#### Eye Movements as Indicators of Visual and Cognitive Processing

by

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#### Eye Movements as Indicators of Visual and Cognitive Processing

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### Abstract

Natural tasks, such as catching a ball, involve the decision whether, when, and where to act. This dissertation examines the relationship between eye and hand movements during goal-directed manual interceptions that require rapid sensorimotor decisions. Human observers viewed and predicted the motion path of a briefly presented moving target and intercepted it at its assumed end position. Observers naturally tracked the moving target to guide interceptive hand movements. To probe the tight eye-hand link, I investigated the effect of perceptual-motor training on eye and hand movement quality (Chapter 2). Results indicate a mutual benefit of training eye and hand movements. Eye movement training alone was not sufficient to improve hand movement accuracy. However, training that required an active sensorimotor decision (eye or hand interception) enhanced eye movement quality.

Next, I tested the role of eye movements during go/no-go decisions. Observers predicted whether targets passed through (go required) or missed (no-go required) a strike box. Observers' eye movements differentiated between decision outcome (go vs. no-go) on a trial-by-trial basis with an overall accuracy of 76% (Chapter 3). Moreover, I found that different eye movement phases were linked to a two-stage decision process. Whereas eye velocity during pursuit initiation corresponded to go/no-go decision accuracy, pursuit maintenance was related to successful interception timing (Chapter 4).

Finally, I investigated the role of movement constraints on decision accuracy by manipulating response modality (button press vs. interceptive hand movement) and eye movements (free viewing vs. fixation; Chapter 5). Decision formation occurred earlier but less accurately when an interceptive hand movement had to be planned and executed. Eye movements (compared to fixation) enhanced decision accuracy regardless of response modality. These results indicate that perceptual decision formation occurs dynamically, relying on the continuous updating of sensory information until an action is required.

In sum, this dissertation provides evidence that eye movements are directly related to neural signatures of perceptual decision making. Furthermore, eye and hand movements show interdependencies during visual predictions and manual interception. This work highlights the potential of studying eye movements as continuous readouts of ongoing sensorimotor and cognitive processes during natural tasks.

### Lay Summary

In many interceptive sports, athletes only have mere seconds to decide whether, when, and where to intercept the ball. To succeed at such goal-directed actions, human observers must rapidly identify and predict motion trajectories of moving objects. Here, I investigated how eye movements contribute to visual predictions during manual interceptions. First, I tested the effect of perceptual-motor training and found a benefit of concurrent eye-hand training, which highlights the behavioural interdependency between eyes and hands. Second, I studied how eye movement relate to rapid go/no-go decision formation. I showed that characteristic eye movements predict observers' decision outcomes and that accurate eye movements benefit accurate decision making. Finally, I found that the action required to indicate a decision (button press vs. interceptive hand movement) shapes decision-specific eye movement patterns and perceptual processes. Overall, my work reveals that eye movements are a sensitive and continuous measure of ongoing visual and cognitive processes.

### Preface

I was the lead on all projects presented in this thesis. My responsibilities included all aspects of conception, design, stimulus programming, data collection, analysis, interpretation, and manuscript composition. Data collection was assisted by undergraduate research assistants. Miriam Spering supervised all aspects of this thesis and provided feedback and edits to the manuscripts that resulted from this work. All studies were approved by the UBC Behavioral Research Ethics Board, certificates H13-01645 (Chapter 2), and H12-02564 (Chapter 3-5).

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**Chapter 4**. This material is currently prepared for submission. A version of this material has been presented as a talk at the Gordon Conference on Eye Movements and the Vision Sciences Society 2019 Annual Meeting. Fooken, J. & Spering, M. (2019). *Eye decide: Eye movement initiation relates to decision accuracy in a go/no-go interception task.* Program No.: 21.12.

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In memory of Jenny Campbell

Wish you were here.

### **Chapter 1**

### Introduction

Accurately perceiving and predicting the trajectory of moving objects is essential to successfully navigate through our dynamic visual environment. When playing catch in the park or crossing a busy intersection during rush hour, humans rely on eye movements to gather sensory information and guide everyday actions. Reaching action goals often requires a sequence of perceptual decisions. For example, the decision whether to initiate a movement is often followed by the decision when and where to act. The aim of this dissertation is to investigate the contribution of eye movements to dynamically evolving visual predictions under different task demands and action requirements. In Section 1.1 of this Introduction, I present an overview of the functional and neural properties of different types of eye movements. In Section 1.2 I discuss how eye movements relate to visual motion perception and provide a background on perceptual learning and decision making. Section 1.3 reviews the link between eye and hand movements for different action goals and task constraints. Finally, I summarize research objectives and provide an overview of each study presented in this dissertation in Section 1.4.

#### **1.1** Functional role of eye movements for vision

Daily activities require a clear and stable perception of the objects around us. However, the human fovea, that is, the area of highest visual acuity on the retina, constitutes less than 1% of the visual field and visual resolution declines rapidly in the periphery (Jacobs, 1979; Wertheim, 1894). To maintain a sharp and focussed view of our visual surroundings, humans rely on different types of eye movements. Saccades are quick gaze shifts that serve to align the fovea with objects of interest. Saccades occur frequently ( $\sim$ 2-3 times per second) during free viewing and visual exploration (Leigh and Zee, 2015). Two other types of visually-guided eye movements, vergence and smooth pursuit eye movements, aim to stabilize the image of the viewed object on the fovea. Vergence refers to the coordinated movement of both eyes to focus and track objects in depth. Smooth pursuit eye movements are slow and continuous rotations of the eye that align the fovea with moving targets. Smooth pursuit occurs naturally in response to visual motion and during self motion (Carpenter, 1988). Saccades, vergence, and smooth pursuit are complemented by two evolutionary

older reflexes that further stabilize the viewed scene on the retina: the vestibulo-ocular reflex and the optokinetic nystagmus. Finally, micro-saccades, tremor, and drift prevent objects from fading perceptually when observers fixate on a stationary object. In this dissertation, I will focus on two types of visually-guided eye movements: smooth pursuit and saccades.

#### 1.1.1 Characteristics of smooth pursuit and saccades

Saccades are high-velocity eye movements that rapidly redirect observers' gaze from one object of interest to another (Dodge, 1903). Saccades can reach a peak velocity of 900 °/s and last between 30-100 ms (Leigh and Kennard, 2004). Yet, it takes on average 200 ms to initiate saccades (Carpenter, 1988), suggesting that the planning and preparation of saccadic eye movements require considerable computation by the central nervous system. Saccades of an amplitude of  $20^{\circ}$  or smaller show a constant relationship between amplitude, peak velocity, and duration, called the main sequence (Bahill et al., 1975; Becker and Fuchs, 1969). In natural settings, larger saccades (>  $20^{\circ}$ ) are usually accompanied by head movements (Freedman, 2008). Due to the short duration of each movement, saccades are not regulated by visual feedback. Instead, an efference copy—or corollary discharge—of the motor command regulating motoneurons of the eyes is also sent to related brain areas (Bridgeman, 1995). Visual perception is mostly suppressed during saccades, presumably to avoid motion blur (Burr et al., 1982; Castet and Masson, 2000; Ross et al., 2001). Yet, saccades serve as an important orienting mechanism and even though visual input is rapidly displaced during saccades, predictive remapping of visual attention enables perceptual stability (Rolfs et al., 2011).

There are several types of saccades characterized by their function, size, and latency. Visually guided saccades are either triggered exogenously by a visual event in the periphery or endogenously when actively exploring the visual environment. However, saccades are not necessarily directed at visual targets. For example, observers can look at the opposite direction of a visually-cued location (antisaccade; Munoz and Everling, 2004) or at a remembered location (memory guided saccades; Pierrot-Deseilligny et al., 2004). Finally, saccades are also elicited in response to moving targets to correct for errors during tracking (catch-up saccades; de Brouwer et al., 2002) or to direct gaze to the predicted target location (predictive saccades; Hayhoe et al., 2012). In this dissertation, I will examine saccades that occur during tracking of visual targets, that is, catch-up and predictive saccades.

Smooth pursuit eye movements occur in response to motion of small visual targets (Lisberger et al., 1987; Rashbass, 1961; Robinson, 1965). Compared to saccades, smooth pursuit is considerably slower (1-100°/s Meyer et al., 1985) and continuously aims to reduce retinal slip, that is, the error between eye velocity and target velocity. The latency of initiating smooth pursuit eye movements is on average 100-150 ms (Carl and Gellman, 1987; Lisberger et al., 1987; Robinson, 1965) and latencies to correct for unexpected target motion changes are of similar magnitude (Schwartz and Lisberger, 1994). Pursuit latency also depends on visual target properties, such as size or contrast (Spering et al., 2005; Tychsen and Lisberger, 1986), and the predictability of the motion path (Bahill and McDonald, 1983; Barnes and Asselman, 1991; Kowler, 1989). Smooth pursuit has classically been separated into two phases (Lisberger et al., 1987). During the

first  $\sim$ 140 ms (open-loop phase) pursuit eye movements are mainly driven by visual motion (retinal image velocity). After the initial phase, the difference between eye and target motion is minimized by a negative feedback control mechanism (closed-loop phase; Krauzlis and Lisberger, 1989). Eye movement control during closed-loop pursuit has been suggested to be regulated by an efference copy signal of the motor command (Crapse and Sommer, 2008) or by proprioceptive feedback—afferent signals from the stretch receptors in the ocular muscles (Lisberger et al., 1987; Weber and Daroff, 1972).

Eye movement responses described in this dissertation were elicited in response to fast moving  $(>30^{\circ}/s)$ , disappearing visual targets. Pursuit of disappearing targets can be maintained for a short time if target motion is predictable, however, pursuit gain will drop over time, that is, eye velocity will no longer match target velocity (Barnes, 2008; Becker and Fuchs, 1985) and variability of smooth pursuit during the blanking period is compensated by saccades (Orban de Xivry et al., 2006). For target velocities exceeding 30°/s smooth pursuit eye movements are often complemented by catch-up saccades (de Brouwer et al., 2002). Catch-up saccades correct for eye position and velocity error that accumulate during tracking when the eye moves relatively slower than the target. Figure 1.1 shows an example of smooth pursuit and saccadic eye movements in a task in which observers were asked to track and intercept a target moving along a predictable motion path. Smooth pursuit was initiated around the time of target motion onset (see slight increase in eye position and velocity around the time of target onset in Fig. 1.1A and 1.1B). The short pursuit latency indicates that the observer anticipated target motion onset due to past experience (Barnes and Asselman, 1991; Kowler, 1989). After  $\sim$ 250 ms a catch-up saccade brought the eye back on the target. The observer then smoothly tracked the target for  $\sim 250$  ms. Finally, a predictive saccade to the assumed target end position was initiated around 600 ms after target onset. This example illustrates that smooth pursuit and saccades are complementary eye movements following and predicting the motion path of moving targets (Orban de Xivry and Lefèvre, 2007).



**Figure 1.1:** Eye movements in response to a fast (40 °/s) moving target. Eye position (A) and eye velocity (B) compared to target position and velocity (black line) during tracking. Periods of smooth tracking (solid blue line) are complemented by saccades (dashed blue line).

#### **1.1.2** Neural correlates of smooth pursuit and saccades

The anatomical pathways of smooth pursuit and saccadic eye movements have extensively been studied in human and non-human primates and have been described in detail in the literature (e.g., Ilg, 1997; Keller and Heinen, 1991; Krauzlis, 2004, 2005; Leigh and Zee, 2015; Sparks, 2002; Thier and Ilg, 2005; Wurtz and Goldberg, 1989). Traditionally, smooth pursuit and saccades have been viewed as two separate anatomical systems. However, more recently behavioural and neurophysiological evidence have revealed considerable overlap between the two systems (Krauzlis, 2004, 2005; Orban de Xivry and Lefèvre, 2007). Here, I will briefly outline key areas and primary pathways that are involved in the control and generation of smooth pursuit and saccades (Fig. 1.2).

- *Primary visual cortex*. Visual input is detected by the retina and transmitted to the lateral geniculate nucleus (LGN) via retinal ganglion cells. From the LGN visual input signals enter the primary visual cortex (V1). Neurons in V1 recognize basic visual features, such as orientation, direction, and spatial frequency and are also sensitive to local motion (Movshon et al., 1985).
- *Lateral intraparietal area*. The lateral intraparietal area (LIP) is involved in the direct control of saccades and smooth pursuit. Stimulation of the LIP can elicit both types of eye movements (Kurylo and Skavenski, 1991). Functionally, the LIP represents, encodes, and updates spatial movement goals (Duhamel et al., 1997; Morris et al., 2012).
- Middle temporal and medial superior temporal areas. The middle temporal (MT) and medial superior temporal (MST) areas are the site of motion integration and the processing of higher-level motion signals, such as 3D motion or optic flow. In humans, area MT is referred to as MT+/V5. Both areas are related to the generation and guidance of smooth pursuit eye movements (Dürsteler and Wurtz, 1988; Newsome and Pare, 1988). Area MT receives inputs from speed-sensitive and direction-selective neurons in area V1 (Majaj et al., 2007; Movshon and Newsome, 1996). Neurons in area MT encode target acceleration, speed, and direction (Lisberger and Movshon, 1999). Neural activity in area MST is related to pursuit maintenance (Dürsteler and Wurtz, 1988) and is sensitive to extra-retinal signals during pursuit (Gu et al., 2006; Ilg, 2008; Newsome and Pare, 1988).
- *Frontal eye fields.* The frontal eye fields (FEF) are involved in the planning and initiation of eye movements (Hanes and Schall, 1996). Stimulation of neurons in FEF or FEF<sub>SEM</sub>—the smooth pursuit subregion of the FEF—evoke saccadic (Bruce et al., 1985; Robinson and Fuchs, 1969) and smooth pursuit eye movements (Gottlieb et al., 1993; Lisberger, 2015; Tanaka and Lisberger, 2002), respectively. The primary input to FEF comes from areaa MT/MST, LIP, and the supplementary frontal eye fields (SEF; Fukushima, 2003). Neurons in the SEF are involved in the control of anticipatory smooth pursuit eye movements (de Hemptinne et al., 2008; Missal and Heinen, 2004).
- *Superior colliculus*. The superior colliculus (SC) is a layered structure in the midbrain that plays a key role for the control of saccades. A retinotopic map in the intermediate layers of the SC controls

orienting eye, head, and body movements that can be evoked by stimulating the SC (Freedman et al., 1996; Sparks, 1999; Wurtz and Albano, 1980). The SC is thought to be involved in target selection and generally encodes movement goals for both saccades and pursuit (Dash et al., 2015; Krauzlis, 2005; Krauzlis et al., 2013).

- Brainstem nuclei (PON, PMN, VN). Cortical oculomotor areas (LIP, MT/MST, FEF, and SEF) and the SC project to the precerebellar pontine nuclei (PON) and the premotor nuclei in the reticular formation (PMN) involved in the motor control of saccadic and pursuit eye movements. Omnipause neurons in medial pontine reticular formation gate eye movements by fully pausing tonic activity during saccades (Keller, 1974) and decreasing activity during smooth pursuit (Missal and Keller, 2002).
- *Cerebellum*. The two main oculomotor regions in the cerebellum are the ventral paraflocculus VPF and the midline oculomotor vermis (Verm). Neural activity in the cerebellum provides a final preparation of the eye movement motor commands that are projected either directly or indirectly to oculomotor nuclei in the brainstem. Damage to the cerebellum drastically impairs saccades and smooth pursuit, but does not eliminate eye movements completely (Leigh and Zee, 2015).



**Figure 1.2:** Lateral view of a macaque monkey brain. Anatomical pathways for pursuit and saccadic eye movements are indicated schematically. Pursuit specific areas MT and MST are highlighted by red-dashed circle, all other areas have been associated with pursuit and saccades. For clarity arrows do not always correspond to direct anatomical connections. CN = caudate nucleus (basal ganglia); FEF = frontal eye field; LIP = lateral intraparietal area; MT = middle temporal area; MST = medial superior temporal area; PMN = brain stem premotor nuclei; PON = precerebellar pontine nuclei; SC = superior colliculus; SEF = supplementary eye field; SNr = substantia nigra pars reticulate (basal ganglia); Verm = oculomotor vermis (cerebellum); VN = vestibular nuclei; VPF = ventral paraflocculus (cerebellum). (Modified from Krauzlis, 2005).

#### **1.2** The interaction between visual perception and eye movements

Our perception of the world is tightly linked to when and where we move our eyes. Sensory information gathered by the visual system guides dynamic, goal-directed actions, such as catching a ball, but also aids the identification of a target amongst distractors, such as finding maple syrup on the supermarket shelf. Visual processing has been proposed to serve two separate functions: action and perception (Goodale, 2011; Goodale and Milner, 1992; Mishkin and Ungerleider, 1982). Vision for action is thought to be mediated by a dorsal cortical pathway through the posterior parietal cortex. The dorsal stream enables the required sensorimotor transformation for bottom-up visual guidance of movements. Vision for perception is proposed to be regulated by a ventral cortical pathway through the infero-temporal cortex. In the ventral stream, visual information facilitates object identification by shape, colour, or orientation recognition. The suggested independent processing of dorsal and ventral stream has since been challenged in the literature and it is clear that there are interdependencies between the two pathways (e.g., Franz et al., 2000; Lee and Van Donkelaar, 2002; Yeatman et al., 2014). The main focus in this dissertation is the link between eye movements and motion perception to goal-directed actions (hand movements). This section also introduces the concepts of perceptual-motor training and perceptual decision making.

#### **1.2.1** Motion perception and smooth pursuit eye movements

Accurate motion perception is important for planning and monitoring goal-directed movements in dynamic environments. To enable accurate tracking of moving objects, the visual system has to extract speed and direction. In primates, motion perception and smooth pursuit eye movements are tightly linked (Spering and Montagnini, 2011). Evidence for shared processing mechanisms comes from electrophysiological studies in non-human primates that show similar neural activity in areas MT and MST during motion perception (Newsome et al., 1989; Newsome and Pare, 1988; Rudolph and Pasternak, 1999) and the control of smooth pursuit eye movements (e.g., Dürsteler and Wurtz, 1988; Komatsu and Wurtz, 1988; Section 1.1.2). Similarly, shared mechanisms of motion perception and smooth pursuit have been observed in healthy human observers using neuroimaging (Huk and Heeger, 2000) and common deficits were reported in a motion-blind patient (Marcar et al., 1997). Behaviourally, motion perception and pursuit are similarly sensitive to motion direction (Krukowski and Stone, 2005) and target speed (Gegenfurtner et al., 2003; Stone and Krauzlis, 2003), although dissociations can occur when motion is ambiguous or the task allows continuous perceptual judgements (e.g., Simoncini et al., 2012; Spering and Carrasco, 2015; Spering et al., 2011a; Tavassoli and Ringach, 2010).

Importantly, tracking a moving object with smooth pursuit eye movements increases the accuracy of predicting the target's future path in time and space (Bennett et al., 2010; Spering et al., 2011b). Moreover, the rate and direction of corrective saccades during smooth pursuit influences motion perception. Compared to tracking moving targets with pure smooth pursuit, target velocities are perceived as faster when pursuit is accompanied by forward saccades, and as slower when backward saccades occur (Goettker et al., 2018).

Thus, motion perception seems to be influenced by target properties as well as by internal mechanisms such as the efference copy of the ongoing oculomotor command.

#### 1.2.2 Perceptual training and motor action

The accuracy of perception does not only depend on the quality of visual input and neural noise levels, but it is also tightly linked to past experience of the observer (Cheung and Bar, 2012). Some expert advantages, such as perceptual-cognitive skills in sports (Mann et al., 2007; Ripoll and Latiri, 1997), may be associated with superior oculomotor strategies in athletes (Bahill and LaRitz, 1984; Land and McLeod, 2000; Takeuchi and Inomata, 2009). Moreover, expert observers also show more accurate perception than novices in simple object recognition tasks (e.g., Tanaka and Taylor, 1991). The observed expert advantage raises the question whether basic perceptual performance can be trained, and if so, whether perceptual expertise in one task can transfer to another.

Specificity versus generalization of perceptual learning-the long-lasting experience-dependent enhancement of identifying and discriminating sensory stimulus features-has been extensively debated and reviewed in the literature (e.g., Ahissar and Hochstein, 2004; Fahle, 2005; Fine and Jacobs, 2002; Seitz and Dinse, 2007). Many studies show that perceptual learning in the visual domain is highly specific and does not transfer across untrained visual locations, features, or modalities (e.g., Ahissar and Hochstein, 1996, 1997; Crist et al., 1997; Fiorentini and Berardi, 1981; Polat and Sagi, 1994; Saffell and Matthews, 2003; Schoups et al., 1995). Yet, there is evidence that some transfer from perceptual learning to visual function is possible. For example, visual acuity improved in amblyopic patients after training in contrast detection and Vernier acuity tasks (Levi and Li, 2009). Transfer of learning from perception to untrained eye movements has been found in observers that performed a motion discrimination task while fixating and later showed improved smooth pursuit eye movements (Szpiro et al., 2014). Even broader transfer has been reported in observers that trained the perceptual system using action video games (Green and Bavelier, 2012; Li et al., 2016), resulting in improved selective attention (Green and Bavelier, 2003) and spatial resolution of the visual system (Green and Bavelier, 2007). Finally, an improvement of baseball on-field performance was reported in college baseball players after training basic visual functions (Deveau et al., 2014) and similar transfer of training has been suggested for athletes (Faubert, 2013; Parsons et al., 2016). Therefore, transfer of perceptual learning seems possible if training activates larger perceptual networks (e.g., Green and Bavelier, 2012) or if the trained and tested function share similar neural pathways (e.g., Szpiro et al., 2014). Training eye movements that are closely linked to visual perception may therefore aid accurate visual predictions and goal-directed actions.

