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The utility of visual motion for goal-directed reaching

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Summary

Visual information is crucial for goal-directed reaching. Recently a number of studies have shown that motion in particular is an important source of information for the visuomotor system. For example, when reaching for a stationary object, nearby visual movement even when irrelevant to the object or task can influence the trajectory of the hand. Although it is clear that various kinds of visual motion can influence goal-directed reaching movements, it is less clear how or why they do so. In this chapter, we consider whether the influence of motion on reaching is unique compared to its influence on other forms of visually guided behavior. We also address how motion is coded by the visuomotor system and whether there is one motion processing system that underlies both perception and visually guided reaching. Ultimately, visual motion may operate on a number of levels, influencing goal-directed reaching through more than one mechanism, some of which may actually be beneficial for accurate behavior.

9.1 Introduction

Visual motion is constantly produced as we move our eyes and head and as objects move in the world. The visuomotor system, therefore, faces a serious challenge in that it must register target as well as background motion and then segment these different sources of motion in order to direct actions to objects. Over the last three decades, a broad and expanding literature has examined how the visuomotor system processes and uses visual motion in goal-directed behavior. Although there is still a great deal that remains unknown, a coherent picture is beginning to emerge, and the results of recent studies have overturned traditional intuitions about what sorts of visual motion information are used to guide action.

9.1.1 *Moving objects*

The use of visual motion by the visuomotor system has been studied in a number of different situations, including that from moving objects, entire scenes, or just backgrounds (Fig. 9.1). Of these, the visual motion of objects has been studied most extensively. This is not surprising, as some of the most impressive human motoric abilities involve goal-directed behaviors to moving objects on brief time scales. Sports such as baseball, cricket,

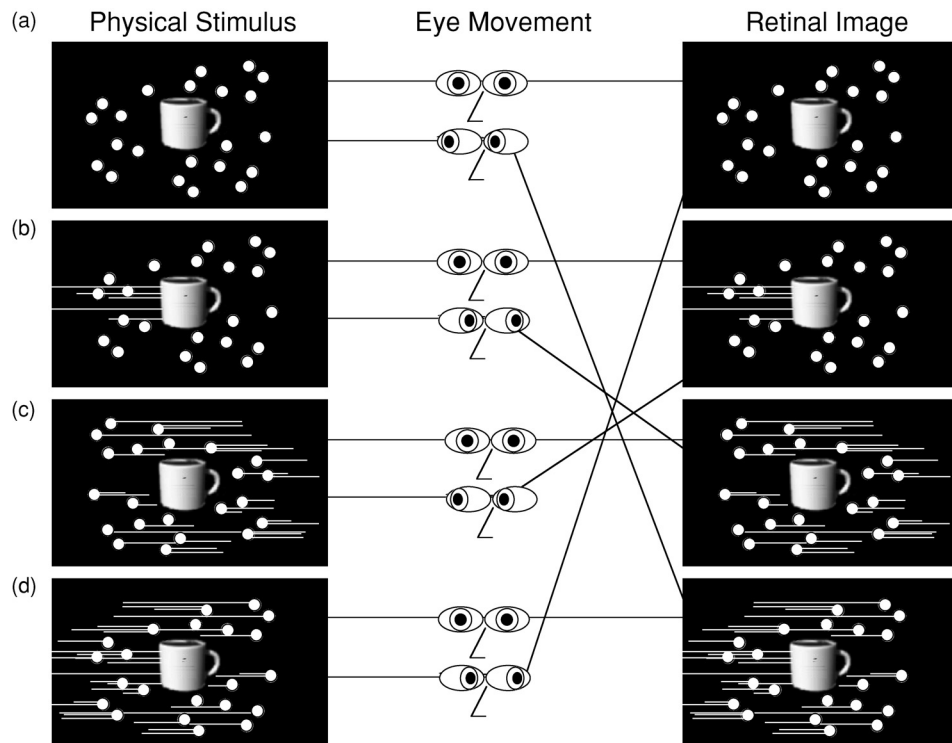


Fig. 9.1 Several types of retinal motion (right panel) produced by various combinations of physical stimuli (left panel) and eye movements (or head or body movements, middle panel). The mug represents a target object and the white dots a structured background. (A). A physically static world can create either a static retinal image or one that moves opposite the direction of an eye movement. (B). A moving object with a static background can produce the same retinal image (with no ego motion) or retinal motion of the background alone (with fixation of the target). (C). The movement of the background alone (e.g., fixating the stereo as we drive in a car) can produce background motion with a retinally static target. (D). The movement of targets with the background can produce coherent static or moving retinal images. Because different combinations of physical stimuli and eye movements can produce identical patterns of retinal motion, the visuomotor system needs to segment target motion from motion of the background.

jai-alai, and others present ample evidence that the human brain is capable of rapidly coding object position and motion (Land & McLeod 2000; Gray 2002), and that there are predictive mechanisms at work (Savelsbergh et al. 1991; Tresilian 1993; Regan 1997). The motion complex MT+ (the human homologue of monkey MT and MST) appears to play an important role in these abilities (Schenk et al. 2005).

9.1.2 Moving backgrounds

Although moving objects provide a means of testing the limits of the visuomotor system, motion of individual target objects is not the only type of motion we face. More commonly,

we face situations in which the target and background move together (Fig. 9.1D) or the target is stationary while the background moves (Fig. 9.1C). This is because the world (often including the target object) is usually stationary while we are moving. This not only causes retinal motion of the target but retinal motion of the entire scene. Similarly, even when the target object is moving in the world, we often move our eyes and head to track the object. In both instances, there is background retinal motion that the visuomotor system must explicitly distinguish from the target object (and then either ignore or use it if it is informative).

