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Smooth Pursuit Eye Movements to Isoluminant Targets

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Braun DI, Mennie N, Rasche C, Schütz AC, Hawken MJ, Gegenfurtner KR. Smooth pursuit eye movements to isoluminant targets. *J Neurophysiol* 100: 1287–1300, 2008. First published July 9, 2008; doi:10.1152/jn.00747.2007. At slow speeds, chromatic isoluminant stimuli are perceived to move much slower than comparable luminance stimuli. We investigated whether smooth pursuit eye movements to isoluminant stimuli show an analogous slowing. Beside pursuit speed and latency, we studied speed judgments to the same stimuli during fixation and pursuit. Stimuli were either large sine wave gratings or small Gaussians blobs moving horizontally at speeds between 1 and 11°/s. Targets were defined by luminance contrast or color. Confirming prior studies, we found that speed judgments of isoluminant stimuli during fixation showed a substantial slowing when compared with luminance stimuli. A similarly strong and significant effect of isoluminance was found for pursuit initiation: compared with luminance targets of matched contrasts, latencies of pursuit initiation were delayed by 50 ms at all speeds and eye accelerations were reduced for isoluminant targets. A small difference was found between steady-state eye velocities of luminance and isoluminant targets. For comparison, we measured latencies of saccades to luminance and isoluminant stimuli under similar conditions, but the effect of isoluminance was only found for pursuit. Parallel psychophysical experiments revealed that different from speed judgments of moving isoluminant stimuli made during fixation, judgments during pursuit are veridical for the same stimuli at all speeds. Therefore information about target speed seems to be available for pursuit eye movements and speed judgments during pursuit but is degraded for perceptual speed judgments during fixation and for pursuit initiation.

INTRODUCTION

Visual motion analysis provides important information for perceptual judgments of object movements and for other perceptual phenomena: perceptual grouping, image segmentation, depth perception. Furthermore, motion signals are critical for the generation and maintenance of smooth pursuit eye movements (Krauzlis and Lisberger 1994; Lisberger et al. 1987; Rashbass 1961; Robinson 1965). Neural systems for visual motion perception and for smooth pursuit eye movements seem to be closely related and to share the same sensory input for the detection and analysis of motion (Britten 2003; Krauzlis 2004, 2005; Lisberger and Movshon 1999; Lisberger et al. 1987; Movshon et al. 1990; Newsome et al. 1985; Page et al. 1994).

At the core of the extrastriate cortical pathway for the analysis of visual motion are two key areas: the first is the relatively small middle temporal area (MT/V5), which contains a high proportion (>90%) of direction-selective cells (Lagae et al. 1994; Saito et al. 1989), which are also partly tuned for speed and are capable of encoding acceleration in their population response (Krekelberg et al. 2006; Lisberger and Movshon 1999; Mausell and Van Essen 1983; Priebe and Lisberger 2004; Priebe et al. 2003). Adjacent to MT are the dorsal and lateral parts of the medial superior temporal area (MST). While the dorsal part is involved in the analysis of complex field motion caused by ego motion, the lateral part (MSTl) seems to be concerned with the analysis of object movements in the external space and pursuit (Duffy and Wurtz 1991a,b; Dürsteler and Wurtz 1988; Komatsu and Wurtz 1988; Newsome et al. 1988; Saito et al. 1986; Tanaka and Saito 1989; Tanaka et al. 1993). The direction and speed discrimination performance of MT neurons has been closely linked to monkeys' perceptual performance through recording, microstimulation and lesion studies (Britten et al. 1992; Liu and Newsome 2005; Newsome and Paré 1988; Rudolf and Pasternak 1999; Salzman et al. 1990, 1992). Lesions of MT result in retinotopic deficits of pursuit initiation (Newsome et al. 1985), whereas lesions to MSTl are followed by pronounced directional deficits during maintained pursuit toward the lesioned brain hemisphere (Dürsteler and Wurtz 1988). The importance of area MT for the perception of motion was furthermore established by studies in human patients (Vaina et al. 2001; Zihl et al. 1983). In neuroimaging studies, the human MT/MST complex (hMT) is typically the region showing the largest activation with motion stimuli (Culham et al. 2001; Tootell et al. 1995; Watson et al. 1993; Zeki et al. 1991), and transcranial magnetic stimulation over area hMT selectively disrupts visual motion processing (Hotson et al. 1994).

However, there is also evidence that area hMT is not the sole extrastriate area for visual motion perception. In fMRI experiments, area V3A and other regions of the parietal and superior temporal sulcus are also activated by motion stimuli (Culham et al. 2001; Orban et al. 1995; Sunaert et al. 1999; Tootell et al. 1995). Several types of motion stimuli, which can clearly be seen perceptually by primates, elicit rather weak responses in area MT. For example, some types of higher-order motion stimuli defined by contrast alternations, motion, or color give rise to motion percepts but are only weakly represented by neuronal activity of MT neurons (Albright 1992; Gegenfurtner et al. 1994; O′Keefe and Movshon 1998; Smith et al. 1998). Colored motion stimuli, where motion is defined by chromatic contrast alone, have been central in understanding the representation of higher-order motion. Initially it was thought that motion defined by chromatic borders alone could not be seen (Livingstone and Hubel 1984, 1987; Ramachandran and Gregory 1978). However, after extensive study, it has become increasingly clear that motion blindness for colored stimuli

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occurs only under very special circumstances, namely in the periphery of the visual field with slow speeds and low spatial frequencies (for a recent review, see Cropper and Würger 2005). Under foveal viewing conditions, the primate visual system is highly sensitive to motion defined by color at low temporal frequencies (<4 Hz) (Derrington and Henning 1993; Gegenfurtner and Hawken 1995a; Stromeyer et al. 1995). While the sensitivity at high temporal frequencies decreases more rapidly for color than for luminance, motion of colored stimuli at high temporal frequencies can still be seen reliably. Because motion and color interact very differently at low and high temporal frequencies, it has been argued that two different mechanisms, a slow and a fast one underlie these two temporal regimes. The slow mechanism is color-opponent and shows high sensitivity to color but is not able to signal the speed of these patterns reliably. The fast mechanism has a weaker sensitivity to color but has the capability to reliably signal the speed of motion (Gegenfurtner and Hawken 1996).

Because MT neurons are not color-opponent and prefer temporal frequencies >4 Hz, the magnocellular pathway, including area MT, is a likely neuronal substrate for the fast motion pathway (for recent review, see Born and Bradley 2005). Processing of slowly moving isoluminant patterns is more likely due to a pathway including extrastriate visual areas V2, V3, and potentially V4 (for recent review, see Lennie and Movshon 2005). Here we explored the perception of slow and fast luminance and isoluminant motion stimuli and asked whether different processing pathways are used for the initiation and maintenance of smooth pursuit eye movements. Because at slow speeds chromatic isoluminant stimuli are perceived to move much slower than comparable luminance stimuli (Cavanagh et al. 1984; Gegenfurtner et al. 2003), we investigated whether smooth pursuit eye movements to isoluminant stimuli show an analogous slowing. We were also interested in whether active tracking improves speed perception.