#### 1.2.3 Perceptual decision making

Processing and perceiving visual information is inextricably linked to the formation of a perceptual decision. For instance, perceiving the speed and direction of an approaching car will guide collision avoidance. To successfully act in natural environments, humans need to detect, differentiate, and categorize sensory stimuli and link the extracted information to behavioural consequences (Gold and Shadlen, 2007; Heekeren et al., 2008; Platt, 2002). On the one hand, perception of low-level visual features, such as motion or orientation, is related to selectively tuned early neural activity. On the other hand, perceptual decisions have to inform higher-level brain regions to guide complex actions. Our understanding of perceptual decision making has been advanced by studying single-cell responses in macaque monkeys during simple motion discrimination tasks (Bennur and Gold, 2011; Britten et al., 1992; Celebrini and Newsome, 1994; Crapse et al., 2018; Gold and Shadlen, 2000, 2003; Horwitz and Newsome, 2001; Shadlen and Newsome, 1996; Yates et al., 2017). In human observers, neural signatures of perceptual decision making have been studied behaviourally (Fooken and Spering, 2019; Hagura et al., 2017; Joo et al., 2016; McSorley and McCloy, 2009; Selen et al., 2012) and measured using neuroimaging (Donner et al., 2009; Heekeren et al., 2004; Heinen et al., 2006; Liu and Pleskac, 2011; Pape and Siegel, 2016; Philiastides, 2006). Based on experimental evidence, computational, mathematical, and conceptual models of decision making have been developed into theoretical frameworks (Cisek, 2006; Glimcher and Fehr, 2013; Noorani and Carpenter, 2016; Ratcliff et al., 2016; Smith and Krajbich, 2019).

Decision-sensitive neural activity is found in brain regions related to sensory processing and oculomotor control (Schall, 2013), including LIP (Roitman and Shadlen, 2002; Shadlen and Newsome, 2001; Yates et al., 2017), MT (Britten et al., 1996, 1992), SEF and FEF (Gold and Shadlen, 2000; Kim and Shadlen, 1999; Kim et al., 2005; Yang and Heinen, 2014; Yang et al., 2010), SC (Basso and Wurtz, 1997; Crapse et al., 2018; Horwitz and Newsome, 2001), and the basal ganglia (Ding and Gold, 2013; Wei et al., 2015). Importantly, neural signatures arise before observers indicate their choice behaviourally. For example, single-cell neural activity of area MT in awake, behaving monkeys that view random-dot motion stimuli predicts the perceived motion direction before monkeys report their choice (Newsome et al., 1989). Neural responses also reflect stimulus features related to perceptual uncertainty, such as the level of motion coherence or the ambiguity of a target's motion path. Similarly, decision-sensitive activity in the motor cortex reflects the buildup of the upcoming choice (Donner et al., 2009; Kaufman et al., 2015; Pape and Siegel, 2016; Thura and Cisek, 2014) and has been shown to influence eye and hand movement dynamics (Hagura et al., 2017; Joo et al., 2016; McSorley and McCloy, 2009; Selen et al., 2012). Perceptual decision making and sensorimotor control may therefore be continuous processes that dynamically interact and update each other to guide accurate motor behaviour.

Taken together, the literature reviewed in this section indicates a strong link between eye movements and perception. Yet, the discussed specificity of perceptual learning indicates that they are separate processes that do not necessarily transfer. Next, I will outline the importance of eye movements during eye-hand coordination.

#### **1.3 Eye-hand coordination**

One of the earliest theories on visual control was proposed by Gibson (1979) who suggested that relevant visual information is gathered to control actions. Gibson argued that our perceptual system is attuned to

visual information that enables us to readout environmental properties necessary to guide actions. In line with Gibson's idea, humans naturally shift their gaze to objects and locations of interest before they initiate a movement towards them (Hayhoe and Ballard, 2005; Land, 2006). Temporal and spatial demands for the visual system may change with varying cognitive goals. For example, reaching towards a coffee cup requires more accurate visual control than knocking it over. Whereas gaze control depends on action goals, hand movement planning and execution depend on current visual information. Thus, eye and hand movement processing is tightly coupled and interdependent.

Currently, there are two main theories of how visual control guides everyday actions. In line with Gibson's idea, on-line control proposes that current visual information is used to update and correct ongoing movements, whereas model-based approaches suggests that internal representations of physical laws and constraints control our movements (Zhao and Warren, 2015). Most goal-directed actions, including interceptive hand movements, rely on on-line control when visual information is available. However, if vision is occluded or unreliable, observers depend on context-specific heuristics, predictive mechanisms, or experience and memory (de la Malla and López-Moliner, 2015; Diaz et al., 2013a; Hayhoe, 2017; McIntyre et al., 2001). In this section, hand movements towards stationary objects and manual interception of moving targets will be discussed. Finally, neural correlates of eye-hand coordination will briefly be outlined.

#### 1.3.1 Eye movements during stationary object handling

When interacting with static objects, gaze patterns are closely linked to the observer's behavioural goal. During everyday tasks, such as tea or sandwich making, the temporal and spatial pattern of fixations and saccades are related to task relevant objects and action sequences (Hayhoe et al., 2003; Land et al., 1999; Land and Hayhoe, 2001). Similarly, when pointing towards or grasping for an object, gaze dwells on future contact points before the hand reaches its goal (Gribble et al., 2002; Neggers and Bekkering, 2000; Smeets et al., 1996; Vazquez et al., 2017; Voudouris et al., 2018). When manipulating the grasped objects, gaze leads the ongoing hand movement, landing on obstacles to avoid collision and anchoring to the end points of the reach (Ballard et al., 1992; Johansson et al., 2001; Land et al., 1999). However, during object handling, gaze is not only linked to current visual information, but also influenced by memory and expectation. For example, observers frequently look at remembered locations of an object while recreating a toy model, even if building blocks are repeatedly and randomly relocated while observers look away (Aivar et al., 2005). Similarly, during visual search, observers' fixations are biased towards remembered and expected object locations (Hollingworth, 2012; Võ and Wolfe, 2012). Gaze patterns and eye movements during natural tasks may therefore reveal how human observers integrate sensory information with cognitive processes, such as intention, expectation, and memory.

#### 1.3.2 Eye movements guiding manual interception of moving objects

Manual interceptions of moving targets, such as catching a ball or swatting a fly, require a fine-tuned interplay between the continuous updating of visual information, on-line control of the goal-directed hand movement, and predictive mechanisms (Brenner and Smeets, 2018; Soechting and Flanders, 2008; van Donkelaar et al., 1992; Zago et al., 2009; Zhao and Warren, 2015). Despite the high temporal and spatial demands of acting at the right time and place, humans are generally able to accurately intercept moving targets, using different movement modalities, including catching (Chapman, 1968; Montagne et al., 1999; Peper et al., 1994), pointing (Brenner and Smeets, 1996; Brouwer et al., 2005; Lee et al., 1997), or batting (Gray, 2002; Mann et al., 2013; Tresilian and Lonergan, 2002). Interception accuracy and precision is generally influenced by movement and task constraints. For example, if the size of the movement goal is small and target speed is fast, spatial accuracy may have to be traded for temporal precision (Brenner and Smeets, 2015; Fitts and Peterson, 1964; Newell et al., 1979; Schmidt, 1969; Tresilian et al., 2003). Moreover, interception performance usually degrades when the target is occluded and observers use a combination of predictive and on-line control to compensate for the missing visual information (de la Malla and López-Moliner, 2015; Mrotek and Soechting, 2007). Thus, the visual system seems to optimally integrate sensory information with ongoing movement plans to guide accurate visual predictions.

Whereas many studies have proposed how visual control contributes to the accuracy and dynamics of interceptive hand movements, the continuous role of eye movements during manual interceptions has received less attention. Observers that are instructed to intercept a continuously moving target naturally track it with smooth pursuit eye movements (Mrotek and Soechting, 2007), indicating that the tight link between smooth pursuit and visual prediction (Spering et al., 2011b) extends to interceptive control (Brenner and Smeets, 2011). When participants are instructed to fixate while intercepting moving targets, hand movement latency increases and end point accuracy decreases (Brenner and Smeets, 2010; de la Malla et al., 2017; van Donkelaar and Lee, 1994). In a free viewing condition, the rate of catch-up saccades is generally suppressed shortly after hand movement initiation (Mrotek and Soechting, 2007) and smoother tracking is associated with more accurate interceptions (Fooken et al., 2016). Moreover, the timing of smooth pursuit and saccades is critical: corrective saccades that occur close to the time of interception are associated with larger end point errors (Fooken et al., 2016; Goettker et al., 2019). Similarly, in ball sports, athletes follow and predict the ball's motion path by tracking the target with eye and head movements in combination with distinct saccades to anticipated bounce or contact locations (Bahill and LaRitz, 1984; Diaz et al., 2013b; Higuchi et al., 2018; Land and McLeod, 2000; Mann et al., 2013). Yet, when temporal and spatial task demands are less critical, the timing of eye movements with respect to target motion seems to be more flexible (Cesqui et al., 2015; López-Moliner and Brenner, 2016; López-Moliner et al., 2010). Similar to eye-hand coordination during stationary object handling, eye movements seem to adapt to specific task demands, movement constraints, and cognitive goals.

#### **1.3.3** Neural correlates of eye-hand coordination

Behavioural evidence suggests that eye and hand movements share common neural processing (Crawford et al., 2004). For example, simultaneous eye and hand movements are quicker and more accurate compared to isolated movements (Chen et al., 2016; Danion and Flanagan, 2018; Epelboim et al., 1997; Fooken et al.,

2018; Maiello et al., 2018; Snyder et al., 2002; van Donkelaar, 1998) and eye-hand coupling persists even when the visual system is perturbed (Engel et al., 2000; Kreyenmeier et al., 2017; Soechting et al., 2001). Successful eye-hand coordination requires the brain to transform visual input from a retinocentric reference frame into a body-centred representation (Flanders et al., 1992; Leclercq et al., 2013). However, whether visual space is encoded in egocentric or allocentric coordinates depends on available sensory information and task constraints (Battaglia-Mayer et al., 2003; Hu and Goodale, 2000). Neural activity, integrating eye and hand movements, similarly depends on temporal and spatial task demands (Battaglia-Mayer et al., 2015; Dean et al., 2012; Hwang et al., 2014). Importantly, early visual processing encoding reach movements and saccades show common neural pathways (Fig. 1.3; Vesia and Crawford, 2012).



Figure 1.3: Lateral view of human brain regions involved in eye-hand coordination. VC: visual cortex (V3A); AG: angular gyrus; IPS: intraparietal sulcus; aIPS/mIps anterior/midposterior part of IPS; SPOC: superior parieto-occipital cortex; S1: primary somatosensory area for arm movements (proprioception); BA5: Brodmann's area 5, M1: primary motor cortex; PMd/PMv dorsal/ven-tral premotor cortex; SEF/FEF: supplementary/frontal eye fields; DLPC: dorsolateral prefrontal cortex; PCS/CS: precentral/central sulcus; IPS: intraparietal sulcus; POS: parieto-occipital sulcus; IPS: Intraparietal sulcus; IPS: Intr

Processes related to eye-hand coordination are generally encoded in the posterior parietal cortex (PPC). Disrupting PPC activity using transcranial magnetic stimulation (TMS) during reaching disturbs the integration of eye-position signals and breaks up eye-hand coupling (van Donkelaar and Adams, 2005; van Donkelaar et al., 2000). Similarly, applying TMS to area MT+/V5 and the superior parieto-occipital cortex (SPOC) during manual interceptions causes errors in interceptive timing, accuracy and increases end point variability (Dessing et al., 2013). Successful interception critically relies on accurate motion integration in

area MT+/V5, on-line spatial encoding in SPOC, and predictive mechanisms arising from the parietofrontal network (Reid and Dessing, 2018). Target occlusion during interception also involves the intraparietal cortex (IPS) where memory and predictive representations of the target velocity are thought to be encoded (Assad and Maunsell, 1995; Delle Monache et al., 2017; Eskandar and Assad, 1999). Furthermore, the superior colliculus (see Section 1.1.2) is not only involved in the control of smooth pursuit and saccadic eye movements, but also encodes hand movement goals (Stuphorn et al., 2000) and may therefore play an important role for eye-hand coupling. At an intermediate stage, hand movement motor commands are encoded in the superior (SPL) and inferior (IPL) parietal lobules of the PPC, where visual and somatosensory (i.e., prioprioceptive) information is combined (Andersen and Buneo, 2002). Finally, the parietal–frontal network is involved in deciding and planning actions by relaying spatial information to the frontal motor areas and thereby guiding goal-directed behaviour (Andersen and Cui, 2009).

#### **1.4 Dissertation overview**

The overall research objective of this dissertation is to relate dynamically evolving eye movements to visual predictions, and action outcomes. To investigate the continuous relationship between eye movements and perceptual processing, I developed novel analyses that link the quality of eye movements to visual and behavioural events over time. The results of this work further our understanding of how humans process visual information to guide goal-directed actions.

#### **Research objective of study 1 (Chapter 2)**

Building on previous work that demonstrated a close relationship between smooth pursuit eye movements and interceptive hand movement accuracy and timing (Fooken et al., 2016), I test the differential effect of perceptual-motor training on eye and hand movement quality under different feedback conditions.

#### Research objective of study 2 (Chapter 3)

Given the interdependency between eye and hand movements during manual interceptions, I investigate whether eye movements are a sensitive predictor of observers' decisions to initiate or inhibit interceptive hand movements (go vs. no-go).

#### Research objective of study 3 (Chapter 4)

Go/no-go decisions can be decoded from observers' eye movements. Here I investigate the time course of decision formation and test whether eye movements contribute to accurate decision making.

#### **Research objective of study 4 (Chapter 5)**

Finally, I study the role of temporal and spatial task demands during go/no-go decision making. Different viewing conditions (free viewing vs. fixation) and response modalities (button press vs. interceptive hand movement) are compared to investigate the effect of movement constraints on decision accuracy and interception timing.

In each study, evolving eye movements are continuously analysed in relation to visual input (target motion) and behavioural events (the decision whether, when, and where to intercept). Moreover, the quality and characteristics of eye movements are compared to action outcomes (interception accuracy, decision outcome, and decision accuracy).

### Chapter 2

# Eye movement training is most effective when it involves a task-relevant sensorimotor decision

To guide goal-directed manual interceptions, observers naturally track the moving object with their eyes. In a previous study, we showed that tracking the target with accurate smooth pursuit eye movements was linked to higher interception accuracy and enabled later interceptions (Fooken et al., 2016). The observed close link between eye and hand movement quality raises the question whether training the eye can improve untrained hand movements. Alternatively, eye and hand movements may have to be trained simultaneously to improve visual predictions and interceptive performance. Finally, we ask whether feedback is necessary to enable learning and thereby increase eye and hand movement quality.

#### 2.1 Introduction

Vision and eye movements guide most of our everyday actions. When we reach for an object, our gaze is shifted to the target long before the hand. This predictive gaze behavior serves to gather information about object identity and location, and marks future contact points for hand and fingers (Johansson et al., 2001; Land et al., 1999; Smeets et al., 1996). When performing everyday actions, eye movements reflect the detailed evolution of the hand movement and the requirements of the task (Hayhoe and Ballard, 2005; Hayhoe, 2017). Gaze also leads the target when we interact with moving objects, such as catching a ball, and thus reveals knowledge of the future target path (Diaz et al., 2013b). Moreover, eye movements can be made predictively, for example during an occlusion interval, and scale with visual target properties such as acceleration (Bennett et al., 2007). In this context, it has been shown that more accurate tracking eye movements (smooth pursuit) result in better prediction of an object's trajectory (Bennett et al., 2010; Spering et al., 2011b). Tracking a moving object with smooth pursuit is also associated with higher accuracy in hand

movement planning (Leclercq et al., 2013) and execution (Fooken et al., 2016). It is important to note, however, that pursuit does not necessarily have to be aligned with the target until the moment of interception (Brenner and Smeets, 2011; de la Malla et al., 2017; López-Moliner and Brenner, 2016). Rather, it seems that the initiation of pursuit and subsequent combination with saccades is sufficient to enable successful interception. Correspondingly, ball sport athletes commonly track the ball briefly using a combination of eye and head movements and then saccade to an anticipated bounce or contact location (Bahill and LaRitz, 1984; Diaz et al., 2013). Such a combination of tracking or gaze holding and prediction in eye movement behavior is now considered a basic skill underlying superior athletic performance (Bahill and LaRitz, 1984; Land and McLeod, 2000; Mann et al., 2013; Uchida et al., 2013; Vickers, 2016).

Here we probe the relation between eye and hand movements in a rapid interception task using a perceptual training paradigm. First, we investigate whether eye movement training enhances the ability to perform untrained goal-directed hand movements. Second, we assess whether eye movement training is sufficient to enhance hand movements, or whether it would be more effective if it was combined with hand movement training.

The idea of transfer across modalities—from eve to hand—is based on the known tight link between eve and hand movements. On one hand, such transfer of training does not readily occur in perceptual or motor learning. For example, one of the hallmarks of perceptual learning is its specificity, i.e., lack of transfer to untrained tasks, visual locations, features, or across modalities (Fahle, 2005; Polat and Sagi, 1994). On the other hand, specificity depends on stimulus characteristics and task requirements. Transfer of perceptual learning from one location to another has been observed when the second location was previously sensitized via training an irrelevant task at that location (Xiao et al., 2008) or when the same stimuli were used (Porat and Zohary, 2016). Transfer across tasks, for example, from Vernier acuity and contrast detection to Snellen acuity, has been observed in patients with amblyopia (Levi and Li, 2009) and college baseball players (Deveau et al., 2014), who even seem to improve on-field performance following such training (see also Faubert, 2013). The broadest transfer of perceptual learning beyond the trained task has been found after training with action video games (Green and Bavelier, 2012; Li et al., 2016), resulting in improved selective attention (Green and Bavelier, 2003) and spatial resolution across the visual field (Green and Bavelier, 2007). Transfer of learning across modalities, from perception to eye movements, is possible if the task requires responses with similar underlying processing mechanisms. Szpiro et al. (2014) trained observers in a motion discrimination task during fixation and found generalization to untrained smooth pursuit eye movements. Transfer of learning has also been observed in other modalities, such as the somatosensory system: tactile perceptual learning can transfer to untrained fingers (Dempsey-Jones et al., 2016).

To address the question whether eye movement training is sufficient to enhance hand movement accuracy, we define and measure performance improvements in hand movement accuracy following isolated training (eye movements are trained, hand is not trained) or combined training (eye and hand movements are trained simultaneously). In an effort to address a bidirectional relation between eye and hand movements, we also investigate the effect of isolated or combined training on eye movement accuracy and precision. A comparison of effects of different training protocols will allow us to evaluate whether eye movement training alone is sufficient to improve the eye, or whether there are added benefits of involving the hand in training, indicating transfer.

We assessed participants in a motion prediction task that required rapidly intercepting a moving object with the hand. In this task, participants viewed a target moving along a curved trajectory—akin to a lateral view of a batted baseball. Importantly, the target was shown only briefly, and participants had to extrapolate its motion trajectory before intercepting it in a dedicated area on the screen. Ultra-short target presentation durations make this task difficult (Fooken et al., 2016) and therefore suitable for a training paradigm. Eye and hand movements were recorded simultaneously. Testing and training with different training protocols occurred over a period of five consecutive days; we also assessed the longer-term retention of learning in a follow-up session one week after training. Some of the training protocols involved an active movement towards the assumed target position and external performance feedback on whether the eye or hand successfully reached the target. Performance feedback is widely considered an important component in training across modalities (Gray, 2009; Herzog and Fahle, 1999; Sigrist et al., 2013; Swinnen, 1996; Wolpert et al., 2011). It might accelerate learning (Fahle and Edelman, 1993; Werner and Bock, 2007) and facilitate transfer (Deveau et al., 2014; Salmoni et al., 1984; Swinnen et al., 1997; Tanaka and Watanabe, 2017). We manipulated external performance feedback to investigate and compare feedback effects on eye and hand movement (see below, Hypotheses).

#### 2.2 Materials and Methods

#### **Participants**

We recruited 50 right-handed undergraduate students (mean age = 24.2 years; SD = 3.5; 29 female) with corrected-to-normal visual acuity and no history of disease interfering with normal eye movement function. The experimental protocol adhered to the Declaration of Helsinki and was approved by the UBC Behavioral Research Ethics Board. Participants gave written informed consent prior to participation and were unaware of the purpose of the experiment. Each participant was randomly assigned to one of five groups (n = 10 each): four training groups that were tested at least five times and one control group that was tested at least twice (see Table 1). Sample size per group is comparable to other studies investigating training effects on eye or finger movements (Dempsey-Jones et al., 2016; Porat and Zohary, 2016). Remuneration was \$8 per hour for each session; a bonus of \$20 was paid upon completion of all five sessions. All 50 observers completed the study, and 41 of them returned for the follow-up session one week later (\$10 remuneration).

#### Visual stimuli and apparatus

Stimuli, apparatus, and task were based on methods developed in Fooken et al. (2016), and are reproduced here for the reader's convenience. Observers had to track and intercept a briefly presented, small, black Gaussian dot with diameter 2 degrees of visual angle (°), shown at a luminance of 5.4 candela per meter squared (cd/m<sup>2</sup>). The stimulus moved across a uniform gray background equally divided into a lighter gray

"tracking zone" on the left (35.9 cd/m<sup>2</sup>) and a darker gray "hit zone" on the right (31.5 cd/m<sup>2</sup>; Fig. 2.1a). The physical trajectory of the target was simulated to be the natural flight of a batted baseball. Visual stimuli were back-projected using a PROPixx video projector (VPixx Technologies, Saint-Bruno, QC, Canada) with a refresh rate of 60 Hz and a resolution of 1280 (H)  $\times$  1024 (V) pixels. Observers sat at a distance of 46 cm from the screen with their head supported by a chin and forehead rest. The screen was a 44.5 cm  $\times$  36 cm translucent display consisting of non-distorting projection screen material (Twin White Rosco screen, Rosco Laboratories, Markham, ON, Canada) clamped between two glass panels and fixed in an aluminum frame. Stimulus display and data collection were controlled by a Windows PC with an NVIDIA GeForce GT 430 graphics card running Matlab 7.1 and Psychoolbox 3.0.8 (Brainard, 1997; Pelli, 1997).

