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The role of eye movements in manual interception: A mini-review

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ABSTRACT

When we catch a moving object in mid-flight, our eyes and hands are directed toward the object. Yet, the functional role of eye movements in guiding interceptive hand movements is not yet well understood. This review synthesizes emergent views on the importance of eye movements during manual interception with an emphasis on laboratory studies published since 2015. We discuss the role of eye movements in forming visual predictions about a moving object, and for enhancing the accuracy of interceptive hand movements through feedforward (extraretinal) and feedback (retinal) signals. We conclude by proposing a framework that defines the role of human eye movements for manual interception accuracy as a function of visual certainty and object motion predictability.

1. Introduction

Hitting a baseball or saving a soccer penalty kick are among the hardest tasks an athlete can accomplish. To successfully intercept a moving object, such as a flying ball, we have to move our hands to the right place at the right time—a process that requires accurate judgment of the object's motion path and precise movement timing. Relevant information about the moving object, such as motion direction and speed, is provided by motion-sensitive brain areas along the visual processing hierarchy (Bradley & Goyal, 2008). The sensorimotor transformation from visual input to motor commands does not occur instantaneously and thus leads to systematic delays: it takes approximately 100 ms (ms) to adjust hand movements to any change in object motion direction or velocity (Brenner & Smeets, 1997). Aiming toward the location where the object was most recently seen will therefore inevitably lead to intercepting at a location the object has already passed. To overcome the sensorimotor delay and accurately intercept a moving object, humans have to form an accurate prediction of the object's path based on current visual motion signals and past visual experience (Fiehler, Brenner, & Spering, 2019). The interaction between visual prediction and the continuous control of visually-guided hand movements makes manual interception an important problem to study, which can elucidate mechanisms underlying sensory signal integration for prediction and motor control. Investigating how biological systems intercept moving objects accurately and precisely is therefore key to understanding goal-directed behaviour in dynamic environments.

In recent years, there has been an increasing interest in understanding the role of active vision during natural goal-directed behaviour in the field (Hayhoe and Ballard, 2005; Hayhoe, 2017; Land, 2006). Previous reviews have highlighted that interceptive actions rely on internal models (Zago et al., 2009), on-line visual control (Brenner & Smeets, 2018; Zhao & Warren, 2015), and predictive mechanisms (Fiehler et al., 2019). Here, we focus on another aspect of vision: the role of eye movements. In particular, we ask whether and how eye movements contribute to accurate visual predictions and manual interceptions. Linking eye movements to interceptive hand movements advances the field by tying together two lines of research: the continuous interaction between eye movements and vision (Gegenfurtner, 2016) and the important role of vision for manual interception (Brenner & Smeets, 2018; Zhao & Warren, 2015).

This review focuses on ecologically-inspired laboratory studies investigating the relationship between eye and hand movements and using precise, high-resolution, and synchronized recording of eye and hand movement dynamics. Although laboratory studies add artificial

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movement constraints, they allow researchers to probe the functional role of eye movements during manual interception. Even though many laboratory findings might translate to real-world interceptions, we acknowledge that natural interceptive behaviour typically occurs in open, 3D environments and includes a vast range of binocular eye, head, and whole-body movements.

We start this review by describing different types of eye movements and outlining their advantages and disadvantages during interception tasks. We then discuss whether and how tracking the moving object with the eyes benefits interception accuracy. Finally, we propose a possible conceptual model of the functional role of eye movements during manual interception and give an outlook of emerging problems in the field.

2. Eye movements during visually-guided manual interception

2.1. Type of eye movements

Human observers use a repertoire of eye movements to gather visual information for perception and visually-guided action. Holding the image of an object stable on the fovea—the small, central area on the retina with the highest density of photoreceptors—allows high-acuity vision of the object. During fixation, retinal image motion must be reduced to prevent blur of higher spatial frequencies (Burr & Ross, 1982). At the same time, head movements and small, fixational eye movements ensure sufficient retinal image motion during fixation to prevent fading caused by absolute stabilization (Martinez-Conde & Macknik, 2017; Rolfs, 2009). Because the fovea only covers ~1% of the visual field and visual resolution declines drastically in the periphery (Jacobs, 1979), humans and many other animals shift their eyes to align the fovea with an object by making quick, high-velocity eye movements called saccades (Land, 2019). Making a saccade to an object of interest not only provides foveal vision of the object, but also allows the observer to use two types of extraretinal signals about the eye position: (1) Proprioceptive feedback, which is derived from the stretch receptors in the ocular muscles (Steinbach, 1987; Bridgeman & Stark, 1991), and (2) efference copy (or corollary discharge) signals, which provide an internal copy of the oculomotor command (Bridgeman & Stark, 1991; Bridgeman, 1995; Sommer & Wurtz, 2008; Crapse & Sommer, 2008) and can be used as a feedforward signal in action and cognition (Subramanian, Alers, & Sommer, 2019).

Saccades play an important role during visually-guided actions towards stationary objects: when reaching for or manipulating objects, observers commonly make a saccade toward the object that the hand approaches (e.g., Ballard et al., 1992; Barany et al., 2020; de Brouwer, Flanagan, & Spering, 2021; Horstmann & Hoffmann, 2005; Johansson et al., 2001; Neggers & Bekkering, 2000). Despite the advantages of using saccades to locate objects of interest (using retinal and extraretinal signals; Wilmut, Wann, & Brown, 2006), saccades may not be the optimal type of eye movement for sampling visual motion information. During saccades, images move rapidly across the retinae while the eyes are moving at peak velocities of up to 900°/s for 30–100 ms (Carpenter, 1988). Yet, the rapid image motion caused by saccadic eye movements is typically not perceived by observers and accurate motion perception of moving objects may not be available (Binda & Morrone, 2018; Castet, 2010).

To ensure continuous and accurate motion perception, humans naturally track moving objects with their eyes using another type of eye movement: smooth pursuit. Smooth pursuit eye movements are slow, continuous rotations of the eyes that align the foveae with a moving object by closely matching the eyes' velocity to the object's velocity (Dodge, 1903; Ilg, 1997). Smoothly aligning the eyes with a moving object not only allows high-acuity vision of the object, but also provides the observer with extraretinal input. Whereas initial (open-loop) pursuit is mainly driven by retinal velocity signals, ongoing (closed-loop) pursuit is driven by an efference copy of the pursuit command, allowing observers to match eye velocity to object velocity using negative feedback control (Krauzlis & Lisberger, 1994; Robinson, Gordon, & Gordon, 1986). The availability of efference-copy signals during smooth pursuit might explain why observers' motion prediction is enhanced during pursuit as compared to during fixation, where no efference-copy signals are produced (Bennett et al., 2010; Spering et al., 2011). Yet, whether and how oculomotor efferent signals contribute to object motion prediction during manual interception remains unclear. One goal of this review is to evaluate and discuss the evidence for shared prediction between eye and hand movements and the use of oculomotor extraretinal signals to guide manual interception.

Fixation, smooth pursuit, and saccades do not work in isolation (Fig. 1). For example, when object motion is relatively fast or temporarily occluded, the eyes lag behind the moving object. Thus, smooth pursuit is often accompanied by catch-up saccades that realign the eyes to the moving object (de Brouwer et al., 2002; Orban de Xivry et al., 2006; for a review, see Orban de Xivry & Lefèvre, 2007). Throughout this review, we use the term catch-up saccades to describe saccades that complement smooth pursuit by bringing the eyes back to the moving object. The term predictive saccade refers to saccades that move the eyes ahead of the target to locations of interest, such as the interception area (Fig. 2). We do not differentiate between types of fixational eye movements because these small eye movements (e.g., microsaccades) appear to be more relevant for high-precision manual tasks (Valsecchi & Gegenfurtner, 2015) than for interceptive hand movements that require gross motor control. Throughout the review we use the broad term fixation to describe when observers keep their gaze relatively stable at a stationary location of interest for longer periods of time.

One goal of this review is to assess whether eye movement quality relates to interception accuracy. A standard measure to evaluate the quality smooth pursuit eye movements is pursuit gain—the relative velocity of the eye with respect to object velocity. A pursuit gain of 1 indicates that the observer tracks the moving object smoothly and at its exact speed, a gain smaller than 1 indicates that the eye is lagging behind the target. Correspondingly, the eye position error—the distance between the eyes and the object—provides a measure of the spatial alignment between eye and object. Catch-up saccade frequency and amplitude provide further criteria of tracking quality. Moreover, the latency and end-point position of the predictive saccade—the saccade that aligns the eyes with the interception location—are additional measures of the temporal and spatial dynamics of eye-hand coordination during manual interception. These detailed eye movement measures require the use of high-resolution eye tracking systems. Recent developments in movement tracking devices (e.g., mobile eye trackers and video-based motion capture systems for body and hand movements) have facilitated the simultaneous recording of eye and body movements during manual interception on a 2D-screen, in virtual reality, and in the field.