9.1.3 Benefits of visual motion: optic flow

One potentially useful type of background retinal motion information extensively studied is optic flow. As we move around the world, characteristic patterns of retinal motion are produced that may be informative about our body movements (Lee 1980; Gibson 1986). For example, moving forward through a stationary scene produces expanding optic flow. Many species of animals, including humans, use this kind of optic flow to gauge and adjust posture (Lee & Aronson 1974; Lee & Reddish 1981; van Asten et al. 1988; Previc 1992; Warren et al. 2001). It has been shown that neurons in visual area MST respond to different kinds of optic flow (e.g., expanding, contracting, shearing (Saito et al. 1986; K. Hikosaka et al. 1988; Tanaka & Saito 1989; Duffy & Wurtz 1991a, 1991b). Physiological experiments in monkeys have demonstrated that stimulation of neurons showing optical flow preferences (in MST) influences judgments of heading (Britten & van Wezel 1998). Consistent with the monkey physiology, neuroimaging studies in humans indicate that there is a homologue of the MST area that exhibits preferential activation to patterns of optic flow (Greenlee 2000; Dukelow et al. 2001; Huk et al. 2002). However, many other high-level motion areas that respond to complex visual motion, such as biological motion and inferred motion (Culham et al. 2001), do not show the selectivity for optic flow.

Optic flow is not simply a property of backgrounds or scenes, but may be used for visually guided behaviors toward or away from individual objects. One possible by-product of optic flow computations is time-to-collision (τ ; Lee & Reddish 1981). As an object looms or approaches our eyes the expanding retinal image (optic flow) may afford information about the time-to-collision. Physiological evidence in pigeons (Wang & Frost 1992) as well as behavioral evidence in humans and diving gannets suggests that the visual system may use a derivative of optic flow information to estimate time-to-collision (Savelsbergh et al. 1991; Regan 1997), although this is controversial (Tresilian 1993).

9.1.4 Visually guided reaching with background motion

The evidence that visual motion is used to guide behavior so far comes from studies of posture and timing (e.g., tau). Recently, however, it has been found that background retinal motion can influence the direction of reaching movements as well. For example, when subjects reach a stationary target, a moving background can cause shifts in the trajectory

of the reaching movement and endpoint consistent with the direction of the background motion (Mohrmann-Lendla & Fleischer 1991; Brenner & Smeets 1997; Yamagishi et al. 2001; Whitney et al. 2003; Saijo et al. 2005).

The effect of background motion on reaching is distinct from the effect of optic flow on posture. Most forms of optic flow (especially expanding and contracting flow fields) are perfectly predictive of head movement and largely predictive of whole-body movements. It is therefore intuitive that this sort of visual information could be used to control posture, locomotion, or body position. On the other hand, the influence of background motion on reaching is counterintuitive because it is neither predictive of hand position or motion, nor is it predictive of the relationship between the hand and the target. Several authors have proposed explanations for the influence of background motion on reaching, but the issue remains controversial. In this chapter we review the evidence for the influence of visual motion on reaching, consider alternative underlying mechanisms, and discuss whether the effects are a beneficial adaptation.

9.2 Object motion and the double-step paradigm

When reaching to a moving object, the visuomotor system could predict future hand position relative to the current hand position by using a forward model (Desmurget & Grafton 2000). This could allow for rapid corrections in response to either target or effector (hand or mouse) displacements and may help reduce the error introduced by sensory and motor delays. An important question over the last decade has been to evaluate what sorts of visual information are used for online control of reaching.

Many studies investigating goal-directed reaching to moving targets demonstrate that the visuomotor system monitors target motion (or perhaps relative position or motion between the hand and moving object) and uses this information to guide the hand. Comparable results have been obtained whether the target physically jumps (Goodale et al. 1986; Pelisson et al. 1986; van Sonderen et al. 1988; van Sonderen et al. 1989; Paulignan et al. 1991b; Prablanc & Martin 1992; Day & Lyon 2000; Brenner & Smeets 2003) or moves continuously (Brenner et al. 1998; Schenk et al. 2004). Subjects are able to make rapid corrections to ongoing behavior.

One of the strongest examples of the speed with which the visuomotor system can respond to changing visual information is the perturbation or double-step paradigm (Bridgeman et al. 1979). In this technique, a target is presented to which subjects reach. During the reach, the target can be displaced in position. The reaction of the hand to the displaced target occurs within 100–150 ms (Goodale et al. 1986; Pelisson et al. 1986; van Sonderen et al. 1988; van Sonderen et al. 1989; Castiello et al. 1991; Paulignan et al. 1991b; Prablanc & Martin 1992; Brenner & Smeets 1997). Even if the displaced target is presented during a saccade, preventing awareness of its displacement, subjects can still make fast and accurate corrections (Bridgeman et al. 1979; Goodale et al. 1986; Pelisson et al. 1986). Although very different measurements of the visuomotor reaction to perturbed targets have been used (including derivatives of hand position, such as velocity and acceleration), the results have been uniformly similar. The brevity of the reaction time – the visual feedback

delay – shows that visual information is important in the online control of action even late into the movement (Desmurget & Grafton 2000).

The double-step paradigm has provided a rich source of information about how the visuomotor system programs and executes action. For example, it has shown that the fast visual feedback necessary for motor control is not dependent upon awareness of the target's displacement or motion (Goodale et al. 1986; Pelisson et al. 1986). This points to a direct route independent of conscious vision and provides support for, at least, the moderate form (Jacob & Jeannerod 2003) of the dual visual systems hypothesis (Trevarthen 1968; Schneider 1969; Ingle 1973; Goodale & Milner 1992). Double-step studies have also demonstrated that reaching movements can be guided and modified online, whether or not subjects fixate on a static point (Goodale et al. 1986; Pelisson et al. 1986; van Sonderen et al. 1988; van Sonderen et al. 1989; Castiello et al. 1991; Paulignan et al. 1991b; Prablanc & Martin 1992; Brenner & Smeets 1997; Diedrichsen et al. 2004). This is important for evaluating the hypothesis that the hand is guided or anchored by the direction of gaze (Paillard 1982; Binsted et al. 2001; Neggers & Bekkering 2001). Although it is generally true that we reach where we are looking (Ballard et al. 1992; Pelz et al. 2001; Soechting et al. 2001), this is not exclusively the case, and bimanual tasks (particularly bimanual double-step tasks) provide adequate evidence for not needing to fixate the endpoint goal of the hand (Diedrichsen et al. 2004). The double-step paradigm has provided even stronger evidence that corrections to fast-reaching movements can occur on an extremely brief time scale, even without changes in eye position and based only on peripheral retinal information (Paillard 1996). Therefore, although eye position certainly contributes to visuomotor control, and foveal location or gaze direction may be an important source of information with which to guide the hand, it is only one of many sources of information that contribute to visually guided behavior.