**Table 2.1:** Training protocols for five groups. Notes: Training on days 2–4 could include eye movements only (eye), or combined eye and hand movements (hand); it either involved external performance feedback (FB) or not. Pre- and posttest were identical across groups. Number of observers during follow-up testing varied by group.

Group	Mean	Gender	Pre-test	Train	ing (days	s 2-4)	Post-test	Follow-
(n = 10  each)	age (SD)	( <i>n</i>	(day 1)	eye hand		FB	(day 5)	up <i>n</i>
		female)						(day 12)
(1) eye no FB	24.5 (3.8)	6	$\checkmark$	√			$\checkmark$	9
(2) eye FB	25.6 (4.2)	6	$\checkmark$	$\checkmark$		$\checkmark$	$\checkmark$	9
(3) eye-hand no FB	23.9 (3.6)	6	$\checkmark$	$\checkmark$	$\checkmark$		$\checkmark$	10
(4) eye-hand FB	24 (2.3)	6	$\checkmark$	$\checkmark$	$\checkmark$	$\checkmark$	$\checkmark$	5
(5) no training	23 (3.3)	5	$\checkmark$				$\checkmark$	8

*Testing sessions.* Observers were tested before training (pre-test) and after training (post-test and followup test) using the following procedure and task (Fig. 2.1b): Each trial began with fixation on a stationary ball presented  $14^{\circ}$  to the left from screen center; fixation duration was randomized (500-700 ms). The ball then moved to the right at one of three speeds (25, 30,  $35^{\circ}/s$ ) and disappeared after a short presentation duration (100, 200, or 300 ms) before reaching the hit zone (see Fig. 2.1a). Speed and presentation duration were randomized within each block of trials. Observers were instructed to track the ball smoothly with their eyes, to continue to track it after it disappeared, and to intercept it with their index finger at an assumed position anywhere within the hit zone. Interceptions were always made in the ipsilateral (right) half of the screen and observers returned their hand to a table-fixed resting pad after each trial. Feedback on manual





b Track-intercept task (pre & post test)



#### C Group and training types



**Figure 2.1:** Experimental procedure and design. Stimuli moved at one of three different speeds, resulting in three trajectory types (a), and were presented for either 100, 200, or 300 ms. An example trial sequence from the pretest track-intercept task is presented in (b). Each trial started with fixation in the "tracking zone", followed by stimulus motion for 100–300 ms. Observers were instructed to track the target with their eyes even after it disappeared, and to intercept it anywhere within the "hit zone" with their index finger (red dot). Performance feedback was given after each trial (black dot). On training days (c), observers were instructed to either track the target with their eyes (groups 1 and 2), or to intercept with their finger (groups 3 and 4). Only groups 2 and 4 received performance feedback during training (black dot); group 3 received feedback about their finger end position (red dot); group 5 was not trained and served as the control group.

interception performance was provided at the time of interception; a red dot indicated interception location and a black dot indicated true target position (Fig. 2.1b). Performance feedback was visible for 500 ms; the next trial started in immediate succession. Each pre- or post-testing session (162 trials) took approx. 20 minutes.

*Training sessions*. Training protocols (groups 1-4; days 2-4) differed with regard to response modality (eye alone or combined eye-hand) and visual feedback (2.1); Fig. 2.1c). Groups 1 and 2 did not move their hand during training. Group 1 was instructed to track the target with their eyes into the hit zone; the target never reappeared, and observers received no performance feedback. Group 2 was asked to track the target

and to actively intercept it with their eyes. To be recognized as final eye position ("hit" or "intercept"), observers had to hold their gaze within a 1.4 degree radius of the assumed target position in the hit zone for 200 ms. They received feedback about where the target was relative to their eye: a red dot indicated their final eye position, and a black dot showed true target position. Observers in groups 3 and 4 were asked to track the target with their eyes and to intercept it with their finger, just as they did during testing. Group 3 received no feedback (only interception position, not true target position, was shown) and group 4 received the same full performance feedback as during testing. Training sessions included three blocks of 162 trials each (486 trials total) and took approx. 60 minutes to complete. Group 5 served as a control and received no training; these participants were only tested twice and did not come into the lab on training days.

#### Eye and hand movement recordings and analysis

We recorded right eye position with a video-based eye tracker (tower-mounted Eyelink 1000, SR Research Ltd., Ottawa, ON, Canada) at a sampling rate of 1000 Hz. At the start of each block of trials, the measurements were calibrated by asking observers to fixate on a small visual target appearing successively at nine different locations on the screen; this procedure was repeated for validation. All data were analyzed off-line using custom-made routines in Matlab for the detection of saccades and pursuit onset (Fooken et al., 2016). Saccades were excluded from pursuit analysis and analysed separately. We computed relative eye velocity (calculated as gain: frame-by-frame eye velocity divided by target velocity in the interval 140 ms after pursuit onset to interception) as the parameter defining pursuit quality. We also computed the cumulative amplitude of catch-up saccades, i.e., the total distance covered by saccades. To investigate how closely the eye landed relative to the final position of the target position,  $p_{tar}$ , and the final eye position  $p_{eye}$  at the time the trial finished. The trial finished either when the target was intercepted manually (pre- and posttest; groups 3 and 4), the target was intercepted with the eyes (group 2), or the target reached the end of its trajectory (group 1). Eye interception error (or accuracy) was then calculated as the Euclidean distance  $d_{eye} = || p_{tar}-p_{eye} ||$ .

During all testing sessions, and during training sessions that involved the hand (groups 3 and 4), movements of observers' right index finger were tracked with a magnetic tracker (3D Guidance trakSTAR, Ascension Technology Corp., Shelburne, VT, USA) at a sampling rate of 240 Hz. A lightweight sensor was attached to the observer's fingertip with a small Velcro strap. Calibration of measurements obtained with the trakSTAR relied on a 5-point procedure in which observers were asked to point to the location of a visual target appearing successively at five locations with their index finger and keep their finger at this location until the next target appeared. This procedure immediately followed eye tracker calibration at the start of each trial. We recorded the 2D finger interception position in x- and y-screen-centered coordinates for each trial. To analyse manual interception accuracy, we first defined the finger hit position,  $p_{finger}$ , as the 2D position of the finger when it first makes contact with the screen. The target position at that time is denoted as  $p_{tar}$ . Interception accuracy is the interception error, calculated as the Euclidean distance  $d_{finger} = || p_{tar} - p_{finger} ||$ . We also analysed interception precision, defined as the statistical variance, indicating spatial variability of xand y-interception positions. All trials were manually inspected, and those with eye blinks (4.3% of all tri- als), hand movement onset prior to target onset (1%), or undetected finger end position (2%) were excluded from further analysis.

#### Hypotheses and statistical analyses

Hypotheses are graphically presented in Figure 2.2. First, we expected that movement accuracy would improve in all training groups as compared to the control group. This improvement might be limited to the trained modality, i.e., hand movement accuracy will increase when training involves moving the hand and eye movement accuracy will increase after training that involves the eye (Hypothesis 1a; Fig. 2.1a). Alternatively, the improvement might transfer across modalities, i.e., hand movement accuracy will increase after eye movement training and eye movement accuracy will increase after hand movement training (Hypothesis 1b; Fig. 2.2a). Second, we expected that external performance feedback based on an active interceptive movement might boost movement accuracy for each modality (Hypothesis 2; 2.2b). Alternatively, if transfer was found (Hypothesis 1b) feedback might enhance performance across modalities.

Differences between groups, and the hypothesis that each training group improved within the given response modality more than the control group, were examined using one-way ANOVA with factor group. Inter-group differences were examined using a post-hoc Dunnett's test to account for potential dependencies in multiple comparisons between each training group and the control group (Dunnett, 1955). With n - k degrees of freedom (sample size minus number of groups),  $\alpha = 0.05$ , five groups, and a sample size of n = 10 per group, the critical value above which a Dunnett's test would be significant is t = 2.89. We also compared training groups with regard to response modality and whether or not feedback was given using repeatedmeasures ANOVA with factors modality and feedback. Changes across training days were investigated with repeated-measures ANOVA with factor day. In all groups and sessions, speed and presentation duration were varied to increase stimulus uncertainty. Based on previous studies using the same paradigm, we expected that these stimulus conditions would systematically affect eye and hand movements (Fooken et al., 2016; Kreyenmeier et al., 2017), and we replicate and report those results here. Effects of speed and presentation duration were analysed using repeated-measures ANOVA with factors speed and duration; this analysis was conducted on data averaged across training groups for the pre-test. However, we had no specific hypotheses regarding interactions between training groups and stimulus conditions, and thus pooled across speeds and presentation durations when testing our main study hypotheses. Statistical analyses were conducted in IBM SPSS Statistics Version 24 (Armonk, NY, USA).

#### 2.3 Results

Our results focus on the effects of training on eye and hand movement accuracy (Hypothesis 1, Fig. 2.2a) and describe how performance changed from pre-test to post-test. We also consider the role of external feedback in task versions requiring active interception (Hypothesis 2, Fig. 2.2b), and day-to-day improvements across training days.



**Figure 2.2:** Schematic predictions of training effects. The graphs in (a) illustrate expected improvements after training as compared to the control group within each modality (Hypothesis 1a, H0 not shown) and potential boost across each modality (Hypothesis 1b, transparent bars). Graphs in (b) illustrate the expected effect of feedback on performance (Hypothesis 2, transparent bars). If feedback had no effect on eye and hand movement, accuracy results would be equivalent to panel (a).

#### Effects of target properties on eye and hand movements

We varied speed and presentation duration—two variables that can be expected to strongly influence eye and hand movements. Replicating previous results (Fooken et al., 2016), pursuit was more accurate when the target was presented for a longer duration and when it moved at a slower speed: relative eye velocity increased with increasing presentation duration (F(2,98) = 115.4, p < .001,  $\eta_p^2 = .70$ ) and with decreasing

speed (F(2,98) = 247.9, p < .001,  $\eta_p^2 = .84$ ). Manual interceptions were most accurate (smallest interception error) when the target was presented for a longer duration (F(2,98) = 58.3, p < .001,  $\eta_p^2 = .54$ ) and when it moved at a medium speed (F(2,98) = 38.53, p < .001,  $\eta_p^2 = .44$ ), indicating a speed-range effect (see Fooken et al., 2016).

In general, observers tended to intercept early in the hit zone and close to the medium-speed target trajectory, in line with a speed-range effect. These patterns were observed across all groups, despite high individual variability in interception strategy (e.g., early vs. late in the hit zone). Figure 2.3 shows 2D interception positions during pre- and post-test for four representative observers; two observers from the control group, for whom we would expect the smallest performance increase, and two from group 4 (eye-hand training with feedback), for whom we would expect the largest performance increase.



**Figure 2.3:** 2D interception positions of two representative observers in group 5 (no training; top row) and two observers in group 4 (eye-hand training with feedback; bottom row); each data point denotes interception position in one trial in the pretest (closed symbols) or posttest (open symbols). Target speeds are denoted by line color and presentation durations by symbol type.

Whereas absolute interception position and timing (later interceptions were made further into the hit zone) differed between individuals, they did not differ significantly between groups and did not change from pre to posttest. This observation was confirmed using a multivariate ANOVA with *group* as fixed factor, yielding no significant group effects on differences between x-interception position (F(4,45) = 1.71, p = .16,  $\eta_p^2 = .13$ ) or y-interception position (F < 1) in pre-test versus post-test. Our main analyses therefore

focus on interception accuracy and precision, rather than on absolute position.

**Training the hand enhanced hand movement accuracy and precision irrespective of external feedback** We calculated finger interception error, i.e. the 2D distance between finger and target end position at time of interception, to evaluate hand movement accuracy. Interception error was overall smaller after training as compared to before training in all groups (Fig. 2.4a). The largest percentage improvements can be seen in groups that trained while using their hand (Fig. 2.4b,c). These observations were confirmed by significant comparisons (Dunnett's *t*) between hand-training groups with the control group (group 3: p =.05, Cohen's d = 1.2; group 4: p = .02, d = 1.41), implying that training the hand in a manual interception task improved interception accuracy. Performance in the eye-training groups did not improve significantly compared to the control group (group 1: p = .53, d = 0.27; group 2: p = .27, d = .65), reflected in an overall non-significant effect of the factor group (F(4,45) = 2.2, p = .08,  $\eta_p^2 = .16$ ). These results indicate that hand movement accuracy only improved when the hand was engaged during training, whereas isolated eye movement training did not benefit the hand.

Notably, the interception performance level achieved after training remained stable or continued to increase one week later (see Fig. 2.4d). A repeated-measures ANOVA with within-subjects factor *time* (post vs. week test) and between-subjects factor *group* revealed a significant main effect of *time* (F(1,35) = 5.93, p = .02,  $\eta_p^2 = .15$ ) and a significant *group* × *time* interaction (F(4,35) = 2.97, p = .03,  $\eta_p^2 = .25$ ). Note that these statistics are based on observers who participated both in the post-test and in the week test (n = 41). Hence, they do not exactly match post-test means shown in Figure 2.4b for n = 50.

Whereas feedback did not modulate hand movement accuracy after training—no significant main effect of *feedback* on post-test performance (see Fig. 2.4c), and no *feedback* × *modality* interaction (all F < 1)—it did affect the time course of learning. Figure 2.4b shows improvements in interception accuracy relative to pre-test for each day. When feedback was given (group 4), interception accuracy increased across training days, saturated on day 3, and remained stable during post-test. When no feedback was given and observers had no knowledge of the target end position (group 3), interception accuracy decreased across training days, indicating that observers hit further away from the target in the absence of feedback. Performance in this group recovered during post-test when observers received feedback, reaching the same performance level as the group that had received feedback throughout training. These observations were confirmed by a repeatedmeasures ANOVA with factors *feedback* and *day*, yielding a significant main effect of *day* (F(5,65) = 7.3, p < .001,  $\eta_p^2 = .36$ ) and a *feedback* × *day* interaction (F(5,65) = 4.13, p = .003,  $\eta_p^2 = .24$ ). In sum, hand movement accuracy increased significantly following training that involved the hand. These improvements occurred irrespective of feedback, even though feedback modulated performance during training days.

It is noteworthy that performance increased even in the absence of any training (see control group data in orange in Fig. 2.4), posing the question whether the pre-test alone might have been sufficient to provide full and extensive training of the task. We investigated this possibility by analysing average interception error during the pre- and post-test in bins of 9 trials. Figure 2.5 shows average binned interception errors for two groups—group 5 (no training) as the group that improved the least (Fig. 2.5a), and group 4 (eye-hand



**Figure 2.4:** Training effects on manual interception accuracy. (a) Interception error (in degrees) during pretest versus posttest. Each data point is the mean 2D interception error for one observer across all trials; larger data points with 2D error bars are group means. Data points falling above the unity line indicate higher error during the posttest; data points below the unity line denote higher error during the pretest. (b) Change in interception accuracy (degree) in comparison to the pretest, with error during pretest set to zero, for all testing and training days. (c) Percentage accuracy increase (error decrease) in posttest relative to pretest. Asterisks denote significant results of Dunnett's *t* test, \**p*, 0.05. (d) Absolute interception error averaged across observers that came for the week follow up for post- (darker) compared to week-test (lighter). Asterisks denote significant results of pairwise *t* test, \**p*, 0.05, \*\*\**p*, 0.001. Error bars in all panels denote standard errors of the mean.

training with feedback) that improved the most (Fig. 2.5b). For both groups, interception error decreased during the first half of the pre-test, and then remained stable at a level of around 3 deg on average across all speeds. Even though the control group's performance improved at the start of the post-test in the absence of training, overall interception error was higher ( $M = 2.4 \pm 0.13$  deg) than for the eye-hand training group ( $M = 2.1 \pm 0.16$  deg), indicating that additional training was useful. This group continued to improve on training days, and reached an overall higher level of accuracy. Most importantly, neither group achieved ceiling performance at any time.


Figure 2.5: Mean interception error in response to three different speed conditions over time; (a) Group 5 (no training), and (b) group 4 (eye-hand training with feedback). Values for pre- and posttest are averaged within bins of nine trials. Values for training days are averaged across session (n = 486 trials). Filled symbols denote group mean; open symbols are means per subject.

Finally, we investigated effects of training on interception precision, the spatial variability of x- and yinterception positions. Figure 2.6 shows mean variance for each group before and after training and reveals large improvements in precision for the four training groups, especially along the horizontal axis (timing; i.e., how far into the hit zone observers intercepted; see Fig. 2.3). The control group also improved, but to a much smaller extent (Fig. 2.6e), maintaining relatively large spreads in horizontal and vertical directions (see also Fig. 2.3a).



**Figure 2.6:** 2D interception variance (precision) in pretest (outer ellipse) as compared to posttest (inner ellipse) for all groups averaged across conditions and observers.

#### Training the eye differentially enhances eye movement performance

Training effects on eye movements were quantified by calculating two main performance measures: interception error of the eye (i.e., eye position relative to final target position), and relative eye velocity (i.e., eye velocity relative to target velocity).

Similar to the pattern observed for manual interception error, the eye interception error decreased with training (main effect of *group* on accuracy improvement in post-test relative to pre-test; F(4,49) = 2.96, p = .03,  $\eta_p^2 = .21$ ; Fig. 2.7a). When no feedback was given and observers had no knowledge of the target end position (group 1), eye interception accuracy decreased across training days (Fig. 2.7b). Performance in this group recovered during post-test when observers received feedback, reaching the same performance level as the group that had received feedback throughout training. However, we observed no significant overall intergroup differences due to large improvements in the control group (Fig. 2.7c). Across all groups, observers' final eye and hand positions were closely linked, indicating that observers pointed where they looked, within  $1.9 \pm 0.32$  deg in the pre-test, and  $1.5 \pm 0.25$  deg in the post-test.

Figure 2.8 shows mean eye velocity profiles for all test and training days for each group. Observers commonly initiated smooth pursuit in anticipation of the predictable motion direction; the frequency of occurrence of these anticipatory movements increased with exposure to the task (compare pre- and post-test velocity values at time 0, when the target started moving). At around 100-150 ms after target onset eye velocity increased rapidly, but never reached target speed, decreasing again after reaching a peak at around



**Figure 2.7:** Training effects on eye interception accuracy. (a) Interception error (in degrees) during pretest versus posttest. Each data point is the mean 2D interception error for one observer across all trials; larger data points with 2D error bars are group means. Data points falling above the unity line indicate higher error during the posttest; data points below the unity line denote higher error during the pretest. (b) Interception accuracy increase (degree) relative to the pretest, with error during pretest set to zero, for all testing and training days. (c) Percentage accuracy increase (error decrease) in posttest relative to pretest.

300 ms. Pursuit's transient nature in this task is due to limited target presentation duration (100-300 ms), and the peak at 300 ms indicates that observers attempted to maintain pursuit up to the maximum visible target duration. Accordingly, relative eye velocity (gain) values were on average  $0.25 \pm 0.11$ . The eye velocity profiles reveal an increase in eye velocity from pre-test to post-test in training groups 2-4 (compare colored dotted and dashed lines in panels b-d). In these groups, performance also improved across training days from day 1 to day 3 (compare light and dark grey lines). By contrast, group 1 showed only a slight increase, and the control group showed no increase in eye velocity.

We quantified the observed effects of training by calculating relative eye velocity, i.e. the mean of the ratio of eye versus target velocity at each time frame between 140 ms after onset to time of interception, as a measure of eye movement accuracy. Training effects emerged early during the pursuit response and built up over time, reaching a peak at around 250 ms after stimulus onset, just before the eye started to decelerate. Correspondingly, relative eye velocity increased up to 20% in the training groups, whereas the control group's relative velocity slightly decreased from pre to post-test (Fig. 2.9a-c). These findings were confirmed by a significant main effect of *group* on relative velocity improvement in post-test in comparison to pre-test (F(4,49) = 3.65, p = .01,  $\eta_p^2 = .25$ ). Similar to what we observed for hand movement accuracy, eye movement performance differences were significant in both hand-training groups regardless of feedback (group 3: p = .01, d = 1.32; group 4: p = .006, d = 1.16). Accordingly, we found no main effect of feedback on post-test relative velocity in training groups (F(1,36) = 1.88, p = .18,  $\eta_p^2 = .05$ ), and no *feedback* × *modality* interaction (F(1,36) = 1.82, p = .19,  $\eta_p^2 = .05$ ).

Eye movement improvements were also significant in the eye training group that received feedback (p = .005, Cohen's d = 1.63), but not in the eye training group without feedback (p = .13, d = .81). Again,



Figure 2.8: Mean eye velocity traces as a function of time relative to target motion onset across all observers (n = 10 per group; one panel per group). Saccades were replaced by linear interpolation. Line style denotes testing or training day.

feedback modulated the time course of learning (compare green lines in Fig. 2.9b). This observation was confirmed by a main effect of *feedback* on relative eye velocity for the two eye-movement training groups (F(1,18) = 17.21, p = .001,  $\eta_p^2 = .49$ ), but not for the hand-training groups (F < 1). This differential modulatory effect of feedback on eye and hand movement training was reflected in a significant *feedback* × *modality* interaction (F(2,36) = 25.07, p < .001,  $\eta_p^2 = .59$ ) during training days, and across all testing and training days (F(1,10) = 6.01, p = .03,  $\eta_p^2 = .38$ ).

