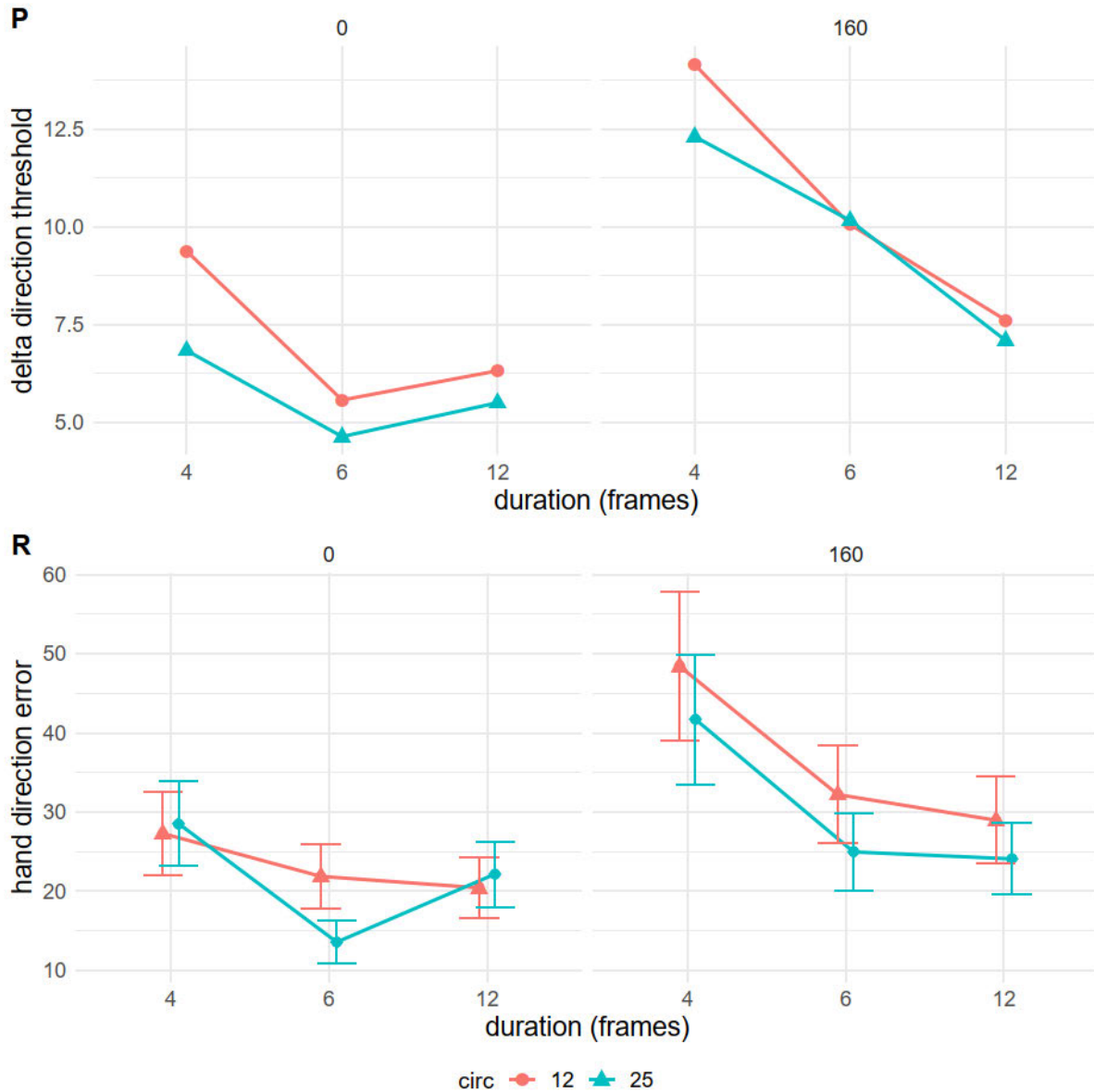
Note. The above graph shows the effect of duration, bandwidth and circle size. bdw refers to the directional noise bandwidth (0° or 160°), duration refers to the framerate (4, 6 or 12 frames) and circle refers to the circle size (either 12° or 25° of visual angle). **P** refers to the perceptual task and **R** refers to the reaching (or pointing) task. Error bars represent standard error of the mean.