2.2. Eye movements enable and limit high-acuity vision

Interacting with visual objects typically requires high-acuity vision of the object and environment to guide ongoing hand and body movements. The inherent problem of the visual system is that our eyes can only gather high-acuity vision at a single point of interest at any given time due to conjugate yoking of eye movements in humans (Land, 2019). Because of these constraints on the oculomotor system, natural eye movement behaviour is adapted to task demands. During goal-directed actions, eye movements serve at least three main functions (Fig. 1A): they (1) allow visual feedback of the ongoing hand movement, (2) enable high-acuity vision during fixation at critical locations along the object's path or planned interception area, and (3) provide continuous information about an object's motion during tracking of the moving object. In the following paragraphs, we describe patterns of oculomotor behaviour associated with each of these three functions and how the observed eye movement patterns support successful manual interception.

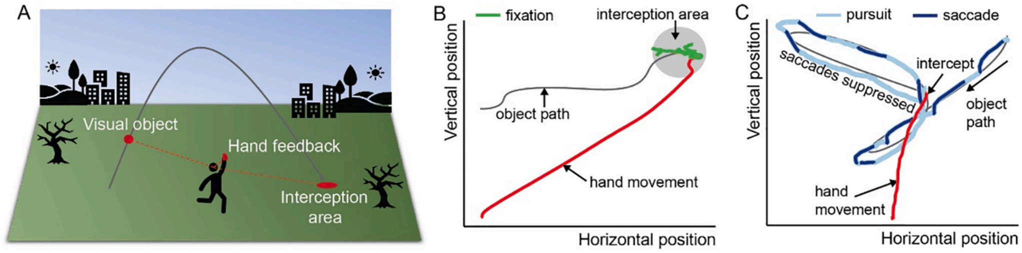

Fig. 1. Function of eye movements during manual interception. (A) Observers may view three critical locations when trying to intercept a moving object: the hand, the interception area, or the moving object. Additionally, observers may look at critical locations ahead of the moving object, such as the bounce location of a ball. (B) Eye movements when intercepting a moving object that always passes a predefined interception area. Observers fixate (green) the interception area while moving their hand (red) to where they intercept the object. Adapted from de la Malla et al. (2019). (C) Eye movement patterns when intercepting a moving object that can be intercepted anywhere along the object path (grey). Observers track the object with a combination of smooth pursuit (light blue) and saccades (dark blue). Shortly before the hand (red) intercepts the object, saccades are suppressed. Adapted from Mrotek and Soechting (2007). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

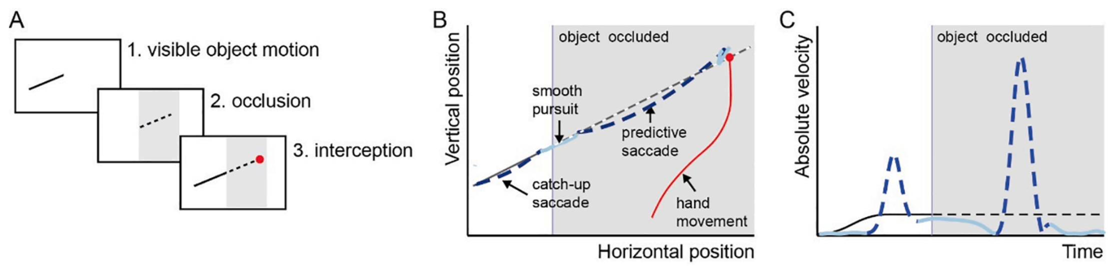

Fig. 2. Eye movements during manual interception of occluded objects. (A) In occlusion paradigms the moving object disappears after an initial visible phase. Observers intercept the moving object at a predicted location. (B) 2D eye position during manual interception of an occluded target. A catch-up saccade is elicited to align the eye with the moving target followed by a brief phase of smooth tracking until a predictive saccade brings the eye ahead of the target to the estimated interception location. (C) Absolute eye velocity across time for the same interception trial. Data from Fooken and Spering (2020).

2.2.1. Looking at the hand provides visual feedback of the interceptive movement

Successful interception of moving objects requires accurate on-line control of the ongoing hand movement (Brenner & Smeets, 2018). In addition to proprioceptive feedback from the limb, viewing the hand during goal-directed actions can provide observers with information about the current effector position. Congruently, visual feedback of the moving hand contributes to accurate on-line control of reaching movements toward stationary objects (Saunders & Knill, 2004). When an object is stationary during reaching, observers can afford to move their eyes away from the object and toward their moving hand once the object of interest has been localized. In contrast, a moving object's position changes continuously during manual interception and looking away from the moving object can lead to inaccurate motion estimation (Brenner & Smeets, 2010; de la Malla, Smeets, & Brenner, 2017; van Donkelaar & Lee, 1994; see also Section 3.1). Sampling foveal visual feedback of the hand during manual interception is therefore characterized by only brief shifts of the eyes toward the effector (Delle Monache, Lacquaniti, & Bosco, 2015).

One way to experimentally test whether observers rely on visual hand feedback during manual interception is to occlude the hand during the movement. Restricting vision of the hand is associated with higher variability in movement kinematics (speed, hand path) and in interception accuracy, as compared to when the hand is fully visible (van Donkelaar & Lee, 1994). These results indicate that on-line control of goal-directed hand movements is impaired when vision of the effector is fully blocked. To investigate whether high-acuity vision of the ongoing hand movement is necessary for accurate and precise manual interception, visual feedback of the occluded hand can be manipulated by shifting the position of a visual cursor that indicates the hand position. For example, delaying visual feedback between cursor and the actual hand movement introduces a mismatch between proprioceptive and visual feedback signals. Here, observers could benefit from looking at the visual cursor to gather accurate visual information of the ongoing hand movement. Remarkably, even when visual feedback is shifted, observers keep their eyes on the moving object rather than the visual cursor (Cámara et al., 2018). Gathering high-acuity visual feedback of the ongoing hand movement only occurs when observers have to accurately move their hand along a predefined movement path (Cámara et al., 2020). These results suggest that peripheral vision is sufficient to complement somatosensory hand feedback signals during manual interception.

2.2.2. Fixation provides stable high-acuity vision at areas of interest

Observers commonly fixate relevant visual objects and future contact points during many goal-directed actions in everyday life (Land, 2006). Such fixations allow observers to locate objects of interest in their environment, to direct their hands towards the next action site, and to check whether the chosen action was successful (Land and Hayhoe, 2001). When intercepting a moving object, observers cannot fixate the object of interest because it continuously changes its position. However, other areas of interest remain constant throughout the interception. For example, when observers have to intercept a moving object that always passes through a known and predefined interception location (e.g., the exit of a marble run) fixating the designated interception area aids accurate target localization, precise hand movement control, and interception feedback that can be used to guide the hand in subsequent interceptions (Fig. 1B; de la Malla, López-Moliner, & Brenner, 2012; Brenner & Smeets, 2015a; de la Malla et al., 2019). One way to experimentally test the need for high-acuity vision at the interception area is to impose movement constraints that require hand movement precision either related to the moving object or the interception area. Indeed, if observers need to move their hand towards a small interception area (e.g., when intercepting through narrow barriers), observers fixate the interception area during interception. Conversely, if the moving object is small (and the interception area is large) observers track the moving object until it is intercepted in the designated interception area (Brenner & Smeets, 2011). Other areas of interest that observers may fixate during manual interception include task-relevant future locations along an object's path, such as a goal (Brenner & Smeets, 2007) or a bounce location (Diaz et al., 2013; Mann et al., 2019). Taken together, these results indicate that observers keep their eyes at the location that requires the most precise hand movement control for interception (e.g., a small interception area or a small moving object).

The finding that observers predictively fixate an area of interest resembles eye movement patterns observed during natural behaviour (Hayhoe & Ballard, 2005; Land, 2006). For example, athletes predictively move their eyes to and fixate critical contact locations in ball sports, such as the predicted bounce location in cricket (Land & McLeod, 2000; Mann et al., 2019) or table tennis (Ripoll, 1989; Rodrigues, Vickers, & Williams, 2002). The timing and duration of such fixations depends on the need for accurate visual information at the interception area and on the degree of object motion predictability; both are highly task-dependent.

