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Contrast and Assimilation in Motion Perception and Smooth Pursuit Eye Movements

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Spering M, Gegenfurtner KR. Contrast and assimilation in motion perception and smooth pursuit eye movements. *J Neurophysiol* 98: 1355–1363, 2007. First published July 18, 2007; doi:10.1152/jn.00476.2007. The analysis of visual motion serves many different functions ranging from object motion perception to the control of self-motion. The perception of visual motion and the oculomotor tracking of a moving object are known to be closely related and are assumed to be controlled by shared brain areas. We compared perceived velocity and the velocity of smooth pursuit eye movements in human observers in a paradigm that required the segmentation of target object motion from context motion. In each trial, a pursuit target and a visual context were independently perturbed simultaneously to briefly increase or decrease in speed. Observers had to accurately track the target and estimate target speed during the perturbation interval. Here we show that the same motion signals are processed in fundamentally different ways for perception and steady-state smooth pursuit eye movements. For the computation of perceived velocity, motion of the context was subtracted from target motion (motion contrast), whereas pursuit velocity was determined by the motion average (motion assimilation). We conclude that the human motion system uses these computations to optimally accomplish different functions: image segmentation for object motion perception and velocity estimation for the control of smooth pursuit eye movements.

INTRODUCTION

The relationship between neuronal activity in the middle temporal visual area (MT) and perceptual judgments of motion has been demonstrated convincingly in the monkey (Newsome et al. 1988, 1989; Salzman et al. 1990). Neurons in monkey brain area MT also provide visual motion signals for the control of smooth pursuit eye movements (Groh et al. 1997; Komatsu and Wurtz 1988; Lisberger and Movshon 1999; Newsome et al. 1985). Similarly, patient studies and imaging studies in healthy observers revealed that the MT complex in humans is closely related to motion perception (Huk and Heeger 2000; Marcar et al. 1997; Tootell et al. 1995). Generally, psychophysical studies in monkeys and humans have shown an excellent agreement between perceptual judgments of motion direction or velocity and pursuit eye movements (Beutter and Stone 2000; Braun et al. 2006; Gegenfurtner et al. 2003; Krukowski and Stone 2005; Osborne et al. 2006; Stone and Krauzlis 2003; Watamaniuk and Heinen 1999). Although area MT and the adjacent middle superior temporal area (MST) might not be the final sites for the processing of motion information for motion perception, as indicated by a study showing that neuronal activity in these cortical areas does not

code direction of second-order motion or moving auditory stimuli (Ilg and Churan 2004), these areas evidently play a major role in processing motion information for perception and pursuit. Motion perception and pursuit seem to be controlled by the same computations and feature similar thresholds for discriminating changes in speed or direction.

Many of these studies used situations in which a single object moved across a uniform gray background. Here we ask whether the close relationship between both behaviors also holds in more complex and dynamic situations. When motion information from multiple sources has to be integrated, either from two moving objects presented simultaneously to the observer (Lisberger and Ferrera 1997; Recanzone and Wurtz 1999) or from a combination of a visual and an electrical motion signal evoked by microstimulation in area MT (Groh et al. 1997), the initial pursuit response follows the average motion signal. This early vector averaging response in pursuit can shift toward a winner-take-all behavior when the exposure duration to the two potential target stimuli is increased before pursuit onset (Recanzone and Wurtz 1999) or when the second object appears during the steady-state phase of the eye movement and its direction and speed are highly predictable (Sperring et al. 2006). Vector averaging is also the most commonly used strategy in steady-state pursuit when a target moves across a full-field visual background (Masson et al. 1995; Niemann and Hoffmann 1997) or within a visual context (Sperring and Gegenfurtner 2007). When the context moves along with the pursuit target, eye velocity increases; when the context moves opposite to the pursuit target, eye velocity decreases. Some studies report an increase in initial eye acceleration and velocity for oppositely moving contexts in humans (Niemann and Hoffmann 1997; Sperring and Gegenfurtner 2007) and monkeys (Born et al. 2000). However, brief velocity injections in a moving context during ongoing pursuit produced very clear results. Eye velocity increased and decreased transiently with increasing and decreasing context velocity, respectively (Kodaka et al. 2004; Lindner et al. 2001; Schwarz and Ilg 1999; Sperring and Gegenfurtner 2007; Suehiro et al. 1999).

However, the computational mechanisms underlying the integration of multiple motion stimuli for velocity perception are less clear. In experiments on induced motion, Duncker (1929) demonstrated that motion in one part of the visual field can influence motion perception in another part of the scene. When observers fixated a stationary target, this stimulus appeared to move in the direction opposite to a moving surround.

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These early results follow a different computational strategy than pursuit responses to multiple moving stimuli and seem to reflect inhibitory rather than excitatory mechanisms. Indeed, vector averaging is not the only motion-integration algorithm that has been found in the brain. 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 that extend the area of the classical receptive field, indicating a reinforcing surround. The other type does not respond to these stimuli, indicating an antagonistic surround. Excitatory and inhibitory center-surround interactions have been assumed to be related to the processing of global and local motion, respectively (Born and Tootell 1992). These mechanisms in receptive field organization could be the neuronal correlate of different algorithms for motion integration, such as motion averaging and motion contrast.

It is the aim of this study to directly compare motion perception and steady-state pursuit eye movements in response to a moving target that is surrounded by a dynamic visual context to test whether motion integration for perception and pursuit maintenance follows similar computational mechanisms. To this end, we analyzed motion perception and pursuit eye movements in human observers in response to step changes in target and context velocity. In each trial, pursuit target and visual context were independently perturbed simultaneously to briefly increase or decrease in velocity. Observers accurately tracked the target and estimated whether target velocity had increased or decreased. In contrast to most paradigms used in previous studies, but similar to the challenges of the real world, target velocity judgments were made more difficult by an additional motion signal from the visual surround. Based on previous results, we predict the following possible outcomes for perceived and pursuit velocity. If the observer succeeds in discounting context motion, responses will follow target velocity. If the observer takes into account context motion, the corresponding motion signal can either be added to or subtracted from target motion, resulting in the use of average motion signals (assimilation) or relative motion signals (contrast). If perception and oculomotor action are driven by the same visual signal, the pattern of results should be the same for perception and pursuit.

