BRAIN RESEARCH 1225 (2008) 76–85

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Review

Contextual effects on motion perception and smooth pursuit eye movements

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ARTICLE INFO

Article history:
Accepted 15 April 2008
Available online 30 April 2008

Keywords:
Smooth pursuit eye movements
Motion perception
Visual context
Vector averaging
MT

ABSTRACT

Smooth pursuit eye movements are continuous, slow rotations of the eyes that allow us to follow the motion of a visual object of interest. These movements are closely related to sensory inputs from the visual motion processing system. To track a moving object in the natural environment, its motion first has to be segregated from the motion signals provided by surrounding stimuli. Here, we review experiments on the effect of the visual context on motion processing with a focus on the relationship between motion perception and smooth pursuit eye movements. While perception and pursuit are closely linked, we show that they can behave quite distinctly when required by the visual context.

Contents

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doi:10.1016/j.brainres.2008.04.061

1. Introduction

The analysis of visual motion is a fundamental ability of the visual system and plays a functional role in scene perception and the control of motor action (Nakayama, 1985). Visual motion signals are crucial for the generation of smooth pursuit eye movements (Lisberger and Westbrook, 1985; Tychsen and Lisberger, 1986). Because of their close connection to motion perception, pursuit eye movements have been studied extensively to gain a better understanding of how visual motion signals control motor behavior, and how the sensory and motor system interact on a cortical level. We review studies that compare motion perception and pursuit, in particular in complex and dynamic visual situations. While there is good agreement between perception and pursuit in many simple situations, we show that they can have distinctly different functional properties when more complex stimuli are used.

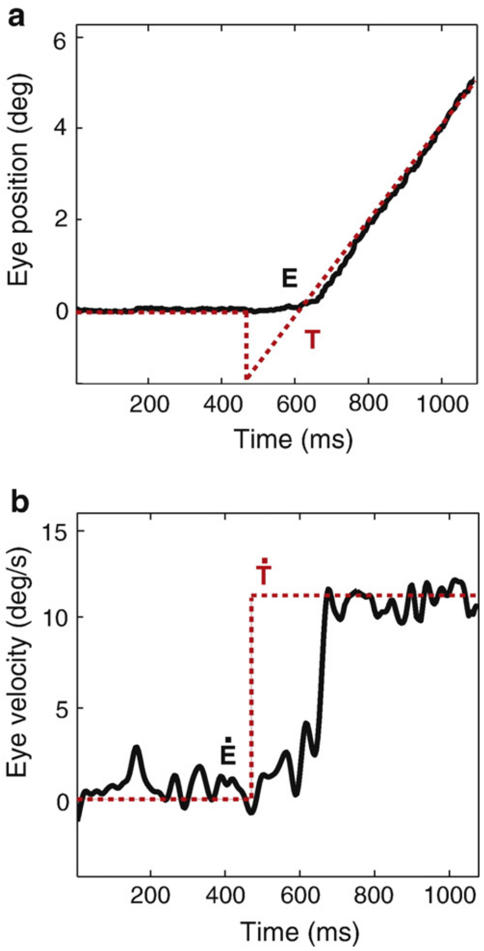

Fig. 1 – (a) Position and (b) velocity responses to a rightward moving target. The target (T) initially steps to the left for 1.8 deg, and then starts to move back across the fovea. This so-called step-ramp procedure (Rashbass, 1961) prevents early catch-up saccades. The eye (E) does not respond to the retinal position error created by the target step, but follows the smooth motion to the right. After a latency of ~100 ms, the eye accelerates and reaches steady-state velocity after ~150–200 ms, marking the beginning of the closed-loop phase. Eye velocity oscillates around target velocity at a frequency of ~2 Hz.

2. Properties of smooth pursuit eye movements

Pursuit eye movements are slow rotations of the eyes that serve to keep gaze on a moving visual object of interest. By compensating for object motion pursuit eye movements enhance high acuity vision (Carpenter, 1988; Ilg, 1997; Land, 1999; Leigh and Zee, 2006). Even though pursuit eye movements are considered slow with respect to their velocity, they are quite fast with respect to their latency, which is on the order of 80–150 ms in humans, and 65–120 ms in monkeys (Carl and Gellman, 1987; Lisberger et al., 1987; Robinson, 1965). Human observers are usually able to track a target moving in the range of 1–100 deg/s. However, pursuit is often too slow, especially when target velocity exceeds 30 deg/s. To compensate for retinal image slip, smooth eye motion is supported by catch-up saccades (DeBrouwer et al., 2002; Rashbass, 1961).

