Exp Brain Res (2005) 162: 394–400
DOI 10.1007/s00221-004-2154-0

RESEARCH NOTE

David Whitney · Melvyn A. Goodale

Visual motion due to eye movements helps guide the hand

Received: 7 May 2004 / Accepted: 16 October 2004 / Published online: 15 January 2005

Abstract Movement of the body, head, or eyes with respect to the world creates one of the most common yet complex situations in which the visuomotor system must localize objects. In this situation, vestibular, proprioceptive, and extra-retinal information contribute to accurate visuomotor control. The utility of retinal motion information, on the other hand, is questionable, since a single pattern of retinal motion can be produced by any number of head or eye movements. Here we investigated whether retinal motion during a smooth pursuit eye movement contributes to visuomotor control. When subjects pursued a moving object with their eyes and reached to the remembered location of a separate stationary target, the presence of a moving background significantly altered the endpoints of their reaching movements. A background that moved with the pursuit, creating a retinally stationary image (no retinal slip), caused the endpoints of the reaching movements to deviate in the direction of pursuit, overshooting the target. A physically stationary background pattern, however, producing retinal image motion opposite to the direction of pursuit, caused reaching movements to become more accurate. The results indicate that background retinal motion is used by the visuomotor system in the control of visually guided action.

Keywords Visual perception · Motion · Position · Visuomotor · Reaching · Pointing · Action

D. Whitney (✉)
The Department of Psychology & The Center for Mind and Brain, The University of California, Davis, CA 95616, USA
E-mail: dwhitney@ucdavis.edu
Tel.: +1-530-297-4451
Fax: +1-530-792-1489

M. A. Goodale
The Department of Psychology,
The University of Western Ontario,
London, Ontario, N6A 5C2, Canada

Introduction

Goal-directed reaching often occurs during complex movements of the body, the eyes, and the world. As a result, there is so much motion information on the retina that it would seem to be a hindrance rather than a help in determining how the body has moved. Indeed, a single pattern of retinal motion can be produced by many different types of ego-motion. Because of this many-to-one mapping, it would appear that the visuomotor system must discount retinal motion to successfully guide the hand to an object. Other sources of information would, on the face of it, provide more reliable information. For example, extra-retinal information, such as efference copy of eye and body movement commands, proprioceptive information about limb and eye position, and vestibular information about body position contributes to the control of reaching movements (Hallett and Lightstone 1976; Hansen and Skavenski 1985; Jeannerod 1988; Gauthier et al. 1990; Bridgeman and Stark 1991; Blouin et al. 1995; Andersen et al. 1997; Desmurget et al. 1998).

Nevertheless, retinal motion information produced by an eye movement could be used when reaching to an object. To test this, we asked subjects to reach to the remembered location of a static target while tracking a moving object with their eyes. There were three different backgrounds that could be visible during the smooth pursuit: a stationary background or a background that moved with or against the direction of pursuit.

Materials and methods

Three right-handed subjects participated in the experiments. The experiments were approved by the University of Western Ontario's ethics review board, and have been conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All subjects gave their informed consent prior to their inclusion in the experiment.

Stimuli in the reaching experiment were presented on an NEC CRT monitor, driven by a Mac G4 computer. Subjects were seated in a dark room 45 cm from the monitor, with a chin and forehead rest to stabilize the head. A static fixation point (0.3×0.3 deg; 32 cd/m^2) was initially presented at a random eccentricity within 9.1–17.9 deg to the left or 9.1–17.9 deg to the right of center. After 1180 ms, a stationary target (0.3×1.5 deg; 0 cd/m^2) was presented for 23.5 ms at one of seven random horizontal positions (±7.3, ±4.9, ±2.5, 0 deg; negative values indicate that the target was located to the left of center). The target was located 12.7 deg below the fixation point. After a randomly determined period from 494–729 ms, the fixation point began to move (15.0 deg/s). If the fixation point was initially located to the left of center, it always moved rightward, and if the fixation point was to the right of center, it always moved leftward. In this way there was no uncertainty about the direction of pursuit. Subjects were instructed to pursue the fixation point with their eyes. Coincident with the initiation of the fixation point's motion, two gratings were presented (sinusoidal luminance modulations; 40×10.5 deg and 40×12.5 deg, respectively; 0.16 cycles/deg; 95% Michelson contrast; vertically separated by 3.1 deg; see Fig. 1). The gratings either drifted in the direction of the fixation point's movement (15.0 deg/s), opposite the fixation (−10.9 deg/s), or were stationary. The starting position and direction of pursuit were random on each trial. The direction and speed of the surrounding grating's motion was also random on each trial. The fixation point (pursuit object) was vertically separated from the top grating by 1.0 deg. Within 529–647 ms after the initiation of the fixation point's movement an audible tone was presented, signaling to subjects that they should reach as quickly as possible to the remembered location of the target (in other words, hit the monitor with their right index finger). After subjects responded and brought their right hand back to the starting position, they were allowed to start a new trial by pressing a key with the other hand (self paced).