Post-hoc tests. There was a significant effect of duration on precision, with greater errors for 4 (M = 10.2, SD = 5.89) than 6 frames (M = 7.32, SD = 4.90) (t(233) = 4.14, p < .001) as well as for 6 than 12 frames (M = 6.60, SD = 3.59) (t(233) =

Figure 7

Mean Directional Error for the Perceptual and Reaching Task Collapsed Across Participants
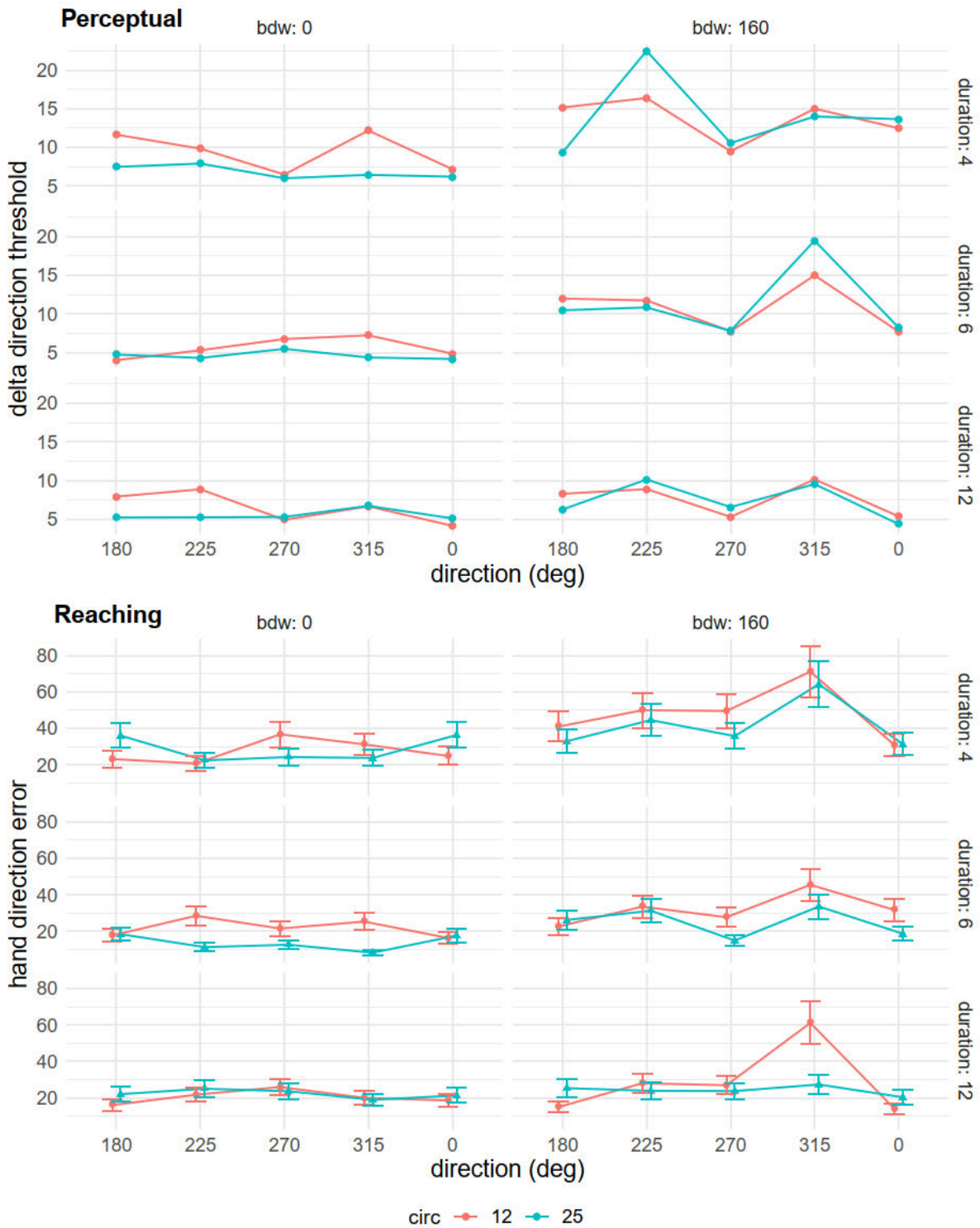
Note. The above graph shows the average directional error across averaged for the six participants. bdw refers to the directional noise bandwidth (0 or 160), duration refers to the framerate (4, 6 or 12 frames). Error bars represent standard error of the mean.

2.66, p = .025), in contrast to the results for the perceptual task. There was also a significant effect of directional noise bandwidth on precision with significantly greater direction error for the 160° condition (M = 9.82, SD = 5.75) than the 0° condition (M = 6.35, SD = 3.68) ($t(234)$ = −8.53, p < .001). These effects are shown in figure 5 for both the perceptual and reaching task.