METHODS

Stimulus generation and presentation

Observers were seated in a dark room facing a Sony Triniton F-900 23-in monitor with a refresh rate of 100 Hz. At a viewing distance of 92 cm, the active screen area subtended 26.5° of visual angle in the horizontal and 14° in the vertical direction on the subject's retina. The screen was viewed binocularly. The subject's head was fixed using a bite bar made of dental medical material and two support points at the forehead. Visual stimuli were generated by a Cambridge Research System VSG 2/3 graphics board with a frame rate of 100 Hz. Each gun of the CRT was linearized by a look-up table to give a 12-bit intensity resolution.

Color space

The sinusoids were modulations symmetric around a central white point with Judd-corrected (Judd 1951) C.I.E. xyY coordinates (0.32, 0.36, 32.6). The grating stimuli were modulated around the white point between red (CIE xyY 0.39, 0.324, 32.6) and green (0.23, 0.407, 32.6) so as to isolate the red-green color opponent mechanism (Derrington et al. 1984; Krauskopf et al. 1982). The Gaussian blobs were defined by color modulations from the white point in the red or the green direction. The C.I.E. coordinates of the stimuli were transformed into cone excitations using the primaries determined by Smith and Pokorny (1975). Maximal modulation between red and green resulted in an 11.5% rooted mean squared cone contrast of the L- and M-cones.

Observers

Three to six highly trained observers including two of the authors (mean age: 27.5 yr, 4 female, 2 male) participated in the different experiments. In the pursuit experiment with a small Gaussian target, two of the six observers were authors; in all other experiments, only one of the authors participated. All observers had normal color vision and eye movements; two of them were slightly myopic. All procedures were conducted with the approval of the local Ethics Committee and in compliance with the declaration of Helsinki.

Eye movement recording and fixation control

The position of the right eye was measured with a double-Purkinje-image infra-red eye tracker (Crane and Steele 1985) (Fourward Technologies, Generation Vl). Viewing was binocular with natural pupils through a 45° angled glass plate with a transmittance >90%. The horizontal eye position was sampled with an A/D converter at 500 Hz at 12-bit precision and stored on disk for later analysis.

Analysis of eye traces

Position traces were recorded for 500 ms prior to the onset of the stimulus movement until stimulus offset. Eye velocity signals were obtained by digital differentiation of eye position signals over time. Steady-state velocity was computed as the average eye speed during a 250-ms interval starting 500 ms before stimulus motion offset. For the detection of saccades during that interval, a histogram of the instantaneous velocities was compiled to compute the limits for detection of velocities above and below the dominant velocity distribution. For each saccade, a period of 16 ms before and a period of 70 ms after the saccade were removed from the trace, and only pursuit segments >50 ms were included in the analysis. The detection of saccades by the algorithm was confirmed by visual inspection of each trace.

For the analysis of pursuit initiation, the eye position signals were filtered by a second-order Butterworth filter with a cut-off frequency of 30 Hz. The eye velocity signals were filtered by a Butterworth filter with a cut-off frequency of 20 Hz. For each trial, the onset and acceleration of smooth pursuit was determined with the method used by Schütz, Braun, and Gegenfurtner (2007): in the time interval from 80 to 300 ms after stimulus motion onset, starting with every sample, regression lines with a length of 80 ms were fitted to the velocity trace. All regression lines with an $R^2 < 0.7$ and a slope $<10°/s^2$ or $>200°/s^2$ were discarded. From the remaining regression lines, the one with the highest R^2 was selected. The intercept of the selected regression line and the time axis was defined as pursuit onset. The slope of the selected regression line was defined as acceleration on this trial. All single traces were visually inspected to verify that the observer was able to follow the instructions, that the eye position was tracked correctly, and that the algorithms detected pursuit onset correctly. Traces with saccades during initiation were also discarded during visual inspection.

Psychophysical determination of isoluminance

The subjective point of isoluminance for each observer was determined with a minimum motion experiment (Hawken et al. 1994). On a gray background, two vertical sine wave gratings of 0.82 cpd appeared simultaneously for 1 s in two separate rectangular windows above and below a central black fixation square (0.2°). The distance between the two windows was 0.5°. Each window had a height of 5.3° and a width of 14°. The two gratings drifted horizontally in opposite directions. One of them was a luminance grating and served as standard for the speed comparison. For the luminance grating, we chose a contrast of 12.5%, which closely matched the RMS-cone-contrast of the color stimuli. The comparison grating was a red-green sine wave, which was modulated by changing the contrast of the red and green components antagonistically in nine steps around the point of photometric isoluminance to fully explore small variations around the point of photometric isoluminance. The luminance contrasts of the red-green gratings were −12.5, −6.25, −3.125, −1.5625, 0, 1.5625, 3.125, 6.25, and 12.5%, where negative values indicate that the green stripes were brighter than the red stripes and positive values that the red stripes were brighter than the green ones. Measurements using a luminance defined comparison grating were interleaved with the red-green comparison gratings to evaluate the variability of the observer's judgments. For a single trial, the standard luminance grating was presented randomly either in the upper or lower window and the red-green test grating appeared in the other window. The observer was instructed to compare the speeds of the two gratings at straight ahead gaze without breaking central fixation. After each trial, he/she reported the position of the faster grating by pressing one of two buttons. A two alternative forced-choice procedure was used to drive a staircase that adjusted the velocity of the red-green test stimulus until it was perceived to move with the same speed as the standard. Four different experiments were run in which the speed of the standard luminance grating was 0.78, 1.56, 3.12, or 6.25 Hz, corresponding to speeds ranging from 0.95 to 7.6°/s.

During each trial, the observer's eye position relative to fixation was observed by the experimenter on an oscilloscope screen. When an observer moved his/her eyes away from the fixation spot, executed a saccade to the gratings, or pursued one of them, he/she was reminded to keep central fixation. Because our observers had participated in other eye movement and psychophysical experiments, they were able to keep stable fixation and moved their eyes very rarely. Following training, three test sessions were run with each observer for each speed. On a given day, only three tests with different standard speeds in a random sequence were run with each observer, lasting less than an hour.