Similar to what we observed for hand movement performance, eye accuracy remained unchanged compared to post-test when tested one week later (see Fig. 2.9d). A repeated-measures ANOVA with withinsubjects factor *time* (post vs. week test) and between-subjects factor *group* revealed no effect of *time*  $(F(1,35) = 1.58, p = .22, \eta_p^2 = .04)$  and no *group* × *time* interaction (F < 1). Again, these statistics are based on subjects who participated in the week test (n = 41), resulting in the difference to post-test data shown in Figure 2.9b for n = 50. In sum, eye movement accuracy increased significantly either when training involved the hand, or when external performance feedback was given, as was the case in task versions that involved a sensorimotor decision.

It is important to note that performance differences between the two isolated eye training groups (Fig. 2.9b,c) could result either from the fact that only one of these groups received external performance feed-



**Figure 2.9:** Training effects on eye movement accuracy. (a) Relative eye velocity during pretest versus posttest. Each data point is the mean relative velocity for one observer across all trials; larger data points are group means. Data points falling above the unity line indicate higher relative velocity during the posttest; data points below the diagonal denote higher relative velocity during the pretest. (b) Relative velocity change in comparison to the pretest, with relative velocity during pretest set to zero, for all testing and training days. (c) Percentage velocity increase in posttest relative to pretest. Asterisks denote significant results of Dunnett's t test, \**p*, 0.05, \*\**p*, 0.01. (d) Relative velocity averaged across observers that came for the week follow up for post (darker) compared to week-test (lighter). Error bars in all panels denote standard errors.

back, or from differences in eye movement behaviour. Whereas group 1 merely tracked the target, group 2 was asked to intercept with their eyes, triggering a goal-directed movement at the assumed target position. As a result of this instruction, observers in groups 1 and 2 produced eye movement patterns that differed both qualitatively and quantitatively, resulting in overall higher eye interception accuracy in group 2 (see also Fig. 2.7b). Observers in group 1 tracked the target for longer periods of time, using a combination of smooth pursuit and saccadic eye movements (see example in Fig. 2.10a,c), whereas observers in group 2 made an early saccadic eye movement towards the target, thus terminating the trial (Fig. 2.10b,d). Congruent with these observations, observers in group 1 initiated their final saccade on average 500 ms later than group 2 (latency group 1:  $M = 1169 \pm 39$  ms; group 2:  $M = 503 \pm 12$  ms). Moreover, observers in group

1 made on average twice as many saccades as compared to group 2 (group 1:  $M = 4.3 \pm 0.24$ ; group 2:  $M = 2.4 \pm 0.14$ ), resulting in a larger cumulative saccade amplitude (group 1:  $M = 31 \pm 1.9$  deg; group 2:  $M = 15 \pm 0.5$  deg). These results indicate that performance differences between both groups are likely modulated by differences in task, rather than the fact that external performance feedback was given.



**Figure 2.10:** (a) Horizontal and vertical eye position for a representative observer in group 1 (eye training no feedback) for two single trials during a training day. Black line denotes average target path shown until time of interception, the vertical gray line denotes point of target disappearance at 200 ms. (b) Eye position of a representative observer in group 2 (eye training with feedback) in two trials in which the target disappeared after 200 ms. In both panels the target entered the hit zone at 1,000 ms after target onset. (c) Horizontal and vertical eye position as a function of time for one representative trial from the same observer as in (a). (d) Horizontal and vertical eye position for the same observer as in (b).

#### 2.4 Discussion

This study investigates under which circumstances perceptual-motor learning transfers across modalities, and the mechanisms underlying performance improvements in eye and hand movements. Using a motion prediction task and comparing five different types of training, we report three key findings. First, eye movement training does not transfer to hand movements, despite known close links between both modalities in

tasks that involve goal-directed hand movements. Second, eye movements improve most when training involves an interception (either eye or hand). Third, external performance feedback has relatively little influence on training outcome.

#### Eye movement training does not transfer to hand movements

Eye movements are usually made spontaneously when observers engage in visually-guided manual tasks such as reaching, grasping, pointing or hitting. Eye and hand movements are spatially and temporally coordinated: gaze leads the hand by up to 1 second (Ballard et al., 1992; Land, 2006; Sailer et al., 2005; Smeets et al., 1996), and gaze locations are anchored to future contact points on the target, indicating strong spatial coupling (Brenner and Smeets, 2011; Cesqui et al., 2015; Gribble et al., 2002; Neggers and Bekkering, 2000; van Donkelaar and Lee, 1994; Vazquez et al., 2017). Many of these studies have focused on the saccade-to-reach relationship. Using the same motion prediction task as in the current study, we recently extended these findings to smooth pursuit, revealing a close relationship between the accuracy of pursuit and the accuracy of manual interceptions (Fooken et al., 2016). This link was closest at the time of interception, indicating a common spatiotemporal framework for the control of smooth pursuit and interceptive hand movements. One potential consequence of such common mechanisms would be that improvements in one domain—the eye—should transfer to the other—the hand. Yet, the current study showed that training eye movements alone was not sufficient to improve hand movements, revealing no transfer from eye to hand (Fig. 2.3). This result was obtained regardless of the type of eye movement training employed (i.e., with or without feedback). Transfer of learning across modalities might only be possible if task requirements are strongly aligned and rely on the same processing mechanisms. Szpiro et al. (2014) observed transfer from perception to pursuit in a motion discrimination task that required perceptual estimation of the target's motion direction. There is considerable overlap in the neural mechanisms underlying motion perception and smooth pursuit (Lisberger, 2010; Osborne et al., 2005; Spering and Montagnini, 2011), facilitating transfer from motion perception to motion tracking. Even though there is evidence for interdependency between the neural control of eye and hand movements, particularly within posterior parietal cortex (Battaglia-Mayer et al., 2015; Buneo and Andersen, 2006; Cui and Andersen, 2007; Snyder et al., 1997), both types of movement are ultimately controlled by effector-specific networks. Moreover, there is little research on the neural mechanisms underlying pursuit-hand coordination, and the extent of overlap between the cortical architecture underlying each type of movement is unclear. Finally, our current task was more complex and required not only processing of sensory motion information, but also trajectory prediction, based on past experience. Lack of transfer could indicate that the process of integrating sensory with experience-based information might differ for pursuit and hand movements.

In sum, our finding of lack of transfer from eye to hand is congruent with much of the perceptual learning literature indicating specificity of learning (Fahle, 2005). It emphasizes the importance of designing training tasks whose requirements mimic real-world requirements across diverse areas of application (e.g., a particular type of move in sports, or clinical rehabilitation).

#### Eye movements improve most when training involves a sensorimotor decision

We found that training smooth pursuit eye movements alone was also not sufficient to improve eye movement accuracy. Our training group 1 merely viewed the target briefly and tracked it with their eyes; these observers never saw the target end position in the hit zone. As a result, neither eye nor hand movements improved as compared to the control group. This finding is consistent with literature on eye movement training, showing only marginal improvements in pursuit velocity gain after training (Guo and Raymond, 2010; Szpiro et al., 2014). Yet, some studies have reported beneficial effects of smooth pursuit training. Experimentally naïve monkeys showed higher pursuit velocity and fewer catch-up saccades after many rigorous training sessions (Bourrelly et al., 2016). Moreover, engaging in contralesional pursuit improved functional recovery in human patients with visual neglect (Kerkhoff et al., 2014, 2013). These studies differ from ours in many aspects—study subjects, type of stimulus and task, and probably most importantly, duration and intensity of training. It is possible that prolonged pursuit training over many weeks could have increased pursuit performance in our study. Congruent with this assumption, group 1 was the only group displaying a small trend towards further improvement when tested again one week after training had been completed (Fig. 2.3d; 2.5d).

Interestingly, when pursuit training was paired with the instruction to make an eye movement toward the assumed target position in the hit zone (group 2), eye movements improved considerably. This improvement could be due to a combination of factors, including the preparation and execution of a goal-directed saccadic eye movement (Fig. 2.6), the predictive sensorimotor decision underlying this saccade, or motivational aspects related to external performance feedback. Feedback did not differentially affect eye movement performance in groups where training involved the hand (Fig. 2.5c). It is therefore unlikely that the difference between the two eye-training groups was entirely driven by feedback. Instead, differences in eye movement behavior, most notably an early goal-directed saccade and overall shorter and more accurate tracking in group 2, could underlie the finding that training in group 2 was more effective. Making an interceptive saccade comprises a different behavioral goal than just tracking a moving target without any task related to its trajectory; it requires prediction based on experience from previous trials (location of feedback) and integration with current sensory information (initial launch trajectory). Eye movements generally reflect the requirements of visual-motor tasks such as reaching, grasping, or walking (Hayhoe and Ballard, 2005; Hayhoe, 2017). Along the same lines, the behavioral goal of intercepting the target with the eyes might determine the need for accurate trajectory prediction, which in turn can only be achieved with accurate pursuit (Spering et al., 2011b).

Finally, we acknowledge that we attributed beneficial effects of training that engaged the hand to the fact that the hand performed a goal-directed movement, involving a sensorimotor decision. Alternatively, improvements might be possible just based on engaging the hand in any kind of movement. This possibility could be tested by including a control group that engages in an independent pointing or hand movement task, not training the observer in the primary task.

#### External performance feedback did not modulate training

Providing external performance feedback generally boosts effects of training in visual (Deveau et al., 2014) and motor tasks Swinnen (1996) (Sigrist et al., 2013). Gray (2009) compared swing accuracy in a baseball batting simulator when giving visual, auditory, or tactile feedback, respectively, to a no-feedback condition. Swings were more accurate when feedback was given, and visual feedback produced the greatest accuracy. However, feedback might not be critical for learning to occur: beneficial effects of training have been repeatedly reported in the absence of feedback (Herzog and Fahlet, 1997; Liu et al., 2010; Szpiro et al., 2014). In our study, feedback significantly altered performance on training days (Fig. 2.3b; 2.5b) but did not significantly modulate training outcome.

It is possible that effects of external performance feedback were attenuated by the existence of both visual as well as internally generated feedback. In versions of the task that involved hand movements, observers were always able to see their own hand and thus received a strong visual feedback signal. Moreover, with every movement we make, the brain sends a copy of the movement command—an efference copy or corollary discharge—back to sensory brain areas, which then integrate these feedback signals with sensory input (Bridgeman, 1995; Crapse and Sommer, 2008; Sommer and Wurtz, 2008). Another source of internal feedback information comes from proprioceptive information signaling the position of the eye in the orbit, or the arm in space (Ren et al., 2006; Vercher et al., 1997). Visual and internally generated feedback information might have boosted training across all training groups in our study, rendering external performance feedback less important than in studies involving perceptual judgments, where no visual or internally-generated feedback is automatically available.

Seeing the hand while it moves, especially close to the time of interception, provides important information needed to correct movements online (de la Malla et al., 2012) and boosts spatial accuracy (de la Malla and López-Moliner, 2012). Further evidence for beneficial effects of visual and internally-generated feedback on motor task performance comes from the neglect literature. Patients with hemispatial neglect (e.g., following stroke) show severe biases in processing visual information presented in their contralesional hemifield. Yet, they can be surprisingly accurate when performing motor tasks, such as goal-directed hand movements, in their blind hemifield (Harvey et al., 2002; Harvey and Rossit, 2012; Himmelbach and Karnath, 2003). This finding has been attributed in part to the availability of visual information (seeing the arm move in space); it could also be due to internally-generated feedback (efference copy and proprioceptive feedback).

#### Conclusion

Our results highlight the importance of a naturalistic task design to successfully train observers' sensorimotor performance. Learning only occurs when the training task involves a sensorimotor decision, here: an active interception of the target either by eye or hand movement. We found no direct transfer of training from eye to hand, indicating that cross-modality transfer likely requires co-activation of the neural networks underlying trained effectors. Our results also revealed only little influence of external performance feedback on training outcome, indicating that internally generated feedback during learning may be sufficient to boost eye and hand movement accuracy and precision.

### **Chapter 3**

## Decoding go/no-go decisions from eye movements

In the previous study we showed that sensorimotor learning only occurred when observers actively decided when and where to intercept (hand or eye). Our results also demonstrated the importance of naturalistic task design when investigating eye-hand dependencies. In real-world scenarios observers are often required to decide whether to move at all before judging when and where to act. To address this question, the current study relates eye movements to the decision whether to initiate or inhibit an interceptive hand movement (go vs. no-go).

#### 3.1 Introduction

Every baseball fan loves the sound of a hitter's bat colliding with the baseball to hit a home run. Just prior to this magical moment, the batter has to decide whether to swing at the pitch by rapidly decoding and predicting the ball's motion trajectory. Perceptual decisions in such situations rely on a hierarchy of brain areas involved with sensory processing and motor control (Gold and Shadlen, 2007; Hanks and Summerfield, 2017; Heekeren et al., 2008; Schall, 2013). Importantly, activity in these brain areas is altered prior to the choice response. Reliable neural signatures, reflecting the outcome of an upcoming perceptual decision, have been observed across different tasks and species (Bennur and Gold, 2011; Crapse et al., 2018; Ding and Gold, 2013; Gold and Shadlen, 2000; Heinen et al., 2006; Kim et al., 2005; Liu and Pleskac, 2011; Pape and Siegel, 2016; Pho et al., 2018; Shadlen and Newsome, 1996; Yates et al., 2017). However, the link between decision signals and continuous motor actions such as smooth-pursuit eye movements is less well understood.

Here we ask whether decision outcome in a rapid go/no-go interception task can be reflected in humans' eye movement responses on a trial-by-trial basis. Many of the brain areas involved in the control of eye movements also carry decision signals. In natural tasks, these decision signals are ultimately linked to the action outcome—for example, batters will only swing at pitches they judge to be hittable. Eye movements

closely reflect task requirements and action goals and provide a continuous update of the action space (Brenner and Smeets, 2017; Hayhoe, 2017; Hayhoe et al., 2012; Johansson et al., 2001; Land et al., 1999; Smeets et al., 1996). Moreover, eye movements are modulated by decision formation even when the eye movements are task irrelevant—for example, when they are not indicating the choice response in a visual-discrimination task (Joo et al., 2016). Given the close link between neural activity in oculomotor areas and decision formation, and between perceptual decisions and action goals, we propose that eye movements might be a sensitive indicator of decision outcome.

We developed a rapid interception task called EyeStrike, in which observers had to make a perceptual decision and predict whether a briefly presented moving target would pass or miss a designated strike box (Figure 3.1A). Similar to ocular baseball, a paradigm developed by Heinen and colleagues (Kim et al., 2005), observers were instructed to withhold an action if they judged the target to be outside the strike box (no-go) and to otherwise initiate an action (go). In contrast to ocular baseball, observers in EyeStrike were asked to track the visual target during decision formation with their eyes and to indicate their choice by withholding or initiating an interceptive hand movement. This allowed us to decode decision making from a continuous natural eye-movement response. We related observers' eye movements to the decision outcome (go vs. no-go). Congruent with decision signatures in neural activity, we found that go/no-go decisions were reflected in distinct eye-movement responses on a trial-by-trial basis, and that eye-movement-based prediction accuracy was related to observers' decision accuracy. Model prediction accuracy was higher for easy versus hard task versions and increased with increasing signal strength, suggesting that eye-movement signatures also reflect sensory-signal accumulation toward a decision threshold.

#### 3.2 Materials and Methods

#### **Observers**

We collected data from 45 male observers (26 members of the University of British Columbia male varsity baseball team and 19 age- and gender-matched non-athletes; mean age:  $20.6 \pm 1.9$  years) with normal or corrected-to-normal visual acuity; 39 were right-handed, six were left-handed (dominant hand was defined as the throwing hand). All observers were unaware of the purpose of the experiment. The experimental protocol adhered to the Declaration of Helsinki and was approved by the University of British Columbia Behavioral Research Ethics Board; observers gave written informed consent prior to participation.

#### EyeStrike paradigm

Observers were asked to track a moving target, a black Gaussian dot  $(SD = 0.38^{\circ})$  with a diameter of  $2^{\circ}$  of visual angle, and to predict whether the target would pass ("go" response required) or miss ("nogo" required) a designated strike box (Figure 3.1A and B). We instructed observers to withhold a hand movement in miss trajectories and to intercept the ball with their index finger while it was in the strike box in pass trajectories. Depending on the target speed, observers had a time window of 150-170 ms to intercept the target inside the box. Each interception started from a table-fixed position and was made with the dominant hand.

Each trial started with drift correction during fixation on a target presented  $15^{\circ}$  to the left or right of the screen center. During drift correction, the eye had to be within a  $1.4^{\circ}$  radius of the fixation target for 0.5-1 s. Stimulus motion was always into the ipsilateral field—that is, for right-handed observers, stimulus motion was from left to right (see example trial in Figure 3.1A), and vice versa. Then the stimulus followed a linear, diagonal path that either hit or missed a darker gray (31.5 cd/m<sup>2</sup>) strike box that was  $6^{\circ} \times 10^{\circ}$  in size and offset by  $12^{\circ}$  from the center to the side of interception (Figure 3.1B). Stimulus velocity followed natural forces (gravity, drag force, Magnus effect; (Fooken et al., 2016)). Easy trajectories clearly passed through (launch angle:  $\pm 5^{\circ}$ ) or clearly missed the strike box (launch angle:  $\pm 12^{\circ}$ ). Difficult trajectories passed (launch angle:  $\pm 7^{\circ}$ ) or missed (launch angle:  $\pm 10^{\circ}$ ) the strike box close to its corners. Importantly, the target disappeared shortly after launch, yielding different degrees of motion-signal strength. A combination of different viewing durations (100-300 ms) and stimulus speeds (36°/s or 41°/s) resulted in visible trajectory lengths ranging from  $3.6^{\circ}$  (short or weak signal strength) to  $12.3^{\circ}$  (long or strong signal strength). All conditions were randomized and equally balanced. We instructed observers to track the target with their eyes and to follow its assumed trajectory even after it had disappeared. Each trial ended either when observers intercepted the target or when the target reached the end of the screen (1-1.1 s). At the end of each trial observers received feedback about their performance; target end position was shown, and correct or incorrect decisions were indicated (see Figure 3.1A). Each observer performed a familiarization session (16 trials; full trajectory visible), followed by 384 experimental trials in which the target disappeared.



**Figure 3.1:** Experimental procedure and design. (A) Observers were asked to fixate on a small black Gaussian dot  $(\pm 15^{\circ})$  from screen center). After 0.5–1 s, the target moved along a diagonal linear path and disappeared after being shown briefly (100-300 ms). Observers had to withhold a hand movement if the target missed a strike box (no-go) and intercept the target inside the strike box if it passed through (go). Observers received feedback about their interception position (red disk) in pass trials and about the target's final position (black X) in all trials. (B) Paradigm design. The target launched either upward or downward at one of four angles (5°, 7°, 10°, or 12°). Trajectories that passed or missed close to the corners of the strike box (7° and 10°) were more difficult.

We defined four response types following conventions in the literature (Kim et al., 2005; Yang et al., 2010). Trials were classified as correct go if observers made an interception (i.e., touched the screen) in response to a pass trajectory and as incorrect go if they moved their hands more than halfway to the screen during a miss trajectory. Trials were classified as correct no-go or incorrect no-go if observers withheld a hand movement or moved their hand less than halfway to the screen in response to a miss or pass trajectory, respectively. Decision accuracy was calculated as the percentage of all correct go and no-go responses.

#### Visual display and apparatus

The visual target was shown at a luminance of 5.4 cd/m<sup>2</sup> on a uniform gray background (35.9 cd/m<sup>2</sup>). Stimuli were back-projected onto a translucent screen with a PROPixx video projector (VPixx Technologies, Saint-Bruno, Canada; refresh rate: 60 Hz; resolution:  $1,280 \times 1,024$  pixels). The displayed window was  $44.5 \times 36$  cm or  $55^{\circ} \times 45^{\circ}$  in size. Stimulus display and data collection were controlled by a PC (NVIDIA GeForce GT 430 graphics card), and the experiment was programmed in Matlab 7.1 using Psychoolbox 3.0.8 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). Observers were seated in a dimly lit room at 46 cm distance from the screen with their head supported by a combined chin and forehead rest.

#### Eye- and hand-movement recordings and preprocessing

Eye-position signals from the right eye were recorded with a video-based eye tracker (EyeLink 1000 tower mount; SR Research Ltd., Ottawa, Canada) and sampled at 1000 Hz. Eye movements were analyzed offline using custom-made routines in Matlab. Eye velocity profiles were filtered using a low-pass, second order Butterworth filter with cutoff frequencies of 15 Hz (position) and 30 Hz (velocity). Saccades were detected based on a combined velocity and acceleration criterion: Five consecutive frames had to exceed a fixed velocity criterion of 50°/s; saccade on- and offsets were then determined as acceleration minima and maxima, respectively, and saccades were excluded from pursuit analysis. Pursuit onset was detected in individual traces using a piecewise linear function fitted to the filtered position trace (Fooken et al., 2016).

Finger position was recorded with a magnetic tracker (3D Guidance trakSTAR; Ascension Technology Corp., Shelburne, VT) at a sampling rate of 240 Hz; a lightweight sensor was attached to the index fingertip of the observer's dominant hand with a small Velcro strap. The 2-D finger interception position was recorded in screen-centered x- and y-coordinates. Each trial was manually inspected, and a total of 345 trials (2%) were excluded across all observers due to eye- or hand-tracker signal loss.

#### Eye-movement data analyses

The stimulus characteristics in this paradigm triggered tracking behavior that most closely resembled short periods of smooth pursuit and catch-up saccades (de Brouwer et al., 2002; Fooken et al., 2016). To evaluate this tracking behavior we analyzed eye-movement position and velocity relative to target position and velocity and extracted the following pursuit measures: horizontal eye-position error, defined as the mean deviation across the entire trial (from eye-movement onset to stimulus offset) of horizontal eye position relative to horizontal target position; eye velocity relative to target velocity (gain) during the closed loop phase (140 ms after pursuit onset until interception); pursuit latency; and open-loop velocity (pursuit onset until

the start of the closed-loop phase). We further extracted the number of catch-up saccades, the latency of the initiation saccade and each trial's targeting saccade (i.e., in pass trials this is the saccade into the strike box), and average saccade amplitude.