METHODS

Observers

Observers were from a pool of six female undergraduate students (mean age: 24.3 ± 1.2 yr) from the University of Giessen, Germany. All observers were trained in eye-tracking experiments, but naïve as to the purpose of the experiments, and had normal visual acuity. Experiments were in accordance with the principles of the Declaration of Helsinki for the protection of human subjects. We report results from five separate experiments. Observers AE and AM participated in all five experiments. Observers AK, CB, and CF participated in three experiments and CO took part in two experiments (see following text).

Eye movement recording and visual stimuli

The position of each observer's right eye was measured with a dual-Purkinje-image infrared eye tracker (Fourward Technologies Generation 6.1, Buena Vista, VA) at 500 Hz. The eye-tracking setup and the recording and calibration procedures were identical to those

described in our previous studies (Spering and Gegenfurtner 2007). Eye velocity profiles were obtained off-line by digital differentiation of eye position signals over time, and eye velocity was filtered using a low-pass filter with a cutoff at 60 Hz. The pursuit target was a Gaussian dot ($SD = 17$ pixels, 0.47°) presented at 50% contrast. A visual context consisted of two vertically oriented sinusoidal gratings with a spatial frequency of 0.5 c/deg and 100% contrast, presented above and below the target trajectory. The context had the same mean luminance as the background. The two sinusoidal gratings were 1.1° apart and randomly shifted in phase by 0 to 0.5 cycles.

Experimental design and procedure

Each trial started with 500-ms central fixation in the presence of a stationary context. On disappearance of the fixation spot, the target appeared at 10.5° to the left or right of fixation and moved horizontally toward the center of the monitor with a velocity of $11.3^\circ/s$. The context initially moved at the same velocity as the target. After 500 ms, target and context were briefly perturbed in velocity for 100 ms to move slower (5.6 or $8.4^\circ/s$) or faster (14.1 or $16.9^\circ/s$) than before perturbation. In control trials, target and context velocity remained unchanged at $11.3^\circ/s$. Step changes in velocity in target and context were independent, yielding 25 conditions (5 target velocities \times 5 context velocities). After the perturbation interval, target and context stepped back to their initial velocity for 400 ms. Trials with leftward and rightward horizontal target motion and different conditions were equally balanced and randomized within a block of trials. Observers were instructed to smoothly track the horizontal target. After each trial, observers had to judge whether the target had increased or decreased in velocity during the perturbation interval, by pressing an assigned button for "slower" or "faster."

Additional experiments were manipulations of the basic procedure described earlier. First, we repeated the basic experiment, but with a longer perturbation duration (250 ms). We also used different context velocities before perturbation (slower: $8.4^\circ/s$ or stationary: $0^\circ/s$) with a 100-ms perturbation interval. Further, we tested the effect of a context moving opposite to the target at a velocity of $-11.3^\circ/s$. Here, the context was also perturbed into the opposite direction with the same range of perturbation velocities and the same duration as in the basic experiment (-5.6 to $-16.9^\circ/s$). Each observer completed between two and four blocks of 200 trials for each experiment in sessions lasting 45–60 min.

Analysis of eye movement data and perceptual judgments

Eye movement data were preprocessed following methods described in detail previously (Spering and Gegenfurtner 2007). Briefly, saccades were detected in horizontal and vertical eye velocity profiles by applying a combined position and acceleration criterion. Time intervals in which a horizontal or vertical saccade was detected were then removed from the horizontal eye velocity trace. The interval for analyzing mean horizontal eye velocity was centered around the peak of the perturbation effect. We averaged across a time interval of 150 ms, starting 100 ms after the onset of the velocity perturbation. All trials were visually inspected to verify that the algorithm for saccade detection identified all saccades. Error trials, defined as trials with blinks, trials with saccades in the analysis interval, or trials in which the eye tracker lost the signal, were excluded. The proportion of excluded trials ranged from 8% (100-ms perturbation experiment) to 24.5% (opposite-motion experiment). We also excluded these trials from the analysis of perceptual judgments. Because we did not find any systematic differences between rightward and leftward pursuit, trials were averaged across both motion directions.

The four possible result patterns (Fig. 1) yielded model predictions following the general form $R = (w1 * t) + (w2 * c) - k$, where R represents the observer's perceptual or pursuit response; t is target velocity; c is context velocity; and $w1$ and $w2$ represent weighting

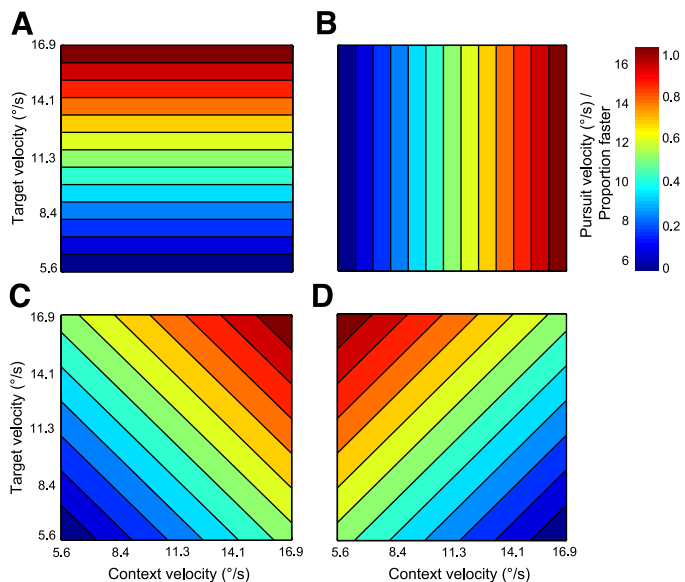


FIG. 1. Model plots for behavioral responses to velocity perturbation. Target and context initially moved at 11.3°/s and were independently perturbed in velocity to move at 5.6, 8.4, 11.3, 14.1, or 16.9°/s during the perturbation interval. Pursuit velocity or perceptual velocity judgment “slower” (blue) vs. “faster” (red) follows (A) target velocity, (B) context velocity, (C) a weighted average of target and context velocity (motion assimilation), and (D) the relative velocity difference between target and context velocity (motion contrast).