Pursuit experiments with large grating stimuli

In the first experiment, a red fixation square was present in the center of the screen on a gray background for 1 s. When the fixation square disappeared, a vertically oriented sine wave grating with a spatial frequency of 0.3 cpd appeared in a 10 × 10° window and drifted within the aperture with a speed of 2.57, 5.15, or 10.3°/s randomly to the left or right. The sine wave grating was either a red-green isoluminant grating or a luminance grating of 12.5% contrast, which matched the RMS-cone-contrast of the isoluminant stimuli. To the red-green photometric isoluminant stimuli, we added increments and decrements of luminance contrasts of −10, −5, −2, 0, 2, 5, or 10% to study effects of contrast variations around isoluminance. The negative contrast values indicate that the green bars were brighter than the red bars of the gratings. Observers were asked to pursue the gratings as precisely as possible. Four observers were tested with pursuit stimuli presented at the seven color contrasts and one luminance contrast at each of the three speeds. We ran ≥1,000 trials per observer resulting in 40 trials per each of the 24 conditions.

The purpose of this experiment was to determine whether pursuit eye movements show a slowing similar to that observed in psychophysical speed judgments of moving chromatic stimuli and, if so, to determine the point of minimal eye velocity in response to moving chromatic gratings: the isoluminant point for pursuit.

To make a comparison between pursuit to luminance gratings and red-green chromatic gratings, a second series of experiments was run. For the red-green gratings, we used, for each observer, the luminance contrast that produced minimum motion psychophysically. Experimental conditions were the same as in the preceding text except that four grating speeds were used (1.29, 2.57, 5.15, or 10.3°/s) and randomly interleaved over trials. The stimuli were either luminance gratings with 12.5% contrast or red-green gratings with a matching RMS-cone-contrast whose luminance contrasts were fixed at the individual observer's subjective isoluminant point. Six sessions with 200 trials were completed with four observers resulting in 150 trials per condition for each observer.

During the analysis, it turned out to be difficult to reliably extract pursuit parameters from individual trials for initiation at the lowest grating speed, i.e., 1.29°/s (see also Hawken and Gegenfurtner 2001). Because the results were more variable and we were not sure whether this additional variability was inherent or due to our analysis, we decided not to present the single trial results for the grating speed of 1.29°/s. The average responses for the 1.29°/s speed are presented and were fully compatible with our conclusions.

Pursuit experiments with blobs

Most investigations of smooth pursuit eye movements have used spatially localized targets. Therefore in a separate series of experiments pursuit was tested with small target stimuli that had a Gaussian luminance profile to avoid chromatic aberration caused by sharp edges. The space constant of the Gaussian was 0.5°. Again two kinds of stimuli were used: the luminance stimulus was modulated around the neutral gray with a contrast of 12.5% and the chromatic stimuli were always green with luminance contrasts of −10, −5, −2, −1, 0, 1, 2, 5, or 10%. Here negative contrasts indicate that the green stimuli were darker than the neutral gray background. A step ramp paradigm (Rashbass 1961) was used in these experiments. After the offset of a red central fixation spot, the pursuit target blob appeared randomly either to the left or right of fixation; then it moved toward the center and across the screen for one second. The target speeds of 1.14, 2.28, 4.55, and 9.1°/s and the two directions were randomly chosen on each trial. The distance between the target onset location and the fixation spot depended on the speed of the target motion and was chosen so that the center of the screen was reached by the target 200 ms after motion onset. At least four sessions with 200 trials were run with each of six observers after a training session.

Latency measurements of pursuit and saccadic eye movements

Small Gaussian blob targets with the same spatial extent as described in the preceding text were also used to specifically compare the effect of color and contrast on the initiation of both smooth pursuit and saccadic eye movements. In this experiment, saccade and pursuit trials were interleaved. We used the gap paradigm for saccades to obtain saccadic latencies in the range of pursuit latencies and to obtain more compact latency distributions (Fischer and Ramsperger 1986; Krauzlis and Miles 1996; Saslow 1967). For the saccade condition, a fixation spot was first presented at the central screen location. After an unpredictable interval between 500 and 1,000 ms, the fixation spot disappeared and the target appeared 2.6° randomly to the left or right of fixation after a gap of 200 ms. In the pursuit condition the target appeared 2.6° to the left or right of fixation and moved back toward the center and across the screen with a speed of 10.5°/s. Pursuit and saccade targets were either achromatic with a contrast of 12.5, 25, or 100% or red photometric isoluminant with the background and cone contrast matched to that of the low-contrast luminance (12.5%) blob. Three observers were tested in four sessions with 200 trials each. Because this paradigm introduces a gap only in the saccade condition, we ran an additional control experiment on the same subjects where we compared saccadic latencies for the gap and no-gap conditions in response to isoluminant targets and the low-contrast luminance targets.

Speed perception during central fixation or pursuit

Speed perception of moving isoluminant and luminance gratings was measured psychophysically with a memory paradigm (McKee 1981) under two conditions: during central fixation and during pursuit. Before each session observers were told to keep in mind the standard speed for later comparisons. Ten times at the beginning of each block and on occasional (≤5%) trials during the test session indicated by a red fixation spot the standard luminance grating appeared and moved at a fixed standard speed randomly left- or rightward. Four standard speeds (1.29, 2.57, 5.15, or 10.3°/s) were used in separate sessions. In the test phase indicated by a green fixation spot, an isoluminant test grating of 10 × 10° (or on occasions the standard grating) appeared after a fixation period of 1 s and moved left- or rightward at different speeds for 1 s. After each trial, the subject gave his/her speed judgment, e. g. whether the grating had moved faster or slower than the remembered standard by pressing an assigned button.

In the fixation condition, the observer was asked to maintain continuous fixation of the central fixation spot, which was always present during the presentation of the moving standard luminance grating at the beginning and during the presentation of the moving luminance and chromatic test gratings. The stability of the observer's eye position was continuously monitored by the experimenter on an oscilloscope screen. In general, observers were able to maintain fixation and were reminded to do so when they occasionally started to deviate from the fixation spot or to initiate pursuit. Eye position traces were stored, and inspection of the traces showed that observers did not show any systematic deviations from fixation.

In the pursuit condition, the central fixation spot disappeared when the standard luminance grating or the test grating appeared and the observer was asked to follow the moving grating with his/her eyes as precisely as possible before giving his/her speed judgment. For each observer, we used the individual's isoluminant point determined by the minimum motion experiment. Again the eye movements were monitored on-line by the experimenter. Analysis of the stored traces indicated that the traces did not differ systematically in gain or latency from the ones obtained in trials without psychophysical judgments.

Each block lasted ~15 min. After each test session, a break of 15 min was introduced to allow the observer to forget the previous standard speed. Four sessions with 200 test trials each were run with four observers for each condition, e.g., speed judgment during central fixation and speed judgment during pursuit.

The fixed duration of stimulus movement used in these experiments leads to a potential confound of speed with the distance the individual grating bars travel. While there is some evidence that observers do not use such spatial or temporal cues during fixation (Henning and Derrington 1994; McKee et al. 1986), they could use the final eye position to infer speed in the pursuit condition. To exclude that possibility, we ran a control experiment on two naïve observers, where the duration of the stimulus was randomly chosen between 750 and 1500 ms. Two standard speeds (2.57 and 5.15°/s) were used.