2.2.3. Tracking moving objects enables continuous high-acuity vision

When aiming to intercept a moving object, observers commonly keep their eyes on the object, tracking it with a combination of smooth pursuit and catch-up saccades (Fig. 1C; Binaee & Diaz, 2019; Delle Monache et al., 2015; Diaz et al., 2013; Fooken et al., 2016; Fooken & Spering, 2020; Mrotek & Soechting, 2007; Barany et al., 2020). Whereas smooth pursuit enables continuous foveation of the moving object, catch-up saccades can compensate for position and velocity errors when object motion is unpredictable or relatively fast (de Brouwer et al., 2002). The occurrence of catch-up saccades during smooth pursuit not only depends on properties of the moving object but also on the visuomotor demands of the task. For example, the rate of catch-up saccades decreases after hand movement onset and observers rely exclusively on smooth pursuit eye movements close to the time of manual interception of fully visible objects (see smooth pursuit prior to interception in Fig. 1C; Mrotek & Soechting, 2007; Soechting & Flanders, 2008). These findings imply that different types of eye movements optimally support different phases of interceptive actions. Whereas early catch-up saccades support a reduction of position error to accurately encode a target's trajectory before the hand movement is initiated, smooth pursuit allows continuous updating of the target's trajectory close to the time of interception (Mrotek, 2013).

These laboratory findings are paralleled by eye movement behaviour in real-world activities. For example, during catching or in striking sports, observers naturally track the moving object with a combination of eye and head movements until the hand aligns with the moving object at the time of interception (Bahill & LaRitz, 1984; Cesqui et al., 2015; Higuchi et al., 2018; Yeo et al., 2012). Interestingly, a phase of smooth tracking is observed shortly before athletes intercept the ball (Hayhoe et al., 2012; Land & McLeod, 2000; Mann et al., 2019), indicating that keeping the eyes on the moving object during the interceptive movement is important for accurate perception and prediction of object motion.

2.2.4. Summary

In sum, experimental and real-world evidence indicate that during manual interception observers typically track the moving object with their eyes (Fig. 1C) or fixate an area of interest (Fig. 1B). Foveal vision of the hand is usually not necessary to guide the interceptive hand movement (Cámara et al., 2018, 2020). High-acuity vision of the interception area is especially required when manual interception is constrained to a small and predefined interception area or when high-precision hand movements are required to approach the interception area (Brenner & Smeets, 2011). During most interceptive tasks, maintaining high-acuity vision of the moving object is critical and can be achieved by smooth pursuit of the moving object—avoiding saccades and fixation—prior to the interception. To understand why observers commonly track the moving object during manual interception, we discuss the functional link between eye movements and interceptive hand movements in the following section.

3. Functional relationship between eye and hand movements

3.1. Are eye movements beneficial for manual interception?

We started this review by noting that successful interception of moving objects requires accurate motion processing and the ability to predict the object's motion in order to overcome sensorimotor delays. Tracking the moving object with the eyes may enhance accurate manual interception by allowing observers to continuously update their prediction of the object's trajectory (Brenner & Smeets, 2018; Fiehler et al., 2019). High-acuity retinal signals from the object aid to quickly detect and react to any changes in the object path. Additionally, tracking the moving object with the eyes provides extraretinal input that contributes to accurate predictions. The role of smooth pursuit in forming such motion predictions is commonly investigated with occlusion paradigms, where the moving object is temporarily occluded or disappears after an initial presentation (Fig. 2A; Becker & Fuchs, 1985; Barnes, 2008). Compared to smooth pursuit of a visible object, where the eye closely matches the object's speed (Fig. 1B), pursuit velocity in response to an occluded object decreases transiently after occlusion, and pursuit is accompanied by catch-up saccades (Fig. 2B,C; Orban de Xivry et al., 2006). Toward the end of the occlusion period, smooth pursuit predictively accelerates to catch up with the target upon its reappearance, a response that is driven purely by extraretinal and cognitive signals (Barnes, 2008; Fiehler et al., 2019). Importantly, predictive pursuit velocity scales with the object's pre-occlusion speed, indicating that observers rely on signals accumulated during initial pursuit to form a prediction of the object motion (Bennett et al., 2007). Perceptual motion prediction is enhanced when a moving object is tracked with smooth pursuit eye movements, compared to fixation (Bennett et al., 2010; Spering et al., 2011). Interestingly, schizophrenia patients with failure in forming or utilizing efference-copy information during smooth pursuit do not benefit from actively tracking a disappearing target (Spering et al., 2013; Thakkar, Diwadkar, & Rolfs, 2017; Bansal, Ford, & Spering, 2018). Oculomotor extraretinal signals are therefore associated with enhanced motion perception and prediction. Further, there is evidence that efference signals aid accurate pointing (Wilmut et al., 2006) and planning during manual tracking (Leclercq, Blohm, & Lefèvre, 2013). However, it is less clear whether and how efference-copy signals during pursuit provide a similar benefit for manual interception.

One way to directly test whether eye movements aid accurate manual interception is by asking observers to fixate at a predefined location during the manual interception task and compare interception performance during fixation and free viewing. Indeed, observers intercept moving objects less accurately when fixating as compared to when eye movements are allowed (Dessing et al., 2009a, 2009b). One reason for inaccurate interception performance is that observers tend to overestimate object speed during fixation, compared to when eye movements are unrestricted, leading to interceptions ahead of the moving object (van Donkelaar & Lee, 1994). Alternatively, instructing observers to fixate could be viewed as a secondary task that might require additional cognitive resources, thus leading to a reduction in interception accuracy.

Another approach to investigate the role of eye movements for interception is to present observers with ambiguous motion stimuli. For example, when an aperture moves in one direction while an internal pattern drifts in a different direction, the perceived global motion is biased in the direction of the internal drift (Tse & Hsieh, 2006; Lisi & Cavanagh, 2015). Similarly, manual interception of double-drift stimuli is also biased in the direction of the internal pattern motion (de la Malla et al., 2017; Lisi & Cavanagh, 2017). Observers systematically intercept moving objects that contain drifting stripes ahead of the object (or behind the object) when internal drift is in the same (or opposite) direction as the aperture (de la Malla et al., 2017). Importantly, this systematic error only occurs when observers have to maintain fixation and not during free viewing. Interestingly, saccadic eye movements directed toward double-drift stimuli follow the trajectory of the aperture rather than the perceived direction, suggesting that eye movements are less affected by certain perceptual biases (Lisi & Cavanagh, 2015; 2017). Another example of conflicting motion signals during manual interception is the presence of visual backgrounds. In naturalistic environments, objects typically move in front of static or moving contexts. In this case, observers need to segregate the retinal motion signals caused by the object and the background (Spering & Gegenfurtner, 2008). Transient background perturbations lead to interception errors in the direction of background motion (Brenner & Smeets, 2015b). In contrast, systematic errors in manual interception and predictive saccade end points caused by long-lasting contextual motion (Soechting, Engel, & Flanders, 2001) can be avoided when observers track a moving object in front of the context (Kreyenmeier, Fooken, & Spering, 2017). Together, these results indicate that tracking the moving object with the eyes helps manual interception through enhanced segregation of conflicting motion signals (either caused by internal drifts or external contexts).

3.2. The link between eye movement quality and interception accuracy

Keeping the eyes on the moving object is associated with more accurate interception compared to when eye movements are restricted. Yet, we do not understand to what extent changes in the quality of one movement affect the other, or the exact nature of the link between the eye and hand movement systems. In the following, we summarize results from key studies that simultaneously recorded eye and interceptive hand movements (Table 1). To compare findings across experiments we highlight two main differences in visual constraints imposed by the task design. First, we differentiate between moving objects that remain fully visible during the task (high visual certainty; Fig. 3A) or are occluded prior to interception (low visual certainty; Fig. 3B). Second, we identify whether the object trajectory is highly predictable (following a simple motion profile; Fig. 3A) or less predictable (more complex and subject to change over time; Fig. 3C). We define complex motion profiles as those in which a moving object suddenly changes direction, velocity, or acceleration, such as a fast-moving prey in the natural environment (Fig. 3C). We also consider profiles of objects exposed to natural forces, such as gravity or drag force, as following a complex motion profile, even though naturalistic priors and internal models can aid motion predictability during manual interception (Bosco et al., 2012; Delle Monache, Lacquaniti, & Bosco, 2019; Zago et al., 2009).

In the following, we discuss two main types of correlational findings: within- (trial-by-trial) and across-observer correlations. We treat within-observer correlations as an indication of a functional link between eye and hand movements. The exact nature of this link and whether eye movements are causally related to interception accuracy remains unclear. Across-observer correlations of mean eye and hand movement measures are more difficult to interpret. Across-observer differences in eye movement quality could be related to inter-individual differences in general motion perception and extrapolation that might be dissociated from hand movement control. In the final part of this section, we discuss studies that experimentally manipulate object motion in such a way that tracking eye movements are altered during manual interception. Causing systematic interception errors by perturbing oculomotor behaviour can possibly provide evidence for the underlying mechanisms that link eye and hand movement control during manual interception.