Infrared emitting markers were attached to the right index finger of each subject. The position of the index finger was recorded at 250 Hz with an Optotrak (Northern Digital, Waterloo, Ontario, Canada). The initial position of the hand was ~40 cm from the monitor. The reaction time (reaching movement onset) was defined as the moment the hand's velocity reached 50 mm/s. The endpoint of the reaching movement was defined as the moment the index finger hit the monitor (marked by the instantaneous deceleration of the hand). There were seven possible target positions, two directions of pursuit, and three types of background motion for a total of 42 conditions. Each subject participated in 18 trials for each condition for a total of 756 trials (comprising three sessions of 252 trials each). For each of the background motion conditions, the normalized endpoint position of the hand was calculated for each target position as a function of the direction of pursuit. To determine this, the average endpoint position of the hand was calculated for each target position within each background condition (21 means). The difference between the endpoint for each trial minus the mean of the respective condition gives a normalized difference score, independent of pursuit direction. Comparing the normalized scores for leftward and rightward pursuit gives

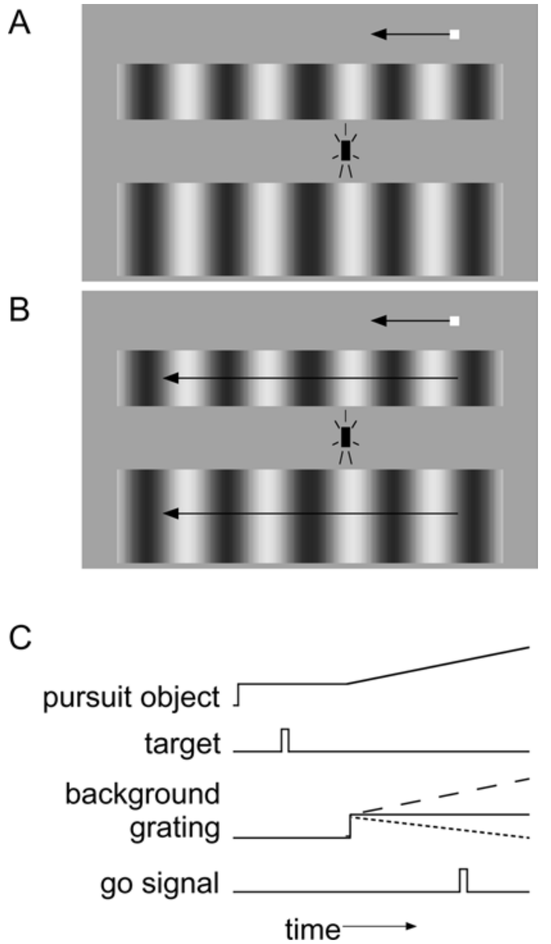


Fig. 1A–C Stimulus and protocol used in the experiment. **A** The target (*black rectangle*) was presented on a blank screen while subjects fixated on an object (*white square*). After the target disappeared, the white object began to move and the subjects were instructed to smoothly pursue the object with their eyes. In one condition, there was a physically stationary background grating visible as soon as the eye movement was initiated. In two additional conditions, the background grating could either move in the same direction as the pursuit object (**B**) or in the opposite direction (condition not shown). The background grating (either moving or stationary) did not appear until after the pursuit eye movement began, so any differences between the results for the three conditions cannot be explained by a difference in the stimulus when the eye was stationary. **C** The sequence of events in each trial. Subjects fixated on the pursuit object that was initially stationary and then began to move. While subjects fixated the stationary pursuit object, a stationary target was briefly presented. When the pursuit object began to move, a background grating was simultaneously presented. The grating was either stationary (*solid line*), moving in the direction of pursuit (*dashed line*), or moving in a direction opposite the pursuit (*dotted line*). At an unpredictable moment during the pursuit eye movement, an audible beep was presented, signaling that the subject should reach to the remembered location of the target an estimate of the pursuit-dependent shift in the endpoint of the reaching movement. The pursuit-dependent shift in the hand's position is shown in Fig. 2 for the three different background conditions.