RESULTS

Perceived speed for grating targets at and near isoluminance

As expected (Cavanagh et al. 1984), in the minimum motion experiment, all observers showed a strong dependence of their speed judgments on the luminance contrast of the near-isoluminant chromatic gratings when they compared the velocities of red-green gratings to luminance gratings moved at slow speeds. At certain red/green contrast ratios, much higher velocities of the red-green grating were required to produce the percept of equal velocity with the standard luminance grating. For each observer, the results of three test sessions for each of the standard speeds were averaged and used to determine luminance contrast ratio as his/her subjective point of isoluminance. Figure 1*A* shows for four observers the perceived relative speed of the red-green grating for the constant drift speed of the luminance grating of 1.9°/s as a function of increments or decrements of luminance contrast added to the photometrically determined isoluminant red and green grating components. For each observer, the perceived relative speed of the red-green grating continuously decreases to a minimum at a certain contrast ratio <10% luminance contrast. At this minimum, observers perceived the red-green grating to move on average 29.5% (range: 22–38%) slower than the luminance comparison grating moving at 1.9°/s.

When the speed of the comparison grating was increased, the perceptual slowing for the isoluminant grating decreased for all observers. Figure 1*B* shows the relative perceived speed of the same observers as in *A* for the speed comparisons with a luminance grating moving at a speed of 7.6°/s. At this higher speed, the dependence of speed judgments on the luminance contrast ratio of the red-green gratings was relatively small. One observer perceived a speed reduction of 13% for the red-green grating for the speed comparison at 7.6°/s. All other observers perceived the speed of the chromatic gratings as veridical or only slightly reduced at the different levels of luminance contrast. These results confirm earlier studies (Cavanagh et al. 1984; Hawken et al. 1994) that reported relative perceived slowing of chromatic gratings mainly for slow comparison speeds but not for speeds >5°/s. These findings were supported by an ANOVA revealing significant main effects of velocity [$F(1,3) = 16.8$, $P < 0.05$] and luminance contrast [$F(8,24) = 3.4$, $P < 0.01$] as well as an interaction between the two [$F(8,24) = 2.8$, $P < 0.05$].

We used these individually determined minima in perceived speed at low speeds as an indication of each subject's perceptual point of isoluminance. There are of course other methods to determine subjective isoluminance, such as flicker photometry (e.g., Stockman and Sharpe 2000) or the minimally distinct border technique (Tansley and Boynton 1978). In our case, minimum motion method is ideal because it does produce reliable minima for each subject, and we could use the exact same stimuli in some of the pursuit experiments.

Pursuit eye movements for grating targets at and near photometric isoluminance

The goal of our study was to investigate the effect of isoluminance on smooth pursuit eye movements during the phase of initiation and steady state and to compare pursuit performance in these two phases with perceptual speed judgments across a range of target velocities. In the first pursuit experiment, observers were instructed to pursue as precisely as possible luminance and isoluminant gratings with different red/green contrast ratios drifting at 2.57, 5.15, or 10.3°/s. Here we wished to test whether there would be pursuit slowing for isoluminant stimuli that was comparable to the perceptual slowing described in the preceding text.

Figure 2 shows for the same four observers as in Fig. 1 the latencies of pursuit initiation for slow (2.57°/s)- and fast

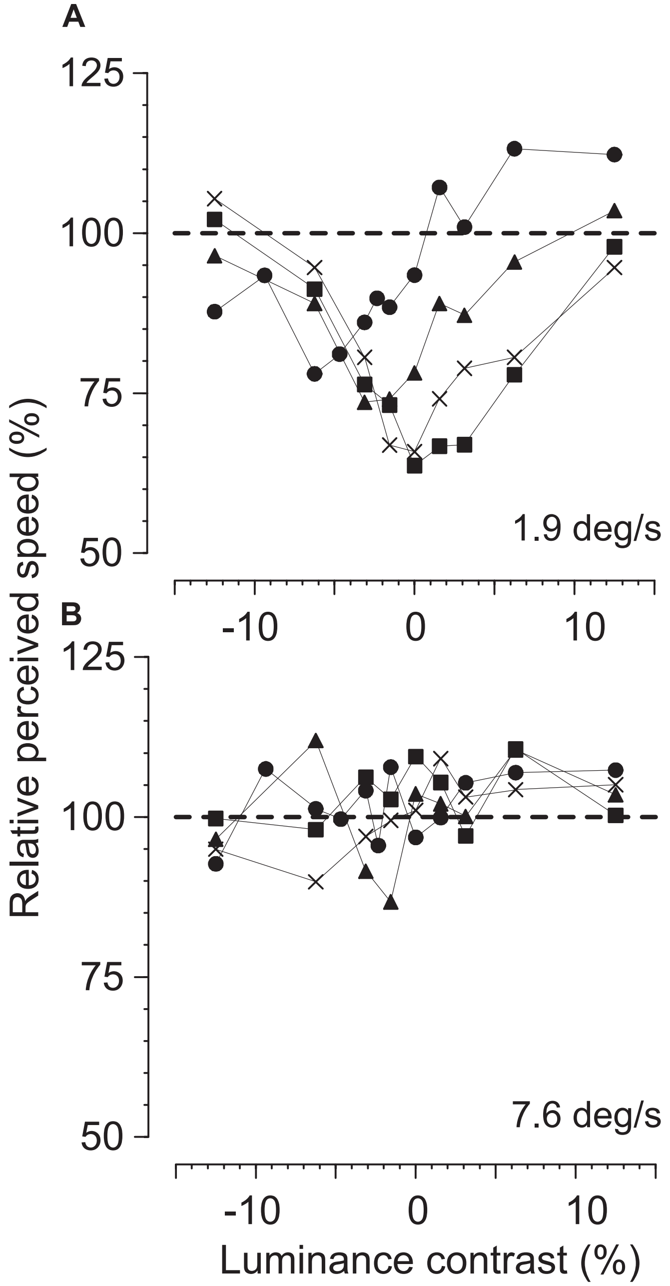

FIG. 1. Psychophysical measurements of the subjective point of isoluminance with the minimum motion paradigm for 2 different speeds of the standard luminance grating. Its speed was 1.9°/s in *A* and 7.6°/s in *B*. The 2 graphs show perceived relative speeds of red-green gratings for 4 observers as indicated by different symbols. Observers had to compare the speed of the standard grating with that of the red-green gratings presented with different luminance contrast ratios close to photometric isoluminance (0) as indicated by the *x* axis. Luminance contrast was subtracted or added to the red and green grating components, negative values indicate that the green stripes were brighter than the red stripes, positive values that the red stripes were brighter than the green stripes. The speed of the red-green gratings was adjusted by a staircase to reach an equal percept of speed. The *y* axis gives the relative speed (equal to velocity of standard luminance grating/velocity of red-green grating required to match the speed of the luminance grating). At the slow speed of 1.9°/s (*A*), all observers perceives a strong slowing of >25% at a certain red-green contrast ratio whereas at the faster speed of 7.6°/s (*B*), the dependence of perceived speed on contrast effect is much smaller. The error bars show SDs.