factors with values of 0.5 for motion assimilation and values of 1 and -1 for motion contrast, respectively. To hold for cases in which results follow motion contrast, a constant factor k , initial eye velocity 11.3°/s or neutral perceptual judgments 0.5, has to be subtracted. Following standard methods, we computed the correlation coefficients between mean pursuit velocity during the analysis interval or perceptual judgment and the model predictions for each observer. Based on the results of previous studies on multiple motion signals, we put emphasis on testing assimilation versus contrast predictions. The assimilation and contrast model predictions were uncorrelated. Class boundaries were determined by a conservative statistical criterion (Movshon et al. 1985).

RESULTS

Perception follows motion contrast; pursuit follows motion assimilation

In the first experiment, we tested the effect of brief (100-ms) velocity perturbations in a pursuit target and a surrounding context in five observers (AE, AK, AM, CB, CO). Initially, the context moved into the same direction as the target at the same velocity. Results for one representative observer (CB) are depicted in Fig. 2A and show that context perturbations generally affected pursuit velocity. With target velocity kept constant, eye velocity transiently increased for increasing context velocity and decreased for decreasing context velocity. Eye velocity changed time-locked to perturbation onset after about 100 ms and started to increase or decrease steeply. It reached a velocity peak approximately 140 ms after perturbation onset and decreased or increased to a baseline velocity of about 11.3°/s with occasional overshoots. Results followed this time course irrespective of the perturbation duration (Fig. 2, A and B). The magnitude of the effect was similar for both perturbation durations. The transient change in eye velocity in response

to the velocity change for either perturbation duration was not due to a corrective saccade. The analysis included only trials in which no saccade occurred during the relevant time interval for analysis after the perturbation (see METHODS). For the experiment with the 100-ms (250-ms) perturbation duration, we collected 2,800 (3,400) trials in total and excluded 224 (361) trials due to saccades during the analysis interval. However, we did observe corrective saccades before and after the analysis interval in some of the remaining trials. In 5.2% (3.8%) of the remaining trials, a saccade was detected before the analysis interval with a mean latency of 55.7 ± 10.6 ms (57.2 ± 13.7 ms) with respect to the perturbation onset. In 16.1% (20.2%) of the remaining trials, a saccade was made after the relevant analysis interval. These saccades had a mean latency of 303 ± 16.2 ms (305.3 ± 16.1 ms) with respect to the perturbation onset. In neither of the two experiments can these early or late corrective saccades account for the systematic changes in eye velocity with different perturbation velocities in target and context. In addition, we occasionally noted that observers anticipated target motion before motion onset (for example, see

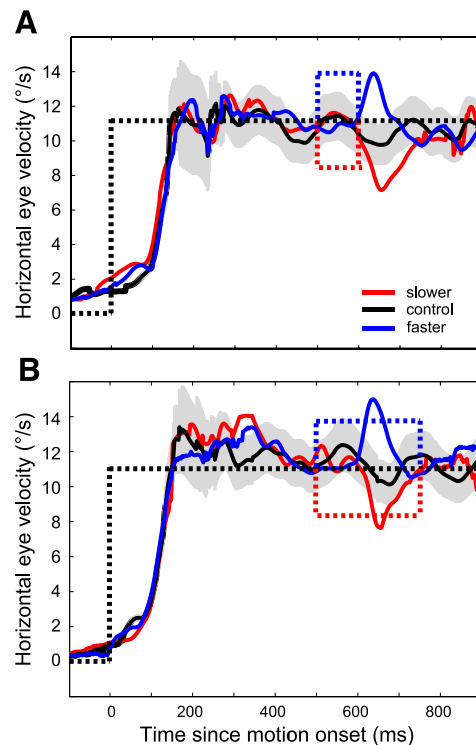


FIG. 2. Smooth pursuit eye velocity profiles in response to step changes in context velocity. Two panels show responses to 2 different perturbation durations: 100 ms (A) and 250 ms (B). Pursuit responses are mean filtered and desaccaded horizontal eye velocity traces averaged across trials with rightward and leftward target motion for observer CB, plotted from 100 ms before target motion onset. In trials with motion to the left pursuit responses were inverted. Context velocity perturbation started 500 ms after target motion onset. In all conditions plotted here, target velocity was unchanged at 11.3°/s (black dotted line). Context was perturbed to move slower (red, 8.4°/s), faster (blue, 14.1°/s), or was unperturbed (black, 11.3°/s). Shaded gray area depicts the SD of horizontal eye velocity in the control condition. All data plotted here are based on 32 trials per condition. In A, between 14 to 32 trials were used in the control condition; in B, 12 to 31 trials were used. Variation in the number of trials is explained by the fact that samples with saccades were removed from the velocity trace. Note that during the relevant interval for analysis, the algorithm detected no saccades in A and one saccade in B. Trials in which a saccade was detected during the analysis interval were excluded from the analysis.