In separate experimental sessions, using a stimulus similar to that in the first experiment, smooth pursuit eye movements were measured with a table-mounted eye tracker (Applied Science Laboratories, Bedford, Massachusetts, USA), at 240 Hz. The velocity of the eye movements was calculated for each of the three experimental conditions. The stimulus and procedure were identical to the first experiment, except that subjects did not make fast reaching movements to the monitor, as these disrupt eye movement recordings, and reduce the reliability of the measurements. Stimuli were presented on a Macintosh LCD display with a refresh rate of 72 Hz. A chin and forehead rest were provided to stabilize the subject's head at a distance of 54 cm from the monitor.

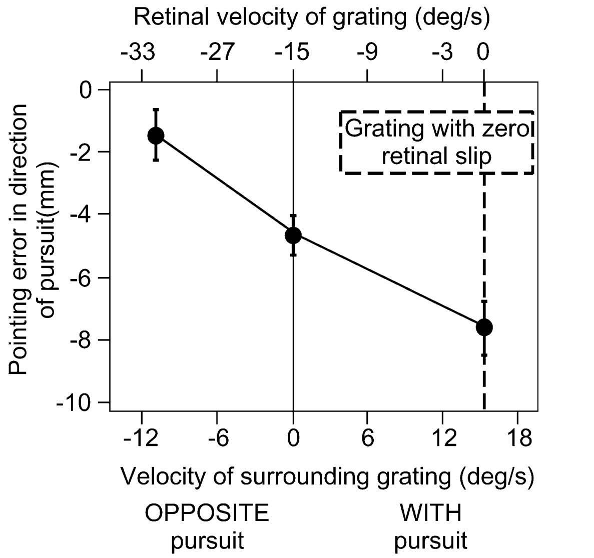


Fig. 2 Results for the first experiment: the error in pointing movements (ordinate) as a function of the background velocity. Negative values along the ordinate indicate that the endpoint of the reaching movement deviated in the same direction as pursuit (0 represents an accurate reach). The direction of background motion (with or against the direction of pursuit) is indicated by the positive and negative values along the abscissa, respectively. The physical motion of the grating is plotted on the bottom; the retinal speed of the gratings, due to the pursuit eye movement, is plotted along the top. The vertical dashed line shows the physical speed of the grating that created a retinally stationary image (no retinal slip). The data show a roughly linear relationship between the background velocity and the error in the pointing movement; the error in the pointing movement varied as a function of the background velocity. Interestingly, when the grating moved at the same velocity as the pursuit object, producing a retinally stationary image, the reaching movements were strongly shifted in the direction of the eye movement. However, when there was a physically stationary background, producing retinal slip opposite to the direction of pursuit, the reaching movements were more accurate

Results and discussion

Figure 2 shows the results of the experiment. When subjects pursued a moving object over a background that drifted at the same speed as their pursuit (retinal slip of the background was therefore 0), subjects overshot the remembered location of the target. Although the background was retinally stationary, pointing movements deviated in the direction of the pursuit eye movement by about 8 mm. A retinally stationary background may therefore be akin to having no visible background (see Yee et al. 1983). When the background was physically stationary (therefore moving across the retina at ~15 deg/s), the endpoints of the pointing movements did not overshoot the target as much (~4.5 mm error); this was a significant reduction in the pointing error (least significant effect was for subject CP, $t_{(15)} = 2.7$, $P < 0.02$). When the background moved opposite the direction of pursuit, pointing movements deviated even less (~1.5 mm error). There was a significant overall effect of background motion on the pointing movements (least significant effect was for CP, $F_{(2,23)} = 46.9$, $P < 0.001$). Within the range of background velocities tested here, there is a roughly linear relationship between the background velocity and the magnitude of the pointing error.