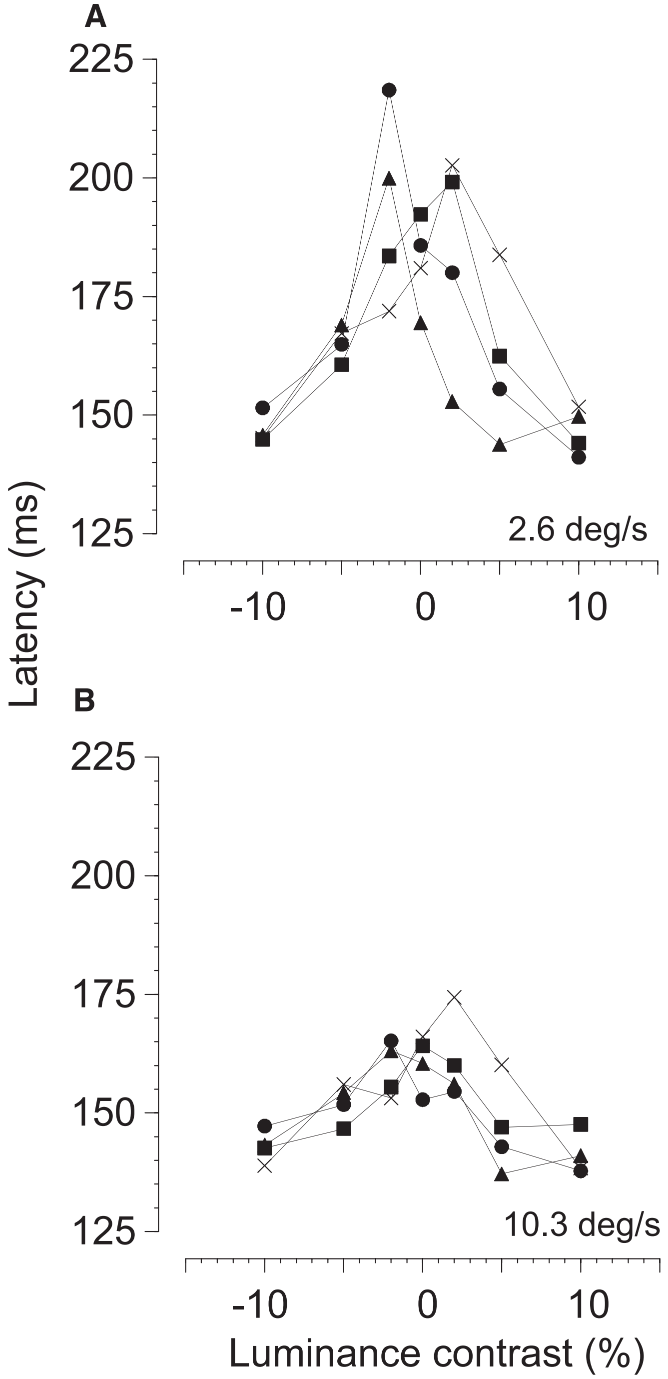

FIG. 2. Average latencies of pursuit initiation for slow and fast moving red-green gratings presented at different luminance contrasts. The data are from the same 4 observers and are plotted with the same symbols as in Fig. 1. When the gratings moved at a speed of 2.6°/s as shown in *A*, pursuit latencies of all observers increased by 50 ms at a certain luminance contrast ratios of the red and green grating components as indicated by the *x* axis. The individual peaks of latency are slightly different from each other, but all are distributed around photometric isoluminance or 0% contrast. When the gratings moved at a speed of 10.3°/s as shown in *B*, the effect of luminance contrast ratios on pursuit latencies for the red-green grating was smaller; latencies increased by ~20 ms.

(10.3°/s)-moving red-green gratings with different added luminance contrasts. At the slow speed (Fig. 2*A*), a pronounced increase in latency is present for all observers for chromatic grating stimuli of low luminance contrasts. For each observer, the peak of latency increase is slightly different and lies at a certain luminance contrast distributed ~0%. On average, latencies for chromatic gratings close to or at isoluminance increased by 49.7 ms or 27% compared with luminance gratings of 12.5% contrast. At a speed of 10.3°/s (Fig. 2*B*), the effect of luminance contrast on pursuit latencies of chromatic gratings was significant, but the difference between luminance and isoluminance were smaller than for the slow speed. On average, the maximal latencies increase was 20 ms or 12%. A repeated-measures ANOVA revealed a significant main effect of speed [$F(2,6) = 47.9$, $P < 0.001$], luminance contrast [$F(7,21) = 8.270$, $P < 0.001$], and their interaction [$F(14,42) = 3.630$, $P < 0.001$]. A comparison of the individual points of isoluminance for pursuit (Fig. 2*A*) and perception (Fig. 1*A*) shows that there is relatively good, but not exact, agreement. Observers with their perceived velocity minima on the negative contrast side (green brighter) of Fig. 1*A* also have their latency maxima in Fig. 2*A* on the negative contrast side and vice versa for observers where red is brighter at isoluminance.

The steady-state velocities were on average reduced by ~5% when the eye speed at its minimum was compared with the values for chromatic gratings with 10% luminance contrast added and by 5.7% when compared with the dark gray and light gray luminance gratings. This reduction of steady-state eye velocity is small compared with the dramatic slowing of >25% observed psychophysically. Over all subjects, the different red-green contrast ratios had a small but significant [$F(7,14) = 3.6$, $P < 0.05$] effect on the steady-state velocities.

Smooth pursuit of gratings: comparison between luminance and isoluminance

In the preceding experiments, we used small contrast variations around the point of photometric isoluminance to determine, precisely, for each observer his/her notch in perceived speed or eye speed. Due to the large number of stimulus conditions in these experiments, we obtained only a relatively small number of eye traces for each condition. Unfortunately, this was not sufficient to obtain reliable estimates of all parameters for pursuit initiation. We therefore adopted the individually determined points of isoluminance for a second series of experiments with gratings and simply compared pursuit responses of the individually determined isoluminant stimuli to luminance stimuli of 12.5% contrast at four different target speeds. In Fig. 3, the average eye velocity traces with respect to the onset of target motion are shown for luminance (solid lines) and isoluminant (dashed lines) grating stimuli for one representative observer (*A*) and for the average of all four observers (*B*). Although the average traces for isoluminant and luminance gratings for all four grating speeds reach similar steady-state velocities 400 ms after target onset (see Fig. 4*B*), it is quite obvious that there is a consistent delay for all eye velocity traces for pursuit of isoluminant gratings. Also pursuit acceleration is reduced for the isoluminance condition when compared with the luminance condition. This was investigated more closely by looking at the statistics of the individual traces.