3.5 Comparing the Perceptual and Reaching Task

3.5.1 Combined precision estimates

An LMM was used to compare the perceptual and reaching task. This model used the same parameters as the above models, it combined the two precision variables as an outcome variable and included task as an additional fixed effect. The fixed effects explained 36% of the variance ($R^2_{GLMM(m)}$ = 0.36) and the random and fixed effects combined explained 51% of the variance ($R^2_{GLMM(c)}$ = 0.51). Significant main effects were found for directional noise bandwidth ($F(1, 759)$ = 30.15, p < .001), duration ($F(2, 758)$ = 14.25, p < .001), direction ($F(4, 759)$ = 3.72, p = .005), and task "($F(1, 483)$ = 127.82, p < .001). No significant main effect was found for circle size ($F(1, 758)$ = 2.32, p = .12).

Post-hoc tests. As was expected, errors were significantly greater for the reaching task (M = 27.9, SD = 29.4) than for the perceptual task (M = 7.88, SD = 5.01) ($t(489)$ = 11.1, p < .001). Errors were also significantly greater for the 160° (M = 26.2, SD = 28.2) than the 0° directional noise bandwidth (M = 16.6, SD = 22.8). Significantly greater error was found for the 4 (M = 28.6, SD = 29.8) than the 12 frame (M = 17.7, SD = 25.2) conditions ($t(759)$ = 4.96, p < .001) and the 4 and 6 frame (M = 17.6, SD = 20.7) conditions ($t(758)$ = 4.48, p < .001). No significant differences were found between the 6 and 12 frame conditions ($t(759)$ = 0.32, p = 1.00).

4. Discussion

This study considers how we use visual information in the form of motion trajectory prediction in order to make perceptual judgements and engage in interceptive movements. We were interested in comparing differences between the way the visual information is used in making perceptual judgments and reaching movements. This is a particularly salient instance of a more general strategy of prediction it is believed we use to contend with neural processing delays and more efficiently engage with our environment. However, comparing these two systems is difficult because of differences in task demands for each modality. We compared the tasks across several different parameters, varying the signal strength (noise bandwidth, duration), the area extrapolated across (two different circle sizes) over five mean directions. We obtained movement latency, movement time, accuracy and precision measurements for the reaching task. This precision estimate allowed us to compare the precision of the perceptual task to that of the reaching task across conditions. For the perceptual task we measured precision using a two-alternative forced-choice design to determine a precision estimate to compare to the reaching task. Previous work has indicated that increased stimulus duration should result in greater precision and higher directional noise bandwidths should result in lower precision (Watamaniuk et al., 1989). Both of which were supported in this study for the perceptual task and partially for the reaching task (no difference was found between the 6 and 12 frame condition for the reaching task).

4.1 Movement Latency

Measuring movement latency was thought to give us some insight into whether a degraded motion signal (in the form of increased directional noise in particular) would result in people delaying their movements in order for signal processing to occur. While there was a significant relationship between stimulus duration and movement latency the results obtained are somewhat ambiguous as there was no significant difference between the longest and shortest durations (4 and 12 frames),

however, latencies were significantly faster for the 6 frame condition than either. It is important to note that there was quite high variability between participants in their movement latency, with very little variance explained by the manipulations. Bandwidth had more of an effect on movement latency with a $32ms$ difference between the conditions, with the more ambiguous 160° stimulus resulting in longer movement latencies. This would accord with participants requiring longer on average to integrate the motion signal for the 160° condition, though the substantial variability amongst participants must again be considered.

4.2 Movement Time

Movement time increased with longer durations indicating that people may have made use of visual information obtained during the movement. This is backed up by the length of the movement times (~400-600ms) combined with the movement latency (<500ms) compared with the length of the sensorimotor loop (the length of delays introduced by the nervous system, ~200ms, Wolpert et al., 2012). This could mean that feedback mechanisms were being used to facilitate corrective movements based on additional information obtained from the stimulus. That only the 0° condition (the less ambiguous visual information) resulted in longer movement times across durations further indicates that participants might have been using visual information obtained throughout the reach (see 3). This accords with previous findings indicating that the presence of visual information throughout a reach can determine endpoint precision (Ma-Wyatt & McKee, 2007). This is also in line with findings around motion perception indicating that we need time to integrate motion information. The time it takes varies, for more coherent motion takes ~80-120ms and for more noisy stimuli can take up to 400ms (Grzywacz et al., 1995). Though this effect was clear, again, there was considerable variability amongst participants in their movement times, with the fixed effects of the model only explaining a small proportion of the variance. This indicates differences in the way that participants were accomplishing the task, which combined with the similarly large amount of variance in

movement latency potentially indicates either that participants had differing abilities with regards to the task, different understandings of the task or employed different strategies when completing the task.

4.3 Movement Accuracy

Despite this individual variability, participants were reasonably accurate as is shown in figure 4. A considerable amount of the variance in accuracy seems to be from single participant in the 12° condition is readily observed in figure 4. This indicates that while the task was difficult, and there was sizeable variability in people's precision, that they were in fact able to complete the task - the task was difficult but not impossible.