3.2.1. Eye movements as predictors of manual interception accuracy within observers

At the moment of intercepting a moving target, observers' eyes are typically aligned with the interception location, resulting in a strong positive correlation between eye position error at the time of interception and manual interception error within-observers (Kreyenmeier et al., 2017; Li et al., 2018; Soechting et al., 2001). However, to probe the functional role of pursuit eye movements during manual interception, eye movement quality throughout the interception has to be considered. Several studies have found that different smooth pursuit measures (pursuit gain and eye position error) are good predictors for interception accuracy on a trial-by-trial basis (Table 1). For example, when observers intercept a disappearing simulated fly ball, eye position error and manual interception error are positively correlated on a trial-by-trial basis (Fooken et al., 2016; Fooken & Spering, 2020). A within-observer relationship between eye movement quality (position error and pursuit gain) and hand movement accuracy is observed across different task demands, such as interception of moving objects in virtual reality (Binaee & Diaz, 2019) or in a naturalistic visual context (Kreyenmeier et al., 2017). These findings also extend to real-world actions: longer periods of smooth tracking are associated with a higher probability of catching a thrown ball (Cesqui et al., 2015).

Whereas several studies indicate that smooth pursuit quality is predictive of interception accuracy, others did not find within-observer correlations between eye and hand movement measures (de la Malla et al., 2017; Goettker et al., 2019). In these studies, observers had to intercept a moving object that remained visible and followed a simple motion profile (Fig. 3A). In contrast, in all studies that found a within-observer correlation, the moving object was either occluded or followed a complex motion trajectory with changing direction and velocity profiles (Fig. 3B). These results suggest that the role of eye movements is more important when object motion is uncertain and accurate interception requires a higher degree of prediction.

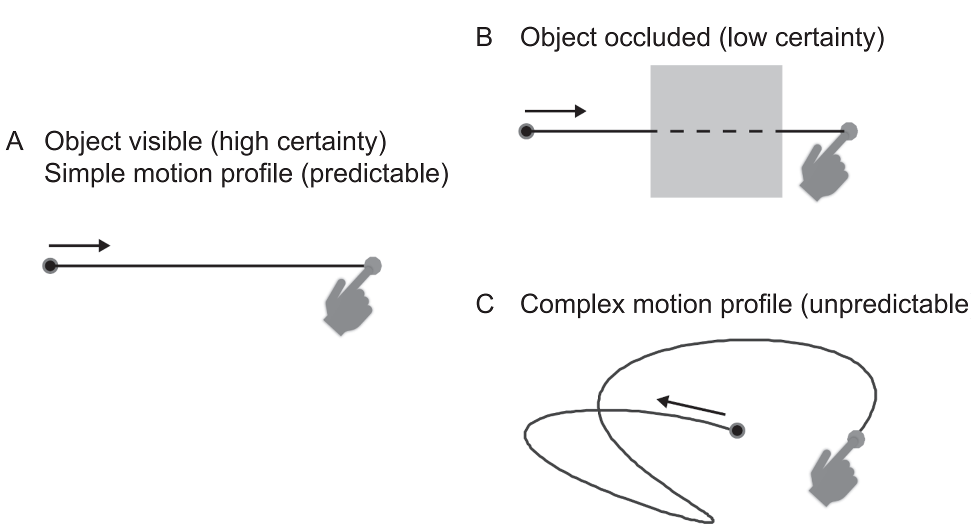

Fig. 3. Examples of visual constraints in different task designs. (A) Objects with high visual certainty and motion predictability are visible during the entire trial and follow a simple motion profile (constant direction and velocity). (B) Temporary occlusion of the object reduces visual certainty (without affecting motion predictability). (C) Objects that follow complex motion profiles (changing motion direction and velocity over time) are less predictable but may still provide continuous visual feedback if they remain visible (high visual certainty).

Table 1
Key studies relating eye movement to hand movement accuracy during manual interception. Visual constraints refer to the visual certainty and motion predictability of the moving object. Movement accuracy is compared for different eye and hand movement measures. A link between eye and hand movements is either observed (✓), not observed (×) or not shown.

Visual constraints		Motor performance		Eye-hand link		Article
Certainty	Predictability	Eye	Hand	Within	Across	
Visible	Simple	Pursuit gain	Timing error	×	Not shown	De la Malla et al. (2017)
Visible	Simple	Position & velocity error	Timing error	×	Not shown	Goettker et al. (2019)
Occluded	Complex	Position error, pursuit gain	Interception error	✓	Not shown	Binaee & Diaz (2019)
Occluded	Complex	Timing error	Timing error	✓	Not shown	Kreyenmeier et al. (2017)
Visible	Complex	Pursuit duration	Catching performance	✓	×	Cesqui et al. (2015)
Occluded	Complex	Pursuit gain	Timing error	✓	✓	Fooken & Spering (2020)
Occluded	Complex	Position error	Interception error	✓	✓	Fooken et al. (2016)
Visible	Simple	Pursuit gain	Timing error	Not shown	✓	Brenner & Smeets (2011)
Visible & occluded	Complex	Pursuit duration, pursuit gain	Interception error	Not shown	✓	Delle Monache et al. (2015)

3.2.2. Across-observer differences in oculomotor control do not systematically affect interception performance

Whereas within-observer correlations indicate a link between eye and hand movement control, across-observer correlations between the same measures are more difficult to interpret. Although most laboratory studies find that observers with higher smooth pursuit quality also show more accurate hand movements (Table 1), these findings may not extend to real-world interceptions. Although large inter-individual difference in both eye movements (pursuit duration and frequency of catch-up saccades) and catching performance are observed, these differences do not necessarily result in a positive across-observers correlation between pursuit quality and interception accuracy (Cesqui et al., 2015). Therefore, a superiority in oculomotor control is not necessarily linked to superiority in hand movement control. These findings are supported by the observation that observers can flexibly allocate their eye movements during catching (López-Moliner & Brenner, 2016). When observers have to perform a secondary task during catching, saccades away from the ball can happen at any time during the catch. Importantly, different individual eye movement patterns are not associated with differences in catching performance (López-Moliner et al., 2010). Taken together, the findings from real-world catching suggest that inter-individual differences in oculomotor control are not directly linked to differences in interception accuracy. Instead, these studies suggest that different oculomotor patterns can lead to similarly successful interception performance.

Another important factor that may influence individual eye and hand movement performance is experience. When observers view an object moving in front of a naturalistic, pictorial backgrounds (similar to the background in Fig. 1A) expectation about natural forces, such as gravity, can affect eye movement patterns (Delle Monache et al., 2019). Generally, eye movements are most accurate when the object moves with naturalistic compared to altered (either zero or double) gravity. Importantly, this effect is even stronger in the presence of a naturalistic compared to a uniform background (Delle Monache et al., 2019), indicating that the visual context interacts with the observer's prior believes about how objects naturally fall. This finding is in line with the notion that gravity can act as a strong prior for perception and action control (Jörges and López-Moliner, 2017). Whereas gravity is a constant naturalistic prior across observers, other external factors, such as expertise can be linked to inter-individual differences. It has been proposed that professional athletes in interceptive sports have superior perceptual-cognitive skills (Mann et al., 2007). Whether athletes also show similar superior oculomotor function is less clear. Recent studies suggest that athletes move their eyes more consistently during interceptive tasks but are not necessarily more accurate (e.g., Fooken & Spering, 2019; Mann et al., 2013). Moreover, a transfer from oculomotor training to on-field performance—which would indicate a functional role of eye movements—remains debated (Appelbaum & Erickson, 2018).

3.2.3. Perturbing oculomotor control to probe functionality

Thus far, we revealed that accurate eye movements (1) enhance motion processing and (2) aid accurate prediction in manual interception tasks. Correlations between eye movement quality and interception accuracy are typically observed when the object motion exhibits a lower degree of visual certainty (due to occlusion) or lower predictability (due to complex motion profiles). As for many scientific questions in experimental psychology and neuroscience (Marinescu, Lawlor, & Kording, 2018), we want to go beyond a general relationship between eye and hand movements and understand the causal link between eye movements and manual interception. A direct link between eye and hand movements has been suggested in the form of shared internally generated feedback signals. For example, smooth pursuit is boosted when tracking of the moving object is accompanied by manual tracking (Danion & Flanagan, 2018) or when the object motion is self-generated by moving the hand (Bennett et al., 2012; Chen, Valsecchi, & Gegenfurtner, 2016; Maiello, Kwon, & Bex, 2018). Similarly, an extraretinal (efference copy) signal of the oculomotor command might be used as a feedforward signal to form a prediction guiding eye and interceptive hand movements. One way to investigate the role efference copy during manual interception is to restrict eye movements completely (Section 3.1). However, retinal motion signals are drastically changed during fixation, compared to free viewing. A less confounded approach to test such a feedforward model is to investigate whether an altered oculomotor command introduces systemic effects in manual interception.