#### Statistical analysis

Varsity baseball players and non-athletes did not differ significantly in overall eye- and hand-movement accuracy. These results were averaged across groups. However, group differences are reported for decision-related performance in EyeStrike. Effects of task difficulty and signal strength on decision-making accuracy were examined using repeated-measures analysis of variance with the between-subjects factor of player (baseball player vs. non-athlete) and within subjects factors of difficulty and strength. Differences between conditions (e.g., easy vs. hard) were evaluated using Welch's two-sample *t* tests. All statistical analyses were performed in R. To identify the pursuit and saccade measure that predicted decision outcome best, we ran a logistic regression model. We trained trial-by-trial eye movement data to be fitted to a binomial categorization (go vs. no-go) using a generalized linear model implemented with the Caret package in R (Kuhn, 2008). Variable importance was evaluated using the Caret function varImp. To evaluate the relationship between single eye-movement predictors (position error and targeting-saccade latency) and behavior (go vs. no-go), we report the accuracy of all cross-validation iterations and Cohen's unweighted kappa, a measure of agreement for categorical prediction (Kuhn, 2008).

#### **Choice probability**

To simulate decision outcomes based on eye movement behavior in EyeStrike, we adopted a method based on signal-detection theory (Green and Swets, 1966). In this framework, the paradigm can be viewed as a two-alternative choice task in which hand movement (go vs. no-go) is the decision outcome and eyemovement behavior is the measure used to predict the response. To evaluate the validity of eye movements as decision predictor, we calculated receiver operating characteristic (ROC) curves. The method to calculate the ROC curve of a given eye-movement measure was as follows: We divided the range between minimum and maximum measured value in 100 equal steps. We then formulated a set of decision rules: We predicted that observers would move their hands based on a continuous criterion starting with the maximum value (100% go prediction) and decreasing by equal step sizes until the minimum value was reached (100% nogo prediction). Choice probability can then be evaluated by calculating the area under the curve (AUC), which yields an estimate of the probability that the observer's behavior (go vs. no-go) has been predicted correctly (Bamber, 1975; Kang and Maunsell, 2012). The AUC was calculated using trapezoidal numerical integration using the Matlab function trapz. Permutation tests were used to assess the significance of choice-probability data (Mayo and Sommer, 2013).

#### 3.3 Results

We related eye movements to rapid go/no-go decisions using our EyeStrike paradigm, in which a visual stimulus passed or missed a designated strike box. We assessed interceptive hand movements (decision outcome) and eye movements under different levels of uncertainty and motion-signal strength. Uncertainty was manipulated by varying task difficulty; different target launch angles resulted in trajectories that either clearly or closely passed or missed the strike box, resulting in easy or hard trajectories (Figure 3.1B). Motion-signal strength was manipulated by limiting target-viewing duration. Different combinations of viewing durations and target speeds resulted in visible trajectory lengths ranging from short  $(3.6^\circ)$ , producing a noisy or weak motion estimate, to long  $(12.3^\circ)$ , producing a less noisy, or strong, motion-signal estimate.

#### **Decision-making accuracy**

We defined decision-making accuracy as the ratio of correct go and no-go decisions across all trials for each observer. Observers across groups performed well in EyeStrike, with 82.3% (SD = 1.2%) average decision accuracy. Overall, decision accuracy was higher for pass trajectories ( $M = 90.4\% \pm 0.8\%$ ) than for miss trajectories ( $M = 74.1\% \pm 2.0\%$ ), t(44) = 6.86, p < 0.001 (compare data points in light gray vs. dark gray shaded areas in Figure 3.2A). Observers made more accurate decisions for easy trajectories ( $M = 90.0\% \pm 1.3\%$ ) compared to hard ones ( $M = 74.7\% \pm 1.3\%$ ; Figure 3.2B), reflected in a significant main effect of difficulty, F(1, 43) = 466.0, p < 0.001. Observers also made more accurate decisions with increasing visible trajectory length: Decision accuracy varied between  $76.3\% \pm 1.5\%$  for the shortest trajectory and  $83.5\% \pm 1.4\%$  for the longest trajectory, reflected in a main effect of strength, F(5, 215) = 20.8, p < 0.001 (Figure 3.2C). This improvement with increasing motion-signal strength was stronger in easy than in difficult trials, reflected in a significant Difficulty × Strength interaction, F(5, 215) = 9.4, p < 0.001.



**Figure 3.2:** Decision-making accuracy in EyeStrike. (A) Decision accuracy (ratio of all correct go and no-go responses to all trials) and incorrect responses for each launch angle; each open circle reflects the average for one observer; horizontal lines represent group averages (N = 45). (B) Decision accuracy for easy compared to hard decisions. Open circles reflect the observer average, separated by baseball players (black) and nonathletes (purple). (C) Decision accuracy for short, medium, and long target presentations. Averages of all observers are indicated by bar height.

#### Eye-movement signatures in pass and miss trials

Briefly presented moving targets in EyeStrike reliably elicited a combination of smooth-pursuit and saccadic

eye movements. In response to target motion onset, observers either initiated smooth pursuit (73% of all trials) or maintained fixation and then initiated a saccade toward the target. Observers strongly anticipated the target's motion direction and initiated pursuit rapidly (mean pursuit latency:  $29 \pm 4$  ms), thus maximizing pursuit in the presence of ultrashort presentation durations. The target disappeared after 100-300 ms and traveled approximately 800 ms before entering the strike box (see time markers in Figure 3.3A).



Figure 3.3: Eye- and hand-movement behavior in EyeStrike. (A) 2-D eye position from a single representative observer for four possible trial outcomes, showing tracking of the target (gray solid line) with a combination of smooth pursuit (solid colored lines) and saccades (dashed colored lines). The time course of the trial is indicated by 100-ms time stamps. Each circle marks the end of a 100-ms interval (filled black circles: target visible; filled gray circles: target has disappeared). In go responses (upper panels), observers moved their hand (gray trajectory) to intercept (red disk) the target inside the strike box. In no-go responses (lower panels), observers withheld a hand movement. Colors indicate correct go (green), correct no-go (blue), and incorrect decisions (red). (B) Heat map of all interception trials across observers. Total number of interceptions in each square was counted and is indicated by shade. Observers' hand movements naturally curved toward the lower half of the strike box.

For go responses (Figure 3.3A, upper panels), observers tended to follow the target closely with their eyes until making a targeting saccade into the strike box. For nogo responses, observers' eye movements followed the trajectory to the strike-box corner where they assumed the target to miss, using a combination of pursuit and saccades (Figure 3.3A, lower panels). In interception trials (correct/incorrect go), observers initiated their hand movement with a latency of 416 ms (SD = 8 ms) on average, and they intercepted close to the final eye position (Euclidean distance between eye and finger at time of interception:  $2.5^{\circ} \pm 0.5^{\circ}$ ). Observers' interception positions were clustered around the actual target position, even though they were instructed to hit anywhere inside the strike box (Figure 3.3B).

#### Decoding decisions from eye movements

In order to decide whether or not to initiate a hand movement, observers had to discriminate trajectories as either pass or miss. Figure 3.4 shows the absolute eye position relative to the target trajectory for two representative observers (Figure 3.4A and 3.4B) and averaged across all observers (Figure 3.4C). Eye position differed clearly between go and no-go responses (compare green and blue traces). In incorrect trials—observers either moved their hand to intercept a target that missed the strike box or withheld a hand movement when the target passed the strike box—eye positions followed a path in between pass and miss trajectories, going toward the corners of the strike box (see average final vertical eye positions in Figure 3.4C). In incorrect trials, eye movements may therefore reflect observers' indecision as to whether the target would pass or miss the strike box.

Next, we investigated which eye-movement parameters best captured the observed differences between pass and miss trials and might therefore indicate decision outcome. We analyzed standard smooth pursuit measures, relative velocity (gain), absolute and relative eye-position error, and saccade measures (number, latency, amplitude of initial and targeting saccade). To select the eye-movement parameters that best reflected decision outcome, we included all extracted pursuit and saccade measures in a logistic regression model. The model identified relative (horizontal) eye-position error ( $\kappa = 0.25$ ) and latency of the targeting saccade ( $\kappa = 0.28$ ) as the best predictive measures for go/no-go responses. Both these measures are related to the timing of the eye movement rather than the absolute spatial position of the target.

Horizontal eye-position error across all trials was significantly more positive during go ( $M = 1.55 \pm 0.22$ ) compared to no-go responses ( $M = 0.01 \pm 0.19$ ), t(44) = 8.00, p < 0.001 (Figure 3.5A), indicating that the eye tended to be ahead of the target when a go decision was made. Observers made overall fewer saccades in trials in which they decided to go ( $M_{go} = 2.46 \pm 0.06$  vs.  $M_{no-go} = 2.89 \pm 0.07$ ), t(44) = 8.96, p < 0.001, indicating smoother tracking, and initiated the targeting saccade earlier than for no-go responses ( $M_{go} = 558 \pm 9$  ms vs.  $M_{no-go} = 700 \pm 11$  ms), t(44) = 14.2, p < 0.001 (Figure 3.5B). The observed time-binned frequency of targeting saccades indicates that this eye-movement measure differentiated between go and no-go responses starting at 300-350 ms after target onset (Figure 3.5B). At the 450-ms time point, a targeting saccade was approximately four times more likely to have occurred in a go trial than in a no-go trial, indicating clearly different saccade-pattern signatures for different decision outcomes.



**Figure 3.4:** 2-D eye position relative to target trajectories. (A) Eye position for Subject 4 (baseball player) and (B) eye position for Subject 22 (non-athlete). In both panels, each line represents a single trial (384 per observer). Eye position followed the target trajectories (thin gray lines) for go (green lines) compared to no-go responses (blue lines). Eye position in incorrect trials (go and no-go) falls between pass and miss trajectories (red lines). (C) Eye position during the first 750 ms of each trial averaged across all observers (N = 45). Filled circles indicate final vertical eye position for all correct and incorrect decision outcomes.

#### Accuracy of eye-movement-based decision indicators

The observed differences in eye movements between go and no-go responses might allow us to read out decision outcomes based on either of the two eye movement parameters identified as best predictors by the regression model. We applied a method adopted from signal-detection theory (Green and Swets, 1966), which has also been used to decode decision outcomes from single-neuron activity in visual-discrimination tasks (Britten et al., 1992; Celebrini and Newsome, 1994; Kang and Maunsell, 2012; Yang et al., 2010). Following this method, EyeStrike can be viewed as a two-alternative forced-choice task in which hand movement (go vs. no-go) is the decision outcome and eye-movement behavior is the measure used to detect the response. For each trial, the model can either correctly predict a go (hit) or no-go response (correct versus incorrect predictions depends on the chosen decision criterion. With a conservative criterion we predict a no-go response in most trials. This will yield a low number of incorrect go predictions (false



**Figure 3.5:** Eye-movement measures during go (green) and no-go (blue) responses. (A) Frequency of average position error across all trials and observers. Vertical lines indicate the group average for go and no-go responses. (B) Frequency of targeting saccades initiated at a given time with respect to stimulus onset. Both panels are for N = 45.

alarms), but it will also lead to relatively few correct go predictions (hits). Conversely, a liberal criterion will lead to a high hit rate, but also to many false alarms. With a continuously changing decision criterion we can calculate ROC curves (Green and Swets, 1966) for each observer reflecting the trade-off between prediction success (hit) and error (false alarm) on a trial-by-trial basis. We calculated the AUC for each observer's ROC curve to obtain an estimate of the goodness of the model's prediction of individual observers' go/no-go responses. An AUC of 100% indicates that eye movements perfectly reflect go/no-go decisions; an AUC of 50% is equivalent to a random prediction or chance.

Figure 3.6A and 3.6B shows individual ROC curves for Subjects 16 (baseball player) and 45 (nonathlete), separated by task difficulty. Subject 16's go/no-go response could be predicted with 98% accuracy using eye-position error as the decision criterion, whereas targeting-saccade latency as the criterion yielded predictions of  $\geq$  85% accuracy. Conversely, Subject 45's decision outcome was best predicted by targetingsaccade latency (82% accuracy). These representative examples illustrate that eye-position error was the better predictor for some observers (n = 23), whereas targeting-saccade latency was the more sensitive predictor for others (n = 22). We formed two subgroups of observers based on which of the two predictors was more sensitive, and calculated ROC curves across observers within each group while taking task difficulty into account (Figure 3.6C). For both groups, go/no-go responses could be predicted well above chance (mean AUC: 76%). Importantly, predictions were above chance for each of the tested 45 observers (range: 60%-98% in measured data vs. 46%-54% in permutation test), t(45.6) = 25.77, p < 0.001. Predictions were overall more accurate for easy (mean AUC: 77%) compared to hard trajectories (mean AUC: 74%), t(44) = 3.23, p = 0.002. Predictions were also more accurate the more reliable the target's motion signal was (Figure 6D), increasing from 74% for the shortest trajectory to 80% for the longest trajectory, t(44) = 5.36, p < 0.001. The finding that our decision prediction based on observers' eye movements increases with motion-signal strength indicates that eye movements reflect the accumulation of sensory evidence over time.



**Figure 3.6:** Decoding decision outcome from eye-movement parameters. (A) Receiver operating characteristic (ROC) curve for a representative observer (baseball player) for whom decision outcome was modeled more accurately by eye-position error (orange). (B) ROC curve for another representative observer (nonathlete) for whom final saccade latency was the better decision predictor (black). (C) Averaged ROC curves across observers whose decision outcome was better predicted by eye-position error (n = 23; orange) versus final saccade latency (n = 22; black). Curves are shown separately for easy (dashed) and hard (solid) trajectories. (D) Averaged group ROC curves separated for long (dashed) and short (solid) target presentations. (E) Relationship between decision accuracy and each observer's area under the curve separated by easy (open circles; dashed regression fit) and hard (filled circles; solid regression fit) target trajectories. Each data point depicts the per-observer average. (F) Relationship between decision accuracy and each observer's area under the curve separated by long (open circles; dashed regression fit) and short (filled circles; solid regression fit) target presentations.

Next we related each observer's AUC to his decision accuracy. We observed a strong positive relationship between AUC and decision accuracy across different levels of task difficulty (Figure 3.6E) and signal strength (Figure 3.6F). Taken together, these results suggest that eye movements are sensitive indicators of decision outcome and differentiate between decisions based on task difficulty and signal strength.

#### Decision making in varsity baseball players versus non-athletes

We tested two populations of observers, college varsity-level baseball players and non-athletes. Both groups were similar in terms of general eye-movement accuracy (no significant main effect of player on any of the reported eye measures). However, decision accuracy was significantly higher for varsity baseball players ( $M = 85.5\% \pm 1.0\%$ ) than for non-athletes ( $M = 78.0\% \pm 2.1\%$ ; compare black with purple data points in Figure 3.2B and 3.2C). This result was reflected in a significant main effect of player, F(1, 43) = 12.0, p < 0.001, in a repeated-measures analysis of variance. Correspondingly, decision predictions using the ROC model were higher for baseball players (mean AUC: 82%) than for non-athletes (mean AUC: 75%), t(33.95) = 3.05, p = 0.004. Decision-prediction accuracy in both groups was equally affected by difficulty and signal strength (Table 3.1).

**Table 3.1:** Decision-prediction accuracy (area under the curve; group average  $\pm SD$ ) for baseball players and non-athletes separated by difficulty (easy vs. hard) and signal strength (strong vs. weak).

	Difficulty		Signal	
	easy	hard	strong	weak
Players	$82.9\pm1.3\%$	$80.9\pm1.3\%$	87.1 ± 1.2%	$80.7\pm1.3\%$
Non-athletes	$76.8\pm1.7\%$	$74.0\pm2.0~\%$	$80.0\pm1.7\%$	$74.7\pm2.2\%$

#### 3.4 Discussion

We developed a rapid interception task that allowed us to systematically evaluate eye movements during go/no-go decisions. Our key findings are that eye movements systematically differed between go and no-go responses, and that these differences could be read out prior to the choice response, thus predicting decision outcome. Prediction accuracy was related to observers' decision accuracy under different levels of task difficulty and motion-signal strength. These results go beyond merely predicting whether or not the hand will move and suggest that human eye movements can be used to sensitively decode and predict decision outcome under different sensory and task constraints.

In EyeStrike, observers naturally viewed a visual target that followed either a pass or miss trajectory (stimulus space) and indicated their choice by initiating or withholding a hand movement (decision out-

come). Stimulus space and decision outcome are linked by an internal machinery that processes sensory information and forms an associated motor command (Gold and Shadlen, 2007; Heekeren et al., 2008; Platt, 2002). In EyeStrike there are two possible choices—go and no-go— which could be reflected in two distinct internal states. However, if the choice is difficult or less reliable—for example, the ball passes or misses close to the corner of the strike box or is visible for a very short time—the two internal states may overlap, potentially causing decision errors. We found that eye movements in incorrect decision trials followed a path in between pass and miss trajectories, and in between eye movements made during correct go and no-go choices (Figure 3.4C). These results indicate that eye movements not only reflect the decision outcome but might also indicate an observer's internal decision state and the confidence with which a decision is reached.

Decision accuracy in behavioral visual-discrimination tasks is typically related to task difficulty and signal strength (or noise level); for example, motion discrimination performance scales with motion coherence (Britten et al., 1992; Lappin and Bell, 1976). Congruently, task difficulty shapes neural activity during decision making. Single-unit recordings in macaque monkeys have shown that neural sensitivity in the middle temporal visual area (Britten et al., 1992) and superior colliculus (Basso and Wurtz, 1997; Horwitz and Newsome, 2001) are closely related to perceptual discrimination performance. Interestingly, subsets of neurons in the supplementary eye field and frontal eye field take longer to decode more difficult perceptual decisions (300-475 ms) compared to easy decisions (175-190 ms) but reflect decision-outcome sensitively regardless of level of difficulty (Yang and Heinen, 2014; Yang et al., 2010). Importantly, the accuracy of predicting decision outcomes based on neural recordings increases with increasing motion-signal strength (Britten et al., 1992; Horwitz and Newsome, 2001) and decreasing task difficulty (Yang et al., 2010). Moreover, saccades evoked by frontal-eye-field microstimulation during perceptual decision making deviate toward the stimulus motion direction. These deviations scale with stimulus signal strength, indicating shared processing of decision formation and oculomotor response (Gold and Shadlen, 2000, 2003).

Similarly, studies in humans have found that easy compared to difficult visual-categorization decisions elicited a greater blood-oxygen-level-dependent response in left dorsolateral prefrontal cortex (Heekeren et al., 2004). Single-trial electroencephalographic analysis has revealed a decision-difficulty component evolving at around 220 ms after stimulus presentation (Philiastides, 2006) for easy compared to difficult visual-categorization decisions. The present results, obtained in a large sample of human observers, suggest that eye movements might sensitively reflect task difficulty and signal strength as well: Model predictions (AUC) were more accurate for easy compared to hard trajectories and for targets that were visible for a longer period of time (stronger signal). An increase in motion-signal strength (i.e., higher coherence, higher contrast, or longer visibility) generally boosts the decision signal, hence potentially strengthening the predictive accuracy of the eye movement signature.

Our findings are also closely related to evidence showing that eye movements can be modulated by decision formation, and that decision making and motor output are closely related. For example, neural population activity in the motor cortex measured using magnetoencephalography has been shown to grad-

ually build up several seconds before execution of a choice response, and to be usable to read out and predict observers' choices in a yes/no motion-detection task Donner et al. (2009); Pape and Siegel (2016). Decision-related modulation has also been found during motor execution. In an earlier study, when a hand movement was perturbed just prior to the choice response, the muscular reflex gain of the perturbed arm was modulated by motion-coherence strength, reflecting ongoing decision formation (Selen et al., 2012). Similarly, saccades indicating choice in a direction-discrimination task have been shown to be initiated earlier and to deviate farther away from the nonselected target with increasing levels of motion coherence—that is, stronger decision signals (McSorley and McCloy, 2009). In another recent study, task-unrelated visually guided saccades, performed in between a visual discrimination and a button-press response, were initiated earlier and faster in the direction congruent with the decision, but they were not modulated if observers viewed the moving stimulus passively, thus directly linking them to the decision (Joo et al., 2016). Taken together, these findings suggest that decision-related processes continuously interact with motor planning and execution.

Eye movements in natural behavior are characterized by task demands and action goals. Many studies have shown convincingly that the eye leads the hand in tasks related to pointing, hitting, catching, or any kind of object-handling behavior (Bekkering et al., 1994; Belardinelli et al., 2016; Johansson et al., 2001; Land et al., 1999; Mrotek and Soechting, 2007). Congruently, there is strong behavioral (Chen et al., 2016; Danion and Flanagan, 2018; Fooken et al., 2016; Leclercq et al., 2013) and neurophysiological (Andersen and Cui, 2009; Crawford et al., 2004; Dean et al., 2012; Hwang et al., 2014; Snyder et al., 2002) evidence for interdependency between eye and hand movements, via either common control or a parallel and coordinated mechanism. Our time-critical decision task reveals different eye-movement dynamics in go versus no-go responses with regard to the targeting saccade of a trial. In go responses, this saccade occurred significantly earlier, thus allowing necessary time for planning an accurate manual interception. In no-go responses, in which the hand movement had to be inhibited, the targeting saccade commonly targeted the corner of the strike box. It had no relevance for leading the hand but might have provided important visual information confirming observers' perceptual decision. Eye movements therefore directly reflect the behavioral consequences of a perceptual decision.