4.4 Precision

A key result from earlier studies that was replicated was the effect of degraded visual stimuli on the performance of both the perceptual and reaching task. This was evidenced in increased error for signals with more directional noise (160° vs. 0°) for both tasks as well as for shorter durations (4 frames > 6 frames > 12 frames) for the perceptual task. These results were partially carried over for the reaching task, though no significant difference was found between the 6 and 12 frame conditions. There was also an interaction effect between directional noise bandwidth and duration for both tasks. This interaction has been demonstrated in previous studies looking at perceptual judgements using similar stimuli (Watamaniuk et al., 1989).

The results for the perceptual task are in line with previous literature that shows that directional precision decreases with larger bandwidths and shorter durations (Watamaniuk et al., 1989). Though in that study much longer durations were used. This was partially supported for the reaching task, though there was no difference found between the 6 and 12 frame conditions potentially indicating that these were equally difficult. Pilot tests showed that 4, 6, and 12 frames at 75Hz were suitable durations for finding an effect, and while this was the case with the perceptual task, there

was no significant difference between the 6 and 12 frame durations for the reaching task. It is possible that a longer duration condition might have shown a greater effect.

4.4.1 Circle size

One unexpected result was that directional error was greater for the smaller 12° than for the 25° circle for the reaching task. An explanation for this might be that, though people were not primed to actually make an interception (they were told to indicate *where* the stimulus would intersect the surrounding circle, rather than *when*), it is possible they nonetheless acted as though they were attempting an interception. This is further supported by the movement time and latency results, both of which were significantly lower for the 12° than the 25° circle. People were altering the timing of their movements according to the size of the surrounding circle.

There are several variables that need to be taken into account when thinking about trajectory interception. The two main variables under control are the timing of the interception (influenced by the size, speed and distance of the target) and the spatial position of the endpoint (i.e. the hand/foot). Brenner and Smeets (2015) suggest that the optimal strategy people use for precise interception involves estimating the time required to intercept a target's path and then adjusting their movement path in space to "fine-tune" the movement and more precisely intercept the target. This is because spatial adjustments are faster than temporal ones (Brenner & Smeets, 2015). The fixed interception point used (i.e. the circle) could mean that a different strategy had was used. As a result of this fixed interception point, participants may have tried to speed up their movements for the smaller circle size, resulting in a speed-accuracy trade-off (i.e. Fitt's Law, Fitts, 1954). This also accords with the above results regarding duration affecting movement times suggesting that visual information obtained throughout the reach could have been used to engage in this fine-tuning for the larger circle size and not for the smaller circle. If participants were influenced by the circle size to increase their speed in order to intercept the signal at the correct time, rather than merely at the correct location, this might necessarily result in less precision.

What is also notable about this finding regarding circle size is that in the 25° condition participants were able to accurately extrapolate the trajectory of a very briefly presented motion signal. Previous studies suggest that trajectory motion produces activity in directional motion detectors that allow people to determine where an occluded moving object should reappear (Watamaniuk, 2005; Watamaniuk & McKee, 1995). These findings present further evidence that this sort of trajectory extrapolation is possible.

Differences in spatial localization capabilities might also account for this. As the 12° circle is much closer to the signal dots, local position judgements may be altering the trajectory estimates so as to decrease precision. However, there was no significant difference between the circle sizes for the perceptual task, which makes this prospect less likely.

4.5   Limitations

A major limitation of the present study is that the task turned out to be more difficult for participants than pilot trials indicated. This was evident for both the perceptual and reaching task. For the reaching task this resulted in much less precision when compared with results from people making reaches when examining simple static stimuli at similar eccentricities (Ma-Wyatt & McKee, 2006). It was also impossible to fit a psychophysical function for some conditions as participants' error rates did not track changes in the stimulus. There was a considerable variability between participants, seen in the gap between the fixed and random effects and in the large error bars. This was particularly surprising for the perceptual task, as we had to remove some data points to which we were unable to fit a psychometric function. For the reaching task, there was evidence of some large directionally specific errors as well. Methods to mitigate these effects are discussed in section 4.6 below.

This could also be due to the nature of the task more generally. For the perceptual task, participants had to make a judgement as to the motion of the stimulus relative to a fixed reference point. The reaching task, on the other hand, contained no such

reference point (largely because this was unnecessary). This difference instantiates different reference frames in the task itself. The perceptual task involves making a judgement in an allocentric reference frame, where the reaching task involves multiple reference frames (allocentric and egocentric).

As will be discussed below, an eye movement-based task could help bridge this gap. Instead of thinking about the task as involving perception and action, it might be more instructive to think of it as involving a reference frame comparison, as this is arguably just as relevant a distinction (Schenk & McIntosh, 2010). Eye movement involves information in a reference frame more closely mimicking the perceptual task (though there is likely considerable interaction between these systems, see Mather and Lackner, 1981), while still involving a motor control element and therefore might be useful to consider in conjunction with the perceptual and reaching metrics.