The pursuit response is usually separated into an open-loop phase (the first 140 ms after initiation), and a closed-loop or steady-state phase (Lisberger et al., 1987; Tychsen and Lisberger, 1986). During the open-loop phase, pursuit is primarily driven by the target's retinal image velocity, because an internal signal about the eye velocity is not yet available to the system. In the early phase of initiation (0–20 ms), the eye starts to accelerate in the direction of the target, and in the later phase (20–100 ms), eye velocity is gradually adjusted to target velocity (see Fig. 1).

During the closed-loop phase, pursuit is maintained by an internal signal, and velocity errors are corrected by reducing retinal image slip (Newsome et al., 1989; Robinson et al., 1986). With the exception of the early open-loop response (0–40 ms), which seems to be largely unaffected by stimulus features, pursuit eye movements clearly depend on the visual properties of the moving stimulus (Lisberger et al., 1987; Lisberger and Westbrook, 1985; Tychsen and Lisberger, 1986; for reviews see Keller and Heinen, 1991; Krauzlis, 2004, 2005; Ilg, 1997; Thier and Ilg, 2005). In this review, we focus on studies that examined the role of non-target visual signals for pursuit initiation and maintenance.

3. Neuronal control of smooth pursuit eye movements

As a basis for understanding the relationship between smooth pursuit eye movements and visual motion processing, we will briefly outline the anatomical pathways underlying the generation of pursuit in the primate brain, with a focus on cortical areas that process visual information. Excellent reviews exist that provide a detailed description of pursuit pathways (Ilg, 1997; 2002; Keller and Heinen, 1991; Krauzlis, 2004; 2005; Leigh and Zee, 2006; Thier and Ilg, 2005) and motion processing in the brain (Born and Bradley, 2005; Britten, 2003).

3.1. *Pursuit pathways in the primate brain*

Visual motion signals are the most important input for the pursuit system. Motion information enters the primary visual cortex (V1) via the magnocellular layers of the lateral geniculate nucleus (LGN). Neurons in area V1 are selective for orientation, direction, and spatial frequency, and respond best to motion signals within local regions of visual space, or to components of complex patterns (Movshon et al., 1985). The integration of local motion signals and the analysis of pattern motion are achieved by area MT (V5), a cortical area in the medial temporal sulcus with large receptive fields (Born and Bradley, 2005; Rust et al., 2006). Microstimulation in area MT during pursuit eye movements results in an increase in steady-state pursuit velocity (Groh et al., 1997). Chemical lesions of area MT in the monkey result in deficits in the perception of velocity of a moving target, and impair pursuit initiation as well as saccades to moving targets (Newsome et al., 1985). Many studies on the relationship between pursuit eye movements and motion perception have therefore focused on this particular brain area. However, motion information for perception and pursuit is also processed in the middle superior temporal area (MST), and possibly in higher cortical areas (Ilg and Churan, 2004).

Neurons in area MST respond to object motion, and are important for pursuit maintenance. Lesions in area MST in the monkey lead to deficits in pursuit for targets moving towards the lesioned hemifield (Duersteler and Wurtz, 1988). Microstimulation in area MST boosts pursuit velocity during tracking towards the stimulated side, and decreases velocity during tracking away from the side of the stimulation (Komatsu and Wurtz, 1989). The dorsal part of area MST (MSTd) is crucial for the analysis of optic-flow information (Duffy and Wurtz, 1991) and direction of heading (Ben et al., 2003). The ventrolateral part of area MST (MSTl) is related to the analysis of object motion in space. MSTl neurons are important for the generation of goal-directed eye and hand movements (pursuit and manual tracking) to a moving object (Ilg and Schumann, 2007). These neurons also discharge before the actual onset of pursuit and to play a role in the generation of predictive pursuit (Ilg and Thier, 2003; Newsome et al., 1988; Thier and Ilg, 2005).