Interestingly, the data in Fig. 2 reveal that the pointing movements were more accurate when there was a physically stationary background, which provided retinal motion cues in a direction opposite to that of pursuit, than when there was no retinal motion. If extra-retinal information about the eye movement (such as efference copy or corollary discharge) was available and accurate, it should have been sufficient to accurately guide the hand to the location of the remembered target. It has been shown that extra-retinal information is not perfectly accurate, however. For example, the magnitude of pursuit and saccadic eye movements can be routinely underestimated (Honda 1990; Blouin et al. 1996), and after an eye movement (or body movement), there are systematic errors in reaching movements to the location of a previously visible target (Henriques et al. 1998; Pouget et al. 2002). Target positions must therefore be updated during or after each eye movement, or at least before the execution of a reach.

Whether background retinal motion is useful for this updating process (and therefore beneficial to reaching) depends on whether targets are coded in body-centered or eye-centered coordinates. If targets were coded in body-centered coordinates, then retinal motion information would not be informative about how the position of the hand has changed relative to the target and would thus not be useful for guiding action (it would be detrimental, if anything). Recent behavioral and neurophysiological studies, however, have demonstrated that targets are actually coded in eye-centered coordinates (Henriques et al. 1998; Batista et al. 1999; Andersen and Buneo 2002; Buneo et al. 2002; Medendorp and Crawford 2002; Pouget et al. 2002). Coding the target and hand in an eye-centered coordinate frame means that every time the body, head, or eye moves, the representation of the hand's position relative to the target must be updated. In this case, retinal motion information could be useful for gauging how the position of the eye has changed with respect to the environment—information that could then be used to update the position of the target relative to the hand (Whitney et al. 2003b).

Our results demonstrate that retinal motion information during a pursuit eye movement influences reaching movements in a systematic way. Extra-retinal signals are therefore not the exclusive source of information used to guide reaching movements—visual motion is used as well. However, this influence of visual motion on reaching could be direct or indirect.

The first possibility is that there is a direct influence: the visual or visuomotor system might shift the representation of targets in the direction of retinal motion. There is strong evidence that this occurs in perception (Ramachandran and Anstis 1990; De Valois and De Valois 1991; Snowden 1998; Nishida and Johnston 1999; Whitaker et al. 1999; Hayes 2000; Whitney and Cavanagh 2000; Fu et al. 2001; McGraw et al. 2002; Mussap and Prins 2002; Edwards and Badcock 2003; Watanabe et al. 2003; Whitney et al. 2003a; Durant and Johnston 2004; Fu et al. 2004; Shim and Cavanagh 2004; for a review, see Whitney 2002), and in visually-guided behavior (Mohrmann-Lendla and Fleischer 1991; Brenner and Smeets 1997; Yamagishi et al. 2001; Ma-Wyatt and McGraw 2003; Whitney et al. 2003b; Ashida 2004), though the influence of visual motion on perception and action may operate on different timescales (Whitney et al. 2003b). This explanation is consistent with the finding that even during fixation, a moving background can influence reaching movements to a stationary object (Brenner and Smeets 1997; Yamagishi et al. 2001; Whitney et al. 2003b).