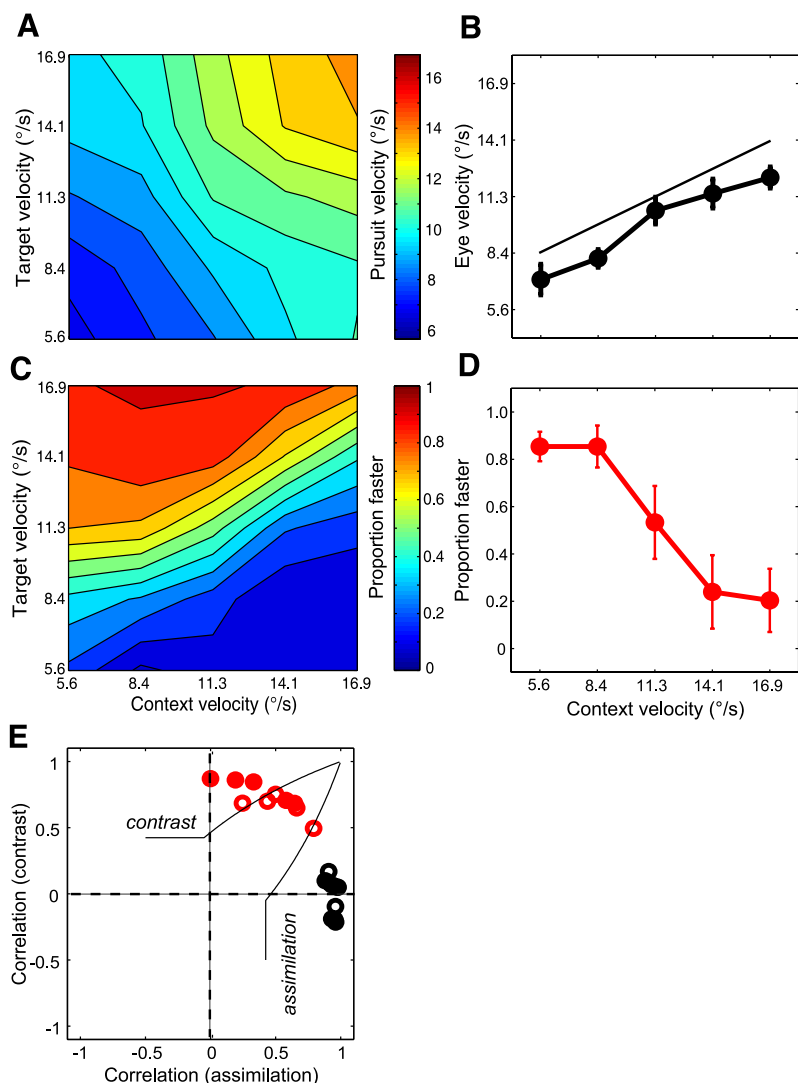


FIG. 3. Mean pursuit and perceptual responses to velocity perturbations in target and context for 5 observers. *A*: mean horizontal eye velocity responses to all target and context perturbation conditions. *B*: eye velocity responses to 5 context perturbation velocities with fixed target velocity ($11.3^\circ/\text{s}$). Individual data points are means \pm SE. Solid black line denotes the prediction of the assimilation model. *C*: mean target velocity judgments in all conditions. *D*: perceptual judgment of target velocity (proportion faster; means \pm SE) for same conditions as in *B*. *E*: scatterplot 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 interval ($n = 5$). 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. 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.

Fig. 2A). However, this behavior was not disruptive to the analysis of perturbation effects during steady-state pursuit.

Across all conditions and all five observers tested in this experiment, pursuit velocity followed predictions of the motion assimilation model. Figure 3A shows results for all perturbation conditions; Fig. 3B shows results for the effect of context perturbations when target velocity was unchanged. Generally, pursuit velocity was faster for contexts moving faster during the perturbation interval and slower for slower moving contexts. These results are similar to those obtained in earlier studies with a full-field textured background (Kodaka et al. 2004; Lindner et al. 2001; Schwarz and Ilg 1999; Suehiro et al. 1999) or a surrounding context (Spering and Gegenfurtner 2007). These authors showed that abrupt changes in background or context velocity transiently affected eye velocity in the direction of the context velocity change. However, the perception of velocity was not tested.

Here we show that results for perceptual judgments were entirely different from pursuit responses (Fig. 3, C and D). When the context moved faster, target velocity was underestimated. For slower moving contexts, target velocity was overestimated. Therefore perceived velocity followed motion contrast. The opposing effects in pursuit and perception become

particularly clear for the condition in which target velocity was unperturbed and any changes in perceived and pursuit velocity are solely due to the context (Fig. 3, B and D).

For each observer's responses across all conditions, separately for perception and pursuit, we calculated correlation coefficients between behavioral responses and model predictions (assimilation vs. contrast). The correlation coefficients reflect the classification of each observer's response as following assimilation or contrast. Figure 3E shows that resulting distributions of correlation coefficients were clearly separated: Perceptual responses were better predicted by the motion contrast model or were unclassified, whereas pursuit responses were better predicted by the assimilation model. The same results were obtained with a longer perturbation interval (250 ms) in five observers (AE, AK, AM, CB, CF; hollow circles in Fig. 3E). Therefore target and context velocity perturbations contrarily affected motion perception and pursuit velocity.