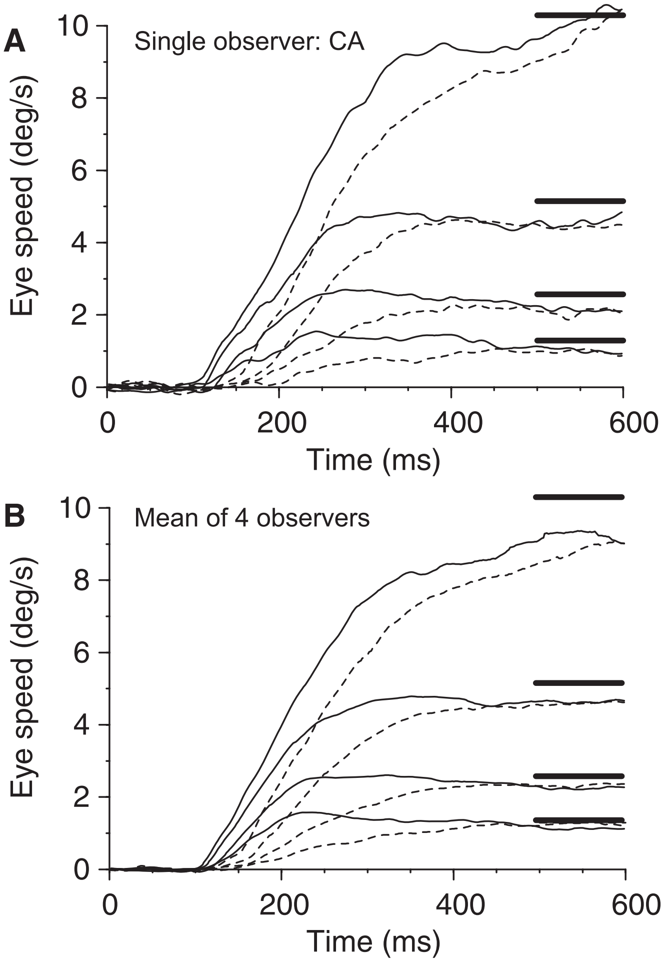

FIG. 3. Averaged eye velocity traces of the naive observer *CA* (*A*) and the grand average of all 4 observers (*B*). The average eye velocity traces are plotted for luminance gratings in black and for red-green isoluminant gratings as dashed traces for all 4 stimulus velocities of 1.29, 2.57, 5.15, and 10.3°/s as indicated by the black lines at the right side. The velocity traces for all red-green gratings are shifted to the right along the *x* axis, indicating the delay of pursuit initiation. After ~400 ms, eye velocity traces for both luminance and isoluminant grating reach quite similar eye speeds (*y* axis).

In Fig. 4*A,* the average pursuit onset latencies for luminance and subjectively isoluminant gratings are plotted for three grating speeds. Data for the slowest speed of 1.14°/s were not entered into the analysis of the individual traces because we could not reliably extract latency and acceleration measures from the individual traces. A repeated-measures ANOVA revealed that pursuit onset latencies for isoluminant gratings were significantly delayed at all three speeds compared luminance gratings moving at the same speed [$F(1,2) = 28.0$, $P < 0.05$]. Also the interaction between color and speed reached significance [$F(2,4) = 14.4$, $P < 0.05$]. The latency difference between luminance and color was larger at the slow speed (51 ms) than at the medium (43 ms) and fast speeds (23 ms). Furthermore, differences were also found for eye acceleration (Fig. 4*B*), which were lower on average by 15.7% for pursuit of chromatic gratings. Here there was a main effect of speed [$F(2,4) = 22.2$, $P < 0.01$], as expected (Lisberger and Westbrook 1985), but the effect of color was only close to significance [$F(1,2) = 13.2$, $P = 0.068$]. For steady-state eye speed (Fig. 4*C*), there was only a trivial effect of speed [$F(2,6) = 64.7$, $P < 0.001$] but not for color.

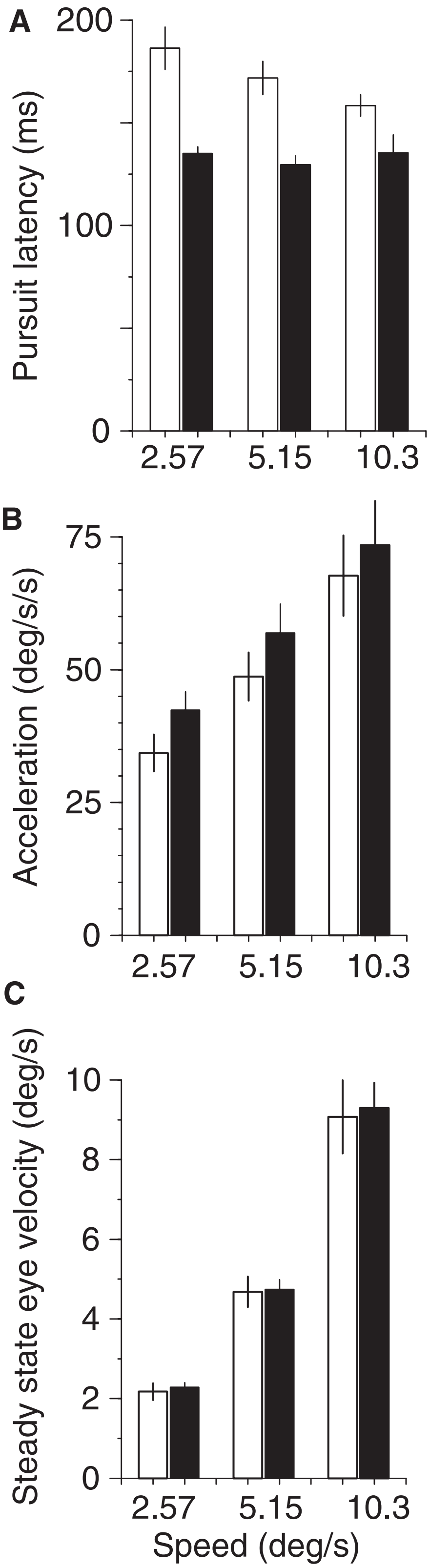

FIG. 4. *A*: average pursuit onset latencies for isoluminant (□) and luminance (■) gratings for 4 observers for the tested stimulus velocities of 2.57, 5.15, and 10.3°/s shown on the *x* axis. Average of eye accelerations (*B*) and steady-state eye velocities (*C*) for the same pursuit eye movements as in *A*. In all 3 graphs, error bars denote ±1 SE. For pursuit of isoluminant gratings, latencies are increased (*A*), eye accelerations decreased (*B*), while the steady-state velocities are only slightly reduced (*C*).