Areas MT and MST have reciprocal connections with frontal and parietal areas with pursuit-related activity, such as the frontal eye fields (FEF), the supplementary eye fields (SEF), the lateral intraparietal area (LIP), and the ventral intraparietal area (VIP). A subregion of the FEF in the ventral inferior part, the frontal pursuit area (FPA), has emerged as one of the most important cortical areas controlling smooth pursuit eye movements (Fukushima, 2003; Krauzlis, 2004). When neurons in the FPA are microstimulated during fixation, pursuit eye movements can be elicited (Gottlieb et al., 1994). Microstimulation during ongoing pursuit leads to a boost in pursuit gain (Tanaka and Lisberger, 2001). The SEF, on the other hand, is involved in coding anticipatory pursuit, as shown by microstimulation in that area (Missal and Heinen, 2004). Single-cell recordings show that a large number of neurons in area VIP are “pursuit neurons” that are highly tuned to direction and velocity, but seem to reflect extraretinal rather than visual information to guide smooth pursuit (Schlack et al., 2003). A pattern of direction-specific pursuit-related activity was also found in single-cell recordings in area LIP (Bremmer et al., 1997).

From cortical areas MT/MST, and parietal and frontal areas, pursuit-related information is transmitted to the pontine nuclei in the brainstem and the cerebellum for the assembly of motor commands from visual and ocular inputs. A second route from extrastriate cortex to the cerebellum goes via the pretectal nucleus of the optic tract (NOT), which is known to control the optokinetic reflex and the ocular following response. A detailed description of cerebellar pursuit control can be found in Leigh and Zee (2006). The network of pursuit areas along the cortico-pontine-cerebellar pathway that emerged from lesioning studies, microstimulation and single-cell recordings in the non-human primate brain is complemented by imaging and patient studies in humans (fMRI: e.g., Konen et al., 2005; patients: e.g., Heide et al., 1996).

4. Contextual effects on pursuit

In our natural environment, objects of interest are usually embedded in a richly structured, dynamic visual context. In order to track such a visual object with the eyes, its motion has to be segregated from other motion signals in the visual context. The spatial integration of target and context motion signals has been studied by having observers track a pursuit target in the presence of a second moving object, or in front of a stationary or moving textured background.

4.1. *Motion signal integration from multiple pursuit targets*

When the visual system is confronted with multiple (in most studies: two) objects that move into different directions and at different velocities, motion information from the two objects is integrated. In a paradigm introduced by Lisberger and Ferrera (1997), a monkey had to fixate a central spot, while two stimuli moved towards the fixation location. Upon reaching the fovea, one of the two stimuli disappeared (the distractor), while the other stimulus continued to move into its original direction (the target), and had to be tracked. No prior information about target identity was given. The monkeys' pre-saccadic open-loop pursuit response followed the vector average of the two stimuli. A similar vector averaging response in open-loop pursuit was obtained when one of the two motion signals was evoked by a visual object, while the other was produced by microstimulating cortical cells in area MT of the awake monkey (Groh et al., 1997). When monkey or human observers were attentionally cued to pursue one of the two objects, pursuit was strongly biased towards the target and followed a winner-take-all response (Ferrera and Lisberger, 1997; Garbutt and Lisberger, 2006; Kowler, 1990), but with a cost in latency (Ferrera, 2000; Ferrera and Lisberger, 1995).

When human observers were informed about target and distractor identity, the oculomotor system compensated for the irrelevant distractor, and the eye vertically curved away from the distractor (Spering et al., 2006). This curvature effect was found in open-loop and closed-loop pursuit. Interestingly, the pursuit response shifted from vertical curvature to winner-take-all behavior, when the time and location of distractor appearance were predictable (Spering et al., 2006).

Curvature effects into the opposite direction to a second stimulus were also obtained in reaching movements (Tipper et al., 1997), and in saccades (Sheliga et al., 1995). These distractor-related curvature effects on eye and hand movements are small but stable, and occur even in response to an ignored (Doyle and Walker, 2001; Spering et al., 2006) or remembered distractor (Theeuwes et al., 2005). Most studies have attributed this effect to the inhibition of a programmed response to the distractor, in line with the premotor theory of attention: The distractor is attended, a motor movement towards the distractor is programmed, and the movement subsequently has to be suppressed (e.g., Rizzolatti et al., 1987; Tipper et al., 1997).