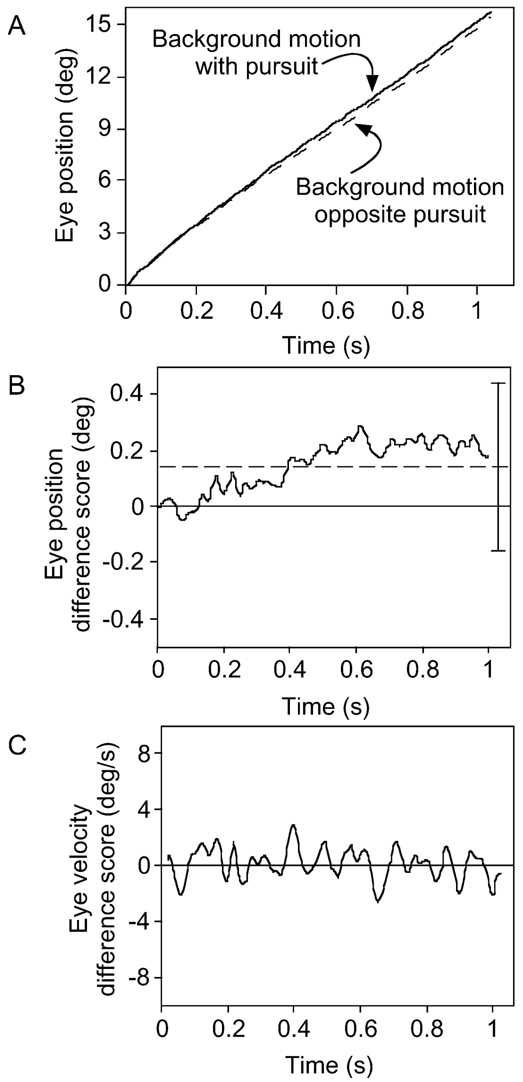
Alternatively, the background motion might influence the eye movement, which could in turn indirectly influence the reach. For example, previous studies have shown that a stationary or moving textured background can influence smooth pursuit (Yee et al. 1983; Collewijn and Tamminga 1984; Keller and Khan 1986; Howard and Marton 1992; Masson et al. 1995; Mohrmann and Thier 1995; Niemann and Hoffmann 1997; Schwarz and Ilg 1999), and additional studies have shown that gaze position can influence reaching (Bock 1986; Enright 1995; Henriques et al. 1998; van Donkelaar and Staub 2000; Neggers and Bekkering 2001; Soechting et al. 2001; Admiraal et al. 2003).

The likelihood that our results are mediated by an indirect mechanism such as an ocular following response or a pursuit asymmetry is mitigated because the pursuit object was not superimposed on the background and the influence of a stationary background is reduced when the pursuit object is separated (for example, in a different depth plane; Howard and Marton 1992). For instance, in recent experiments using stimuli similar to those used here, we found that when the pursuit object was superimposed on or even touching a moving background, pursuit gain was modulated by up to 10% (for instance, pursuing a target in a direction opposite to the background motion reduced gain to ~0.9, consistent with Masson et al. 1995). However, when the pursuit object was separated from the moving background by 0.5 deg, the gain was only modulated by ~2%, a non-significant modulation (Goltz and Whitney 2004). Separating the target from the background motion therefore improves pursuit performance, consistent with previous reports of accurate pursuit in spite of background retinal motion (Lindner et al. 2001; Schweigart et al. 2003). In the experiment here, the separation between the pursuit object and the moving background was 1.0 deg. Figure 3 shows that in this situation there was virtually no difference in the position (Fig. 3B) or speed (Fig. 3C) of the eye. Subjects were able to effectively discount the moving background and maintain accurate fixation on the pursuit object.

Although there is little measurable influence of the background motion on gaze position when the pursuit object is separated from the background, it is conceivable that the background in our experiment could have modulated an internal eye position signal distinct from the measured smooth pursuit. If the background in our experiment modulated an internal eye position signal, like efference copy (perhaps by partial OKN innervation), but the reach was based on a different estimate of eye position (for example, was based solely on efference copy without the addition of OKN; Post et al. 1984; Bridgeman 1986; Leibowitz et al. 1986), then the reach could have systematically deviated in the direction of the background. According to this argument, pursuit could be accurate (Fig. 3) while pointing is not (Fig. 2). This indirect mechanism would also predict the negative slope in the data shown in Fig. 2.

However, these direct and indirect mechanisms do not explain the data completely. Interestingly, the data in Fig. 2 not only show a negative slope, but also show an intercept shift. The pointing error did not intersect zero when the background was retinally or physically stationary. Rather, reaching movements overshot the target in the direction of pursuit, regardless of background, which suggests that there may be a systematic underestimation of the extra-retinal eye movement command. While the direct and indirect influences of background motion on reaching discussed above would predict the negative slope in Fig. 2, the simplified models alone would not predict the shift in the intercept. For example, neither model would predict that a retinal velocity of ~30 deg/s opposite to pursuit should produce more accurate reaching than a retinally or physically stationary background.