Pursuit eye movements for blob targets at and near isoluminance

In our study, we also used small target spots, the typical smooth pursuit target, to study the effect of isoluminance over a range of velocities and to compare the results with those gained with the large grating stimuli. Pursuit is often distinguished from ocular following responses on the basis of stimulus size, voluntary control, and latency. However, there is strong evidence that the dynamics of motion integration for the initiation of ocular following and voluntary smooth pursuit are very similar (Gellman et al. 1990; Masson 2004).

In our third experiment, pursuit initiation and maintenance was studied with 0.5° Gaussian blob targets with six observers. The chromatic stimulus was a green blob either at photometric isoluminance or with four different increments or decrements of luminance contrast added. For comparison, pursuit was also measured to a white luminance defined blob of 12% contrast. Figure 5 shows the average latencies, eye accelerations, and steady-state eye speeds for all target speeds as a function of the luminance contrast of the green target blob. Overall the effect of isoluminance on pursuit eye movements of spot like targets is similar to that seen for the grating stimuli: For the chromatic targets close to or at photometric isoluminance, pursuit latencies increase rapidly around a luminance contrast of 0%. Consistent with the results of delayed latencies for chromatic grating stimuli reported above, there was a large and stable delay of 50 ms (range: 41–64 ms) for pursuit latencies to the small chromatic targets close to isoluminance for all target speeds. In Fig. 5*A*, the average onset latencies of six observers are plotted for the different increments or decrements of luminance contrast added to the green isoluminant blob target moving at all four speeds. It is quite obvious that pursuit latencies increased consistently with the decrease of luminance contrast of the green target independently of target speed. At photometric isoluminance, the onset latencies for pursuit of the blob targets were >260 ms (range: 262–275 ms) independent of their speed. These results show that even at higher target speeds the luminance contrast has a dramatic significant effect on the latency of pursuit initiation [$F(9,45) = 12.5$, $P < 0.001$]. Again target speed had a significant effect [$F(3,15) = 15.1$, $P < 0.001$], and also the interaction of color and speed was significant [$F(27,135) = 3.1$, $P < 0.001$]. A significant effect of color contrast was also found for eye acceleration as shown in Fig. 5*B* [$F(9,45) = 5.1$, $P < 0.001$]. Eye acceleration decreased for all targets at all speeds around a luminance contrast of 0% or photometric isoluminance. As expected and similar to the grating stimuli, target speed had a significant effect [$F(3,15) = 33.9$, $P < 0.001$] on eye acceleration as well as the interaction of color contrast and target speed [$F(27,135) = 2.0$, $P < 0.01$].

However, steady-state eye velocities of the blobs, as shown in Fig. 5*C*, were reduced by <5% for target speeds <5°/s and by 11.8% for a target speed of 9.09°/s. A repeated-measures ANOVA revealed that the effect of luminance contrast on the steady-state velocity was significant [$F(9,45) = 3.3$, $P < 0.01$] as was the effect of speed and the interaction of color contrast and speed. To summarize, similar to the results of the grating stimuli we found for both, latencies of pursuit initiation and eye acceleration a strong negative effect of isoluminance for pursuit of small chromatic targets, and this deficit was also present for the higher speeds.

Comparison of saccadic and pursuit latencies

The rather long delay of 40–50 ms for pursuit initiation to isoluminant targets is remarkable because our isoluminant and luminance stimuli were matched with respect to cone contrast: comparisons were done with luminance targets of 12.5% contrast. In earlier experiments investigating saccadic eye movements and manual pointing responses (White et al. 2006), no latency difference was found between contrast-matched isoluminant and luminance targets for both of these goal-directed movements. Therefore we performed a control experiment and measured pursuit onset and saccadic latencies in a single experiment. Three observers were instructed to make saccadic or pursuit eye movements to a suddenly appearing peripheral blob target. This target was either static or moved horizontally at 10.5°/s toward and across the screen center (step ramp). We used again isoluminant and luminance targets with matched cone contrasts (12.5%), and additional luminance targets with medium (25%) and high (100%) contrast. The comparison of the resulting saccadic and pursuit latencies and pursuit eye accelerations to luminance and color targets of equal cone contrast revealed that only the initiation of pursuit eye movements was consistently delayed by isoluminance (Fig. 6). Compared with pursuit onsets to luminance targets, pursuit onsets to isoluminant targets of all three observers were delayed by 34, 41, and 51 ms, respectively (Fig. 6, compare ■ in the isoluminant and low luminance condition).

Note that here we are not interested in comparing absolute latencies for saccades and pursuit because it is not easily