To summarize, when more than one moving object is present in the visual field, the resulting pursuit velocity can either follow a vector averaging, a motion contrast, or a winner-take-all response. The type of response depends on (1) the stage of the pursuit response, (2) the uncertainty about the identity of the target object, (3) the uncertainty regarding the time and location of distractor appearance, (4) the salience of the two objects, and (5) and the locus of attention. The higher the uncertainty and the more physically equivalent the two objects are, the more likely will the response follow the vector average. When one object is made more salient than the other, either by boosting its physical properties or by directing attention to it, the response shifts to a winner-take-all behavior pattern. Finally, motion contrast responses occur when the distractor is predefined, but unpredictable, and can therefore not be ignored completely. Depending on the nature of the target and distractor, the visual motion system therefore uses different strategies to optimally accomplish different tasks for the motor response: tracking with high precision (winner-take-all), minimizing choice errors (vector averaging), and avoiding motor planning errors (motion contrast).

4.2. *Motion signal integration from pursuit target and visual context*

The segregation of object motion from background motion is usually accomplished by the visual system without much effort (Albright and Stoner, 2002; Roelfsema, 2006). But under some circumstances our visual system fails and cannot resolve the interaction of target and context motion signals. Gestalt psychologist Karl Duncker (1929) provided an early report of a phenomenon termed "induced motion", in which a stationary, fixated target object appeared to move into the opposite direction to a second moving object in the periphery. The second moving object was either a target object of the same size as the fixated object, a frame surrounding the fixation point, or a moving background. In the "Duncker illusion", the visual system seems to rely on the second moving object, the moving frame, or the background as a stable frame of reference. If the second moving object is assumed to be stationary, the foreground object, which is physically stationary, receives an illusory motion component and is perceived to move into the opposite direction to the reference object.

The perceptual effects of induced motion are large and impressive (see Anstis and Casco, 2006; Nawrot and Sekuler, 1990; Zivotofsky et al., 1995), and are responsible for illusions in everyday life, such as perceiving the moon "racing" through the clouds. Illusory motion affects the direction of saccades (Zivotofsky et al., 1998), pointing movements (Soechting et al., 2001), and the initiation of the optokinetic nystagmus (Waespe and Schwarz, 1987). Smooth pursuit eye movements to a single moving object can also be affected by additional motion signals in the vicinity, either from a second moving single object, as outlined above, or from a visual context.

Table 1 summarizes findings from behavioral studies conducted on humans or monkeys, in which eye movement

Table 1 – Overview of results from behavioral studies in humans and monkeys on context effects on pursuit eye movements (adapted from Spering and Gegenfurtner, 2007a)

	No effect	Pursuit enhancement	Pursuit impairment
Context stationary	No effect on velocity (2) No effect on latency (4,11,12)		Reduction in initial acceleration (7,11,12) Reduction in steady-state velocity (1,3,4,5,7,11,14) Longer latency (7,14)
Context moves in pursuit direction	No effect on latency (4,5)	Increase in initial velocity (4) Increase in steady-state velocity (4,5,7) Shorter latency (7)	
Context moves opposite	No effect on latency (4,5)	Increase in initial acceleration (5,7) and velocity (10) Increase in steady-state velocity (7)	Decrease in initial velocity (4) Decrease in steady-state velocity (4,5) Longer latency (7)
Velocity perturbation in pursuit direction	No effect on velocity, if initial context stationary (7,8)	Transient velocity increase, if initial context moving in pursuit direction (3,6,7,8,9,13), or stationary (3,6,9,13)	
Velocity perturbation opposite to pursuit	No effect on velocity (3,6,7,8,9,13)		
Orthogonal context perturbation		Transient velocity increase in perturbation direction (3,9)	Transient velocity increase in opposite direction to perturbation (7)

Numbers in the table correspond to references given in the following. Studies in humans: 1) Collewijn and Tamminga (1984); 2) Kowler et al. (1978); 3) Lindner et al. (2001); 4) Masson et al. (1995); 5) Niemann and Hoffmann (1997); 6) Schwarz and Ilg (1999); 7) Spering and Gegenfurtner (2007a); 8) Spering and Gegenfurtner (2007b); 9) Suehiro et al. (1999). Studies in monkeys: 10) Born et al., 2000; 11) Keller and Khan (1986); 12) Kimmig et al. (1992); 13) Kodaka et al. (2004); 14) Mohrmann and Thier (1995).

responses to target and context motion were measured. Although these studies differ with regard to species, paradigm (i.e., target velocity, type and velocity of context used, instruction), and set-up, there are some clear general tendencies.