First evidence in favor of this hypothesis were recently demonstrated (Goettker et al., 2018, 2019). When a visual object starts to move, observers often make catch-up saccades to compensate for retinal errors that accumulate during open loop pursuit (Fig. 2B). A standard method to avoid such catch-up saccades is the step-ramp paradigm, in which the target jumps backwards before moving towards the eye (Rashbass, 1961). Manipulating the size of the backwards step is associated with different eye movement responses: a large backward step evokes a backward saccade against the motion direction, whereas a small backward step elicits a forward (catch-up) saccade. Importantly, backward and forward saccades during tracking are associated with slower and faster motion perception compared to trials without saccades (Goettker et al., 2018). These errors in perception extend to interception: when observers elicit forward saccades during manual interception, they systematically intercepted ahead of the moving object as compared to trials in which participants track the object smoothly (Goettker et al., 2019). Conversely, backward saccades during smooth pursuit led to interceptions behind the moving object. These findings suggest that altering the oculomotor command leads to systematic, congruent effects in manual interception.

3.2.4. Summary

Several experiments have related eye movements to interceptive hand movements (Table 1). A strong positive relationship between eye movement quality and manual interception accuracy is especially observed when object motion is unpredictable either due to occlusion or because of changes in motion direction and velocity during interception. When object motion is uncertain and more prediction is required, efference copy signals of the eye movement system may aid manual interception performance.

4. Toward a unified framework of eye-hand coordination in manual interception

In this section we introduce one possible conceptual model for the functional role of eye movements during manual interception. When comparing the relationship between eye and hand movements across different experiments (Table 1) a clear picture emerges: the link between eye and interceptive hand movements is modulated by the degree of motion predictability and visual certainty (Fig. 3 and Fig. 4). When object motion is fully predictable (constant motion direction and speed) and visible, a correlation between eye and hand movement accuracy does not necessarily exist (de la Malla et al., 2017; Goettker et al., 2019). Instead, observers may benefit from stabilized, foveal vision at the interception area to guide precise hand movements (e.g., Brenner & Smeets, 2011). Thus, high-acuity retinal signals are predominantly used to guide the hand to the interception area. A link between extraretinal feedforward signals and interceptive control appears to be weaker compared to the retinal signals (Fig. 4A), although efference copy signals of saccades directed to the interception area may additionally contribute to accurate manual interceptions (Wilmut et al., 2006).

In many naturalistic interception tasks, object motion follows a complex motion profile or is (temporarily) occluded from the observers' view (low motion predictability or visual certainty). Here, observers may benefit from closely tracking the moving object with their eyes (Mrotek & Soechting, 2007; de la Malla et al., 2019; Fig. 1C) to continuously update their prediction of the object motion (Brenner & Smeets, 2018). In the case of object occlusion, a prediction has to be derived from the initial object presentation prior to occlusion. Perceptual studies demonstrate that smooth pursuit before occlusion directly aids the formation of motion prediction (Bennett et al., 2010; Spering et al., 2011). Similarly, when observers have to intercept an occluded moving object (low visual certainty) smooth pursuit quality is related to interception accuracy (Binaee & Diaz, 2019; Fooken et al., 2016). When visual certainty or motion predictability are low, retinal and extraretinal (efference copy) signals may both be crucial to estimate object motion for accurate interceptive control (Fig. 4B). Thus, in these studies, a stronger link between eye and hand movements is observed, compared to situations where the object is visible and moves fully predictably.

5. Outlook and conclusion

Eye movements are functionally linked to interceptive hand movements via shared retinal and extraretinal signals (Fig. 4). The strength of the link is modulated by the degree of predictability and visual certainty of the interception task. This conceptual model is derived from exploratory studies that show how different visual and task demands affect eye and hand movement patterns. In addition to exploratory work, more confirmatory studies are necessary to investigate the causal link between eye and interceptive hand movements. One promising direction is to investigate how perturbing the oculomotor command affects goal-directed hand movements (e.g., Goettker et al., 2019) and vice versa (e.g., Cámara et al., 2020) Additionally, quasi-experimental approaches can help to probe the causal link between eye movements and manual interception (Marinescu, et al., 2018).

In this review, we identified different eye movement patterns that enable (1) accurate motion prediction of moving objects, (2) localization of relevant contact areas, and (3) precise hand movement control at interception locations, providing visual feedback of manual errors. However, it should be noted that most of the studies discussed in this review investigated manual interception of objects moving along a two-dimensional plane. To intercept moving objects in a three-dimensional plane, observers use active vision including head, body movements, and binocular eye movements to track moving objects in depth (Gray & Regan, 1998; Regan & Gray, 2000). During real-world interceptions, observers are more likely to rely on naturalistic priors and internal models during manual interception of naturalistically moving objects (Zago et al. 2009, Delle Monache et al., 2019). The rapid development of high-end mobile eye and whole-body tracking devices will allow researchers to study how eye-hand coordination patterns observed in the laboratory translate to real-world tasks. Such ecological approaches can further be complemented by wireless neurophysiological recordings in freely moving monkeys, advancing our understanding of the neurophysiological substrates of action planning and execution (e.g., Berger, Agha, & Gail, 2020). In particular, many research questions regarding the neuronal implementation of efference copy information in action control and cognition are still unresolved (Subramanian et al., 2019).

An open question that future studies need to address is the role of inter-individual differences. Although most studies find across-observer correlations between eye and hand movement accuracy (Table 1), such a positive relationship is not observed during real-world catching (Cesqui et al., 2015), indicating that different eye movement strategies can lead

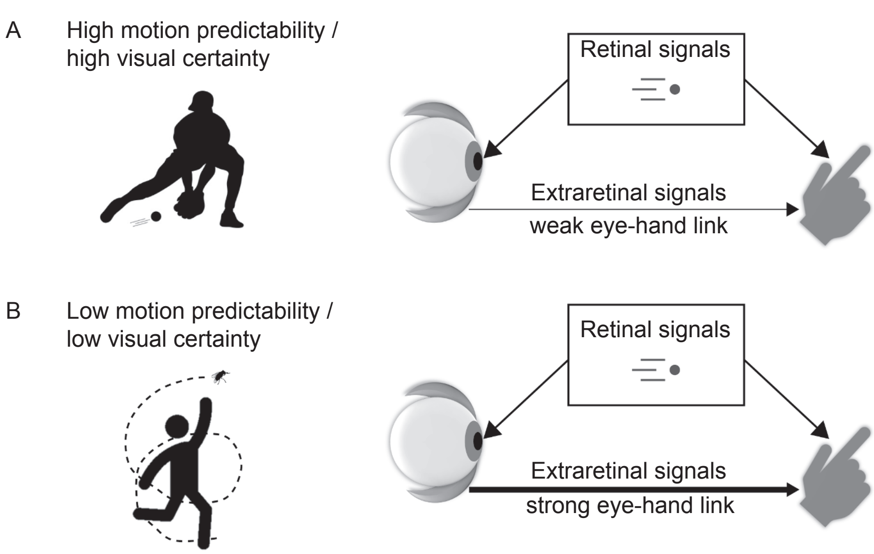

Fig. 4. Possible link between eye and hand movements during manual interception. In addition to shared retinal signals, we propose that oculomotor extraretinal signals are used as a feedforward input to form predictions and guide eye and interceptive hand movements. The importance of the extraretinal signal depends on visual constraints of the interception task. (A) Observers rely predominantly on retinal signals at the interception area when the object moves predictably and remains visible throughout the task, resulting in a weaker eye-hand link. (B) Observers rely on retinal and extraretinal signals when the object moves unpredictably or exhibits a lower degree of visual certainty resulting in a strong eye-hand link.

to similar catching performance (López-Moliner & Brenner, 2016). Modeling oculomotor behaviour during manual interception within the optimal feedback control framework (Scott, 2012) may provide a promising new direction for the field to answer the question whether a single optimal eye movement strategy exists during manual interception.

Another modelling approach is to build a computational system that mimics biological behaviour. Visually-guided and predictive pursuit have previously been modelled using a Bayes-optimal framework (Adams et al., 2015; Nachmani et al., 2020; Orban de Xivry, Coppe, Blohm, & Lefèvre, 2013). Extensions of these models can complement experimental work investigating whether eye and hand movements are controlled by shared or independent signals (Eggert, Rivas, & Straube, 2005; Jana, Gopal, & Murthy, 2017). Importantly, generative models can help tease apart deficits in sensory processing, internally generated feedback, and motor control in different patient groups (e.g., Adams et al., 2015; Bansal et al., 2018; DuBois et al., 2016; Thakkar et al., 2017).

The conceptual model proposed in this review introduces possible mechanisms through which eye movements benefit manual interception and identifies two critical factors that mediate the functional link between eye and hand movements, namely visual certainty and motion predictability. This model unifies current perspectives on the role of eye movements in manual interception and provides a framework for future studies on eye-hand coordination during interception.