What remains unclear from the double-step studies is whether the target position or motion (or both) are used for online guidance of the hand. One might ask whether a distinction should even be drawn between the motion and position of an object, because these properties are necessarily *physically* interdependent. The visual system, however, need not code object motion and position as a single dimension. Along with spatiotemporal sensitive mechanisms that simultaneously code the position and motion of an object (Burr et al. 1986; Geisler 1999; Burr & Ross 2002; Nishida 2004), several visual illusions suggest that the visual system may also have independent mechanisms for coding object motion and position (Whitney 2002). Therefore, it becomes meaningful to ask whether rapid corrections to visually guided reaching are driven by object motion, shifts in the coded locations of targets due to the motion, or a combination of these. Unfortunately, to date this question has not been fully addressed (see Section 5).

9.3 Background scene motion

The above experiments have been extended by showing that both reaching and pointing movements tend to deviate in the direction of background retinal motion (Mohrmann-Lendla & Fleischer 1991; Brenner & Smeets 1997; Proteau & Masson 1997; Yamagishi

et al. 2001; Whitney et al. 2003; Saijo et al. 2005), not just target motion (Smeets & Brenner 1995a). There are several surprising characteristics of this effect. First, even in the presence of a stationary target, background retinal motion influences the reach (Brenner & Smeets 1997; Whitney et al. 2003; Saijo et al. 2005). Second, retinal motion can be separated by many degrees from the target and still be influential (Whitney et al. 2003; Saijo et al. 2005). Third, reaction time to background retinal motion is around 120–150 ms (Brenner & Smeets 1997; Whitney et al. 2003; Saijo et al. 2005), which is just as fast as reactions to changes in target location or motion of the target itself in double-step studies (Prablanc & Martin 1992). Visual motion during either the programming (prior to the reaction) or execution influences the trajectory of the reach (Whitney et al. 2003). Finally, the percept of the target (its motion or position) can be dissociated from the hand's trajectory, demonstrating that the hand does not simply follow perceived target position or motion (Yamagishi et al. 2001; Whitney et al. 2003). Rather, the visuomotor system uses visual motion to directly control the hand.

9.3.1 Underlying cause of background motion's influence on reaching

There is not consensus about the underlying cause of the influence of visual motion of the background on the trajectory and endpoint of goal-directed reaching movements. It has been argued that background visual motion shifts the coded locations of objects (Whitney et al. 2003). This is an “indirect” mechanism, because the visuomotor response is modulated by the target position (or shifted position). Alternatively, it has been suggested that background motion triggers a passive manual following response (Saijo et al. 2005) akin to the ocular following response (Kawano & Miles 1986; Miles et al. 1986; Kawano et al. 1994; Masson et al. 2001). This is a “direct” effect of motion on reaching, as the representation of the target position is not shifted.

To distinguish between direct and indirect influences of visual motion on visuomotor control, it is helpful to consider a distinction made in the visual motion perception literature between velocity- and position-based motion computations. Visual motion could be an inference based on perceiving the position of an object at two time points (Ullman 1979; Nakayama & Tyler 1981; Cavanagh 1992; Del Viva & Morrone 1998; Seiffert & Cavanagh 1998; Derrington et al. 2004). There is evidence for this sort of motion detector (Cavanagh 1992; Lu & Sperling 1995), which may involve attention and could be helpful in tracking camouflaged or second-order (feature or contrast-defined) motion. This mechanism indirectly measures motion and cannot recover it without a means of coding object position. The more familiar, dominant, and common sort of motion detector is sensitive to velocity and is considered a “direct” measure of motion because it does not require multiple samples over space or time (Adelson & Bergen 1985; van Santen & Sperling 1985; Watson & Ahumada 1985). Even when an object position has not been identified or tracked, a velocity detector can still register motion.

The distinction between directly and indirectly sensed visual motion carries over to visuomotor control. When programming and executing reaching movements, the

visuomotor system could, independent of any target representation, monitor visual motion information and use this to guide the hand (Saijo et al. 2005; Gomi et al. 2006). Alternatively, visual motion could influence the coded locations of targets, and it is these target positions that are monitored throughout the execution of the reach (Whitney et al. 2003). Cases of akinetopsia (Zihl et al. 1983) show that patients can perceive object position but not object motion, whereas cases of blindsight (Cowey & Stoerig 1991) reveal an unawareness of object position coupled with intact perception of nonlocalized motion. Although blindsight and akinetopsia are somewhat controversial, the possibility that motion directly and/or indirectly contributes visuomotor control is plausible. Evidence for each possibility is reviewed in the following.

9.3.2 *Shifted target positions*

One explanation for the deviations in the trajectory and endpoints of the reach is that the target position that serves to guide the hand is shifted by background motion (Brenner & Smeets 1997; Whitney et al. 2003). It is well known that visual motion can influence the perceived locations of both static and moving objects (Ramachandran & Anstis 1990; De Valois & De Valois 1991; Nishida & Johnston 1999; Whitaker et al. 1999; Hayes 2000; Whitney & Cavanagh 2000; McGraw et al. 2002) (see Fig. 9.2 and Whitney 2002, for a review). For example, the briefly flashed objects in Figure 9.2C appear shifted in the direction of the nearest visual motion. Is it possible that visual motion shifts either the perceived location or the represented location of targets, thus indirectly causing a deviation in the hand's trajectory? There are three possibilities: The reach may simply follow the perceived shift in target location; the reach may follow a shift in the coded location of the target independent of what is perceived; or the reach may not depend on shifts in the perceived or coded target location.