Therefore both the direct and indirect models require an additional assumption that there is an underestimation of pursuit distance or magnitude when reaching to remembered targets. In the case of the indirect model,



◀

Fig. 3A–C Smooth pursuit eye movements while the background moves in the same direction as or the opposite direction to the target. **A** *Solid* and *dashed* lines show the average eye position for one subject across all trials when the background moved with or against the direction of pursuit, respectively (data are merged such that pursuit direction is always rightward). All missing data (for example, due to blinks) and saccades (defined as instantaneous eye velocities greater than 40 deg/s) were removed; missing frames accounted for less than 2% of the data. Data were collected at and normalized to pursuit onset, which occurred after an initial saccade (because the onset of the target's motion was unpredictable). **B** The difference between the eye position traces for the two conditions in (**A**) in which the background moves with or against the direction of pursuit. The average difference in eye position is 0.15 deg (~1.5 mm, *dashed line*), indicating that when the background moves in the same direction as the pursuit object, the eye is located about 1.5 mm in front of its location when the background moves opposite to the direction of pursuit. This effect, however, is less than one standard error (s.e.m≈0.3 deg, indicated by the *error bar*), and is not significant ($P > 0.05$). Also, note that the difference in the pointing error (>6 mm, see Fig. 2) is over four times the eye position error found here, suggesting that the pointing error is not entirely due to an error in pursuit. **C** The difference between the velocity of the smooth pursuit in the two conditions. A positive score indicates that tracking speed was higher when the background moved with pursuit. The instantaneous velocity of the eye was calculated using a running average of the eye position over a 40 ms window, yielding a smoothed estimate of eye speed; a difference score was then subtracted for each frame (every ~4 ms). The average velocity difference is ~0.16 deg/s, but the large variability shows that there is no systematic or significant difference in eye speed as a function of the direction of background motion. The average velocity difference of ~0.16 deg/s is equivalent to a ~1.8% modulation of pursuit speed as a function of background motion direction (so that, depending on the background motion, the pursuit sped up or slowed down by ~1.8%). Data for two other subjects showed modulations of 2.7% and 1.7%. These are insignificant effects, and are consistent with previous reports that pursuit is essentially accurate, especially when the moving background is separated from the target (Howard and Marton 1992; Schweigart et al. 2003; Goltz and Whitney 2004)

the size of the background could modulate the internal eye position signal used for reaching (such as efference), and since our display did not occupy the entire visual field there could have been an underestimation of pursuit distance that might become more accurate with a larger background. In the direct model, the pursuit underestimation could be due to a systematic encoding error or to delays in coordinate transformations. For example, to reach to an object, the target and hand must be represented in a common coordinate frame, which is likely to be eye-centered (Henriques et al. 1998; Batista et al. 1999; Andersen and Buneo 2002; Buneo et al. 2002; Medendorp and Crawford 2002; Pouget et al. 2002). A coordinate transformation is therefore required, which involves necessary delays. If the eye is moving, this delay would cause underestimation of the distance between the gaze and target positions, because the eye continues to move while the representation of the hand is being transformed into eye-centered coordinates. Ultimately, this delay-induced error would cause the representation of the hand to lag behind the representation of the target (which is already in eye-centered coordinates), which would reveal itself as a systematic underestimate of pursuit amplitude (and an error in reaching). Importantly, however, in both the direct and indirect scenarios, the background visual motion opposite the direction of pursuit serves to reduce this systematic error in goal-directed reaching.

Although the pattern of motion on the retina is not necessarily predictive of how the body has moved, or how the eye has moved relative to the body, it is informative about how the eye alone has moved with respect to the world. If targets are coded in eye-centered coordinates, as is increasingly believed (Henriques et al. 1998; Batista et al. 1999; Andersen and Buneo 2002; Buneo et al. 2002; Medendorp and Crawford 2002; Pouget et al. 2002), then the visuomotor system could adaptively incorporate visual motion information when assigning or updating the positions of objects. This explains why, when a physically stationary background was present in our experiment (providing retinal motion opposite to the direction of pursuit) reaching movements were more accurate than when there was no retinal motion.

Acknowledgements Thanks to Herb Goltz. This work was partially supported by NEI F32 EY013899 to D.W., and a CIHR grant to M.A.G.