CRediT authorship contribution statement

Jolande Fooken: Conceptualization, Visualization, Writing - review & editing. **Philipp Kreyenmeier:** Conceptualization, Visualization, Writing - review & editing. **Miriam Spering:** Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Adams, R. A., Aponte, E., Marshall, L., & Friston, K. J. (2015). Active inference and oculomotor pursuit: The dynamic causal modelling of eye movements. *Journal of Neuroscience Methods, 242*, 1–14. https://doi.org/10.1016/j.jneumeth.2015.01.003.

Appelbaum, L. G., & Erickson, G. (2018). Sports vision training: A review of the state-of-the-art in digital training techniques. *International Review of Sport and Exercise Psychology, 11*(1), 160–189. https://doi.org/10.1080/1750984X.2016.1266376.

Bahill, A. T., & LaRitz, T. (1984). Why can't batters keep their eyes on the ball? *American Scientist, 72*(3), 249–253.

Ballard, D. H., Hayhoe, M. M., Li, F., & Whitehead, S. D. (1992). Hand-eye coordination during sequential tasks. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 337*(1281), 331–339. https://doi.org/10.1098/rstb.1992.0111.

Bansal, S., Ford, J. M., & Spering, M. (2018). The function and failure of sensory predictions. *Annals of the New York Academy of Sciences, 1426*(1), 199–220. https://doi.org/10.1111/nyas.13686.

Barany, D. A., Gómez-Granados, A., Schrayer, M., Cutts, S. A., & Singh, T. (2020). Perceptual decisions about object shape bias visuomotor coordination during rapid interception movements. *Journal of Neurophysiology, 123*(6), 2235–2248. https://doi.org/10.1152/jn.00098.2020.

Barnes, G. R. (2008). Cognitive processes involved in smooth pursuit eye movements. *Brain and Cognition, 68*(3), 309–326. https://doi.org/10.1016/j.bandc.2008.08.020.

Becker, W., & Fuchs, A. F. (1985). Prediction in the oculomotor system: Smooth pursuit during transient disappearance of a visual target. *Experimental Brain Research, 57*(3), 562–575. https://doi.org/10.1007/BF00237843.

Bennett, S. J., Baures, R., Hecht, H., & Benguigui, N. (2010). Eye movements influence estimation of time-to-contact in prediction motion. *Experimental Brain Research, 206*(4), 399–407. https://doi.org/10.1007/s00221-010-2416-y.

Bennett, S. J., O'Donnell, D., Hansen, S., & Barnes, G. R. (2012). Facilitation of ocular pursuit during transient occlusion of externally-generated target motion by concurrent upper limb movement. *Journal of Vision, 12*(13), 1–16. https://doi.org/10.1167/12.13.17.

Bennett, S. J., Orban de Xivry, J.-J., Barnes, G. R., & Lefèvre, P. (2007). Target acceleration can be extracted and represented within the predictive drive to ocular pursuit. *Journal of Neurophysiology, 98*(3), 1405–1414. https://doi.org/10.1152/jn.00132.2007.

Berger, M., Agha, N. S., & Gail, A. (2020). Wireless recording from unrestrained monkeys reveals motor goal encoding beyond immediate reach in frontoparietal cortex. *ELife, 9*, Article 305334. https://doi.org/10.7554/eLife.51322.

Binaee, K., & Diaz, G. (2019). Movements of the eyes and hands are coordinated by a common predictive strategy. *Journal of Vision, 19*(12), 1–16. https://doi.org/10.1167/19.12.3.

Binda, P., & Morrone, M. C. (2018). Vision during saccadic eye movements. *Annual Review of Vision Science, 4*(1), 193–213. https://doi.org/10.1146/annurev-vision-091517-034317.

Bosco, G., Delle Monache, S., & Lacquaniti, F. (2012). Catching what we can't wee: Manual interception of occluded fly-ball trajectories. *PLoS ONE, 7*(11), Article e49381. https://doi.org/10.1371/journal.pone.0049381.

Bradley, D. C., & Goyal, M. S. (2008). Velocity computation in the primate visual system. *Nature Reviews Neuroscience, 9*(9), 686–695. https://doi.org/10.1038/nrn2472.

Brenner, E., & Smeets, J. B. J. (1997). Fast responses of the human hand to changes in target position. *Journal of Motor Behavior, 29*(4), 297–310. https://doi.org/10.1080/00222899709600017.

Brenner, E., & Smeets, J. B. J. (2007). Flexibility in intercepting moving objects. *Journal of Vision, 7*(5), 1–17. https://doi.org/10.1167/7.5.14.

Brenner, E., & Smeets, J. B. J. (2010). Intercepting moving objects: Do eye movements matter? In R. Nijhawan, & B. Khurana (Eds.), *Space and time in perception and action* (pp. 109–120). Cambridge: Cambridge University Press, 10.1017/CBO9780511750540.008.

Brenner, E., & Smeets, J. B. J. (2011). Continuous visual control of interception. *Human Movement Science, 30*(3), 475–494. https://doi.org/10.1016/j.humov.2010.12.007.

Brenner, E., & Smeets, J. B. J. (2015a). How people achieve their amazing temporal precision in interception. *Journal of Vision, 15*(3), 1–21. https://doi.org/10.1167/15.3.8.

Brenner, E., & Smeets, J. B. J. (2015b). How moving backgrounds influence interception. *PLoS ONE, 10*(3), 14–16. https://doi.org/10.1371/journal.pone.0119903.

Brenner, E., & Smeets, J. B. J. (2018). Continuously updating one's predictions underlies successful interception. *Journal of Neurophysiology, 120*(6), 3257–3274. https://doi.org/10.1152/jn.00517.2018.

Bridgeman, B. (1995). A review of the role of efference copy in sensory and oculomotor control systems. *Annals of Biomedical Engineering, 23*(4), 409–422. https://doi.org/10.1007/BF02584441.

Bridgeman, B., & Stark, L. (1991). Ocular proprioception and efference copy in registering visual direction. *Vision Research, 31*(11), 1903–1913. https://doi.org/10.1016/0042-6989(91)90185-8.

Burr, D. C., & Ross, J. (1982). Contrast sensitivity at high velocities. *Vision Research, 22*(4), 479–484. https://doi.org/10.1016/0042-6989(82)90196-1.

Cámara, C., de la Malla, C., López-Moliner, J., & Brenner, E. (2018). Eye movements in interception with delayed visual feedback. *Experimental Brain Research, 236*(7), 1837–1847. https://doi.org/10.1007/s00221-018-5257-8.

Cámara, C., López-Moliner, J., Brenner, E., & de la Malla, C. (2020). Looking away from a moving target does not disrupt the way in which the movement toward the target is guided. *Journal of Vision, 20*(5), 1–18. https://doi.org/10.1167/jov.20.5.5.

Carpenter, R. H. S. (1988). *Movements of the eyes*. London: Pion.

Castet, E. (2010). Perception of intra-saccadic motion. In G. S. Masson, & U. J. Ilg (Eds.), *Dynamics of visual motion processing: Neuronal, behavioral, and computational approaches* (pp. 213–238). New York: Springer.

Cesqui, B., Mezzetti, M., Lacquaniti, F., & D'Avella, A. (2015). Gaze behavior in one-handed catching and its relation with interceptive performance: What the eyes can't tell. *PLoS ONE*, 1–39. https://doi.org/10.1371/journal.pone.0119445. e0119445.

Chen, J., Valsecchi, M., & Gegenfurtner, K. R. (2016). Role of motor execution in the ocular tracking of self-generated movements. *Journal of Neurophysiology, 116*(6), 2586–2593. https://doi.org/10.1152/jn.00574.2016.

Crapse, T. B., & Sommer, M. A. (2008). Corollary discharge across the animal kingdom. *Nature Reviews Neuroscience, 9*(8), 587–600. https://doi.org/10.1038/nrn2457.

Danion, F. R., & Flanagan, J. R. (2018). Different gaze strategies during eye versus hand tracking of a moving target. *Scientific Reports, 8*(10059), 1–10. https://doi.org/10.1038/s41598-018-28434-6.

de Brouwer, Flanagan, J. R., & Spering, M. (2021). Functional use of eye movements for an acting system. *Trends in Cognitive Sciences, 25*(3), 252–263. https://doi.org/10.1016/j.tics.2020.12.006.

de Brouwer, S., Yuksel, D., Blohm, G., Missal, M., & Lefèvre, P. (2002). What triggers catch-up saccades during visual tracking? *Journal of Neurophysiology, 87*(3), 1646–1650. https://doi.org/10.1152/jn.00432.2001.

de la Malla, C., López-Moliner, J., & Brenner, E. (2012). Seeing the last part of a hitting movement is enough to adapt to a temporal delay. *Journal of Vision, 12*(4), 1–15. https://doi.org/10.1167/12.10.4.

de la Malla, C., Rushton, S. K., Clark, K., Smeets, J. B. J., & Brenner, E. (2019). The predictability of a target's motion influences gaze, head, and hand movements when trying to intercept it. *Journal of Neurophysiology, 121*(6), 2416–2427. https://doi.org/10.1152/jn.00917.2017.

de la Malla, C., Smeets, J. B. J., & Brenner, E. (2017). Potential systematic interception errors are avoided when tracking the target with one's eyes. *Scientific Reports, 7* (10793), 1–12. https://doi.org/10.1038/s41598-017-11200-5.