9.3.2A *Dissociating perception and action*

Is the influence of visual motion on reaching due to a visual illusion, or does the visuomotor system rely on visual motion information that bypasses conscious vision? Yamagishi et al. (2001) found that pointing movements to a drifting Gabor pattern were differentially shifted relative to the perceived location of the Gabor (also see Ashida 2004). Although the directionality of the illusion was comparable for perception and action, the magnitudes differed (but c.f., Kerzel & Gegenfurtner 2003, 2005) for counterevidence). Morhmann-Lendla & Fleischer (1991) and Brenner & Smeets (1997) obtained similar results in that the trajectories of reaching movements directed to physically static objects deviated slightly *in* the direction of superimposed moving backgrounds. The perceived position of continuously visible static targets in this situation, however, is generally veridical, while displaying, if anything, induced motion or motion contrast (Brenner & Smeets 1994; Smeets & Brenner 1995b). Similar dissociations between perception and action have been reported in studies of frame of reference, induced motion, and induced Roelofs effects, although their relation to the influence of background motion on reaching is unclear (Bridgeman et al. 1979;

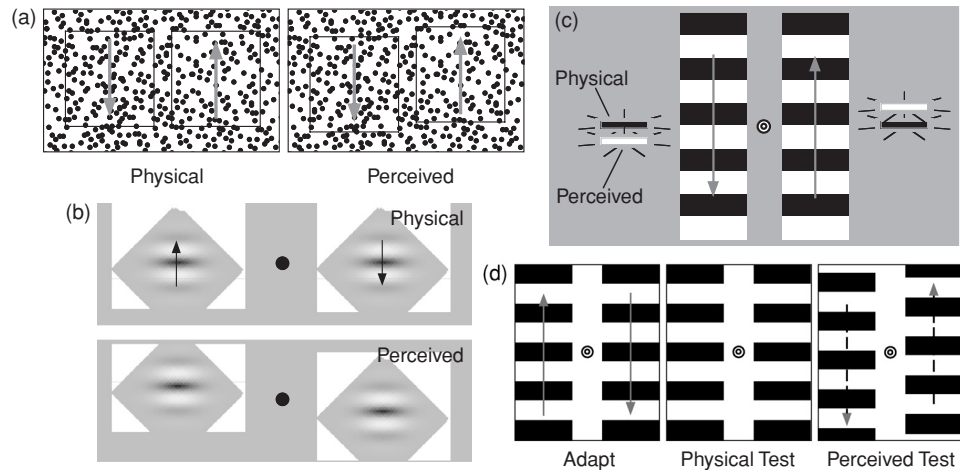


Fig. 9.2 The influence of visual motion on perceived position. (A). Two kinetically defined squares contain dots drifting in opposite directions. The black lines were not visible; the squares were defined only by the relative motion of the drifting dots. The right panel shows the perceived positions of the motion-defined squares, which are displaced in the direction of the motion. (B). Drifting a luminance-modulated carrier (sine wave) inside a static Gaussian contrast envelope causes the static envelope to appear shifted in position, in the direction of the visual motion. The magnitude of the effects in (A) and (B) peak when the luminance of the drifting regions is equated to that of their surroundings. (C). Motion in one region influences the perceived positions of briefly flashed static objects separated from the motion. (D). The motion aftereffect, following motion adaptation, can be accompanied by a concurrent shift in the perceived position of the test pattern. Figure adapted from Whitney (2002) with permission.

Bridgeman et al. 1981; Bridgeman et al. 1997; Sheth & Shimojo 2000; Dassonville et al. 2004; Post & Welch 2004). Nonetheless, a variety of paradigms suggest that the influence of visual motion on reaching is not simply based on misperceiving the target motion or position.

9.3.2B Relative speed of perception and action

In order to gauge the relative time course of motion's influence on visuomotor behavior and perception, Whitney et al. (2003) employed a motion-reversal paradigm that involved presenting a moving pattern for an unpredictable period of time followed by a reversal in its motion. A brief static target was flashed several degrees away from the visual motion at an unpredictable moment – either before, simultaneous with, or after the motion reversal (Fig. 9.3). When the target was presented during continuous motion (well before the reversal), the hand deviated in the direction of the background motion (similar to Mohrmann-Lendla & Fleischer 1991; Brenner & Smeets 1997; Yamagishi et al. 2001). However, when the target was presented just before the motion reversal (circled points in Fig. 9.3B), the hand initially deviated in the direction of the initial visual motion and then abruptly reversed the direction of its deviation (Fig. 9.3C). In other words, the trajectory of the hand closely

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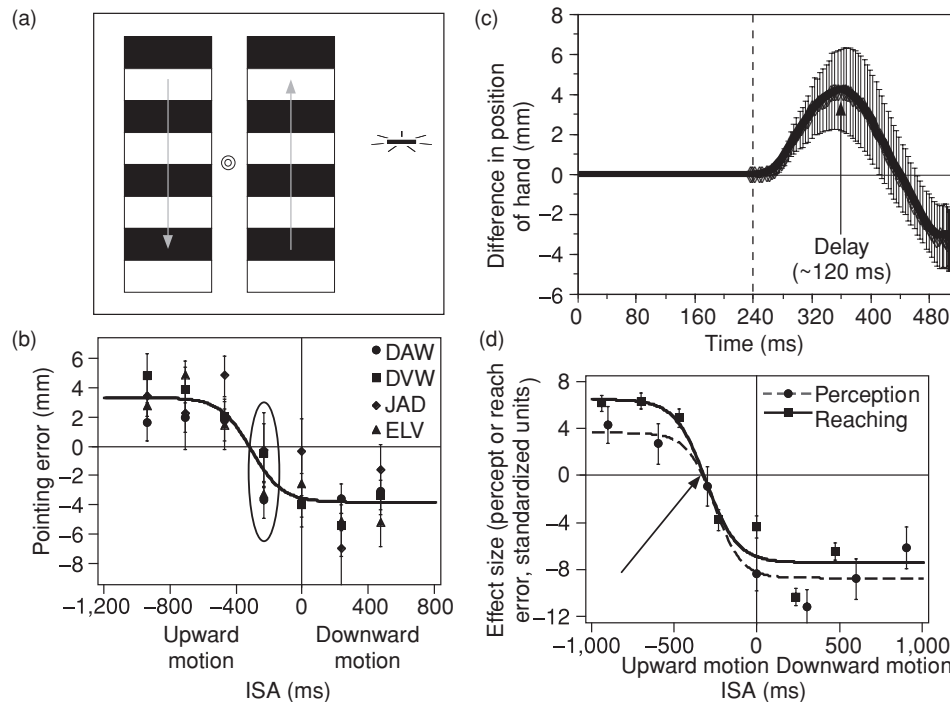