References

Admiraal MA, Keijsers NL, Gielen CCAM (2003) Interaction between gaze and pointing toward remembered visual targets. J Neurophysiol 90:2136–2148

Andersen RA, Buneo CA (2002) Intentional maps in posterior parietal cortex. Annu Rev Neurosci 25:189–220

Andersen RA, Snyder LH, Bradley DC, Xing J (1997) Multimodal representation of space in the posterior parietal cortex and its use in planning movements. Annu Rev Neurosci 20:303–330

Ashida H (2004) Action-specific extrapolation of target motion in human visual system. Neuropsychologia 42:1515–1524

Batista AP, Buneo CA, Snyder LH, Andersen RA (1999) Reach plans in eye-centered coordinates. Science 285:257–260

Blouin J, Gauthier GM, van Donkelaar P, Vercher JL (1995) Encoding the position of a flashed visual target after passive body rotations. Neuroreport 6:1165–1168

Blouin J, Gauthier GM, Vercher JL, Cole J (1996) The relative contribution of retinal and extraretinal signals in determining the accuracy of reaching movements in normal subjects and a deafferented patient. Exp Brain Res 109:148–153

Bock O (1986) Contribution of retinal versus extraretinal signals towards visual localization in goal-directed movements. Exp Brain Res 64:476–482

Brenner E, Smeets JBJ (1997) Fast responses of the human hand to changes in target position. J Motor Behav 29:297–310

Bridgeman B (1986) Multiple sources of outflow in processing spatial information. Acta Psychol (Amst) 63:35–48

Bridgeman B, Stark L (1991) Ocular proprioception and efference copy in registering visual direction. Vision Res 31:1903–1913

Buneo CA, Jarvis MR, Batista AP, Andersen RA (2002) Direct visuomotor transformations for reaching. Nature 416:632–636

Collewijn H, Tamminga EP (1984) Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds. J Physiol 351:217–250

De Valois RL, De Valois KK (1991) Vernier acuity with stationary moving Gabors. Vision Res 31:1619–1626

Desmurget M, Pelisson D, Rossetti Y, Prablanc C (1998) From eye to hand: planning goal-directed movements. Neurosci Biobehav R 22:761–788

Durant S, Johnston A (2004) Temporal dependence of local motion induced shifts in perceived position. Vision Res 44:357–366

Edwards M, Badcock DR (2003) Motion distorts perceived depth. Vision Res 43:1799–1804

Enright JT (1995) The non-visual impact of eye orientation on eye-hand coordination. Vision Res 35:1611–1618

Fu YX, Shen Y, Dan Y (2001) Motion-induced perceptual extrapolation of blurred visual targets. J Neurosci 21:RC172

Fu YX, Shen Y, Gao H, Dan Y (2004) Asymmetry in visual cortical circuits underlying motion-induced perceptual mislocalization. J Neurosci 24:2165–2171

Gauthier GM, Nommay D, Vercher JL (1990) The role of ocular muscle proprioception in visual localization of targets. Science 249:58–61

Goltz HC, Whitney D (2004) The influence of background motion on smooth pursuit: separation matters. J Vision 4:649

Hallett PE, Lightstone AD (1976) Saccadic eye movements towards stimuli triggered by prior saccades. Vision Res 16:99–106

Hansen RM, Skavenski AA (1985) Accuracy of spatial localizations near the time of saccadic eye movements. Vision Res 25:1077–1082

Hayes A (2000) Apparent position governs contour-element binding by the visual system. P Roy Soc Lond B Bio 267:1341–1345

Henriques DY, Klier EM, Smith MA, Lowy D, Crawford JD (1998) Gaze-centered remapping of remembered visual space in an open-loop pointing task. J Neurosci 18:1583–1594

Honda H (1990) The extraretinal signal from the pursuit-eye-movement system: its role in the perceptual and the egocentric localization systems. Percept Psychophys 48:509–515

Howard IP, Marton C (1992) Visual pursuit over textured backgrounds in different depth planes. Exp Brain Res 90:625–629

Jeannerod M (1988) The neural and behavioural organization of goal-directed movements. Clarendon, Oxford

Keller EL, Khan NS (1986) Smooth-pursuit initiation in the presence of a textured background in monkey. Vision Res 26:943–955

Leibowitz HW, Post RB, Sheehy JB (1986) Efference, perceived movement, and illusory displacement. Acta Psychol (Amst) 63:23–34