Delle Monache, S., Lacquaniti, F., & Bosco, G. (2015). Eye movements and manual interception of ballistic trajectories: Effects of law of motion perturbations and occlusions. *Experimental Brain Research, 233*(2), 359–374. https://doi.org/10.1007/s00221-014-4120-9.

Delle Monache, S., Lacquaniti, F., & Bosco, G. (2019). Ocular tracking of occluded ballistic trajectories: Effects of visual context and of target law of motion. *Journal of Vision, 19*(4), 1–21. https://doi.org/10.1167/19.4.13.

Dessing, J. C., Oostwoud Wijdenes, L., Peper, C. L. E., & Beek, P. J. (2009a). Adaptations of lateral hand movements to early and late visual occlusion in catching. *Experimental Brain Research, 192*(4), 669–682. https://doi.org/10.1007/s00221-008-1588-1.

Dessing, J. C., Oostwoud Wijdenes, L., Peper, C. E., & Beek, P. J. (2009b). Visuomotor transformation for interception: Catching while fixating. *Experimental Brain Research, 196*(4), 511–527. https://doi.org/10.1007/s00221-009-1882-6.

Diaz, G., Cooper, J., Rothkopf, C., & Hayhoe, M. (2013). Saccades to future ball location reveal memory-based prediction in a virtual-reality interception task. *Journal of Vision, 13*(2013), 1–14. https://doi.org/10.1167/13.1.20.Introduction.

Dodge, R. (1903). Five types of eye movement in the horizontal meridian plane of the field of regard. *American Journal of Physiology, 8*(4), 307–329. https://doi.org/10.1152/ajplegacy.1903.8.4.307.

DuBois, D., Ameis, S. H., Lai, M., Casanova, M. F., & Desarkar, P. (2016). Interoception in autism spectrum disorder: A review. *International Journal of Developmental Neuroscience, 52*(1), 104–111. https://doi.org/10.1016/j.ijdevneu.2016.05.001.

Eggert, T., Rivas, F., & Straube, A. (2005). Predictive strategies in interception tasks: Differences between eye and hand movements. *Experimental Brain Research, 160*(4), 433–449. https://doi.org/10.1007/s00221-004-2028-5.

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

Fooken, J., & Spering, M. (2019). Decoding go/no-go decisions from eye movements. *Journal of Vision, 19*(2), 1–13. https://doi.org/10.1167/19.2.5.

Fooken, J., & Spering, M. (2020). Eye movements as a readout of sensorimotor decision processes. *Journal of Neurophysiology, 123*(4), 1439–1447. https://doi.org/10.1152/jn.00622.2019.

Fooken, J., Yeo, S.-H., Pai, D. K., & Spering, M. (2016). Eye movement accuracy determines natural interception strategies. *Journal of Vision, 16*(14), 1–15. https://doi.org/10.1167/16.14.1.

Gegenfurtner, K. R. (2016). The interaction between vision and eye movements. *Perception, 45*(12), 1333–1357. https://doi.org/10.1177/0301006616657097.

Goettker, A., Braun, D. I., Schütz, A. C., & Gegenfurtner, K. R. (2018). Execution of saccadic eye movements affects speed perception. *Proceedings of the National Academy of Sciences, 115*(9), 2240–2245. https://doi.org/10.1073/pnas.1704799115.

Goettker, A., Brenner, E., Gegenfurtner, K. R., & de la Malla, C. (2019). Corrective saccades influence velocity judgments and interception. *Scientific Reports, 9*(1), 1–12. https://doi.org/10.1038/s41598-019-41857-z, 5395.

Gray, R., & Regan, D. (1998). Accuracy of estimating time to collision using binocular and monocular information. *Vision Research, 38*(4), 499–512. https://doi.org/10.1016/S0042-6989(97)00230-7.

Hayhoe, M. M. (2017). Vision and action. *Annual Review of Vision Science, 3*(1), 389–413. https://doi.org/10.1146/annurev-vision-102016-061437.

Hayhoe, M. M., & Ballard, D. (2005). Eye movements in natural behavior. *Trends in Cognitive Sciences, 9*(4), 188–194. https://doi.org/10.1016/j.tics.2005.02.009.

Hayhoe, M. M., McKinney, T., Chajka, K., & Pelz, J. B. (2012). Predictive eye movements in natural vision. *Experimental Brain Research, 217*(1), 125–136. https://doi.org/10.1007/s00221-011-2979-2.

Higuchi, T., Nagami, T., Nakata, H., & Kanosue, K. (2018). Head-ee movement of collegiate baseball batters during fastball hitting. *PLoS ONE, 13*(7), 1–15. https://doi.org/10.1371/journal.pone.0200443. e0200443.

Horstmann, A., & Hoffmann, K.-P. (2005). Target selection in eye–hand coordination: Do we reach to where we look or do we look to where we reach? *Experimental Brain Research, 167*(2), 187–195. https://doi.org/10.1007/s00221-005-0038-6.

Ilg, U. J. (1997). Slow eye movements. *Progress in Neurobiology, 53*(3), 293–329. https://doi.org/10.1016/S0301-0082(97)00039-7.

Jacobs, R. J. (1979). Visual resolution and contour interaction in the fovea and periphery. *Vision Research, 19*(11), 1187–1195. https://doi.org/10.1016/0042-6989(79)90183-4.

Jana, S., Gopal, A., & Murthy, A. (2017). Evidence of common and separate eye and hand accumulators underlying flexible eye-hand coordination. *Journal of Neurophysiology, 117*(1), 348–364. https://doi.org/10.1152/jn.00688.2016.

Johansson, R. S., Westling, G., Bäckström, A., & Flanagan, J. R. (2001). Eye-hand coordination in object manipulation. *The Journal of Neuroscience, 21*(17), 6917–6932. https://doi.org/10.1523/JNEUROSCI.21-17-06917.2001.

Jörges, B., & López-Moliner, J. (2017). Gravity as a strong prior: Implications for perception and action. *Frontiers in Human Neuroscience, 11*, 1–16. https://doi.org/10.3389/fnhum.2017.00203.

Krauzlis, R. J., & Lisberger, S. G. (1994). A model of visually-guided smooth pursuit eye movements based on behavioral observations. *Journal of Computational Neuroscience, 1*(4), 265–283. https://doi.org/10.1007/BF00961876.

Kreyenmeier, P., Fooken, J., & Spering, M. (2017). Context effects on smooth pursuit and manual interception of a disappearing target. *Journal of Neurophysiology, 118*(1), 404–415. https://doi.org/10.1152/jn.00217.2017.

Land, M. F. (2006). Eye movements and the control of actions in everyday life. *Progress in Retinal and Eye Research, 25*(3), 296–324. https://doi.org/10.1016/j.preteyeres.2006.01.002.

Land, M. F. (2019). Eye movements in man and other animals. *Vision Research, 162*, 1–7. https://doi.org/10.1016/j.visres.2019.06.004.

Land, M. F., & Hayhoe, M. M. (2001). In what ways do eye movements contribute to everyday activities? *Vision Research, 41*(25–26), 3559–3565. https://doi.org/10.1016/S0042-6989(01)00102-X.

Land, M. F., & McLeod, P. (2000). From eye movements to actions: How batsmen hit the ball. *Nature Neuroscience, 3*(12), 1340–1345. https://doi.org/10.1038/81887.

Leclercq, G., Blohm, G., & Lefèvre, P. (2013). Accounting for direction and speed of eye motion in planning visually guided manual tracking. *Journal of Neurophysiology, 110* (8), 1945–1957. https://doi.org/10.1152/jn.00130.2013.

Li, Y., Wang, Y., & Cui, H. (2018). Eye-hand cordination during flexible manual interception of an abruptly appearing, moving target. *Journal of Neurophysiology, 119* (1), 221–234. https://doi.org/10.1152/jn.00476.2017.

Lisi, M., & Cavanagh, P. (2015). Dissociation between the perceptual and saccadic localization of moving objects. *Current Biology, 25*(19), 2535–2540. https://doi.org/10.1016/j.cub.2015.08.021.

Lisi, M., & Cavanagh, P. (2017). Different spatial representations guide eye and hand movements. *Journal of Vision, 17*(2), 1–12. https://doi.org/10.1167/17.2.12.

López-Moliner, J., Brenner, E., Louw, S., & Smeets, J. B. J. (2010). Catching a gently thrown ball. *Experimental Brain Research, 206*(4), 409–417. https://doi.org/10.1007/s00221-010-2421-1.