Pursuit of a small object on a stationary textured background was generally found to be impaired, and initial acceleration and steady-state velocity were reduced (Collewijn and Tamminga, 1984; Lindner et al., 2001; Masson et al., 1995; Niemann and Hoffmann, 1997; Spering and Gegenfurtner, 2007a; Keller and Khan, 1986; Kimmig et al., 1992; Mohrmann and Thier, 1995). This suppressive effect of a stationary background was retained over a large area of space, and not restricted to the central part of the visual field that directly surrounded the target (Kimmig et al., 1992; Spering and Gegenfurtner, 2007a).

Results concerning the effects of a stationary or moving context on pursuit latency are inconclusive. Generally, context effects on latency can be caused by perceptual, motor, or cognitive mechanisms. It has been suggested that latency effects result from the observer's inability to attend to the target in the presence of a textured context, because the context renders the target less salient (Masson et al., 1995). However, in all studies reported here, the target does not come on suddenly, but is presented before the context appears or starts to move. Studies using single moving targets showed that when a distractor moved into the same direction as a target, latency was decreased. When the distractor moved opposite to the target direction, latency increased, irrespective of whether the monkey attended to the distractor or not (Ferrera and Lisberger, 1995). It is therefore more likely that latency effects (Table 1) are directly related to perceptual or motor factors, rather than to cognitive factors. Alternatively, the delay in pursuit initiation could be caused by the suppression of context-induced optokinetic nystagmus (OKN). When the context is stationary or moving counter-phase to the context, active pursuit of the target causes a retinal image shift of the context opposite to the target direction. Such context-induced retinal image motion drives a passive pursuit or slow-phase optokinetic response into the opposite direction. In order to smoothly track the target, the OKN has to be suppressed (Lindner and Ilg, 2006; Worfolk and Barnes, 1992; Wyatt and Pola, 1984), possibly causing the delay in initiating pursuit.

For moving backgrounds, most studies provide evidence for a spatial averaging of motion signals (motion assimilation). A background moving into the same direction as the pursuit target increased pursuit velocity, whereas a background moving into the opposite direction decreased eye velocity (Masson et al., 1995). Similarly, a brief background perturbation evoked a transient increase in eye velocity into the direction of the perturbation (Kodaka et al., 2004; Lindner et al., 2001; Schwarz and Ilg, 1999; Spering and Gegenfurtner, 2007a,b; Suehiro et al., 1999), when the background was moving into the same direction as the target. Pursuit was not affected by changes in background velocity, when the background moved opposite to the pursuit target. This asymmetry in context effects was attributed to an asymmetry in the suppression of the OKN (Lindner and Ilg, 2006). A background moving opposite to the pursuit target evokes OKN with a slow phase into the opposite direction to pursuit, thereby counteracting the pursuit response. Similarly, a background moving along with the pursuit target evokes an OKN into the same direction as pursuit, thereby boosting eye velocity (Masson et al., 1995; Raymond et al., 1984; Yee et al., 1983). Lindner and Ilg (2006) argue that the suppression of the OKN response during pursuit might be more complete when the background is moving into the direction opposite to the pursuit target.

However, there is some debate over what the effects of an oppositely moving context are. As an alternative to motion assimilation, some studies provide results in line with the idea that relative motion signals (motion contrast) are relevant for controlling pursuit in the presence of a moving background. These studies report an increase in initial acceleration and steady-state velocity, when the background moved into the direction opposite to the pursuit target (Born et al., 2000; Niemann and Hoffmann, 1997; Spering and Gegenfurtner, 2007a). Motion contrast also seems to drive pursuit to a horizontal target in response to brief vertical background perturbations (Spering and Gegenfurtner, 2007a).

Whereas these results in pursuit are similar to the perceptual effects reported for the Duncker illusion, most other studies (Table 1) show that eye movements follow motion assimilation when a dynamic background is present. A direct comparison between perception and pursuit of a moving target surrounded by a visual context is therefore necessary, to resolve the question whether motion signals from target and context are integrated in the same way for pursuit and perception.