#### Conclusion

Previous research has shown that decision-related neural responses can be used to read out an observer's intention even before a choice response is made. Here we show that eye movements carry a decision signature that is sensitive to task difficulty and sensory-signal strength and relates to observers' decision accuracy. Eye movements can be viewed as a continuous readout of ongoing sensorimotor processes and can be studied to further our understanding of perception and cognition in naturalistic tasks (Huk et al., 2018). Even though our results were obtained using a head-restrained paradigm, equivalent eye-movement behavior (i.e., initial tracking followed by a predictive saccade) is commonly observed in head-unrestrained virtual-reality or real-world settings (Bahill and LaRitz, 1984; Land and McLeod, 2000). Our paradigm introduces ecological validity by allowing unrestricted eye movements and by using a natural hand movement to indicate the

choice response. The findings presented here might generalize to decision making in the real-world, such as batting in cricket or baseball. Understanding how humans make decisions in real-world tasks can therefore be significantly aided by evaluating eye-movement responses. Our findings provide a direct link between neural decision signatures and continuous eye-movement responses, thus demonstrating eye movements' capacity to serve as sensitive indicators of neural function outside of directly recording brain activity.

### **Chapter 4**

# Eye movement initiation as the earliest readout of decision formation

In the previous study we showed that eye movements can sensitively predict observers' go/no decisions. Yet, two questions remain: first, do eye movements contribute to accurate decision making? And second, are the observed eye movement differences between go and no-go decisions simply the consequence of hand movement execution or do they reflect decision formation? The current study investigates how eye movements evolve over time and how they continuously link to decision formation and accuracy.

#### 4.1 Introduction

Perceptual decisions in real-world scenarios often require a sequence of interrelated decisions. For example, when a pedestrian steps onto a bike lane, an approaching cyclist has to decide whether to stop or to veer around the obstacle. Depending on the initial decision outcome the cyclist then has to decide how hard to brake or in which direction to swerve. Yet, perceptual decision-making tasks in the laboratory often rely on simple one-step choices. For instance, in classic motion discrimination paradigms, observers have to judge the net direction of a random-dot motion stimulus and indicate their choice by either eye movement or manual response. Such paradigms are powerful tools to study neural signatures of perceptual decision making (Bennur and Gold, 2011; Crapse et al., 2018; Gold and Shadlen, 2000; Liu and Pleskac, 2011; Newsome et al., 1989; Pape and Siegel, 2016; Shadlen and Newsome, 1996; Yates et al., 2017). However, the question how we make sequential decisions is relatively unexplored. This study probes sequential decision making processes using a manual go/no-go interception task and investigates eye movements during two-stage perceptual decisions.

Goal-directed hand, arm, and body movements, such as movements that we engage in during obstacle avoidance, are accompanied by naturally occurring eye movements. Akin to neurophysiological responses in oculomotor and decision-related brain areas (Britten et al., 1992; Celebrini and Newsome, 1994; Horwitz and Newsome, 2001; Yang et al., 2010), eye movements are sensitive to decision formation and outcome

(Fooken and Spering, 2019; Joo et al., 2016; McSorley and McCloy, 2009). For example, smooth pursuit and saccadic eye movement parameters provide reliable estimates of the outcome of go/no-go manual interception decisions in humans (Fooken and Spering, 2019). However, it is possible that eye movements merely reflect the consequences of the observer's choice rather than the decision formation itself. In the example above, stopping the bicycle requires less visuomotor control than veering around the pedestrian, resulting in different movement patterns. The current study examined the role of eye movements during the time course of a two-stage decision process: the decision whether and when to intercept a briefly presented moving target.

#### 4.2 Materials and Methods

This study relates the time course of decision formation during a rapid go/no-go track-intercept task to eye movements. To investigate the relationship between evolving eye movements and task outcome we performed new analyses on a previously published data set (Fooken and Spering, 2019). Paradigm and procedure are identical to the previous experiment and are reproduced here for the reader's convenience. New analyses developed for the current paper are described in detail.

#### Observers

We collected data from 45 observers and excluded three participants who did not follow instructions and moved their hand in more than 80% of trials, regardless of stimulus conditions. The remaining 42 male observers (25 members of the UBC male varsity baseball team, 17 age- and gender-matched non-athletes, mean age  $20.5 \pm 2.0$  yrs) with normal or corrected-to-normal visual acuity; 39 were right-handed, six were left-handed (dominant hand was defined as the throwing hand). All observers were unaware of the purpose of the experiment. The experimental protocol adheres to the Declaration of Helsinki and was approved by the UBC Behavioral Research Ethics Board; observers gave written informed consent before participation.

#### Visual display and apparatus

The visual target was shown at a luminance of 5.4 candela per meter squared (cd/m<sup>2</sup>) on a uniform grey background (35.9 cd/m<sup>2</sup>). Stimuli were back-projected onto a translucent screen with a PROPixx video projector (VPixx Technologies, Saint-Bruno, Canada; refresh rate 60 Hz, resolution 1280 (H)  $\times$  1024 (V) pixels). The displayed window was 44.5 (H)  $\times$  36 (V) cm or 55°  $\times$  45° in size. Stimulus display and data collection were controlled by a PC (NVIDIA GeForce GT 430 graphics card) and the experiment was programmed in Matlab 7.1 using Psychoolbox 3.0.8 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). Observers were seated in a dimly-lit room at 46 cm distance from the screen with their head supported by a combined chin- and forehead-rest.

#### **Experimental paradigm**

Observers were asked to track a small (diameter 2 deg) moving target and to predict whether the target would pass ("go" response required) or miss ("no-go" required) a designated strike box (Fig. 4.1A,B). We instructed observers to withhold a hand movement in miss trajectories and to intercept the ball while it was

in the strike box with their index finger in pass trajectories. Each interception started from a table-fixed position and was made with the dominant hand.

The stimulus followed a linear-diagonal path that either hit or missed a darker grey strike  $(31.5 \text{ cd/m}^2)$  box that was  $6^{\circ} \times 10^{\circ}$  in size and offset by  $12^{\circ}$  from the center to the side of interception (Fig. 4.1B). Stimulus velocity followed natural forces (gravity, drag force, Magnus force; (Fooken et al., 2016)). Launch angles were set to  $\pm 5^{\circ}$ ,  $\pm 7^{\circ}$  (pass trajectories),  $\pm 10^{\circ}$ , or  $\pm 12^{\circ}$  (miss trajectories). Importantly, the target disappeared shortly after launch (100-300 ms). Target speed was either 36 or  $41^{\circ}$ /s. All conditions were randomized and equally balanced (384 trials). We instructed observers to track the target with their eyes and to follow its assumed trajectory even after it had disappeared. Each trial ended when observers either intercepted the target or when the target reached the end of the screen (1-1.1 s). At the end of each trial observers received feedback about their performance; target end position was shown, and correct or incorrect decisions were indicated.

We defined four response types following conventions in the literature (Kim et al., 2005; Yang et al., 2010). Trials were classified as correct go if observers made an interception (i.e. touched the screen) in response to a pass trajectory and as incorrect go if observers moved their hands more than half way to the screen during a miss trajectory. Trials were classified as correct no-go or incorrect no-go if observers withheld a hand movement or moved their hand less than half way to the screen in response to a miss or pass trajectory, respectively. Decision accuracy was calculated as the percentage of all correct go and no-go responses.

#### Eye and hand movement recordings and preprocessing

Eye position signals from the right eye were recorded with a video-based eye tracker (Eyelink 1000 tower mount; SR Research Ltd., Ottawa, ON, Canada) and sampled at 1000 Hz. Eye movements were analyzed off-line using custom-made routines in Matlab. Eye velocity profiles were filtered using a low-pass, second-order Butterworth filter with cutoff frequencies of 15 Hz (position) and 30 Hz (velocity). Saccades were detected based on a combined velocity and acceleration criterion: five consecutive frames had to exceed a fixed velocity criterion of 50°/s; saccade on- and offsets were then determined as acceleration minima and maxima, respectively, and saccades were excluded from pursuit analysis. Pursuit onset was detected in individual traces using a piecewise linear function fit to the filtered position trace.

Finger position was recorded with a magnetic tracker (3D Guidance trakSTAR, Ascension Technology Corp., Shelburne, VT, USA) at a sampling rate of 240 Hz; a lightweight sensor was attached to the observer's dominant hand's index fingertip with a small Velcro strap. The 2D finger interception position was recorded in x- and y-screen-centered coordinates. Each trial was manually inspected and a total of 345 trials (2%) were excluded across all observers due to eye or hand tracker signal loss.

#### Eye movement data analyses

The stimulus characteristics in this paradigm triggered tracking behavior that most closely resembled short periods of smooth pursuit and catch-up. To evaluate tracking behavior over time we analyzed eye movement

quality during different time windows. In a previous study we found that observers characteristically made 2-3 saccades during EyeStrike. We defined the time interval from stimulus onset to the onset of the first saccade as our pursuit initiation time window and the time from first saccade offset to final saccade onset as the pursuit maintenance window (Fig. 4.1C). For both intervals we analyzed eye position and velocity relative to target position and velocity and extracted the following pursuit measures: mean eye and velocity position error, relative eye velocity (gain), and absolute eye velocity. As a temporal measure that is relatively independent of the spatial target position we analyzed the mean saccade rate of each observer over time.

#### Go/no-go separation time

To calculate the time at which the eye movement signature starts to differ, we calculated the saccade rate for each observer and split the data into go and no-go trials. We then compared the saccade rate between go and no-go decisions over time. We calculated a moving average of the saccade rate across a 5 ms time interval and down-sampled the data from 1000 Hz to 500 Hz to decrease the risk of detecting false negatives. We then performed a Mann-Whitney test for each time interval. The separation time was determined as the first time interval of at least three consecutive intervals for which a p-value smaller than 0.01 was achieved.

#### 4.3 Results

Observers (n=42) had to predict whether a briefly presented moving target would pass (go required) or miss (no-go required) a designated strike box (Fig. 4.1A). If observers judged the target to pass through the strike box (go decision), they had to intercept it time critically inside the box. If observers judged the target to miss the strike box (no-go decision), they had to withhold a hand movement. The target was only visible for the first 100-300 ms, then travelled for approx. 500 ms before entering or missing the strike box (Fig. 4.1B).

Relating eye movements to decision formation and outcome (go vs. no-go) revealed three main findings. First, higher eye velocity during pursuit initiation was related to higher decision accuracy (whether to intercept). Second, higher eye velocity during pursuit maintenance was related to better interception timing (when to intercept), suggesting that different stages of decision formation were linked to distinct oculomotor events. Third, the time point at which eye movements differentiated decision outcome coincided with hand movement onset. This result indicates that differences in eye movements for go compared to no-go decisions were not merely a consequence of interceptive hand movements, but they occurred prior to hand movement execution.

#### Time course of decision formation and interception

Observers tracked the target with a combination of smooth pursuit and saccadic eye movements. Target motion onset elicited one of three eye movement responses (Fig. 4.1C): Observers either tracked the target smoothly (5.8% of all trials) or with a combination of smooth pursuit and a catch-up saccade (53.9% of trials)—or they fixated until initiating a saccade to match target speed (40.3% of trials). Five observers initiated pursuit in less than 10% of all trials. All other observers tended to anticipate target motion, initiating their eye movements on average  $40.4 \pm 8.2$  ms before target onset. The initial saccade (i.e. the first saccade



Figure 4.1: (A) Cartoon of the experimental setup. Observers had to judge whether a briefly presented target would pass (go required) or miss (no-go required) the strike box. Judgments were made by initiating or withholding an interceptive hand movement. (B) Task and interception events over time. The target was visible for 100-300 ms, entered the strike box at ~800 ms, and was inside the box for ~180 ms. Observers initiated hand movements between 250 and 650 ms. (C) Exemplary initial eye velocity traces of single trials. Observers elicited three different types of eye movement patterns in response to target motion (black), either fixating until initiating a saccade (blue), tracking the target before initiating a saccade (green), or tracking it smoothly (purple). (D) Exemplary eye position trace of a single trial in which a combination of smooth pursuit (solid green line) and saccades (dashed green line) was exhibited. Target motion onset, initial saccade onset and targeting saccade onset are indicated by vertical dashed grey lines.

in each trial) was then initiated ~240 ms after stimulus onset ( $M = 237.0 \pm 41.6$  ms). The initial saccade was followed by a brief period of tracking before observers initiated a final, targeting saccade at 620 ms ( $M = 620.1 \pm 58.5$  ms) after target onset (Fig. 4.1D). The trial ended when the target reached the end of its trajectory (no-go), or when observers intercepted it (go). In go trials, observers initiated an interceptive hand movement ~400 ms ( $M = 411.9 \pm 45.1$  ms) after stimulus onset and hit the target on average 920 ms ( $M = 916.9 \pm 28.7$  ms) after target onset (Fig. 4.1B). Consequently, go/no-go decision formation had to occur

within the first few hundred milliseconds to allow successful interception.

#### Pursuit initiation is related to decision accuracy

We defined the pursuit initiation period as the time interval from stimulus onset to initial saccade onset. The initial saccade offset was on average 350 ms ( $M = 351.8 \pm 41.1$  ms) after stimulus onset, only 50-ms before the average hand movement onset. The brief time delay suggests that interception decision formation occurred prior to the initial saccade. To investigate whether eye movements before the initial saccade, i.e., during the pursuit initiation phase, contributed to decision formation and accuracy, we analyzed pursuit eye velocity during this interval. Each observers' decision accuracy was calculated as the percentage of all correct go and no-go responses. We found that observers who on average moved their eyes faster during the pursuit initiation period made more accurate decisions (Fig. 4.2A). Eye movement initiation was evaluated by calculating the average eye velocity error (2D velocity difference between eye and target) and absolute eye velocity in the interval from target onset to initial saccade onset. We found a negative correlation between eye velocity error and decision accuracy (Fig. 4.2B) suggesting that initiating smooth pursuit eye movements and thereby decreasing the error between eye and target velocity is linked to accurate target motion prediction and correct decision formation. Furthermore, we found a positive correlation between absolute eye velocity and decision accuracy (Fig. 4.2C). We acknowledge that this correlation could be driven by the cluster of four observers that showed a decision accuracy of less than 75%. However, a positive correlation remains when removing these four subjects from the analysis (r = .4, p = .011), emphasizing the link between eye movement initiation and go/no-go decision formation.



Figure 4.2: Relationship between eye movement initiation and decision accuracy. (A) Initial eye velocity from three observers averaged across all trials (n=384). Subject 15 (yellow) shows the lowest eye velocity during the pursuit initiation phase and had an overall lower decision accuracy (70%) than observers 8 (orange; 83%) and 21 (brown; 88%). (B) Decision accuracy is negatively related to eye velocity error. (C) Decision accuracy is positively related to absolute eye velocity during pursuit initiation. Circles represent averaged values per observer.

#### Pursuit maintenance is related to hitting accuracy

The previous results highlight that pursuit initiation relates to the first stage of go/no-go decisions (whether to intercept). In our task, the decision whether or not to move the hand was followed by the decision when to intercept. Observers were instructed to hit the strike box at the same time as the target was inside. Whereas the spatial position of the target trajectory was restricted to the area of the strike box, observers had to time-critically judge horizontal target motion to successfully intercept the target. We therefore focused on interception timing as a measure of interception accuracy (Fig. 4.3A). Overall observers were on time in 76.0  $\pm$  6.6 %, too early in 17.8  $\pm$  7.5 %, and too late in 6.2  $\pm$  4.5 % of all interception (go-required) trials. Incorrectly timed interceptive hand and eye movement onset, respectively (Fig. 4.3B,C; Table 4.1). Observers moved their hand earlier and faster and initiated the final targeting saccade earlier in trials in which they intercepted too early. Conversely, observers initiated the interceptive hand movement and final targeting saccade later when interceptions were too late.

**Table 4.1:** Hand and eye movement differences for early, on-time, and late hits. Hand and targeting saccade latencies are relative to stimulus onset. The targeting saccade was defined as the final saccade of each trial.

	Hand latency	Hand peak velocity	Targeting sac. latency
Early hit	$372.3 \pm 38.7 \text{ ms}$	$59.7 \pm 6.3 \text{ cm/s}$	$607.4 \pm 55.3$ ms
On-time	$426.8 \pm 44.4 \text{ ms}$	$57.3 \pm 5.5 \text{ cm/s}$	$642.3 \pm 55.1 \text{ ms}$
Late hit	$513.6 \pm 61.4 \text{ ms}$	$57.6\pm6.7~\text{cm/s}$	$675.4\pm78.2\ ms$

Values indicate group averages  $\pm$  standard deviation.

Manual interceptions were commonly preceded by a final targeting saccade with the eye landing 58.6  $\pm$  22.6 ms before the hand in the strike box. Therefore, the decision of when to intercept was most likely formed after the initial saccade (go/no-go decision interval) but prior to the targeting saccade. We defined the pursuit maintenance phase as the time from initial saccade offset to targeting saccade onset (Fig. 4.1D) and analyzed eye movement quality. In the maintenance interval, we found a positive relationship between relative eye velocity (mean ratio of eye and target velocity) and timing accuracy (Fig. 4.3D). Positional measures of tracking quality (2D or horizontal eye position error, saccade amplitudes) were not related to timing accuracy. These results indicate that to accurately judge the target speed and successfully time the interception in go trials, observers benefit from matching eye and target velocity during pursuit maintenance.

#### Eye movement separation coincides with hand movement onset

To determine at which point in time eye movements differentiated decision outcome (whether to intercept) we investigated the change in saccade rate—a temporal measure that is relatively independent of the spatial



**Figure 4.3:** (A) Timing accuracy depended on the timing of the interception. If the target had not yet reached the strike box at the time of interception the observer was too early; if it had already left the strike at the time of interception the observer was too late. Finger velocity (B) and saccade rate (C) separated by early (light pink), on-time (green), and late (dark pink) hits reflect timing errors. (D) Relationship between timing accuracy and relative eye velocity during maintenance phase.

target position—for go compared to no-go decisions. For each observer, saccade rates were compared between alternate decision outcomes in 2 ms intervals (see Materials and Methods; Fig. 4.2A). The time at which saccade rates first differed significantly (Mann-Whitney test, p < 0.01) was determined to be the go/no-go separation time (Fig. 4.4A,B). Using this method, we were unable to find a separation time for three observers until after the offset of the second saccade. Separation times for these observers differed by two or more standard deviations from the group mean and were excluded from this part of the analysis. For the remaining 39 observers the mean separation time was 395 ms (range 326-520 ms; Fig. 4.4C). The same set of observers initiated the hand movement in go trials on average at 411 ms (range 320-536 ms; Fig. 4.1B). These results indicate that the time at which eye movements start to reflect decision outcome coincides with hand movement onset. Therefore, eye movement patterns that reflect go/no-go decisions are not simply a consequence of hand movement execution, but an indicator of the ongoing decision formation.

#### 4.4 Discussion

In this study we related continuously evolving eye movements to two-stage perceptual decisions in a go/nogo interception task. We showed that eye movement quality during pursuit initiation is related to decision accuracy and that accurate smooth pursuit eye movements during pursuit maintenance are linked to interception timing accuracy. These findings suggest that smooth pursuit eye movements continuously contribute to dynamic decision formation. Finally, we show that eye movements distinguish go/no-go decisions early on and are not merely a consequence of motor execution. These results emphasize that eye movements are a sensitive indicator of dynamic multi-stage decision processes.

Eye movements are closely related to cognitive goals in a variety of everyday tasks that require an interaction with objects, such as brick stacking or sandwich making (Hayhoe and Ballard, 2005; Hayhoe,



**Figure 4.4:** Eye movement separation for go vs. no-go decisions. (A) Change of *p*- value and (B) saccade rate over time comparing go and no-go decision trials. Separation time for this representative observer was 428 ms. (C) Saccade rates for go vs. no-go decisions averaged across all observers that showed a differentiation (n=39).

2017; Johansson et al., 2001; Land et al., 1999). A particularly strong link between eye movements and action is seen in the context of goal-directed hand movements. It is commonly observed that the eye leads the hand during pointing, hitting, or catching (Bekkering et al., 1994; Belardinelli et al., 2016; Brenner and Smeets, 2011; Land and McLeod, 2000; Mrotek and Soechting, 2007). We recently showed that eye movements reliably decoded go/no decisions based on the observation that go decisions were associated with earlier targeting saccades to guide the interceptive hand movement (Fooken and Spering, 2019). Yet, it is not known whether eye movements are simply the consequence of a perceptual decision or if they reflect decision formation over time. The current study reveals that eye movements differentiate the decision whether or not to intercept as early as hand movement onset, indicating that eye movements reflect go/no-go decisions before hand movement execution. The concurrence of eye movement separation time and hand movement onset is further evidence for the close interdependency of eye and hand movements and common neural processing (Andersen and Cui, 2009; Crawford et al., 2004; Hwang et al., 2014). However, the neural and behavioural link between motor- and decision-related activities is less well understood.

On the one hand, perceptual decisions can be biased by motor actions: Participants indicating their choice in a motion discrimination task by left or right handed reaches that were associated with different mechanical loads were perceptually biased towards the effortless side even though they were not aware of the increased motor cost (Hagura et al., 2017). On the other hand, eye and hand movements are modulated by prior perceptual decisions. When observers made visually guided (Joo et al., 2016) or choice-indicating (Mc-Sorley and McCloy, 2009) saccades just after a perceptual judgement, saccades in the decision-congruent direction were initiated earlier and faster. Moreover, when observers' hand movements are perturbed during manual choice responses, muscular reflex gains scale with stimulus motion strength, suggesting that senso-rimotor control is linked to ongoing perceptual decision making (Selen et al., 2012). Taken together, these findings indicate that there is a continuous crosstalk between perceptual decision processes and evolving

motor plans.

Further evidence of the close relationship between motor and perceptual processing comes from studies of neural activity in the motor cortex in human and non-human primates. Neural population activity measured by magnetoencephalography in human observers were predictive of decision outcome in a motion detection task before observers indicated their choice (Donner et al., 2009; Pape and Siegel, 2016). Furthermore, electrophysiological recordings of the dorsal premotor and primary motor cortex of macaque monkeys revealed that neural activity reflects changes of mind during reach target selection when the position of correct targets has to be updated dynamically (Kaufman et al., 2015; Thura and Cisek, 2014). These results suggest that the readout of sensory information is continuously coupled to motor preparation and execution.