There is also the question of differences in the temporal nature of the two tasks. If we consider that the use of online or model-based control when engaging in interception may be largely task dependent (Zago et al., 2009), then visual information may also be used in a task dependent manner. The perceptual task contains no element of timing, where most tasks involving manual interception do. If we consider, as Brenner et al. (2016) suggest, that people first decide *when* they will intercept a target, engaging in a movement, before making more precise spatial corrections based on updated visual information (as it is faster to make spatial adjustments than temporal ones, see: Brenner et al., 1998).

4.6   Future directions

When examining the data for the reaching task there were much larger directional errors for some directions than others, and this effect varied across participants. This may have been a function of the way in which the step sizes for the stimulus were chosen. As is common when using this kind of stimulus the step size of the motion signal was adjusted for each participant . For this trial the step size was only varied participant to participant and not by direction, resulting in directional differences that

were difficult for some participants to discriminate demonstrate disproportionately large errors.

Given the somewhat surprising finding around precision and circle size for the reaching task, one potential avenue might be to further investigate this effect. Some additional manipulations that could be used would be to examine the effect would be to use more that two different circle sizes. This could help determine whether this increase in precision scales with circle size and, if so, the limits of this effect. Another potential manipulation would be to increase the size of the stimulus (e.g. to use a 25° RDC for the 25° circle condition, rather than a 12° RDC) to determine whether this effect of circle size is due to motion extrapolation, movement error, or to local position-based effects (Westheimer & McKee, 1977). This could, however, also introduce a new confound, as people have been shown to have better motion detection and discrimination when observing larger RDCs (Heinen & Watamaniuk, 1998).

Based on the way that mean movement time increased with stimulus duration, it could be helpful to look at how this visual information is being used. Examining hand movement data could provide further information as to how people are using visual information. By measuring peak velocity of the movement we could determine whether people are making last minute corrections based on visual information obtained throughout the reach.

As mentioned above, in addition to changes to the stimulus, it would also be informative to conduct a study tracking smooth pursuit eye movements, in addition to the reaching and perceptual data. This could use a similar stimulus setup to the one in the current study (though perhaps with some alterations discussed above to accommodate some of the limitations). As oculomotor performance has been studied in a similar manner previously, and it has been found, using a similar stimulus, that after accounting for inherent motor noise, oculomotor and psychophysical performance showed evidence that they are governed by a common motion processing stage, limiting performance for both systems (Kowler & McKee, 1987; Stone & Krauzlis, 2003;

Watamaniuk & Heinen, 1999). Comparing the way that these two motor systems use visual information would allow us to further understand the interaction between the perception and different motor systems. As mentioned above, it may also provide additional insight into how visual information is used in different reference frames.

4.7 Conclusion

This study aimed to further investigate the complex interrelationship between visual perception and hand movements. While we managed to find patterns of differences between our conditions, including increased directional noise in a motion signal causing decreases in precision and effects on movement time, there was also considerable variability between participants. The perceptual and movement systems are methodologically difficult to analyse, as it is difficult design experiments that dissociate the modalities in order to compare them. Nonetheless, analysing these systems together provide does provide some insight into how humans are able to account for processing delays. The interaction between motion processing and trajectory interception involves examining two important predictive processes people use to engage with the environment. This is also a particularly explicit instance of a more general class of predictive strategies it is thought we use to engage with the world. It is clear from this study that much further research can be done in examining the interaction between motion perception, trajectory extrapolation and movement using these types of stimuli. By combining low level motion perception (briefly presented motion stimuli) and reaching movements it is possible to get closer to understanding how visual information is used to inform interceptive movements.

References

Adams, R. A., Shipp, S. & Friston, K. J. (2013). Predictions not commands: Active inference in the motor system. *Brain Structure & Function*, *218*(3), 611–643. https://doi.org/10/f4wkqx

Adelson, E. H. & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A*, *2*(2), 284–299. https://doi.org/10.1364/josaa.2.000284

Batista, A. P., Buneo, C. A., Snyder, L. H. & Andersen, R. A. (1999). Reach Plans in Eye-Centered Coordinates. *Science*, *285*(5425), 257–260. https://doi.org/10/fd5x89

Bernshteĭn, N. (1967). *The Coordination and Regulation of Movements*. Pergamon Press.