5. Contextual effects on pursuit and motion perception

Generally, psychophysical studies in humans and monkeys have shown an excellent agreement between perceptual judgments of motion direction or velocity, and pursuit eye movements (Watamaniuk and Heinen, 1999; Beutter and Stone, 2000; Stone and Krauzlis, 2003; Gegenfurtner et al., 2003; Krukowski and Stone, 2005; Braun et al., 2006; Osborne et al., 2006). A tight link between motion perception and pursuit eye movements has also been implied by neurophysiological studies that demonstrated the involvement of the middle temporal visual area (MT) in motion perception (e.g., Newsome and Paré, 1988; Newsome et al., 1989; Salzman et al., 1990), and pursuit eye movements (e.g., Newsome et al., 1985; Komatsu and Wurtz, 1988; Groh et al., 1997; Lisberger and Movshon, 1999). Imaging studies in healthy human observers have underlined the role of area MT in motion perception (e.g., Tootell et al., 1995; Marcar et al., 1997; Huk and Heeger, 2000), and in pursuit eye movements (e.g., Konen et al., 2005; Nagel et al., 2006). Taken together, these results point to a shared motion processing system for perception and pursuit.

Some behavioral studies have found differences between pursuit and motion perception. Churchland et al. (2003) had observers discriminate between the directions of two trajectories along the cardinal or oblique axes. In line with the well-known oblique-effect, direction discrimination performance was better along the cardinal axes, but this anisotropy was not observed in the initial pursuit response. Irrespective of target direction, the eye movement response discriminated equally well between cardinal and oblique object motion. Conclusions about separate computations for perception and pursuit are difficult to draw from this work. A follow-up paper by Krukowski and Stone (2005) with the same paradigm reported an oblique-effect in perception and pursuit. Thus, there is strong evidence for shared motion processing for perception and pursuit.

However, most of the behavioral studies reported here used a classic set-up for smooth pursuit experiments with a single, bright dot moving across a uniform grey background. In the real world, the motion processing system is confronted with a more difficult task when a motion signal has to be extracted from a target of interest moving across a dynamic textured context. If the tight link between perception and pursuit indeed holds for more complex and dynamic visual situations, pursuit and perception should be similarly affected by a moving visual context.

Some studies have looked at motion perception during pursuit eye movements in response to a target surrounded by a context (Raymond et al., 1984; Schweigart et al., 2003). These studies did not directly compare perception and pursuit on the same trial. Zivotofsky (2005) used a variation of the Duncker illusion, in which a pursuit target was moving horizontally across a vertically drifting random dot pattern. The motion percept followed the Duncker illusion, i.e., the target was perceived to move into the opposite direction to background motion direction. Pursuit eye movements, on the other hand, were initiated in the direction of background motion, followed by a gradual shift in the direction of horizontal target motion.

Illusory motion of a visual background has been reported as a consequence of moving the eyes. In the "Filehne illusion" (Filehne, 1922; Mack and Herman, 1973), observers perceive a small background movement opposite to the eye movement direction when a moving target is smoothly tracked across a stationary visual background. This illusion is found in healthy human observers (Haarmeier and Thier, 1998), as well as in a patient with bilateral extrastriate cortex lesions who could not compensate for self-motion induced retinal image motion (Haarmeier et al., 1997). Usually, we are not aware of retinal image motion that results from our own movements, because the retinal motion signal is subtracted from an internal reference signal (efference copy). In the Filehne illusion, however, this comparison between eye-movement (self-) induced and object-motion (externally) induced retinal image motion is incomplete, and the resulting error signal is not compensated.

Spering and Gegenfurtner (2007b) analyzed motion perception and pursuit eye movements in human observers in response to step changes in target and context velocities. In each trial, pursuit target and visual context were independently perturbed simultaneously to briefly increase or decrease in velocity. Observers had to track the target and estimate whether target velocity had increased or decreased. Pursuit eye movements followed the vector average of target and context motion (Fig. 2a). The perceptual response was clearly different from the pursuit response: When target velocity remained unchanged, and the context briefly moved faster, eye velocity increased (vector average or motion assimilation), but target velocity was judged to be slower than before the perturbation (motion contrast). Observers systematically underestimated target velocity when context velocity increased, and overestimated target velocity when context velocity decreased (Fig. 2b). When a moving target is surrounded by a dynamic visual context, perception and pursuit can therefore differ: Perception is driven by a relative velocity signal and follows motion contrast, pursuit is driven by an average velocity signal and follows motion assimilation (Fig. 2c).