López-Moliner, J., & Brenner, E. (2016). Flexible timing of eye movements when catching a ball. *Journal of Vision, 16*(5), 1–11. https://doi.org/10.1167/16.5.13.

Maiello, G., Kwon, M., & Bex, P. J. (2018). Three-dimensional binocular eye–hand coordination in normal vision and with simulated visual impairment. *Experimental Brain Research, 236*(3), 691–709. https://doi.org/10.1007/s00221-017-5160-8.

Mann, D. L., Nakamoto, H., Logt, N., Sikkink, L., & Brenner, E. (2019). Predictive eye movements when hitting a bouncing ball. *Journal of Vision, 19*(14), 1–21. https://doi.org/10.1167/19.14.28.

Mann, D. L., Spratford, W., & Abernethy, B. (2013). The head tracks and gaze predicts: How the world's best batters hit a ball. *PLoS ONE, 8*(3), 1–11. https://doi.org/10.1371/journal.pone.0058289. e58289.

Mann, D. T. Y., Williams, A. M., Ward, P., & Janelle, C. M. (2007). Perceptual-cognitive expertise in sport: A meta-analysis. *Journal of Sport & Exercise Psychology, 29*(4), 457–478. https://doi.org/10.1111/j.1467-6494.2008.00505.x.

Marinescu, I. E., Lawlor, P. N., & Kording, K. P. (2018). Quasi-experimental causality in neuroscience and behavioural research. *Nature Human Behaviour, 2*(12), 891–898. https://doi.org/10.1038/s41562-018-0466-5.

Martinez-Conde, S., & Macknik, S. L. (2017). Unchanging visions: The effects and limitations of ocular stillness. *Philosophical Transactions of the Royal Society B: Biological Sciences, 372*(1718), 20160204. https://doi.org/10.1098/rstb.2016.0204.

Mrotek, L. A. (2013). Following and intercepting scribbles: Interactions between eye and hand control. *Experimental Brain Research, 227*(2), 161–174. https://doi.org/10.1007/s00221-013-3496-2.

Mrotek, L. A., & Soechting, J. F. (2007). Target interception: Hand-eye coordination and strategies. *Journal of Neuroscience, 27*(27), 7297–7309. https://doi.org/10.1523/JNEUROSCI.2046-07.2007.

Nachmani, O., Coutinho, J., Khan, A. Z., Lefèvre, P., & Blohm, G. (2020). Predicted position error triggers catch-up saccades during sustained smooth pursuit. *ENeuro, 7* (1), 1–22. https://doi.org/10.1523/ENEURO.0196-18.2019.

Neggers, S., & Bekkering, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology, 83*(2), 639–651. https://doi.org/10.1016/j.jaap.2006.03.009.

Orban de Xivry, J.-J., Bennett, S. J., Lefèvre, P., & Barnes, G. R. (2006). Evidence for synergy between saccades and smooth pursuit during transient target disappearance. *Journal of Neurophysiology, 95*(1), 418–427. https://doi.org/10.1152/jn.00596.2005.

Orban de Xivry, J.-J., & Lefèvre, P. (2007). Saccades and pursuit: Two outcomes of a single sensorimotor process. *The Journal of Physiology, 584*(1), 11–23. https://doi.org/10.1113/jphysiol.2007.139881.

Orban de Xivry, Jean-Jacques, Coppe, Sebastien, Blohm, Gunnar, & Lefèvre, Philippe (2013). Kalman Filtering Naturally Accounts for Visually Guided and Predictive Smooth Pursuit Dynamics. *Journal of Neuroscience, 33*(44), 17301–17313. https://doi.org/10.1523/JNEUROSCI.2321-13.2013.

Rashbass, C. (1961). The relationship between saccadic and smooth tracking eye movements. *The Journal of Physiology, 159*, 326–338. https://doi.org/10.1016/0196-9781(92)90172-Y.

Regan, D., & Gray, R. (2000). Visually guided collision avoidance and collision achievement. *Trends in Cognitive Sciences, 4*(3), 99–107. https://doi.org/10.1016/S1364-6613(99)01442-4.

Ripoll, H. (1989). Uncertainty and visual strategies in table tennis. *Perceptual and Motor Skills, 68*(2), 507–512. https://doi.org/10.2466/pms.1989.68.2.507.

Robinson, D. A., Gordon, J. L., & Gordon, S. E. (1986). A model of the smooth pursuit eye movement system. *Biological Cybernetics, 55*(1), 43–57. https://doi.org/10.1007/BF00363977.

Rodrigues, S. T., Vickers, J. N., & Williams, A. M. (2002). Head, eye and arm coordination in table tennis. *Journal of Sports Sciences, 20*(3), 187–200. https://doi.org/10.1080/026404102317284754.

Rolfs, M. (2009). Microsaccades: Small steps on a long way. *Vision Research, 49*(20), 2415–2441. https://doi.org/10.1016/j.visres.2009.08.010.

Saunders, J. A., & Knill, D. C. (2004). Visual feedback control of hand movements. *Journal of Neuroscience, 24*(13), 3223–3234. https://doi.org/10.1523/JNEUROSCI.4319-03.2004.

Scott, Stephen H. (2012). The computational and neural basis of voluntary motor control and planning. *Trends in Cognitive Sciences, 16*(11), 541–549. https://doi.org/10.1016/j.tics.2012.09.008.

Soechting, J. F., Engel, K. C., & Flanders, M. (2001). The Duncker illusion and eye–hand coordination. *Journal of Neurophysiology, 85*(2), 843–854. https://doi.org/10.1152/jn.2001.85.2.843.

Soechting, J. F., & Flanders, M. (2008). Extrapolation of visual motion for manual interception. *Journal of Neurophysiology, 99*(6), 2956–2967. https://doi.org/10.1152/jn.90308.2008.

Sommer, M. A., & Wurtz, R. H. (2008). Brain Circuits for the Internal Monitoring of Movements. *Annual Review of Neuroscience, 31*(1), 317–338. https://doi.org/10.1146/annurev.neuro.31.060407.125627.

Spering, M., Dias, E. C., Sanchez, J. L., Schütz, A. C., & Javitt, D. C. (2013). Efference copy failure during smooth pursuit eye movements in schizophrenia. *Journal of Neuroscience, 33*(29), 11779–11787. https://doi.org/10.1523/JNEUROSCI.0578-13.2013.

Spering, M., & Gegenfurtner, K. R. (2008). Contextual effects on motion perception and smooth pursuit eye movements. *Brain Research, 1225*, 76–85. https://doi.org/10.1016/j.brainres.2008.04.061.

Spering, M., Schütz, A. C., Braun, D. I., & Gegenfurtner, K. R. (2011). Keep your eyes on the ball: Smooth pursuit eye movements enhance prediction of visual motion. *Journal of Neurophysiology, 105*(4), 1756–1767. https://doi.org/10.1152/jn.00344.2010.

Steinbach, M. J. (1987). Proprioceptive knowledge of eye position. *Vision Research, 27*(10), 1737–1744. https://doi.org/10.1016/0042-6989(87)90103-9.

Subramanian, D., Alers, A., & Sommer, M. A. (2019). Corollary discharge for action and cognition. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging, 4*(9), 782–790. https://doi.org/10.1016/j.bpsc.2019.05.010.

Thakkar, K. N., Diwadkar, V. A., & Rolfs, M. (2017). Oculomotor prediction: A window into the psychotic mind. *Trends in Cognitive Sciences, 21*(5), 344–356. https://doi.org/10.1016/j.tics.2017.02.001.

Tse, P. U., & Hsieh, P.-J. (2006). The infinite regress illusion reveals faulty integration of local and global motion signals. *Vision Research, 46*(22), 3881–3885. https://doi.org/10.1016/j.visres.2006.06.010.

Valsecchi, M., & Gegenfurtner, K. R. (2015). Control of binocular gaze in a high-precision manual task. *Vision Research, 110*, 203–214. https://doi.org/10.1016/j.visres.2014.09.005.

van Donkelaar, P., & Lee, R. G. (1994). The role of vision and eye motion during reaching to intercept moving targets. *Human Movement Science, 13*(6), 765–783. https://doi.org/10.1016/0167-9457(94)90017-5.

Wilmut, K., Wann, J. P., & Brown, J. H. (2006). How active gaze informs the hand in sequential pointing movements. *Experimental Brain Research, 175*(4), 654–666. https://doi.org/10.1007/s00221-006-0580-x.

Yeo, S. H., Lesmana, M., Neog, D. R., & Pai, D. K. (2012). Eyecatch. *ACM Transactions on Graphics, 31*(4), 1–10. https://doi.org/10.1145/2185520.2185538.

Zago, M., McIntyre, J., Senot, P., & Lacquaniti, F. (2009). Visuo-motor coordination and internal models for object interception. *Experimental Brain Research, 192*(4), 571–604. https://doi.org/10.1007/s00221-008-1691-3.

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