Bosco, G., Monache, S. D., Gravano, S., Indovina, I., Scaleia, B. L., Maffei, V., Zago, M. & Lacquaniti, F. (2015). Filling gaps in visual motion for target capture. *Front. Integr. Neurosci.*, 1–17. https://doi.org/10/gc9zz7

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. https://doi.org/10/c7g6rj

Brenner, E., Smeets, J. B. J. & de Lussanet, M. H. E. (1998). Hitting moving targetsContinuous control of the acceleration of the hand on the basis of the target's velocity. *Experimental Brain Research*, *122*(4), 467–474. https://doi.org/10/b9vs7b

Brenner, E., Rodriguez, I. A., Muñoz, V. E., Schootemeijer, S., Mahieu, Y., Veerkamp, K., Zandbergen, M., van der Zee, T. & Smeets, J. B. (2016). How Can People Be so Good at Intercepting Accelerating Objects if They Are so Poor at Visually Judging Acceleration? *i-Perception*, *7*(1), 1–13. https://doi.org/10.1177/2041669515624317

Brenner, E. & Smeets, J. B. J. (2015). How people achieve their amazing temporal precision in interception. *Journal of Vision*, *15*(3), 1–21. https://doi.org/10/f7dpt8

Brenner, E. & Smeets, J. B. J. (2017). Chapter 4 - Accumulating visual information for action. In C. J. Howard (Ed.), *Progress in Brain Research* (pp. 75–95). Elsevier. https://doi.org/10.1016/bs.pbr.2017.07.007

Brenner, E. & Smeets, J. B. J. (2018). Continuously updating one's predictions underlies successful interception. *Journal of Neurophysiology*, *120*(6), 3257–3274. https://doi.org/10/gg2wv3

Brysbaert, M. & Stevens, M. (2018). Power Analysis and Effect Size in Mixed Effects Models: A Tutorial. *Journal of Cognition*, *1*(1), 9. https://doi.org/10/gcsmn2

Buneo, C. A. & Andersen, R. A. (2006). The posterior parietal cortex: Sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia*, *44*(13), 2594–2606. https://doi.org/10/cckjkg

Cohen, M. A., Dennett, D. C. & Kanwisher, N. (2016). What is the Bandwidth of Perceptual Experience? *Trends in Cognitive Sciences*, *20*(5), 324–335. https:// doi. org/10.1016/j.tics.2016.03.006

Crawford, J. D., Henriques, D. Y. & Medendorp, W. P. (2011). Three-Dimensional Transformations for Goal-Directed Action. *Annual Review of Neuroscience*, *34*(1), 309–331. https://doi.org/10.1146/annurev-neuro-061010-113749

Eggert, T., Rivas, F. & Straube, A. (2005). Predictive strategies in interception tasks: Differences between eye and hand movements. *Experimental Brain Research*, *160*(4), 433–449. https://doi.org/10/cptfwg

Fiehler, K., Brenner, E. & Spering, M. (2019). Prediction in goal-directed action. *Journal of Vision*, *19*(9), 1–21. https://doi.org/10.1167/19.9.10

Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, *47*(6), 381–391. https://doi.org/10.1037/h0055392

Friston, K. J. (2011). What Is Optimal about Motor Control? *Neuron*, *72*(3), 488–498. https://doi.org/10/b3fk4b

Friston, K. J., Daunizeau, J., Kilner, J. & Kiebel, S. J. (2010). Action and behavior: A free-energy formulation. *Biological Cybernetics*, *102*(3), 227–260. https:// doi. org/10/c8zhrp

Friston, K. J., Mattout, J. & Kilner, J. (2011). Action understanding and active inference. *Biological Cybernetics*, *104*(1), 137–160. https://doi.org/10/d5jmw3

Galluci, M. (2019). *GAMLJ: General analyses for linear models*. https://gamlj.github.io/

Gibson, J. J. (1979). *The Ecological Approach to Visual Perception*. Psychology Press OCLC: 914056891.

Goodale, M. A. & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*(1), 20–25. https://doi.org/10.1016/0166-2236(92)90344-8

Grzywacz, N. M., Watamaniuk, S. N. J. & McKee, S. P. (1995). Temporal coherence theory for the detection and measurement of visual motion. *Vision Research*, *35*(22), 3183–3203. https://doi.org/10.1016/0042-6989(95)00102-6

Harris, C. M. & Wolpert, D. M. (1998). Signal-dependent noise determines motor planning. *Nature*, *394*(6695), 780–784. https://doi.org/10.1038/29528

Heinen, S. J. & Watamaniuk, S. N. J. (1998). Spatial integration in human smooth pursuit. *Vision Research*, *38*(23), 3785–3794. https://doi.org/10/dkwrr2

Hogendoorn, H. & Burkitt, A. N. (2019). Predictive Coding with Neural Transmission Delays: A Real-Time Temporal Alignment Hypothesis. *eNeuro*, *6*(2), e0412. https://doi.org/10.1523/eneuro.0412-18.2019

Jackson, S. R. (2010). Is the visual dorsal stream really very visual after all? *Cognitive Neuroscience*, *1*(1), 68–69. https://doi.org/10/ft9k75

jamovi project. (2019). *Jamovi* (Version 1.1). https://www.jamovi.org

Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R. & Broussard, C. (2007). What's new in psychtoolbox-3. *Perception*, *36*(14), 1–16.