Fig. 9.3 Stimulus and results of an experiment demonstrating the influence of visual motion on fast visually guided reaching. (A) A static target was briefly flashed (rectangle) near a drifting grating. The nearby grating initially moved in one direction and then abruptly reversed direction. Subjects reached and hit the target with their index finger. (B) Endpoints of reaching movements. The abscissa shows the interstimulus asynchrony (ISA) between the target presentation and the motion reversal. Data are presented in a manner such that initially the grating drifted upward and then reversed direction and drifted downward. Targets presented well before (after) the motion reversal produced systematic upward (downward) errors in the endpoint of the reach, always in a direction consistent with that of the nearest visual motion. (C) For each given ISA (from B), the difference in the trajectory of the hand (vertical position over time) was calculated as a function of the direction of visual motion. The resulting difference is the modulation in the hand's position as a function of motion direction. At an ISA of ~ -240 ms (C), the net effect of visual motion shows that the hand initially deviates upward, reaches a maximum deviation, and then deviates back downward, mimicking the motion reversal. The difference between the physical motion reversal and the moment of the hand's trajectory – the visuomotor delay – was about 120 ms (arrow). (D) The temporal tuning of visual motion's influence on perceived position (dashed line, circles) and its influence on reaching (solid line, squares). The perceived position of the flashed target (measured using Fig. 9.2D) depends on when it is presented relative to the grating's motion reversal (dashed line). Both the perceived position of the target and the endpoint position of the hand follow a similar time course. Figure adapted from Whitney et al. (2003), with permission.

mimicked the motion reversal – albeit delayed in time. Visual motion therefore influences the trajectory of the hand during both the programming and execution (online) phases of the reach. Consistent with the double-step studies described earlier, the visuomotor delay (the reaction time to a change in visual motion direction) was about 120–150 ms (arrow in Fig. 9.3C). This delay is quite brief, even though the target and influencing motion was separated by many degrees.

To test whether the deviation in the trajectory of the reaching movement depends on perceptual awareness of target position, Whitney et al. (2003) measured the perceived shift in the position of the target (as in Fig. 9.2C) using the same stimulus as above (Fig. 9.3D). When the time courses of the perceptual and motor effects are directly compared (Fig. 9.3D), it is clear that the deviation in the hand occurs as early as the deviation in the perceived position of the target. More importantly, the moment at which a perceptual decision is reached lags behind visual motion's influence on the reach. Figure 9.3D shows that the perceived position of the target depends on visual motion presented at least 300 ms after the target (targets presented at –300 ms ISA do not appear shifted upward despite the fact that they are presented during upward motion. The reason is because their perceived position depends partially on downward visual motion presented more than 300 ms later). Reaching, however, has a delay of about 120 ms (Fig. 9.3C). Therefore, the visuomotor system does not depend upon a later perceptual decision but modifies the hand's trajectory online, whereas the perceived position of the target is still indeterminate. These results demonstrate that hand position cannot be based on the percept (because the direction of the hand's response precedes and is even opposite to the perceived position of the target). Of course, it is entirely possible that the same information is used by visuomotor and perceptual systems; however, it unfolds on different time scales. Regardless, *perceived* target position does not govern the direction or endpoint position of the hand. Other, nonperceptual representations of target position might be responsible for fast, online control of reaching.

9.3.2C Similarities between manual responses to object and background motion

The double-step studies described in Section 9.2 share many common traits with the influence of visual motion on reaching. First, both of the effects involve visual feedback used for online control, occur at very high speeds, and have comparable reaction times of around 100–150 ms (Brenner & Smeets 1997; Whitney et al. 2003; Saijo et al. 2005). In comparison, grip aperture reactions to changes in the visual shape or structure of objects are slower, as are other reactions to higher-level visual features (Paulignan et al. 1991a; Paulignan et al. 1991b; Bock & Jungling 1999; Day & Lyon, 2000; Pisella et al. 2000).

As mentioned before, however, it is debated whether the visuomotor correction in the double-step paradigm is due to changes in target position per se or just the visual motion (or percept of motion) induced by the jumping target. One piece of evidence supporting the former (position matters, not just motion) comes from double-step studies in which the target was defined solely by chromatic differences (Pisella et al. 2000; Brenner & Smeets 2004). Color provides relatively weak input to the magnocellular stream (Livingstone & Hubel 1988; Derrington 2000), and color-defined motion is perceived more slowly

(Cropper & Derrington 1994, 1996), less accurately (e.g., motion standstill; Cavanagh et al. 1984; Cavanagh 1992; Lu & Sperling 1995; Lu et al. 1999), and, at least at low contrasts, with a position-based mechanism (Cropper & Derrington 1994; Seiffert & Cavanagh 1998). Therefore, if reactions to color changes are fast, this would be strong evidence that nonmoving features of objects (i.e., their positions alone) are sufficient to drive fast motor corrections. In one study, using color-defined targets Pisella et al. (2000) found that subjects were slow at overriding (halting) a reaching movement based on changes in the color of the target. This could indicate that visual motion matters for fast manual corrections. However, Brenner and Smeets (2004), measuring correcting responses rather than overriding responses, found that subjects were quite fast at correcting the direction of their pointing movement in response to changes in the color of a target. Therefore, visual motion may not be the only attribute of scenes and objects that can give rise to fast corrections; it may be that target position matters in both the double-step and background motion studies. Unfortunately, the issue is still unresolved because no study has successfully controlled for the luminance of the targets. The stimulus used by Brenner & Smeets (2004) was physically isoluminant, but was not equated psychophysically, so nonlinearities (Anstis & Cavanagh 1983; Lu & Sperling 2001b) could result in apparent brightness differences that could give rise to strong motion signals. Therefore, the double-step experiments need to be repeated with psychophysically equiluminant or second-order contrast-defined stimuli that are detected by a position-based mechanism (Seiffert & Cavanagh 1998). These stimuli would provide definitive data on whether it is the position and/or velocity of targets in the double-step paradigm that drives the hand.