It is well-established that smooth pursuit eye movements and motion perception are closely linked (Kowler, 2011; Spering and Montagnini, 2011). Previous research has shown that engaging in smooth pursuit aids accurate motion prediction, a benefit that is thought to arise from additional motion information provided through efference copy signals during pursuit maintenance (Bennett et al., 2010; Spering et al., 2011b). Here we show that accurate pursuit initiation is related to higher decision accuracy. The initiation window was different from the classic open-loop phase ( $\sim$ 140 ms from pursuit onset) during which pursuit is mainly controlled by retinal motion signals (Lisberger, 2015; Lisberger et al., 1987). However, it is unlikely that pursuit initiation in the interval from stimulus onset to the onset of the initial saccade relies on efference copy signals. Alternatively, higher eye velocity and decision accuracy could arise from predictive mechanisms. Experience, expectation, and learning have been shown to increase eye velocity during the pursuit initiation phase (Carl and Gellman, 1987; Kowler and McKee, 1987). Here we show that faster eye velocity during pursuit initiation is related to higher decision accuracy. It should be noted, however, that we do not show a causal link between accurate eye movement initiation and decision formation. An alternative interpretation of our results could be that observers that were able to perceive and extrapolate motion signals more accurately initiate faster smooth pursuit eye movements. The observed differences in smooth pursuit initiation and the link to decision-making accuracy is a novel finding that needs to be investigated further to identify causality and underlying mechanisms.

We further show that eye velocity during pursuit maintenance is linked to accurate interception timing. These results are closely related to findings showing that more accurate smooth pursuit eye movements are linked to more accurate manual interceptions in time and space (Fooken et al., 2016). In the current study, interception timing was more crucial than spatial accuracy for a successful interception. We found that only relative eye velocity, but not positional error with respect to the target, was linked to timing accuracy. Similarly, corrective saccades during tracking might influence observers' speed perception and interception (Goettker et al., 2018, 2019). These results suggest, that velocity and positional error signals during smooth pursuit eye movements may contribute to different aspects of motion perception.

Neural and behavioural correlates of perceptual decision making have classically been studied using random-dot motion stimuli (Bennur and Gold, 2011; Britten et al., 1992; Celebrini and Newsome, 1994;

Crapse et al., 2018; Gold and Shadlen, 2000, 2003; Hagura et al., 2017; Horwitz and Newsome, 2001; Joo et al., 2016; Liu and Pleskac, 2011; McSorley and McCloy, 2009; Pape and Siegel, 2016; Shadlen and Newsome, 1996; Yates et al., 2017). These studies have gradually added to our understanding of decision networks in human observers (Gold and Shadlen, 2007; Heekeren et al., 2008; Schall, 2013). Yet, real-world scenarios often require more complex perceptual decisions than judging net motion. A series of studies investigating go/no-go decisions in human (Heinen et al., 2006) and non-human primates (Kim et al., 2005; Yang and Heinen, 2014; Yang et al., 2010) revealed neural decision correlates in the supplementary and frontal eye field, an area also associated with the predictive control of eye movements (Fukushima et al., 2006). Akin to neural correlates found during motion discrimination or go/no-go decision tasks, human eye movements are also sensitive to decision outcome and task requirements such as difficulty or signal strength (Fooken and Spering, 2019). In conclusion, eye movements provide a continuous readout of cognitive processes during two-stage decision formation. Because eye movements occur naturally, this may open up new avenues for studying decision making in real-world scenarios.

## Chapter 5

## Eye movement signatures of go/no-go decisions with different task constraints

The previous study indicated that initiating smooth pursuit eye movements improved accurate decision making. In the current study, we directly manipulated viewing condition to test whether eye movements directly contribute to accurate go/no-go decision making. During target presentation, observers were instructed to either fixate on a fixation cross or to freely track the moving target. Furthermore, we investigated the role of hand movement constraints by manipulating response modality. Observers either indicated their go/no-go decision by an interceptive hand movement or by button press. These manipulations allow us to investigate how eye movements contribute to go/no-go decision under different task constraints.

#### 5.1 Introduction

During a ball game, hitters and umpires alike have to decide if a thrown pitch will pass or miss the strike box. Since motor preparation and execution of the baseball swing takes time, the hitter only has 200 milliseconds (ms) to decide whether or not to swing, whereas the umpire can wait to see the full pitch. Situations that require the same perceptual decision but have different temporal demands may therefore be linked to different predictive eye movement strategies. For example, in many ball sports athletes are required to judge when and where to intercept, catch, or kick fast moving balls. In sports in which the ball bounces prior to interception, such as cricket, squash, or table tennis, athletes typically make a predictive saccade to the assumed bounce location and then briefly track the ball smoothly (Land and McLeod, 2000; McKinney et al., 2008; Ripoll and Fleurance, 1988). The timing of the predictive saccade (i.e., the pre-bounce latency) and the duration of post-bounce tracking vary with ball speed and elasticity, indicating that observers are able to adjust their eye movement strategy depending on external and physical constraints (Diaz et al., 2013b). In sports in which there is no bounce prior to interception, such as baseball, athletes track the approaching target with a combination of eye and head movements and typically make a predictive saccade to guide ball-effector contact (Bahill and LaRitz, 1984; Higuchi et al., 2018). These examples illustrate that the eye
movements system is able to dynamically adapt to temporal and spatial task demands.

It has been shown that eye movements benefit accurate motion perception of moving objects in time and space. Motion prediction of target direction and velocity becomes less accurate when observers are instructed to maintain fixation than when they are instructed to smoothly track the ball (Bennett et al., 2010; Spering et al., 2011b). Similarly, restricting eye movements to fixation at or near the starting point of a moving target changes hand movement dynamics, increasing movement latency and decreasing end point accuracy (Brenner and Smeets, 2010; van Donkelaar and Lee, 1994). When observers are allowed to track the moving target with their eyes, higher manual interception accuracy is associated with smoother tracking (de la Malla et al., 2017; Fooken et al., 2016; Goettker et al., 2019). Taken together, these studies show that human observers rely on accurate eye movements to guide visual predictions in time and space. However, whether and how eye movements reflect temporal and spatial task demands for ultra-fast perceptual decisions is not yet known.

In this study, we directly tested the effect of movement constraints (eye and hand) on decision making accuracy in a go/no-go interception task. To investigate effects of temporal task constraints we manipulated response modality (interceptive hand movement vs. button press). We hypothesized that the planning and execution of interceptive hand movements were more time costly (less time for decision formation) than button press responses and were therefore associated with a lower go/no-go decision accuracy (speed-accuracy trade-off). We further tested the contribution of eye movements to accurate decision making by manipulating viewing condition (free viewing vs. fixation). Following results from Chapter 4, we hypothesized that allowing eye movements benefited accurate go/no-go decision making. Overall, the outlined manipulations allowed us to investigate the functional role of eye movements during go/no-go decision making under different task demands.

## 5.2 Materials and Methods

We investigated the effect of response modality in two separate experiments. In experiment 1, observers indicated go/no-go decisions by withholding or executing interceptive hand movements. In experiment 2, observers indicated their choice response by withholding or initiating a button press. In both experiments we manipulated viewing condition and instructed observers to either move their eyes freely or fixate in a predefined location.

### **Observers**

We tested 22 observers (mean age 26.7 yrs, std = 3.9; 12 female) in experiment 1 and 18 observers (mean age 24.1 yrs, std = 3.3; 9 female) in experiment 2. All observers were unaware of the purpose of the experiment and were compensated at a rate of \$10/h. The experimental protocol adheres to the Declaration of Helsinki and was approved by the UBC Behavioral Research Ethics Board; observers gave written informed consent prior to participation.

### Visual stimuli, display, and apparatus

The visual target was a small, black disk (luminance 5.4 candela per meter squared,  $cd/m^2$ ) with diameter 2 degrees moving across the screen towards a darker grey strike box (31.5  $cd/m^2$ ) that was  $6^{\circ} \times 10^{\circ}$  in size and offset by 12° from the center to the side of interception (Fig. 5.1A). These objects were shown on a uniform grey background (35.9  $cd/m^2$ ) and were back-projected onto a translucent screen with a PROPixx video projector (VPixx Technologies, Saint-Bruno, Canada; refresh rate 60 Hz, resolution 1280 (H) × 1024 (V) pixels). Display size was 44.5 (H) × 36 (V) cm with a viewing distance of 46 cm. Stimulus display and data collection were controlled by a PC (NVIDIA GeForce GT 430 graphics card) and the experiment was programmed in Matlab 7.1 using Psychtoolbox 3.0.8 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

### Experimental paradigm and task

Observers were asked to track the target and to predict whether it would pass ("go" response required) or miss ("no-go" required) the strike box (Fig. 5.1A). Initial target velocity was  $36^{\circ}$ /s and followed natural forces (gravity, drag force, Magnus force). Launch angles were set to  $\pm 5^{\circ}$  or  $\pm 7^{\circ}$  for pass trajectories and to  $\pm 10^{\circ}$  or  $\pm 12^{\circ}$  for miss trajectories. The target disappeared at different times after the launch, at 200, 400, 600, or 800 ms, corresponding to a quarter, half, three quarters, or all the way to the left border of the strike box (Fig. 5.1A). All conditions were randomized and equally balanced. We instructed observers to withhold a response (hand movement in experiment 1; button press in experiment 2) in miss trajectories and to intercept the target while it was in the strike box in pass trajectories. Each trial ended when observers either intercepted the target / pressed a button or when the target reached the end of the screen (1.1 s). At the end of each trial observers received visual feedback about their performance; target end position was shown, and correct or incorrect decisions were indicated.

### **Response modality**

We evaluated the effect of response modality on decision making in two separate experiments (Fig.5.1B). In experiment 1, observers were asked to hit the target while it was in the strike box with their right index finger. At the start of a trial, each observer's right hand was resting on a table-fixed computer mouse and the interception movement was initiated from there. Finger position was recorded with a magnetic tracker (3D Guidance trakSTAR, Ascension Technology Corp., Shelburne, VT, USA) at a sampling rate of 240 Hz; a lightweight sensor was attached to the observer's dominant hand's index fingertip with a small Velcro strap. The 2D finger interception position was recorded in x- and y-screen-centered coordinates.

In experiment 2, observers were asked to intercept the target by pressing a button on a button box with their right index finger; in between trials, observers' right hand rested on the button box. After each interception, observers received feedback about the target position at the point of the button press. Button presses were recorded using a RESPONSEPixx button box (VPixx Technologies Inc., Saint-Bruno, Province, Canada).



**Figure 5.1:** Experimental paradigm and movement manipulations. (A) The target launched at different angles and either passed or missed the strike box. The target was visible for a quarter, half, three quarters, or all the way to the left border of the strike box. (B) Observers made their go/no-go judgement either by interceptive hand movements or by button press. (C) Eye movements were either unrestricted (free viewing) or observers had to maintain fixation at one of three fixation positions (denoted f1, f2, and f3).

### Eye movement condition

In both experiments, each observer performed two blocks (120 trials each) of free viewing and two blocks of fixation (Fig. 5.1C). Eye movement condition order was randomly assigned and counterbalanced. In the free viewing condition, we instructed observers to track the target with their eyes and to follow its assumed trajectory even after it had disappeared. In the fixation condition, observers were asked to fixate (within a  $2.5^{\circ}$  radius) at one of three fixation locations: at target launch (-14°), half way between target launch and the strike box (screen centre), or at the border of the strike box (14°; Fig. 5.1C). These fixation positions were chosen to control for target presentation and interceptions in the periphery. Observers were only required to maintain fixation while the stimulus was visible (i.e., the first 200, 400, 600, or 800 ms, depending on target presentation duration). The fixation cross disappeared as soon as the target disappeared and observers were no longer restricted to maintain fixation. During the initial fixation phase, we continuously checked observers' gaze position and showed a warning message if they moved their eyes. In the fixation condition, we had to discard 774 (14.7%) trials in experiment 1 and 192 (4.4%) trials in experiment 2 because observers did not maintain fixation.

### Eye movement recordings and preprocessing

Eye position signals from the right eye were recorded with a video-based eye tracker (Eyelink 1000 tower mount; SR Research Ltd., Ottawa, ON, Canada) and sampled at 1000 Hz. Eye movements were analyzed off-line using custom-made routines in Matlab. Eye velocity profiles were filtered using a low-pass, second-order Butterworth filter with cutoff frequencies of 15 Hz (position) and 30 Hz (velocity). Saccades were detected based on a combined velocity and acceleration criterion: Five consecutive frames had to exceed a fixed velocity criterion of 50°/s; saccade on- and offsets were then determined as acceleration minima and maxima, respectively. Pursuit onset was detected in individual traces using a piecewise linear function fit to

the filtered position trace. Each trial was manually inspected to mark non-detected saccades.

### Analysis of decision accuracy, interception timing, and eye movements

We defined trials in which observers intercepted targets that followed a pass trajectory as correct go and trials in which observers did not respond to a miss trajectory as correct no-go. Decision accuracy was calculated as the ratio of all correct go and no-go decisions over all trials. Interception timing was defined relative to the time of interception. Interceptions in which the target was inside the strike box at the time of interception were defined as on-time, interceptions in which the target had not yet reached the strike box as early, and interceptions in which the target had already left the strike box as late. Timing accuracy was defined as the ratio of all on-time interceptions over all interception trials.

The stimulus characteristics in this paradigm triggered tracking behavior that most closely resembled short periods of smooth pursuit and catch-up saccades. Saccades were excluded from pursuit analysis and we analyzed eye movement position and velocity relative to target position and velocity. We further extracted catch-up saccade number, initiation saccade latency (i.e., first saccade of each trial) and targeting saccade latency (i.e., last saccade of each trial). Finally, we determined the eye separation time between saccade rates for go and no-go decisions described in Chapter 4.

### **Statistical analysis**

We manipulated viewing condition (free viewing vs. fixation) and response modality (interceptive hand movement vs. button press). Effects of viewing condition and response modality on decision-making accuracy and interception timing were examined using repeated-measures ANOVA with between-subject factor experiment (interceptive hand movement vs. button press) and within-subject factors viewing condition. Within-group differences between conditions (e.g. free viewing vs. fixation) were evaluated using Welch two-sample paired *t*-tests. Between-group differences between response modality (interceptive hand movement vs. button press) were evaluated using Welch two-sample unpaired t-tests. All statistical analyses were performed in R.

### 5.3 Results

### Effect of task constraints on eye movements

Observers were either free to track the moving target or had to maintain fixation on one of three fixation positions (Fig. 5.1B). In the free viewing condition, observers typically followed the target's trajectory with their eyes (Fig. 5.1A). For the fixation condition, observers were instructed to maintain fixation until the fixation cross disappeared which coincided with the disappearance of the moving target. Consequently, observers were allowed to make an eye movement to accompany target interception to allow more natural action. However, these targeting saccades were rare and some observers completely refrained from making an eye movements (Fig. 5.2). Overall, we found that observers made no eye movements during the fixation condition in 65% of all trials, only small ( $\leq 1 \text{ deg}$ ) saccades in 15% of the trials, and larger targeting saccades in the remaining 20%.



**Figure 5.2:** 2-D eye position relative to the screen. (A) During free viewing observers tended to follow the target into or outside of the strike box. Both representative subjects (13 and 28) showed similar eye movement characteristics. (B) Observers were instructed to maintain fixation while the target was visible and were allowed to make an eye movement to accompany the interception. Subject 13 made several targeting saccades, especially when the fixation position was on the left, whereas subject 28 refrained from making any eye movements.

Next, we compared eye movements during free viewing with respect to the two different response modalities. For both interception types, observers tracked the target with a combination of smooth pursuit and saccades until initiating a targeting saccade either close to the location where the target would miss the strike box (no-go decision) or into the strike box (go decision) close to the target location at the point of interception  $(M = 2.3 \pm 0.7 \text{ deg})$ . Whereas eye position was similar for both response modalities, we found significant differences in eye movement timing (Table 5.1). In experiment 1, observers initiated the initial saccade earlier (Fig. 5.3). Earlier initial and targeting saccade latencies indicate that interceptive hand movements required earlier movement preparation and hand movement onset. Observers initiated the interceptive hand movement 399.6  $\pm$  49.8 ms after stimulus onset to be able to reach the strike box on time. Interceptions by button press presumably required similar motor preparation, however, after movement initiation responses were almost instantaneous. Consequently go/no-go decision formation had to occur earlier in the interceptive hand movement condition.

To further investigate the time course of the go/no-go decision formation, we compared saccade rates between go and no/go-decision trials for each response modality. The time point at which the go/no-go difference is detectable is an indicator of the time that the perceptual decision has been formed (Chapter 4). Congruent with the idea of earlier decision formation for interceptive hand movement responses, we found

 Table 5.1: Eye movement differences between observers that intercepted the target with their hand (experiment 1) compared to observers that intercepted the target by button press (experiment 2).

	Hand movement	Button press	<i>p</i> -value
Initial saccade latency	$185.2 \pm 30.4 \text{ ms}$	$222.8\pm35.0\ ms$	.001
Targeting saccade latency	$621.6 \pm 66.4 \text{ ms}$	$676.5 \pm 56.1 \text{ ms}$	.007
Mean eye velocity	$8.66 \pm 3.65 \text{ deg/s}$	$6.84 \pm 2.81 \text{ deg/s}$	.083
Eye separation time	$442.6 \pm 108.9 \text{ ms}$	493.4 ± 117.3*ms	.185

Values indicate group averages  $\pm$  standard deviation; *p*-values indicate between group comparisons using Welch two sample unpaired t-tests.

\* For two observers in experiment 2 saccade rates did not differ between go and no-go decisions.

earlier separation times in experiment 1 (interceptive hand movements). Here, separation times ranged from 250-652 ms (Fig 5.3B), whereas separation times for experiment 2 (button press responses) ranged from 294-702 ms (Fig 5.3C). Moreover, saccade rates during go and no-go decisions did not differ significantly for two observers in experiment 2, further indicating that decision formation may happen later in the trial. The change in saccade rates over time also indicates the earlier initiation of the targeting saccade for interceptive hand movements compared to button presses (onset of second peak in Fig. 5.3B,C). Taken together, the observed differences in eye movements indicate observers had less time to integrate motion information during go/no-go decision formation when an interceptive hand movement was required compared to simple button press responses.

### The effect of movement constraints on decision accuracy

Decision accuracy was defined as the ratio of correct go and no-go decisions over all trials for each observer. Decision accuracy ranged from 73.8-98.3% and was therefore above the 50% chance level in all conditions. We found a significant between-group main effect of *response modality* (F(1, 38) = 17.3, p < 0.001) and within-group main effect of *eye movement condition* (F(1, 38) = 49.3, p < 0.001), but no significant interaction (F(1, 38) = 3.6, p = 0.065). Decisions were more accurate for button press responses ( $M = 92.9 \pm 3.0$ %) than for interceptive hand movements ( $M = 87.5 \pm 6.0$ %), indicating that observers benefitted from having more time to reach the go/no-go decision when intercepting by button press. For both response modalities, decision accuracy was higher in the free viewing compared to the fixation condition (Fig. 5.4), suggesting that actively tracking the target enhanced motion estimation and prediction. Lastly, in the fixation condition, we found no main effect of fixation position for either experiment (F(2, 76) = 1.9, p = 0.154), indicating that the fixation detriment was not due to poorer visual acuity or motion information in the periphery.



**Figure 5.3:** Eye movement differences between interceptive hand movement (green) and button press (purple) responses. (A) Mean absolute eye velocity over time averaged across observers and response types. Saccade rates for go vs. no-go decisions over time separated by hand movement response (B) and button press response (C). Mean separation times are indicated by vertical black line and standard deviation by grey shaded box.

### The effect of movement constraints on timing accuracy

Timing accuracy was defined as the ratio of correctly timed interception (i.e. the target was inside the strike box at the time observers touched the screen or pressed the button) over all interception trials. Both early and late interceptions were counted as an incorrectly timed response. Timing accuracy ranged from 55.4-98.5%, indicating a large inter-subject variability. We found a significant within-group main effect of eye movement condition (F(1, 38) = 8.3, p = 0.007), but no between-group main effect of response modality (F(1, 38) = 1.2, p = 0.286). We also found a significant eye movement condition and response modality *interaction* (F(1, 38) = 4.7, p = 0.037) most likely driven by the difference in timing accuracy in experiment 1 (interceptive hand movement; Fig. 5.5A). Allowing eve movements significantly increased observers' ability to intercept the target with their index finger at the right time, suggesting that eye movements guided online correction. Moreover, observers may have needed more time for go/no-go decision formation in the fixation compared to free viewing condition, and consequently had less time to accurately time the interceptive hand movement. In line with this idea, we found that observers initiated their hand movement later ( $M_{fix}$  = 429.2 ± 61.9 ms vs.  $M_{free}$  = 407.5 ± 59.8 ms) and reached the strike box later ( $M_{fix}$  = 903.0  $\pm$  21.7 ms vs.  $M_{free}$  = 893.6  $\pm$  18.0 ms) in the fixation compared to free viewing condition (Fig. 5.5B,C). In contrast, neither timing accuracy, nor interception time differed between viewing conditions for interceptions by button press, suggesting that observers did not rely on eye movements to guide their speed judgement. These results indicate that interceptive strategies and eye-hand coordination change depending on the spatial-temporal demands of the interceptive action.



**Figure 5.4:** Decision accuracy for different viewing condition (blue: fixation; red: free viewing) and response modalities (left: interceptive hand movement; right: button press). Each circle reflects the average decision accuracy for one observer. Group averages are indicated by horizontal lines.