Kowler, E. & McKee, S. P. (1987). Sensitivity of smooth eye movement to small differences in target velocity. *Vision Research*, *27*(6), 993–1015. https://doi.org/10/dvnhhk

Land, M. F. (2009). Vision, eye movements, and natural behavior. *Visual Neuroscience*, *26*(1), 51–62. https://doi.org/10/c87pr5

Lee, D. N. & Reddish, P. E. (1981). Plummeting gannets: A paradigm of ecological optics. *Nature*, *293*(5830), 293–294. https://doi.org/10/bpws8x

Mather, J. A. & Lackner, J. R. (1981). The influence of efferent, proprioceptive, and timing factors on the accuracy of eye-hand tracking. *Experimental Brain Research*, *43*(3), 406–412. https://doi.org/10/cj3jmw

Ma-Wyatt, A. & McKee, S. P. (2006). Initial visual information determines endpoint precision for rapid pointing. *Vision Research*, *46*(28), 4675–4683. https://doi.org/10/fncbn2

Ma-Wyatt, A. & McKee, S. P. (2007). Visual information throughout a reach determines endpoint precision. *Experimental Brain Research*, *179*(1), 55–64. https://doi.org/10.1007/s00221-006-0767-1

Morgan, M. J., Watamaniuk, S. N. J. & McKee, S. P. (2000). The use of an implicit standard for measuring discrimination thresholds. *Vision Research*, *40*(17), 2341–2349. https://doi.org/10.1016/s0042-6989(00)00093-6

Mrotek, L. A., Flanders, M. & Soechting, J. F. (2004). Interception of targets using brief directional cues. *Experimental Brain Research*, *156*(1), 94–103. https://doi.org/10/bbf832

Mumford, D. (1992). On the computational architecture of the neocortex. *Biological Cybernetics*, *66*(3), 241–251. https://doi.org/10/fc636h

Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.2041-210x.2012.00261.x

Newsome, W. T., Britten, K. H. & Movshon, J. A. (1989). Neuronal correlates of a perceptual decision. *Nature*, *341*(6237), 52–54. https://doi.org/10/dmwkcn

O'Regan, J. K. & Noë, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences*, *24*(5), 939–973. https://doi.org/10/b3dbnv

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Multisensory research*, *10*(4), 437–442. https://doi.org/10/fb9s55

Rao, R. P. N. & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, 2(1), 79–87. https://doi.org/10/drddxm

Reichardt, W. (1967). Autocorrelation, a Principle for the Evaluation of Sensory Information by the Central Nervous System. In W. A. Rosenblith (Ed.), *Sensory Communication* (pp. 302–317). The MIT Press. https://doi.org/10.7551/mitpress/9780262518420.003.0017

Santen, J. P. H. V. & Sperling, G. (1985). Elaborated Reichardt detectors. *Journal of the Optical Society of America A: Optics and Image Science, and Vision*, 2(2), 300–321. https://doi.org/10.1364/josaa.2.000300

Scaleia, B. L., Zago, M. & Lacquaniti, F. (2015). Hand interception of occluded motion in humans: A test of model-based vs. on-line control. *Journal of neurophysiology*. https://doi.org/10/f7spzr

Schenk, T. (2006). An allocentric rather than perceptual deficit in patient D.F. *Nature Neuroscience*, 9(11), 1369–1370. https://doi.org/10/fjfbqh

Schenk, T. & McIntosh, R. D. (2010). Do we have independent visual streams for perception and action? *Cognitive Neuroscience*, 1(1), 52–62. https://doi.org/10/csc2gb

Shipp, S. (2016). Neural Elements for Predictive Coding. *Frontiers in Psychology*, 7. https://doi.org/10/f9cc9c

Smeets, J. B. J. & Brenner, E. (2010). Vision for action is not veridical. *Cognitive Neuroscience*, 1(1), 69–69. https://doi.org/10/dj64zm

Snijders, T. A., Bosker, R. J. et al. (1999). An introduction to basic and advanced multilevel modeling. *Sage, London. WONG, GY, y MASON, WM (1985): The Hierarchical Logistic Regression. Model for Multilevel Analysis, Journal of the American Statistical Association*, 80(5), 13–524.