Another similarity between the influence of visual motion on reaching and the double-step paradigm is that both have revealed an important contribution of visual information during the programming as well as the execution (online) phases of the movement. A static target displaced prior to or during a reach influences the direction of the hand's trajectory (Section 9.2). Likewise, visual motion presented before or after a reaching movement is executed (during the programming or the execution phases) influences the direction of the hand (Whitney et al. 2003; Saijo et al. 2005; Gomi et al. 2006). The fact that visual motion during the programming phase of the movement influences a reach suggests that either the predicted reach position or the representation of the target may be shifted by visual motion just as it is when the target position is displaced in double-step experiments.

Although incomplete and necessitating further studies (see Section 9.5), the results reviewed here suggest a possible link between visual motion and double step-induced modifications to the trajectory of the hand. If the link holds, this would suggest that the visuomotor system monitors target positions continuously (or at least frequently) and that visual motion causes updating of target positions similar to actual changes in their locations.

9.3.3 Following responses

Although it is suggested that the visual motion and double-step results are due to the manner in which the visuomotor system represents and updates target positions, there is

another possibility. Visual motion (of the background or the target itself) could influence the hand directly. The “indirect” model assumes that a deviation in the trajectory of reaching movements in the presence of background motion occurs because the visuomotor system has an explicit representation of target position and updates, modifies, or shifts this position representation in the presence of background (or target) motion. Visual motion is important in this account, but only indirectly via an influence on the target positions tracked by the visuomotor system. An alternative is that the visuomotor system has direct access to visual motion, which influences a reach independent of the target representation. The most likely form of this alternative account is a manual following response (Saijo et al. 2005). The following discussion will draw a distinction between the direct (following response) and indirect (shifted target representation) hypotheses.

9.3.3A Background motion modulates smooth pursuit

Before examining the manual following response, it is worth considering the similar but distinct effects of background motion on the eye. It has long been known that the gain of pursuit eye movements (ratio of eye velocity to target velocity) is modulated by the presence and direction of background motion (Yee et al. 1983; Collewyn & Tamminga 1984; Keller & Khan 1986; Howard & Marton 1992; Masson et al. 1995; Mohrmann & Thier 1995; Zivotofsky et al. 1995; Niemann & Hoffmann 1997; Schwarz & Ilg 1999; Lindner et al. 2001, but c.f. Kowler et al. 1984). For example, pursuit gain can be reduced by upward of 10% when there is retinal motion opposite the direction of ocular pursuit (Masson et al. 1995), and this effect is specific to the energy or first-order motion in the display (Masson et al. 2002). Interestingly, however, gain modulation is a function of the distance between retinal motion and the pursuit target (Howard & Marton 1992; Masson et al. 2001; Goltz & Whitney 2004; Whitney & Goodale 2005); increasing the separation between the target and the motion by approximately two degrees is sufficient to abolish the pursuit modulation (Goltz & Whitney 2004; Whitney & Goodale 2005). The influence of visual motion on reaching, however, operates over much larger distances, indicating differential spatial integration (or different gain or weighting functions for eye and reaching movements (Whitney et al. 2003; Saijo et al. 2005).

9.3.3B Ocular following response

In addition to eye movement speed (i.e., pursuit gain), it has also been shown that eye *position* is influenced by background retinal motion (Kawano & Miles 1986; Miles et al. 1986; Kawano et al. 1994; Masson et al. 2001), even in the absence of pursuit eye movements. This has been termed the ocular following response. The latency of this response is much shorter than smooth pursuit eye movements because of a direct neural pathway between cortical regions of visual motion processing and subcortical areas responsible for the generation of eye movement commands (Shidara & Kawano 1993; Kawano et al. 1994).