These results imply that the neuronal systems underlying velocity perception and pursuit velocity control might use different computational analyses for reading out sensory motion signals. Alternatively, the perceptual result might be influenced by the eye movement signal itself. Perceived velocity and direction of motion have been shown to be affected by eye

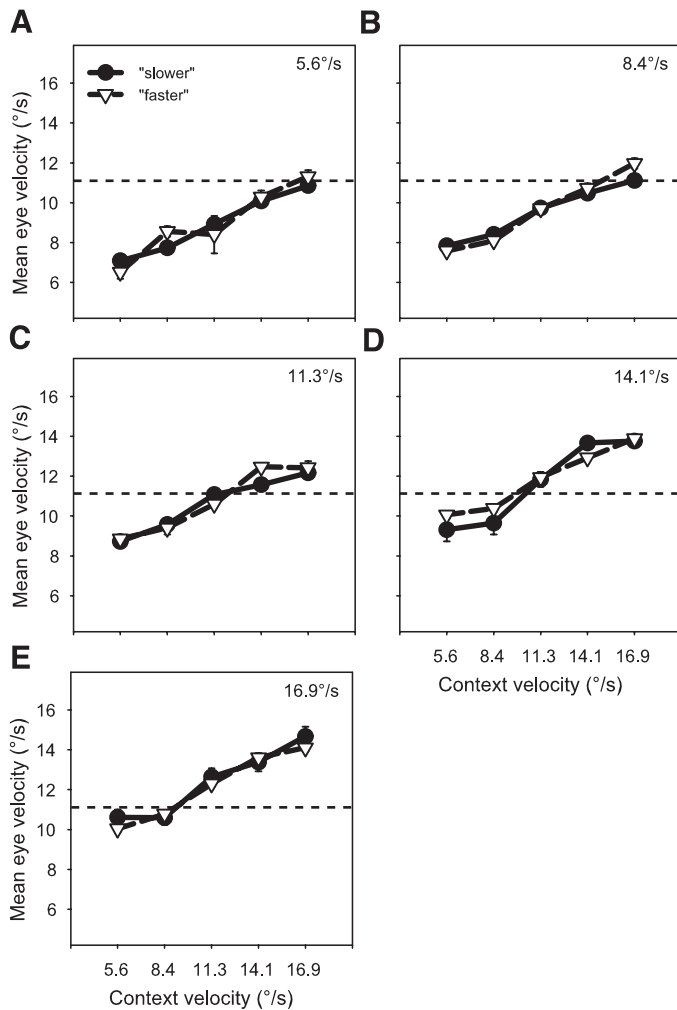


FIG. 4. Horizontal pursuit eye velocity divided by judgment categories for 5 observers in the basic experiment. A–E: results for different target velocities separately. Judgment categories are denoted by symbols (filled circles, “slower”; triangles, “faster”). Individual data points are means \pm SE.

movement signals (Brenner and Van den Berg 1994; Souman et al. 2005). If the perceptual judgments obtained here were due to a compensation for pursuit velocity, the pursuit response should differ between judgment categories and be higher for “slower” judgments than for “faster” judgments. In the 100-ms perturbation experiment, we therefore divided pursuit responses according to observers’ judgments “slower” and “faster” into two categories and compared pursuit velocities across all perturbation conditions between judgment categories. Figure 4 reveals that there were no differences in mean eye velocity responses between judgment categories. We used a multiple regression analysis to test for partial effects of judgment category with target and context velocity as additional predictor variables. As expected, partial regression coefficients for target velocity ($B = 0.89, t = 21.87$) and context velocity ($B = 1.02, t = 25.05$) were significantly different from zero in a two-tailed partial t -test ($P < 0.001$), whereas the regression coefficient for judgment category was not ($B = 0.43, t = 0.37, P = 0.71$). Therefore the perceptual judgment cannot have been caused merely by differences in pursuit velocity.

Simplification of target–context segmentation affects pursuit, but not perception

To further test the assumption that perceptual judgment and pursuit velocity interact, we conducted a series of control experiments in which the initial context velocity was different from target velocity. It is known that with velocity injections in oppositely moving backgrounds there is little or no context effect on pursuit (Kodaka et al. 2004; Lindner et al. 2001; Schwarz and Ilg 1999; Spering and Gegenfurtner 2007; Suehiro et al. 1999). With target and context moving into opposite directions, it becomes easier to segregate target from context motion. In the following experiments, we therefore varied the ease of target–context segmentation. In the first manipulation of the basic experiment, the context moved slower than the target at 8.4°/s until the onset of the perturbation. Four observers were tested in this experiment (AE, AM, CF, CO). Similar to the results reported for the basic experiment, we found that pursuit velocity followed assimilation, and perception went in the direction of the relative motion signal (Fig. 5). The effect in perception was smaller than that in the original experiment (compare Fig. 5D with Fig. 3D) and always remained <0.5 on average. Note that with a context moving at 8.4°/s initially, the context velocity increases during the perturbation interval more often (for perturbation velocities 11.3, 14.1, and 16.9°/s) than