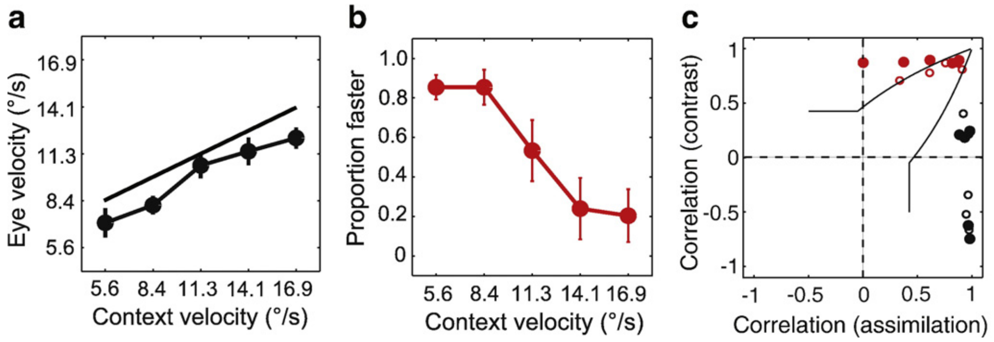

Fig. 2 – Mean pursuit and perceptual responses to velocity perturbations in target and context for five observers from a study by Spering and Gegenfurtner (2007b). (a) Eye velocity responses to five context perturbation velocities with fixed target velocity (11.3°/s). Individual data points are means ± SEM. The solid black line denotes the prediction of the assimilation model. (b) Perceptual judgment of target velocity (proportion faster; mean ± SEM) for same conditions as in (a). (c) Scatter plot of correlations between model predictions for assimilation and contrast and pursuit velocity (black) and perceived velocity (red). Filled circles, 100 ms perturbation interval (*n* = 5); hollow circles, 250 ms perturbation (*n* = 5). Class boundaries divide the plot into zones in which responses are classified as assimilation-type or contrast-type responses. Data points falling in the region marked "assimilation" are better predicted by the assimilation model, data points falling in the "contrast" region are better predicted by the contrast model. The correlation coefficients for these data points significantly differ from each other. Data points falling in between the boundaries are considered as unclassified, which means that responses are well predicted by both models because correlation coefficients do not significantly differ from each other (adapted from Spering and Gegenfurtner, 2007b, p. 1358).

A series of control experiments ruled out alternative explanations for the opposing effects of context motion on perception and pursuit. It was shown that the perceptual effect was not merely the result of a compensation for vector averaging, and therefore independent of the effect on pursuit (Spering and Gegenfurtner, 2007b). When the background moved into the opposite direction to the pursuit target the eye movement was unaffected, while perception still followed motion contrast. In contrast to what has been shown for the Filehne illusion (e.g., Haarmeier and Thier, 1998), the opposing effects in pursuit and perception in the Spering and Gegenfurtner (2007b) study were therefore not due to an inability to compensate for eye movements.

Despite the strong evidence for shared motion processing systems for perception and pursuit, there are some situations in which both types of behavior differ. The opposing effects of a dynamic context reflect the different needs for perception and pursuit. For the perceptual system, it is the most important task to isolate and segment a moving object from the background. This can be done by accentuating speed differences and calculating the relative velocity difference between object and background. Information about the absolute speed is not relevant for this task. For smooth pursuit eye movements, on the other hand, the most immediate demand is to extract a precise velocity signal in order to initiate and maintain an accurate eye movement. Integrating over a larger spatial region will generally improve this calculation, unless the relevant context contains a different motion signal.