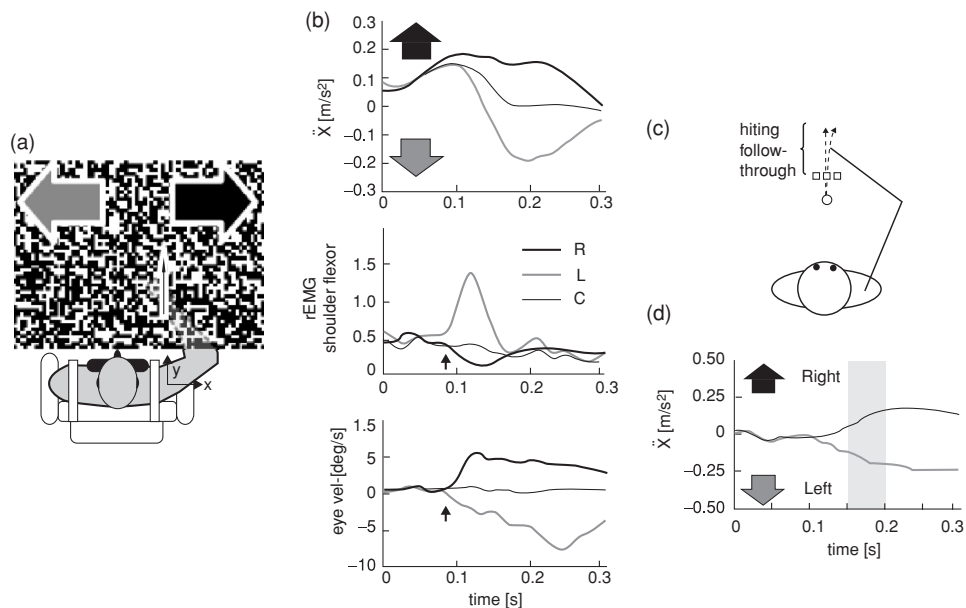


Fig. 9.4 Experimental setup to measure and quantify the manual following response, as well as arm kinetics, muscle, and ocular responses induced by visual motion. (A). Large field visual motion (right or left indicated by large arrows) was presented after the hand traveled 5 cm from its initial position. (B). Top panel: The hand's acceleration in the x-direction (orthogonal direction to the hand path) shows a deviation in the acceleration in the direction of the background motion within about 100 ms (the thick black, thick gray, and thin curves represent the rightward, leftward, and no visual motion conditions, respectively). Middle panel: The normalized and rectified electromyogram (EMG) of the shoulder flexor muscle. Bottom panel: Right eye velocity. The small vertical arrows in the middle and bottom panels show that the shoulder muscle response to visual motion is as fast as the ocular response. (C). Manual following response induced by a large-field visual motion during a follow-through movement, after hitting a target. The stop position of the reaching movement was not specified; subjects were instructed to follow through their reach in the most natural direction. (D). The averaged hand acceleration in the x-direction (the direction of the background visual motion) for those trials in which the background moved rightward or leftward during the follow-through phase of the reach. Figure adapted from Saijo et al. (2005), with permission.

9.3.3C Manual following response

The influence of visual motion on reaching movements (Brenner & Smeets 1997; Whitney et al. 2003; Saijo et al. 2005) is similar, in many respects, to the ocular following response (Gomi et al. 2005, 2006) and may therefore be characterized as a manual following response (Fig. 9.4). Akin to the ocular following response, the manual following response is a short-latency passive deviation in the trajectory of the hand in the direction of large-field visual motion (Brenner et al. 1997; Whitney et al. 2003; Saijo et al. 2005). This response can be elicited without a visible target, suggesting that positional information about the target itself may not be essential to response generation (Saijo et al. 2005).

The manual following response is distinct from several other reported effects. When tracking a moving target with the hand (manual pursuit), background texture (moving or stationary) influences the gain of the manual pursuit – but in a direction opposite that of the manual following response (Masson et al. 1995; Soechting et al. 2001). The manual following response is also not due to the location or movement of the eye (Sections 9.3.3A and 9.3.3B). Although there are coordinated mechanisms serving both ocular and manual responses (Prablanc et al. 1979; Herman & Maulucci 1981; Biguer et al. 1982; Fischer & Rogal 1986; Turrell et al. 1998; Henriques et al. 1998b; Engel et al. 2000; Soechting et al. 2001; Ariff et al. 2002; Henriques et al. 2003), the manual following response induced by visual motion is opposite the pointing error caused by gaze shifts (Henriques et al. 1998b; Henriques et al. 2003). More importantly, the latency of the arm muscle activity is comparable to that of the ocular following response (Saijo et al. 2005) as shown in Fig. 9.4B. If the hand simply followed the eye, one would expect a more substantial delay. Finally, the ocular following response is eliminated when subjects fixate or when visual motion is presented in just one visual field; however, the manual following response remains strong in both of these cases (Whitney et al. 2003; Saijo et al. 2005). These observations diminish the possibility that eye–hand coordination produces the manual following response (see also Section 9.2).

Another possible explanation for motion’s influence on reaching, as discussed above, is that visual motion affects the representation of the target’s position, which could lead to an online correction of the manual movement. Interestingly, however, the quick manual response can be induced without simultaneous presentation of the target and background visual motion (Saijo et al. 2005). More strikingly, the manual following response is still present during “follow-through” movements – even after the target is hit, the arm continues to deviate in the direction of background visual motion (Fig. 9.4C). Because the variation in the trajectory of follow-through movements after contact with the target is different from target-directed reaching, it has been suggested that the trajectory of the follow-through movement is distinct from the target-directed reaching phase (Saijo et al. 2005). From these observations, it appears that at least part of the quick manual response induced by a large-field visual motion is due to the direct influence of visual motion on the arm motor system rather than an indirect effect of visual motion on target representations.

The rapid manual following response occurs for visual motion not only in the fronto-vertical plane (Brenner & Smeets 1997; Whitney et al. 2003) but also in any direction along the horizontal plane (Saijo et al. 2004). This suggests that the manual following response is coded in 3D space rather than retinal 2D coordinates. Moreover, varying motion coherence (Newsome & Pare 1988) causes comparable changes in the following response (Saijo et al. 2005), implicating motion energy computations via motion processing units at a relatively late stage in the visual system – at least beyond the level of primary visual cortex, and most likely in visual area MT+. Using TMS, a recent study directly tested this hypothesis and found that stimulation of MT+ significantly reduced the manual following response (Whitney et al. 2007).

The observations reviewed here suggest that visual motion not only affects the representation of target position but also directly influences manual control. For the sake of efficiency, the visuomotor system analyzes information about the target and background in parallel. Simply disregarding background information would be difficult if not impossible, and for this reason it is necessary to consider how the visual system codes and uses background motion information. To elucidate the potentially diverse functional mechanisms that allow for skilled motor performance, it is important to compare and combine observations from both behavioral and physiological techniques. Together with the results above, a coherent story is beginning to emerge that visual motion information – even that of the background – is tightly linked to motor processing. This linkage operates through a direct influence of motion on reaching (manual following response) and may also involve a secondary indirect influence of visual motion on the represented positions of targets.

9.4 Beneficial uses of visual motion for reaching

Whether or not a distinction is drawn between (direct) motion-induced and (indirect) position-induced visuomotor responses, it is possible that both models operate under normal conditions and make comparable predictions in most circumstances. In fact, the influence of background motion on reaching could be an adaptive and beneficial response that the visuomotor system employs to guide reaching movements. Based on the statistical regularity of motion – the fact that background retinal motion is generally produced by self-movement (especially eye movements), the visuomotor system could access retinal motion as a means of gauging how the eye or body has moved relative to target objects (Whitney et al. 2003).