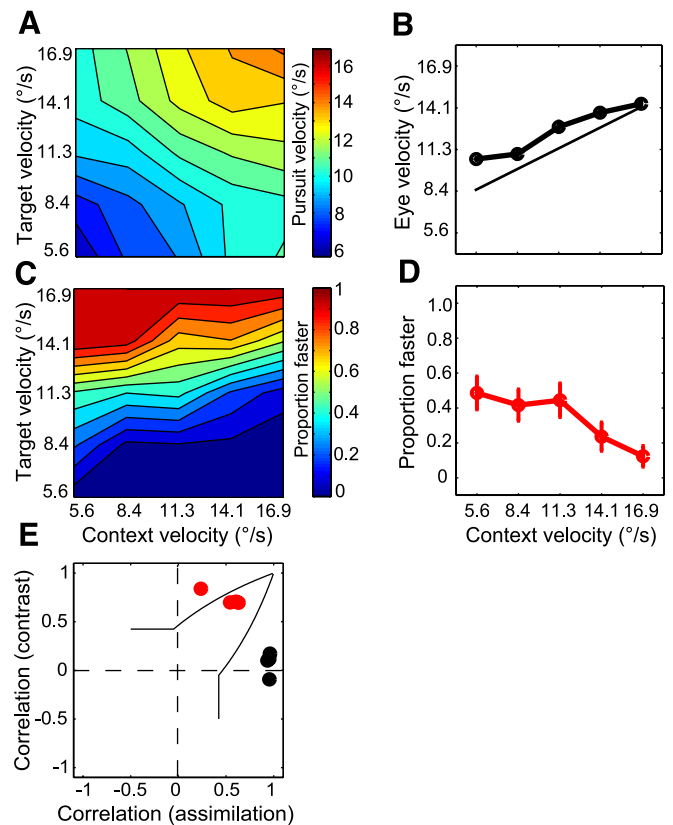


FIG. 5. Results in pursuit and perception for a context moving slower before perturbation for 4 observers. A: pursuit responses for all context and target perturbation velocities. B: pursuit responses for 5 context perturbation velocities and fixed target velocity at 11.3°/s; individual data points are means \pm SE. Solid black line denotes assimilation model prediction. C: perceptual results for all conditions. D: perceptual results for fixed target velocity. E: scatterplot of correlations between model predictions for assimilation and contrast and pursuit velocity (black) and perceived velocity (red). Class boundaries are the same as in Fig. 3E.

it decreases (perturbation velocity 5.6°/s). With perceptual judgments following motion contrast, the observer will respond “slower” more often than “faster” with a higher number of trials in which the context increases in velocity during the perturbation interval.

Next, in a 100-ms perturbation interval, we used perturbation velocities 5.6 to 16.9°/s for the target and -5.6 to -16.9 °/s for a context moving in the opposite direction to the target in five observers (AE, AK, AM, CB, CF). This experiment also tests for an effect of the eye movement on perceptual judgments: If the lack of effect of an oppositely moving context on pursuit is replicated here, and if the effect on perception persists, this would be further proof of the independence of the perceptual effect. Results show indeed that context perturbation had no effect on pursuit velocity (Fig. 6). Irrespective of context perturbation velocity, eye velocity followed target velocity. Note that eye velocity was generally slower than when the context moved along with the pursuit target, in line with earlier findings for opposite context motion on steady-state pursuit (Masson et al. 1995; Niemann and Hoffmann 1997). In previous studies (e.g., Lindner et al. 2001; Schwarz and Ilg 1999), it was assumed that the lack of context perturbation effect on pursuit under these conditions might be due to the observer not perceiving the velocity perturbation in an oppositely moving context. However, we found that perceptual judgments were affected by context perturbations (see Fig. 6, C and D). Target velocity was generally perceived as slower than when the context moved along with the target, but overall, perceptual judgments followed motion contrast. Be-

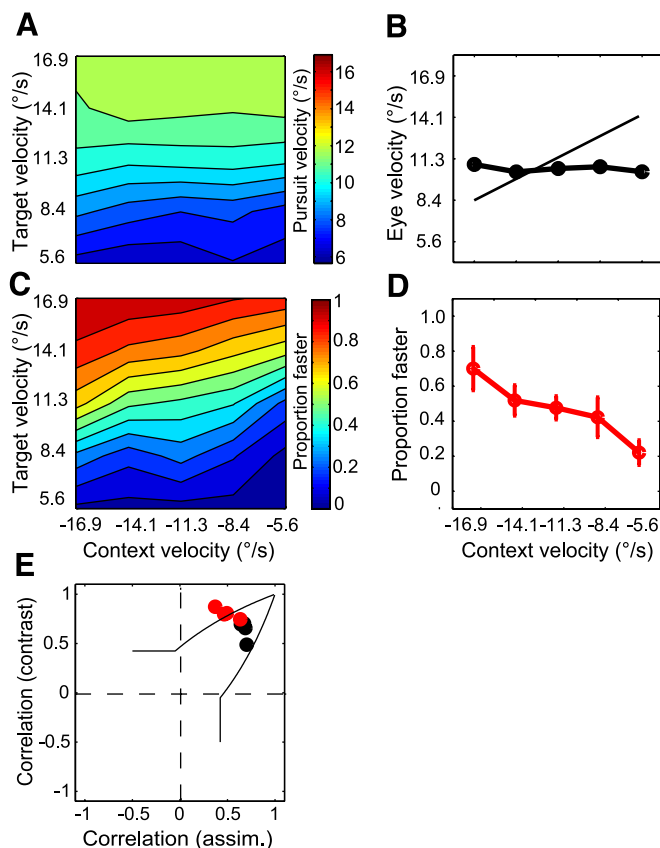


FIG. 6. Results in pursuit and perception for opposite context motion for 5 observers. A–E: results in same order as in Fig. 5.

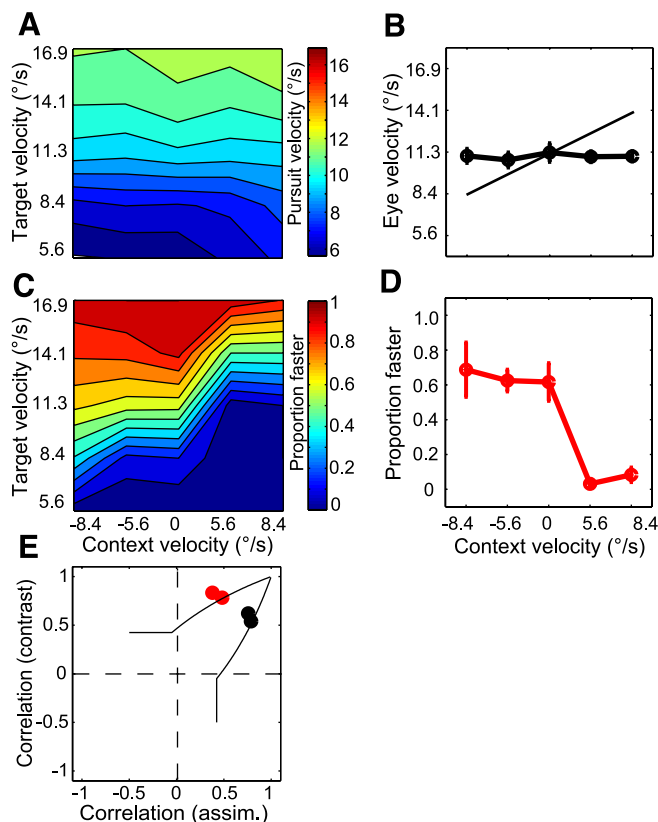


FIG. 7. Results in pursuit and perception for a stationary context before perturbation for 2 observers. A–E: results in same order as in Fig. 5.

cause we do not see an effect on pursuit but on perception only, we assume that the perceptual effect is not likely to be caused by an internal motor feedback signal from the pursuit eye movement.