## 5.4 Discussion

We investigated the effect of eye and hand movement constraints on go/no-go decision formation and interception timing. We show that go/no-go decisions were more accurate when observers had to initiate or inhibit an interception by button press than by hand movement. Next, we showed that eye movements (compared to fixation) enhanced accurate decision making regardless of response modality. In contrast, eye movements improved interception timing only for interceptive hand movements but not for button press responses. Overall, these results indicate that perceptual decision formation occurs dynamically, relying on the continuous updating of sensory information until an action is required.

Our observation that eye movement velocity was higher during goal-directed hand movements is related to evidence showing a benefit of coordinated eye and hand movement execution (Chen et al., 2016; Danion and Flanagan, 2018; Fooken et al., 2018; Maiello et al., 2018; Snyder et al., 2002). However, faster and more accurate tracking of the target was not sufficient to boost decision accuracy to the same level as decisions that were indicated by button press. The observed advantage of responding by button press can be explained in the context of the diffusion decision model (for a review, see Ratcliff et al., 2016). Observers gather sensory information until the accumulated evidence reaches a decision threshold. The rate of evidence accumulation and decision accuracy depend on external factors, such as, stimulus signal strength or viewing times. In our task, observers viewed a briefly presented moving target that either passed (go) or missed (no-go) a strike



**Figure 5.5:** Interception timing for different viewing condition (blue: fixation; red: free viewing) and response modalities (left: interceptive hand movement; right: button press). (A) Timing accuracy for each observer (circles). Group average indicated by horizontal line. (B) Absolute interception time for each observer (circles) per condition and experiment. (C) Finger velocity in experiment 1 (interceptive hand movement) during free viewing (red) compared to the fixation (blue) condition.

box. Go and no-go trajectories were equally likely, resulting in an unbiased starting point half way between the go and no-go decision boundary (Fig. 5.6A). We found that observers made more accurate decisions when responding by button press than when intercepting by hand. The observed advantage may reflect the trade-off between accumulating sensory information for accurate decision formation and allowing sufficient time for movement planning and execution. To allocate sufficient time for interceptive hand movements, observers had to reach go/no-go decisions faster, resulting in a shift of the decision boundary towards the starting point (Fig. 5.6B). Manipulating viewing condition did not directly change the temporal demands of the task. Instead, higher decision accuracy during free viewing compared to fixation indicates different rates of evidence accumulation. At the critical time of decision formation (action initiation required) decision accuracy is consequently higher when eye movements are allowed and evidence is accumulated faster (Fig. 5.6C).

Previous research has shown that decision accuracy depends on stimulus properties, such as the strength of motion coherence in random-dot motion discrimination or phase coherence in object discrimination, with higher levels of coherence or certainty being associated with higher decision accuracy (Basso and Wurtz, 1997; Britten et al., 1992; Horwitz and Newsome, 2001; Lappin and Bell, 1976) and quicker decision formation (Philiastides, 2006; Yang and Heinen, 2014; Yang et al., 2010). Here we show that manipulating viewing condition and response modality affects decision formation similarly. Restricting eye movements led to a decrease in decision accuracy, which may be linked to less accurate motion integration during fixation than during free viewing. These findings are closely related to evidence showing that accurate eye movements aid accurate motion perception and prediction (Bennett et al., 2010; Brenner and Smeets, 2010; Fooken et al., 2016; Goettker et al., 2019; Spering et al., 2011b).

In two-choice decision making tasks, choice-responses are typically indicated either by pressing a but-



**Figure 5.6:** Diffusion decision model of rapid go/no-go decisions. (A) General model of go/no-go decision formation with unbiased starting point (equal probability of go and no-go trajectories). Evidence is accumulated until go or no-go decision boundary is reached at time t. (B) If decision formation needs to occur earlier (compare thand and tbutton) the decision boundary is shifted further towards the starting point which comes at a cost of lower decision accuracy. (C) For higher rates of evidence accumulation it takes less time to reach the decision boundary (compare tfree and tfix). A higher rate of evidence accumulation allows observers to reach a higher decision accuracy at the point in time at which action initiation is required.

ton or by making a goal-directed saccade, both of which are relatively short latency and quick movements. Our results show that manipulating response modality significantly affects the temporal demands of decision formation and consequently decision accuracy. These findings highlight the importance of studying action responses beyond simple button presses, since decisions in the real-world often require dynamic and complex movement planning and execution. Recent studies have shown that neural activity and reflex gains of the motor system relate to decision outcome (Donner et al., 2009; Pape and Siegel, 2016; Salinas and Romo, 1998; Selen et al., 2012). Studying neural signatures in the motor cortex while varying response modality could therefore reveal the interaction between perceptual decision formation and movement preparation and initiation in more detail.

Finally, we found that response modality influenced interception timing differently. Whereas timing accuracy decreased in the fixation condition when an interceptive hand movement was required, viewing condition had no effect on timing accuracy in the button press condition. Studies investigating how human observers estimate time to contact between moving objects and stationary targets often rely on button presses or computer mouse clicks as response modality (Bennett et al., 2010; Bosco et al., 2012; Chang and Jazayeri, 2018; Gray and Regan, 1998; López-Moliner et al., 2007; Smeets et al., 1996). However, in real-world tasks, such as hitting or catching a ball, observers use online control to adjust movement speed once the interceptive action is initiated (de la Malla and López-Moliner, 2015; Montagne et al., 1999; Peper et al., 1994; Zhao and Warren, 2015), whereas button press responses cause an instant interception. The resulting different temporal demands have implications for ongoing visual control and action planning and should be considered in future task designs. Taken together our results reveal that perceptual decision making is a dynamic process that is influenced by movement constraints and task design.

### Conclusion

This study further reveals the importance of task constraints and adds two main research contributions to previous work. First, we show that eye movements are not only beneficial for accurate motion prediction and in guiding interceptive hand movements, but also contribute to accurate go/no-go decision making that occurs shortly after target motion onset (~200-300 ms). These results highlight the interdependence of eye movement control and perceptual decision making, processes that have previously been studied in isolation. Second, we demonstrate that hand movement constraints significantly impact the time course of decision-related processes and actions. Button presses and interceptive hand movements are both manual responses, yet, the required hand movements have different spatial and temporal demands. On the one hand, the planning and execution of an interceptive hand movement is more time costly, resulting in higher temporal demands for initial go/no-go decision. On the other hand, interceptive hand movement direction and speed can be adjusted once a movement is initiated, whereas button presses are all-or-none responses. Studies investigating the relationship between visual perception and manual responses should therefore carefully consider how the chosen response modality affects temporal and spatial task demands and how these relate to real-world decisions.

## **Chapter 6**

# Discussion

This Chapter discusses how results presented in this dissertation are related to the idea of using eye movements as a model for cognitive processes and sensorimotor decision making and outlines practical implications for future studies. First, I will discuss the potential advantages and shortcomings of using eye movements as a model for cognitive processes. Second, I will highlight the importance of studying smooth pursuit and saccadic eye movements as interdependent systems (Chapters 3, 4, and 5). Third, I will discuss the key steps of sensorimotor decision making, including the accumulation of evidence and integration of prior knowledge with sensory input (Chapters 3, 4, and 5). Fourth, I will emphasize the relevance of task design when studying sensorimotor processes (Chapters 2 and 5). Finally, I will outline practical implications of the work presented in this dissertation with a focus on clinical studies and sport applications (Chapters 3 and 5). In this section I will also briefly discuss preliminary results from an ongoing study on eye movements and decision making in Parkinson's patients. I will conclude by summarizing the main research contributions of this dissertation.

## 6.1 Eye movements as a model for cognitive processes

The oculomotor system is a relatively simple and segregated motor system. Human eye movements are controlled by only three pairs of extraocular muscles and neural mechanisms of smooth pursuit and saccadic eye movements are well understood (see Section 1.1.2). Eye movements are known to be affected by cognitive processes, such as, attention, reward, or anticipation (Barnes, 2008; Hutton, 2008). Eye movements are also intertwined with visual perception (Gegenfurtner, 2016); visual perception guides where we direct our gaze to and how we act, whereas motor actions, in turn, influence perception. Eye movements are therefore an ideal model system to study the interdependency between perceptual and motor processes. However, in some cases eye movements are more sensitive to changes in visual stimuli than perceptual responses, demonstrating dissociations between eye movements and perceptual awareness (Spering and Carrasco, 2015). Such dissociations may be related to separate neural processing of visual information for guiding perception (ventral stream) and action (dorsal stream; Goodale, 2014) and to the partial separation of visual and motor processing at a subcortical level (Spering and Carrasco, 2015). The studies presented in this dissertation link eye movements to visual predictions associated with dorsal stream processes. Dissociations between eye movements and action outcomes are therefore unlikely to be discovered. Instead, our results provide further evidence for a tight link between eye movements and goal-directed actions. However, our results go beyond simply relating overall eye movement quality (averaged across all trials) to action outcomes. We present a trial-by-trial model of predicting go/no-go decision outcome based on distinct eye movement patterns (Chapter 3). These results highlight the potential of studying eye movements as markers for cognitive processes in more naturalistic settings in which many task repetitions may not be possible. Furthermore, we show that eye movements are sensitive indicators of ongoing decision processes even within single trials by relating different phases of smooth pursuit and saccades to the timing and accuracy of two-stage sensorimotor decisions (Chapter 4 and 5). Overall, our results highlight the potential of studying eye movements to reveal the timing and sequential nature of cognitive processes.

## 6.2 Smooth pursuit and saccade synergies

In 1967, the Russian scientist Alfred Yarbus demonstrated in an elegant experiment that human observers' gaze patterns were related to task specific instructions that reflected cognitive processes (Yarbus, 1967). This work inspired the idea that eye movements—particularly saccades—provided a window into cognition (Findlay and Gilchrist, 2003). In contrast, smooth pursuit eye movements were originally considered to be primarily driven by visual target motion, complemented by position and velocity error reducing corrective saccades (Lisberger et al., 1987; Rashbass, 1961). Later studies demonstrated that smooth pursuit is influenced by similar cognitive processes as saccades (Barnes, 2008; Kowler, 2011) and that the two eye movement systems are controlled by common neural pathways and function in synergy (Krauzlis, 2005; Orban de Xivry and Lefèvre, 2007). Yet, smooth pursuit and saccadic eye movements are still mostly studied in isolation. In this dissertation both types of eye movements are analysed in relation to each other. For example, the timing of final targeting saccades sensitively predicted observers' go/no-go decision outcome (see Section 3.3, Fig. 3.5). Interestingly, saccade rates for go compared to no-go decisions diverged at the same time as observers initiated manual interceptions (see Section 4.3, Fig. 4.4), providing more evidence for shared neural processing not only between smooth pursuit and saccades, but also between the eye and hand movement system. Moreover, we show that the timing of an initial "catch-up" saccade depends on the temporal demands of the go/no-go decision, that is, observers initiate the saccade later when they have more time to indicate their response (see Section 5.3, Table 5.1). Taken together, these results provide strong evidence that saccades are not only initiated to correct for position or velocity error during tracking, but that smooth pursuit and saccadic eye movements optimally work together to accomplish action goals.

## 6.3 Sensorimotor decision making

Decision-related processes are influenced by current visual information, prior knowledge, expectation, and task constraints. For instance, many real-world decisions happen under strict temporal constraints, that is, decisions have to be reached before a critical event happens to allow time for appropriate action responses. In the literature, these kinds of timed decisions are described by the rate of sensory evidence accumulation, decision boundaries or thresholds, and priors or decision biases (Noorani and Carpenter, 2016; Ratcliff et al., 2016).

### Accumulation of evidence

The rate of evidence accumulation depends on internal factors and the external environment. Neural processing within the brain can vary with neural noise, attention, or wakefulness, whereas external sensory stimuli can be weak, noisy, or ambiguous. A hierarchy of brain areas processes sensory information and forms associated motor commands (Schall, 2001). External changes in stimulus properties lead to changes in the signal to noise ratio and therefore impact signal detection and discrimination (Green and Swets, 1966). For example, a weak level of motion coherence or low contrast decreases the neural response to the visual stimulus and may result in a lower signal-to-noise ratio (Shadlen and Kiani, 2013). Therefore, more time is needed to integrate noisy visual information and reach the same level of decision accuracy. Several results presented in this dissertation reflect changes in evidence accumulation. For example, manual interception accuracy (see Section 2.3) and go/no-go decision accuracy (see Section 3.3, Fig. 3.2) decreased with shorter target duration (weaker signal strength). Similarly, go/no-go decision accuracy was affected by task difficulty—more ambiguous motion trajectories led to an increased number of incorrect decisions. A decrease in the rate of evidence accumulation was also observed when target properties were held constant, but eye movements were restricted during target presentation (see Section 5.4). These results suggest that eye movements enhance the internal readout of accurate motion estimation, revealing further interdependence of perceptual processing and oculomotor control.

### Prior knowledge and decision bias

Visual information may be unreliable or not always be available to inform sensorimotor predictions and decisions. Under uncertainty, humans have to rely on other factors, such as prior knowledge and experience. Behaviourally, priors are integrated with current visual information to guide goal-directed actions—a mechanism that can be described by Bayesian models (Körding and Wolpert, 2006). Prior knowledge can immediately inform sensorimotor decisions (e.g., by receiving performance feedback) or gradually cause a decision bias (e.g., unbalanced outcome likelihood). In all experiments described in this dissertation, target conditions were equally balanced, resulting in a relatively unbiased task design. However, some effects of priors and biases were observed. In all tasks, observers received immediate feedback about how accurate their visual predictions and decisions were. This information helped observers to learn target properties and improve prediction and decision accuracy over time (see Section 2.3, Fig. 2.5).

Another example of the strong influence of prior knowledge and experience on decision making is

presented in Chapters 3 and 4. In these Chapters, a subset of observers were UBC varsity baseball players. In our go/no-go decision task baseball players were more accurate when intercepting fast targets, indicating that they were influenced by in-game timing of decision making and movement initiation ( $\sim$ 200 ms to decide whether to swing and  $\sim$ 400 ms to hit). We also found that players made more accurate go/no-go decisions than a group of age- and gender-matched non-athletes (see Section 3.3, Fig. 3.2). The superior performance of baseball players is unlikely to be driven by more efficient use of priors, because we did not observe any influence of trial history on decision outcome for either groups. Yet, players' ability to accurately judge the target's motion path may be related to enhanced visual-anticipatory skills that could have developed through extensive baseball training and on-field experience (also see section on sport application below). Finally, we found that observers have a natural tendency to initiate rather than inhibit interceptive movements. Moreover, results emphasize that our task design adds ecological validity and observers behaved naturally. To investigate the role of priors and decision bias further, future studies have to directly manipulate study design, such as changing the go/no-go ratio or feedback validity.

## 6.4 Relevance of task design

Our understanding of how visual information is integrated to guide perceptual decisions has been advanced by single-cell recordings of neural activity in non-human primates and by laborious psychophysical experiments in human observers. The advantage of studying perceptual processes in highly-controlled laboratory environments with simple visual stimuli is that neural and behavioural effects are likely not influenced by other sensory or cognitive processes. However, in real-world environments humans are exposed to a variety of sensory input and continuously have to decide whether, when, and where to act. Yet, sensorimotor control and perceptual decision making have largely been studied in isolation. To bridge the gap between understanding low-level perceptual processes and human behaviour in real-world scenarios, the need for studying sensorimotor behaviour using more naturalistic task designs has been proposed (Gallivan et al., 2018; Huk et al., 2018; Spering and Chow, 2018).

Several results presented in this dissertation highlight the relevance of task design with respect to sensorimotor behaviour. First, we show that training observers to passively track a disappearing target was not sufficient to enhance eye or hand movement quality (see Section 2.3, Fig. 2.4 and 2.9). Instead, learning occurred when the task involved a sensorimotor decision, that is, when observers had to actively intercept the target at its assumed end position. These results suggest that developing perceptual-cognitive expertise is linked to experiencing behavioural consequences. Second, we demonstrate that manipulating task constraints influenced how and when perceptual decisions were formed (see Section 5.3, Table 5.1, Fig. 5.3). When observers indicated go/no-go responses by button press compared to interceptive hand movements, decisions were more accurate. The difference in temporal constraints, that is, interceptive hand movements took more time than button press responses, were not only reflected in decision accuracy, but also in observers' eye movement patterns. These results suggest that eye movements are a direct and sensitive readout of ongoing cognitive events (see also Chapters 3 and 4). In all studies, observers naturally elicited eye movements without specifically being instructed to do so (with the exception of the fixation condition in Chapter 5). Sensorimotor decisions (go/no-go decisions and predicted target end points) were indicated by natural interceptive hand movements. Even though our paradigms and experimental setup are a step towards a more naturalistic task design, head and body movements were restrained during all experiments. Head movements are an essential part of visual orienting responses in natural environments and the control of eye and head movement is tightly coupled (Freedman, 2008). With the recent development of accurate and high-resolution portable eye trackers head-free eye movements can be evaluated in the real world (e.g., Matthis et al., 2018). Future studies should therefore test whether results presented in this dissertation will transfer to human decision making in unrestricted environments.

## 6.5 Practical implications

Eye movements occur naturally and can be recorded with high temporal resolution in naturalistic environments. Eye tracking also provides reliable data quality, affordability, and easy portability. Furthermore, the underlying neural mechanisms of eye movements are well understood so that behavioural eye movement data can ultimately be linked to cognitive processes.

### **Clinical studies**

Studying eye movements in clinical populations can aid our understanding of the underlying neural disease mechanisms and can potentially lead to the development of novel diagnostic tools. Eye movement deficits have been associated with many neurological disorders, including psychiatric (Barton et al., 2008; Spering et al., 2013; Trillenberg et al., 2004), neurodevelopmental (Sweeney et al., 2004), and neurodegenerative (Anderson and MacAskill, 2013) disorders. For example, Parkinson's disease (PD) patients frequently suffer from visual dysfunction, such as, changes in colour vision and contrast sensitivity (Weil et al., 2016), and show deficits in smooth pursuit and saccadic eye movement control (Chan et al., 2005; van Koningsbruggen et al., 2009; White et al., 1983). PD is commonly associated with a depletion of dopamine secreting neurons in the basal ganglia (Albin et al., 1989), an area that has also been associated with perceptual decision making (Ding and Gold, 2013). Furthermore, perceptual decision making might be impaired in PD patients when current sensory information has to be integrated with previously learned priors (Herz et al., 2016; Perugini et al., 2016). To investigate whether eye movements deficits affect sensorimotor decision making, we tested twelve PD patients and eight age-matched controls in a preliminary study in our go/no-go decision task (see Section 3.2, Fig. 3.1). PD patients' go/no-go decisions were as accurate as controls', indicating that decision making was preserved. Moreover, patients were able to compensate for motor slowing (low hand movement velocities) by initiating the interceptive hand movement earlier. One potential confound of our study was that overall task performance was very high ( $\sim 85\%$ ). To investigate further whether and how decision making is preserved in PD patients, we are currently testing a more difficult version of the task with varying temporal and spatial demands.

Another potential clinical implication is the use of eye movement and visual training during rehabilitation. Evidence shows that training smooth pursuit eye movements towards the contralesional side in human patients with visual neglect improves functional recovery (Kerkhoff et al., 2014, 2013). Similar benefits have been suggested for visuomotor feedback training in patients suffering from hemispatial neglect (Rossit et al., 2019), indicating that there is a benefit of involving the eye and hand movement system during a training intervention similar to results presented in Chapter 2.

### **Sports application**

Several studies have demonstrated that high-level athletes compared to novices show superior on-field oculomotor strategies (Spering and Schütz, 2016; Vickers, 2016) and rely on enhanced anticipatory (Müller and Abernethy, 2012; North et al., 2009) and perceptual-cognitive (Karlinsky et al., 2015; Mann et al., 2007) skills. These skills relate to athletes' ability to detect, discriminate, and recognize sensory information. In Chpater 3, we observed differences between baseball players and non-athletes in our go/no-go decision task (see Section 3.2, Fig. 3.1). Baseball players made more accurate decisions and their eye movement patterns reflected decision outcome more distinctly. These results suggest that baseball players' on-field experience and expertise affected visual predictions in the laboratory. Our results further indicate that accurate decision making was related to early and accurate eye movement initiation (Section 4.3, Fig. 4.2). Players' superiority could therefore be linked to enhanced eye movement and anticipatory control. Similarly, we found in a previous study that senior compared to junior baseball players were able to accurately track a disappearing target longer, which allowed them to intercept later, a strategy that may provide an advantage in the real world (Fooken et al., 2016). Taken together, we observed differences between baseball players of different experience level and between players and non-athletes on lab-based visual prediction tasks. These results suggest that players have developed perceptual-cognitive skills that transfer from sport-specific to basicvisual performance. Contrary, we found no evidence of transfer when training predictive eye movements of non-athletes in a perceptual-motor training study (Section 2.3). However, our task design did not probe transfer from training visual predictions and manual interceptions to general perceptual cognitive skills. Instead, we tested and trained observers on tasks that required very similar visuomotor control. To investigate the potential of training basic-oculomotor function, future studies could test perceptual-cognitive skills on an unrelated task relying on the same underlying visual mechanisms.

## 6.6 Conclusion

The primary goal of this dissertation was to relate eye movements to visual predictions and action outcomes. Results from a series of four experimental studies suggest that eye movements provide a high-resolution readout of underlying perceptual processes guiding sensorimotor decisions and goal-directed actions. First, eye movements are a continuous measure that can be recorded on-line and underlying mechanisms are well understood. Linking different phases of eye movements to visual and behavioural events can therefore reveal the time frame and sequence of ongoing decision processes. Second, eye movements occur naturally in response to visual stimuli and are closely coupled with hand movement control. Studying eye movements as decision markers therefore allows more naturalistic task designs. Finally, eye movements reflect temporal and spatial task constraints and reliably predict action outcomes. Overall, this dissertation reveals that eye movements are a sensitive indicator of visual and cognitive processing.

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