Although potentially adaptive, this explanation for the findings shown previously is counterintuitive. To reach to a target, the hand and the target must be coded in a common coordinate frame. If reach plans were coded in head, body, or hand-centered coordinates, then retinal motion's influence on reaching would be detrimental because the relative position of the hand and target do not change when the eyes move. A deviation in the hand's trajectory would therefore cause inaccuracy. However, there is evidence suggesting that targets are actually coded in eye-centered coordinates (Henriques et al. 1998a; Buneo et al. 2002; Crawford et al. 2004) and that coordinate transformations only happen on demand (Henriques et al. 1998a). If the common coordinate frame in which reach plans are coded is eye-centered, then every time we reach for an object, the visuomotor system must take into account eye position. Retinal motion in this scenario would be informative about changes in eye position and could be used to help update target (or eye) position for reaching.

9.4.1 Errors in reaching

If visual motion's influence on reaching is beneficial, then what is the error being corrected or compensated? One possibility is an error in extraretinal signals such as an efference copy. If an efference copy were perfect, the visuomotor system could update target positions continuously relative to gaze direction. Thus, the visuomotor system would have perfect

information about relative eye-target positions and would accurately reach to objects. Unfortunately, efference copy signals are not always available, and even when they are available, they are routinely underestimated (i.e., the gain of the mechanism is less than one [Bridgeman 1995]). This is supported by demonstrations such as the Filehne and Aubert-Fleischl illusions (Wertheim 1981; Mack & Herman 1973; Freeman 2001). Underestimating eye movement amplitude (distance traveled) or velocity could cause reaching movements to systematically miss targets. This is especially true when targets are no longer visible after reach initiation. Visual motion could cause a bias in the trajectory of the reach opposite the direction of the eye movement, thereby reducing the systematic underestimation of efference copy. In fact, retinal motion opposite the direction of a pursuit eye movement improves reaching to the remembered position of a static target (Whitney & Goodale 2005).

Another possibility is that there are delays in coordinate transformations that necessitate a compensation mechanism. The target and hand must be coded in a common coordinate frame. Regardless of which frame this is, several transformations are required. Either the target is sequentially transformed from retinal to eye, head, body, and hand-centered coordinates, or the hand is transformed in the reverse order. In both cases, unless transformations are instantaneous (a physical impossibility), there will be a mismatch between the target's physical location and the representation of the hand and target in a common coordinate frame. When reaching to a physically static object during a pursuit eye movement, the delays transforming the representations of the hand and target mean that by the time the reach is executed the eye will have continued along its trajectory, leaving a gap between the actual target location and the reach goal (i.e., an error in programming). Similar to the underestimation of an efference copy, this error would be reduced by retinal motion in a direction opposite that of the eye movement. When retinal motion is not available, on the other hand, this error does manifest itself (Whitney & Goodale 2005).

If the reach errors above are compensated by visual motion, then akinetopsic (motion blind; Zihl et al. 1983) patients might lack this compensation. In fact, these individuals are impaired when reaching to moving targets under free viewing conditions in which they move their eyes (Schenk et al. 2000), indicating that visual motion, and motion area MT+ in particular, is important for visually guided behavior (Schenk et al. 2005). Further studies of motion-blind patients, in which background and target motions are independently manipulated, would help establish the relevance of the background motion, per se. Given the speed with which visual motion is processed (Schmolesky et al. 1998) and that retinal motion correlates perfectly with eye movements, it would be enormously advantageous for the visuomotor system to use background visual motion as a source of feedback information for the control of visually guided reaching.

9.5 Future directions

A great deal of evidence suggests that low-level retinal motion (i.e., first-order luminance-defined motion) influences visually guided reaching. However, do other types of visual motion also exert an influence on reaching? For example, second-order motion (Cavanagh

& Mather 1989; Derrington et al. 2004) or other high-level motion such as transformational apparent motion, inferred motion, attentive tracking, or third-order motion (Cavanagh 1992; Hikosaka et al. 1993; Assad & Maunsell 1995; Watamaniuk & McKee 1995; Lu & Sperling 2001a; Tse & Logothetis 2002; Watamaniuk 2005) may or may not be used by the visuomotor system. Because these types of motion are thought to be processed in dorsal visual motion areas (Culham et al. 2001), if the visuomotor system receives direct and necessary input from these motion areas, we might expect reaching to depend on the percept of motion and not simply on the physical presence of retinal motion.

Further research is needed to determine whether the manual corrections in double-step studies are due, at least in part, to the visual motion produced by the jumping target. Although studies have begun to address this (Pisella et al. 2000; Brenner & Smeets 2004), the question remains. One way forward is to present a target object that moves in one direction while physically shifting in the opposite direction, pitting physical movement (motion energy) against position displacement, similar to what has been done in studies of pursuit (Masson et al. 2002). Ideally, however, the conflicting motion and position information would be specific to the target and not the background. Likewise, the conflicting information should be real – not illusory – as has been used in the past (Brenner & Smeets 1997). Although difficult to imagine, this is precisely what reverse-phi (Anstis 1970; Shioiri & Cavanagh 1990), four-stroke apparent motion (Anstis 1980) and the related missing fundamental illusion (Adelson & Bergen 1985) demonstrate.

9.6 Conclusions

Over the last several decades, the role of visual motion in visually guided action and motor control has been a topic of interest. Numerous studies have examined how eye movements and reaching are guided to moving objects; another group of independent but related studies has examined how posture and locomotion are guided by optic flow. More recently, a third group of studies has investigated the influence of background retinal motion on goal-directed reaching, manual tracking, and eye movements. Although distinct specific hypotheses are addressed by each of these studies, there is a broad consensus that visual motion – of objects themselves, scenes as a whole, or backgrounds alone – is sufficient to drive visuomotor behavior in a systematic, automatic, and fast manner. It is possible that all of these effects are determined by common neural mechanisms of motion processing and that these mechanisms serve one or more adaptive, beneficial roles. Future studies are therefore required, not only to establish the neural underpinnings of motion's influence on action but also to address the functional role(s) that retinal motion plays in motor control.

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