We further tested the effect of a context that remained stationary (0°/s) until the perturbation onset. During the perturbation interval, the context was perturbed to move into the same (5.6 or 8.4°/s) or opposite (-5.6 or -8.4 °/s) direction to the target. We tested two observers (AE, AM) in this experiment. The results are very similar to those obtained with an oppositely moving context (Fig. 7). From this series of control experiments we conclude that the opposing effects in perception and pursuit are independent. The fact that pursuit was not affected by an oppositely moving context, whereas perception was affected, provides further evidence for separate motion-processing algorithms for perception and pursuit.

DISCUSSION

Situational demands determine which motion integration mechanism is used

Our results show that the perception of target velocity and pursuit of a moving target follow different patterns. Whereas a perceptual velocity judgment was driven by a relative motion signal, pursuit velocity followed motion assimilation. The different context effects obtained in this study reflect the different needs for motion perception and eye movement control. In complex and dynamic scenes, the most important task for the perceptual system is 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 to initiate and maintain accurate eye movements. Integrating over a larger spatial region will generally improve this calculation, unless, as in our case, the relevant context contains a different motion signal.

Comparison with other studies

A prominent example for the notion that relative motion signals are vital for the segmentation of image motion is the Duncker illusion (Duncker 1929). Here, motion in one part of the visual field influences motion perception in another part of the scene, and a stationary target usually appears to move in the direction opposite to a moving surround (induced motion). In similar experimental situations, the perception of target motion direction has been shown to follow relative motion (Anstis and Casco 2006; Nawrot and Sekuler 1990; Zivotofsky et al. 1995). However, pursuit eye movements were initiated in the direction of background motion, followed by a gradual shift in the direction of horizontal target motion (Zivotofsky 2005). This result could be due to different latencies evoked by target stimulus and background. The visual background used in the studies by Zivotofsky and colleagues was superimposed on the target trajectory. Two other studies report contrast effects on target motion perception when a pursuit target was surrounded by a visual context moving into the same or opposite direction (Raymond et al. 1984; Schweigart et al. 2003). Raymond et al. (1984) did not measure pursuit eye movements and were therefore not able to directly compare perception and pursuit. Schweigart et al. (2003) compared their perceptual results to an internal pursuit drive signal derived from a model simulation of pursuit velocity control in the presence of a moving visual background. The model includes the assumption that pursuit is essentially unaffected by a moving background and follows target velocity, whereas target velocity perception is assumed to be driven by an internal premotor target velocity signal that differs from the final driving signal for pursuit. Our findings disagree with the assumption that pursuit velocity follows the veridical target velocity signal in the presence of a moving context. In accordance with previous behavioral results obtained with multiple motion signals from two possible target stimuli (Ferrera and Lisberger 1997; Lisberger and Ferrera 1997) or a target and a visual background (Kodaka et al. 2004; Lindner et al. 2001; Masson et al. 1995; Schwarz and Ilg 1999; Spering and Gegenfurtner 2007; Suehiro et al. 1999), we observed a strong effect of the moving visual context on pursuit velocity in the direction of the vector average. The idea that the “choice” of motion processing mechanism depends on the requirements of the task—in our case making a pursuit eye movement or judging an object’s velocity—is not new. Recanzone and Wurtz (1999) suggested that activity in the same neurons in area MT can shift from vector-averaging to winner-take-all behavior, depending on how long the two potential targets were presented before pursuit initiation and on how far they were separated in space. These findings imply that the shift occurs with increasing time to respond to the target and increasing information about its direction and speed (see also

Lisberger and Ferrera 1997; Spering et al. 2006). In the present experiments, stimulus conditions were identical but different tasks required observers to focus on different aspects of the visual scene.

Other studies have reported effects of motion contrast on pursuit eye movements in the presence of a moving visual context. In humans, Niemann and Hoffmann (1997) tested the effect of a full-field textured background that moved continuously into the same or opposite direction to the pursuit target at a constant speed throughout the trial. Depending on the pursuit phase analyzed, there is evidence for contrast-type as well as assimilation-type effects in the pursuit responses obtained in this study. Whereas initial eye acceleration increased in response to an oppositely moving context (contrast), steady-state eye velocity gain decreased (assimilation). Similar contrast effects on initial pursuit acceleration were obtained with a continuously moving version of the peripheral context used in the present study, when it moved into the opposite direction to the pursuit target (Spering and Gegenfurtner 2007). These findings imply that there might be differences in the mechanisms for integrating target and context motion signals during pursuit initiation and maintenance. Whereas initial pursuit seemed to be driven by the relative velocity difference between target and context, steady-state pursuit more often followed an average motion signal in these studies. There are indeed important differences between pursuit initiation and maintenance that might account for the evidence for contrast and assimilation effects, respectively. Whereas open-loop pursuit is mainly driven by a visual signal and internal feedback on retinal target slip is not yet available to the system, closed-loop pursuit follows visual inputs related to a retinal velocity error signal (Lisberger et al. 1987). It is possible that the pursuit system is differentially sensitive to visual motion signals from the background or the periphery during the open- and closed-loop phase. Similar to the idea that motion contrast and assimilation are used to suit different task requirements posed by velocity perception versus pursuit velocity control, 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, it is 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.