Lindner A, Schwarz U, Ilg UJ (2001) Cancellation of self-induced retinal image motion during smooth pursuit eye movements. Vision Res 41:1685–1694

Ma-Wyatt A, McGraw PV (2003) Illusory positional shifts affect both perception and action. J Vision 3:122

Masson G, Proteau L, Mestre DR (1995) Effects of stationary and moving textured backgrounds on the visuo-oculo-manual tracking in humans. Vision Res 35:837–852

McGraw PV, Whitaker D, Skillen J, Chung ST (2002) Motion adaptation distorts perceived visual position. Curr Biol 12:2042–2047

Medendorp WP, Crawford JD (2002) Visuospatial updating of reaching targets in near and far space. Neuroreport 13:633–636

Mohrmann H, Thier P (1995) The influence of structured visual backgrounds on smooth-pursuit initiation, steady-state pursuit and smooth-pursuit termination. Biol Cybern 73:83–93

Mohrmann-Lendla H, Fleischer AG (1991) The effect of a moving background on aimed hand movements. Ergonomics 34:353–364

Mussap AJ, Prins N (2002) On the perceived location of global motion. Vision Res 42:761–769

Neggers SF, Bekkering H (2001) Gaze anchoring to a pointing target is present during the entire pointing movement and is driven by a non-visual signal. J Neurophysiol 86:961–970

Niemann T, Hoffmann KP (1997) The influence of stationary and moving textured backgrounds on smooth-pursuit initiation and steady state pursuit in humans. Exp Brain Res 115:531–540

Nishida S, Johnston A (1999) Influence of motion signals on the perceived position of spatial pattern. Nature 397:610–612

Post RB, Shupert CL, Leibowitz HW (1984) Implications of OKN suppression by smooth pursuit for induced motion. Percept Psychophys 36:493–498

Pouget A, Ducom JC, Torri J, Bavelier D (2002) Multisensory spatial representations in eye-centered coordinates for reaching. Cognition 83:B1–11

Ramachandran VS, Anstis SM (1990) Illusory displacement of equiluminous kinetic edges. Perception 19:611–616

Schwarz U, Ilg UJ (1999) Asymmetry in visual motion processing. Neuroreport 10:2477–2480

Schweigart G, Mergner T, Barnes GR (2003) Object motion perception is shaped by the motor control mechanism of ocular pursuit. Exp Brain Res 148:350–365 (Epub 2002 Nov 2020)

Shim WM, Cavanagh P (2004) The motion-induced position shift depends on the perceived direction of bistable quartet motion. Vision Res 44:2393–2401

Snowden RJ (1998) Shifts in perceived position following adaptation to visual motion. Curr Biol 8:1343–1345

Soechting JF, Engel KC, Flanders M (2001) The Duncker Illusion and Eye-Hand Coordination. J Neurophysiol 85:843–854

van Donkelaar P, Staub J (2000) Eye-hand coordination to visual versus remembered targets. Exp Brain Res 133:414–418

Watanabe K, Sato TR, Shimojo S (2003) Perceived shifts of flashed stimuli by visible and invisible object motion. Perception 32:545–559

Whitaker D, McGraw PV, Pearson S (1999) Non-veridical size perception of expanding and contracting objects. Vision Res 39:2999–3009

Whitney D (2002) The influence of visual motion on perceived position. Trends Cogn Sci 6:211–216

Whitney D, Cavanagh P (2000) Motion distorts visual space: shifting the perceived position of remote stationary objects. Nat Neurosci 3:954–959

Whitney D, Goltz HC, Thomas CG, Gati JS, Menon RS, Goodale MA (2003a) Flexible retinotopy: motion-dependent position coding in the visual cortex. Science 302:878–881

Whitney D, Westwood DA, Goodale MA (2003b) The influence of visual motion on fast reaching movements to a stationary object. Nature 423:869–873

Yamagishi N, Anderson SJ, Ashida H (2001) Evidence for dissociation between the perceptual and visuomotor systems in humans. P Roy Soc Lond B Bio 268:973–977

Yee RD, Daniels SA, Jones OW, Baloh RW, Honrubia V (1983) Effects of an optokinetic background on pursuit eye movements. Invest Ophth Vis Sci 24:1115–1122