The results obtained in Spering and Gegenfurtner (2007b) are for the steady-state phase of pursuit only. Other studies have reported motion contrast effects of background perturbations on initial pursuit acceleration or velocity (Table 1, e.g., Born et al., 2000; Niemann and Hoffmann, 1997; Spering and Gegenfurtner, 2007a). These studies imply that the mechanisms for integrating target and context motion signals might differ during pursuit initiation and maintenance. It is possible that the pursuit system is differentially sensitive to peripheral motion signals during the open- and closed-loop phase. Similar to the idea that motion contrast and assimilation are used to suit different task requirements, contrast and assimilation mechanisms could also be matched to the differential requirements of the open- versus closed-loop pursuit phase. During open-loop pursuit, the system is challenged to produce an eye movement into the correct direction and at a short latency. To achieve this, it seems more important to segment the target from its context than to derive a precise velocity signal. The earliest phase of the pursuit response has indeed been shown to be less sensitive to visual stimulus properties such as velocity (Lisberger et al., 1987). At a later stage of the pursuit response, it seems more important to match eye velocity to target velocity. The precision of the extracted velocity signal is usually enhanced when the system integrates over a large spatial region. Further evidence that different computational mechanisms might be used to extract a velocity signal during the open- and closed-loop phase of pursuit comes from a study by Recanzone and Wurtz (1999). Using a paradigm with two potential pursuit targets, these authors report that activity in MT neurons can shift from a vector averaging to a winner-take-all response with increasing time to respond to the target and increasing information about its motion trajectory. Similarly, Born et al. (2006) show that the integration of motion signals for pursuit changes over time. In this study, monkeys had to smoothly track moving, tilted line stimuli, thereby creating an "aperture problem" situation. Pursuit initiation during the first 40 ms was based on a relatively coarse estimate of local (1D) motion information, resulting in a substantial tracking error into the local motion direction (see also Masson and Stone, 2002). The relative importance of 2D velocity information increased over time, and subsequent pursuit went into the veridical motion direction. In a study on individual differences in the pursuit response, Wilmer and Nakayama (2007) show that open-loop pursuit is determined by low-level motion signals in which stimulus motion is derived directly from luminance changes in the retinal image. Closed-loop pursuit after the first catch-up saccade follows high-level motion signals that rely on salient features in the image that are tracked over time.

In addition to the phase of pursuit, the mechanism used for motion signal integration seems to be most crucially determined by the direction of the context motion. Motion contrast effects on pursuit eye movements were only obtained in studies with contexts moving counter-phase to the target, whereas motion assimilation effects were observed with in-phase context motion (see Table 1).

6. Neuronal correlates of contextual effects

The opposite effects of a dynamic context on perception and pursuit bear resemblance with the properties of receptive fields in area MT. For neurons in area MT, which integrate motion signals over space, a variety of center-surround mechanisms have been described (Allman et al., 1985; Born et al., 2000). One type of MT neurons responds best to wide-field motion stimuli, which extend the area of the classical receptive field, indicating a reinforcing surround. The other type of MT neurons does not respond to these stimuli, indicating an antagonistic surround. The existence of MT neurons with excitatory and inhibitory center-surround interactions has been taken as evidence for parallel processing of global and local motion information in area MT (Born and Tootell, 1992) and in areas that receive projections from MT (Berezovskii and Born, 2000). The perceptual and pursuit responses reported in Spering and Gegenfurtner (2007b) carry a clear signature of antagonistic and reinforcing surrounds. Perceptual responses, resulting from the computation of relative motion signals, might be mediated by motion-sensitive neurons with antagonistic surrounds (local-motion sites) in area MT. Pursuit responses, on the other hand, might be mediated by neurons with receptive fields that spatially sum over larger regions of the visual field (global-motion sites) in area MT. Motion information for perception and pursuit might therefore be processed in separate but parallel processing streams in local- and global-motion sites in area MT.

7. Summary

Given the complexity and variety of our natural environment, our visual system has to be highly adaptable to different contexts and requirements, in order to guide motor action appropriately. In this review, we have summarized studies that provide evidence for the strong influence of context and task on smooth pursuit eye movements. Depending on the nature of the visual context and the requirement for the eye movement, motion signal integration for pursuit can follow different computational mechanisms. We have also provided evidence for separate motion processing mechanisms of target and context motion signals for motion perception and pursuit, with a potential neural correlate of these mechanisms in area MT. Motion perception and pursuit are tightly linked with regard to the brain areas that process the motion signal, but the underlying integration algorithms might differ.

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