These considerations might play a role in explaining the different context effects obtained during pursuit initiation and maintenance in the studies mentioned earlier (Niemann and Hoffmann 1997; Spering and Gegenfurtner 2007), although there is also evidence for motion assimilation-type effects on pursuit initiation. Masson et al. (1995) report that a background moving into the opposite direction to the pursuit target produced a decrease in initial eye velocity. These differences in results might arise from methodological differences concerning the time interval chosen for analyzing initial pursuit velocity

versus acceleration (for a detailed discussion of methodological issues, see Niemann and Hoffmann 1997).

The paradigm used in those earlier studies differs from the paradigm that we used here. In the present study, the effect of a transient velocity change in target and/or context velocity on eye velocity during ongoing pursuit was studied. It therefore seems more reasonable to compare our results to data obtained in studies that used a similar transient velocity shift in a stationary or moving context in humans (e.g., Schwarz and Ilg 1999; Spering and Gegenfurtner 2007) or monkeys (Born et al. 2000). Schwarz and Ilg (1999) found that eye velocity increased or decreased transiently in the direction of a horizontal background motion injection that was applied for 200 ms starting at different time intervals during the open- or closed-loop phase of horizontal pursuit. This assimilation-type effect occurred independently of the start of the perturbation relative to pursuit onset, but was observed only when the background was shifted into the same direction as the target. The same asymmetry was observed in a previous series of experiments by Spering and Gegenfurtner (2007), in which a 300-ms perturbation occurred during the steady-state phase of horizontal pursuit, and with a 100- and 250-ms perturbation in the present study. However, Born et al. (2000) observed the exact opposite effect of a brief background velocity injection that coincided with pursuit onset on initial eye velocity in monkeys. In that experiment, a background was either shifted downward (270°) or to the right and slightly upward (12° from horizontal) for 250 ms, starting at the time of pursuit onset. As a result, horizontal pursuit responses were shifted in the direction opposite to the background motion. Although this contrast effect on open-loop pursuit clearly differs from the assimilation-type response pattern reported in the present study, it resembles the findings that we obtained in previous experiments with vertical motion of a single distractor stimulus (Spering et al. 2006) or with vertical (90 or 270°) context motion injections (Spering and Gegenfurtner 2007) during the closed-loop phase.

It therefore seems that a number of methodological and theoretical considerations play a role in whether assimilation- or contrast-type effects are observed (for discussions, see Born et al. 2000; Niemann and Hoffmann 1997). The differences in results are unlikely to result from differences in the background used (sine-wave grating, random-dot pattern, or line elements) because we observed both types of effects with a sine-wave grating context. Also, the position of the target during context perturbation (central or peripheral location) seems to be of minor importance because assimilation-type effects were observed with different target locations at the beginning of the perturbation interval in the Schwarz and Ilg (1999) study. However, the crucial difference between studies reporting assimilation or contrast in pursuit responses to brief context motion injections seems to be the direction of the context motion during the perturbation interval. Pursuit followed assimilation only when the context was moving into the exact same direction as the pursuit target. For slightly offset from horizontal background motion direction or vertical motion directions, pursuit followed motion contrast. For oppositely moving contexts, pursuit was unaffected.

Several studies have raised the concern that a moving context activates the optokinetic nystagmus (OKN) and that velocity perception could be affected by the interaction of the two eye movement systems (Masson et al. 1995; Raymond et

al. 1984; Yee et al. 1983). If one assumes that the optokinetic system was fully activated by the moving, peripheral context that we used (for discussion see Lindner and Ilg 2006; Worfolk and Barnes 1992), this could in principle contribute to the averaging effect we found on pursuit velocity (see Spering and Gegenfurtner 2007). However, the opposing effects on perception that we report here, especially with oppositely moving contexts, cannot be explained by the interaction of pursuit and OKN.

Neuronal correlates of motion contrast and motion assimilation

Our results point to a clear function of the surround effects that have been observed in cortical area MT (Allman et al. 1985; Born et al. 2000). 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). Similarly, the perceptual and pursuit responses reported here carry a clear signature of antagonistic and reinforcing surrounds. We reason that perceptual responses, resulting from the computation of relative motion signals, are mediated by motion-sensitive neurons with antagonistic surrounds (local-motion sites) in area MT. Pursuit responses, on the other hand, are 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.

The assumption that motion processing for perception and pursuit separates in area MT is similar to a conclusion reached by Churchland et al. (2003). These authors compared perception and pursuit in a paradigm in which observers had to discriminate between the directions of two trajectories along the cardinal or oblique axes. Generally, discrimination performance was better along the cardinal axes (the so-called *oblique effect*). This anisotropy was not observed in the initial pursuit response. Eye velocity direction discriminated equally well between target motion irrespective of direction. These results already point at separate processing systems for perception and pursuit. However, conclusions about separate computations for perception and pursuit are difficult to draw from this work. Churchland et al. (2003) merely reported an effect in one domain and no effect in another, which could have been due to a lack in statistical power. A follow-up paper by Krukowski and Stone (2005) addressed these problems and reported the same oblique effect both in perception and pursuit. The oblique effect these authors were concerned with is a very subtle variation of thresholds showing up when many measurements are averaged. In our study, we show effects into opposite directions in perception and pursuit. These effects are massive and noticeable on individual trials.

The two opposing strategies of contrast and assimilation that we identified in motion processing have also been observed in other domains of vision. As early as in the retina, contrast helps to accentuate differences, whereas assimilation is used to achieve high precision. The chromatic appearance of a visual object can be influenced by the color at nearby locations (Kirschmann 1891) and either shift toward the color of the

inducing object (assimilation) or away from the inducing color (contrast). Similar opposing strategies have been observed for brightness perception (Shapley and Reid 1985). These different computations are used to optimally respond to different task demands at various stages in the hierarchy of visual processing.

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