Sober, S. J. & Sabes, P. N. (2003). Multisensory Integration during Motor Planning. *Journal of Neuroscience*, 23(18), 6982–6992. https://doi.org/10/gg2pqt

Sober, S. J. & Sabes, P. N. (2005). Flexible strategies for sensory integration during motor planning. *Nature Neuroscience*, 8(4), 490–497. https://doi.org/10/cpwhcr

Stone, L. S. & Krauzlis, R. J. (2003). Shared motion signals for human perceptual decisions and oculomotor actions. *Journal of Vision*, 3(11), 725–736. https://doi.org/10/fsrskt

Todorov, E. (2004). Optimality principles in sensorimotor control. *Nature Neuroscience*, 7(9), 907–915. https://doi.org/10/b3p5gj

Todorov, E. & Jordan, M. I. (2002). Optimal feedback control as a theory of motor coordination. *Nature Neuroscience*, 5(11), 1226–1235. https://doi.org/10/drpq85

Tresilian, J. R. (2005). Hitting a moving target: Perception and action in the timing of rapid interceptions. *Perception & Psychophysics*, *67*(1), 129–149. https://doi.org/10/cv84wc

Umberger, B. R. & Miller, R. H. (2017). Optimal Control Modeling of Human Movement. In B. Müller, S. I. Wolf, G.-P. Brueggemann, Z. Deng, A. McIntosh, F. Miller & W. S. Selbie (Eds.), *Handbook of Human Motion* (pp. 1–22). Springer International Publishing. https://doi.org/10.1007/978-3-319-30808-1_177-1

Ungerleider, L. G. & Mishkin, M. (1982). Two Cortical Visual Systems. In D. Ingle, M. A. Goodale & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). MIT Press.

Watamaniuk, S. N. J. (2005). The predictive power of trajectory motion. *Vision Research*, *45*(24), 2993–3003. https://doi.org/10.1016/j.visres.2005.07.027

Watamaniuk, S. N. J. & Heinen, S. J. (1999). Human smooth pursuit direction discrimination. *Vision Research*, *39*(1), 59–70. https://doi.org/10/fjv7ft

Watamaniuk, S. N. J. & Heinen, S. J. (2003). Perceptual and oculomotor evidence of limitations on processing accelerating motion. *Journal of Vision*, *3*(11), 5. https://doi.org/10.1167/3.11.5

Watamaniuk, S. N. J. & McKee, S. P. (1995). Seeing motion behind occluders. *Nature*, *377*(6551), 729–730. https://doi.org/10/fj9p93

Watamaniuk, S. N. J., McKee, S. P. & Grzywacz, N. M. (1995). Detecting a trajectory embedded in random-direction motion noise. *Vision Research*, *35*(1), 65–77. https://doi.org/10/d44kgh

Watamaniuk, S. N. J., Sekuler, R. & Williams, D. W. (1989). Direction perception in complex dynamic displays: The integration of direction information. *Vision Research*, *29*(1), 47–59. https://doi.org/10/fhzxs2

Westheimer, G. & McKee, S. P. (1977). Spatial configurations for visual hyperacuity. *Vision Research*, *17*(8), 941–947. https://doi.org/10/d8bhwd

Wexler, M. & Klam, F. (2001). Movement prediction and movement production. *Journal of Experimental Psychology: Human Perception and Performance*, *27*(1), 48–64. https://doi.org/10/d8z5gm

Whitney, D. & Leib, A. Y. (2017). Ensemble Perception. *Annual Review of Psychology*, *69*, 105–129. https://doi.org/10.1146/annurev-psych-010416-044232

Williams, D. W. & Sekuler, R. (1984). Coherent global motion percepts from stochastic local motions. *Vision Research*, *24*(1), 55–62. https://doi.org/10/bhsh5f

Wolpert, D. M., Diedrichsen, J. & Flanagan, J. R. (2011). Principles of sensorimotor learning. *Nature Reviews Neuroscience*, *12*(12), 739–751. https://doi.org/10/brjqb2

Wolpert, D. M. & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, *3*(11), 1212–1217. https : / / doi . org / 10 / fmxm5h

Wolpert, D. M., Pearson, K. G. & Ghez, C. P. J. (2012). The Organization and Planning of Movement. In E. Kandel (Ed.), *Principles of Neural Science* (Fifth Edition, pp. 743–767). McGraw-Hill Education.

Zago, M., McIntyre, J., Senot, P. & Lacquaniti, F. (2008). Internal models and prediction of visual gravitational motion. *Vision Research*, *48*(14), 1532–1538. https://doi. org/10/brhbjq

Zago, M., McIntyre, J., Senot, P. & Lacquaniti, F. (2009). Visuo-motor coordination and internal models for object interception. *Experimental Brain Research*, *192*(4), 571–604. https://doi.org/10/dhbh6n

Zhao, H. & Warren, W. H. (2015). On-line and model-based approaches to the visual control of action. *Vision Research*, *110*, 190–202. https:// doi. org/ 10.1016/j. visres.2014.10.008