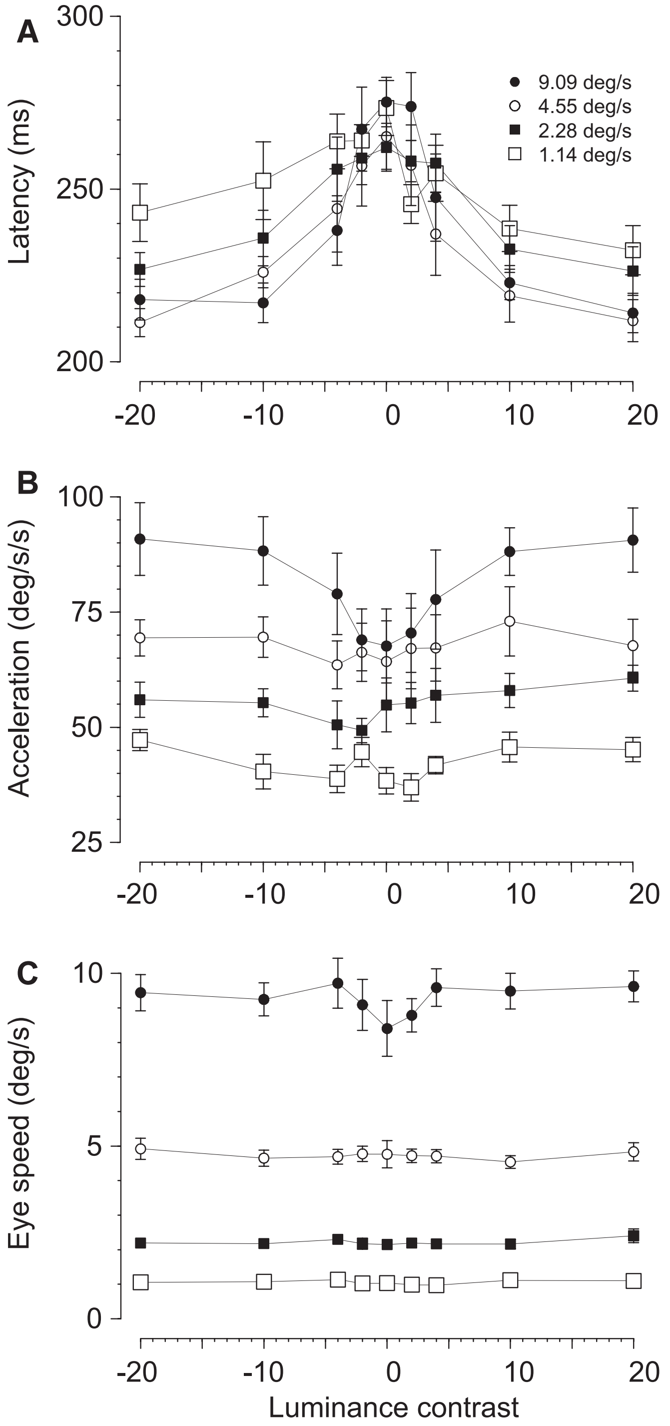

FIG. 5. Average data for 6 observer of pursuit eye movements for blob targets of different contrasts moving at 4 different velocities. *A*: average latencies of pursuit initiation for blob targets moving at 4 different speeds as a function of luminance contrast as indicated by the *x* axis. The green blobs were either brighter (positive values of luminance contrast) or darker (negative values on *x* axis) than the background. Average accelerations (*B*) and steady-state velocities (*C*) of the same pursuit eye movements as in *A*. While at small luminance contrasts around photometric isoluminance the average latencies for all four target velocities increase to >250 ms, average accelerations decrease while the steady-state velocities show mainly for the fastest blob velocity of 9.09°/s a decrease. In all 3 graphs, error bars denote ±1 SE.

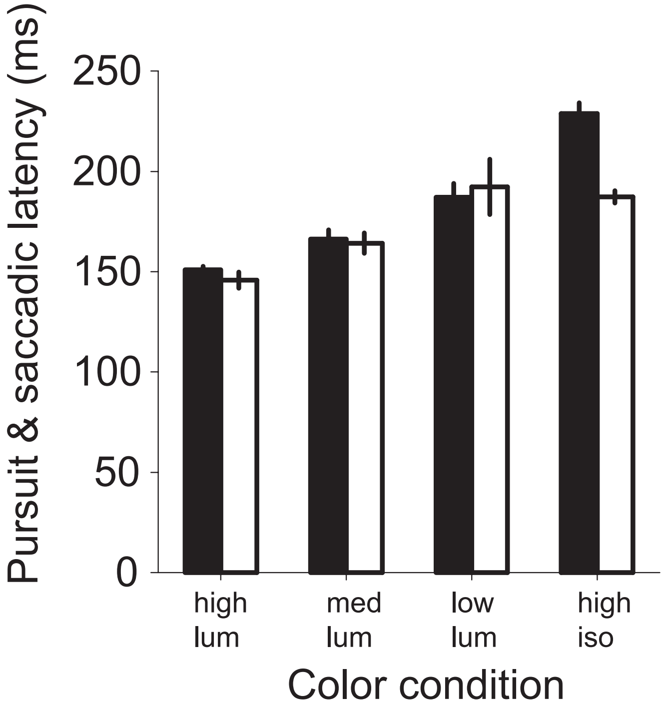

FIG. 6. Average latency data for pursuit (■) and saccades (□) for 3 observers. Three different luminance conditions with high, medium, and low-contrast blobs are shown in the 3 pairs of columns to the left, the isoluminant conditions are shown in the pair of columns to the right. Error bars denote ±1 SE.

possible to match all relevant stimulus parameters. We chose our parameters, most notably the gap in the saccade condition, so that we would obtain similar saccadic and pursuit latencies for the luminance conditions. However, the use of the gap-paradigm for saccades only introduces a potential confound. The gap could, in principle, have differential effects on saccades to isoluminant and luminance targets. We therefore ran a control experiment with the same three observers where saccadic latencies were measured for low-contrast luminance and isoluminant targets under gap and no-gap conditions. Saccadic latencies were similar for luminance and isoluminant targets, both for the gap condition (luminance: 197 ms, isoluminance: 191 ms) and the no-gap condition (luminance: 243 ms, isoluminance: 237 ms). Therefore we can firmly conclude that the longer latencies for isoluminant pursuit are due to mechanisms specific for pursuit.

Figure 7 plots pursuit latency versus pursuit acceleration for all individual trials for a representative observer (DB). With decreasing luminance contrast, acceleration decreases on average from 78 to 66°/s^2, and latency increases from 177 to 224 ms. However, the values for isoluminant targets are different from the ones for even the lowest luminance contrasts. Average acceleration was 47°/s^2 and latency was 252 ms in response to the isoluminant targets.

We also compared pursuit acceleration for all four pursuit targets. While the average pursuit acceleration for all three observers was fairly constant ~65°/s^2 for the three different luminance contrasts (high: 66, medium: 68, low: 63°/s^2), it was clearly reduced for pursuit of the isoluminant target (high iso: 42°/s^2). These differences were significant (*t*-test for independent samples) for all three observers at the $P = 0.01$ significance level. This shows that isoluminant pursuit targets behave quite differently from luminance targets at matched cone contrasts.

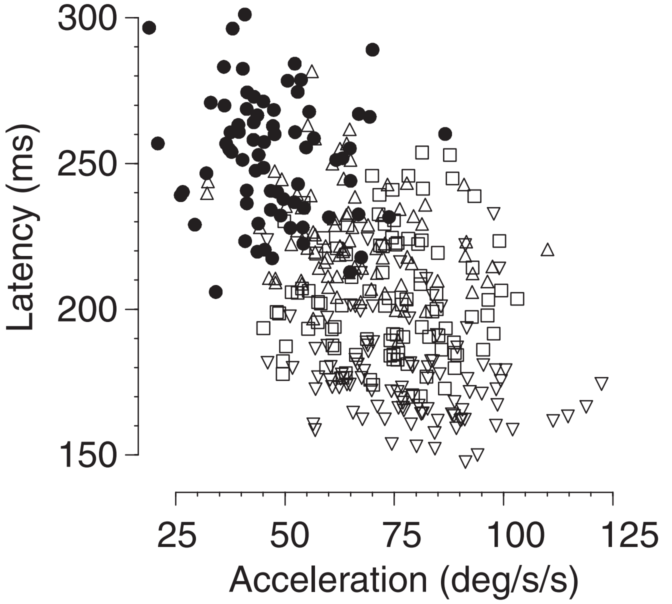

FIG. 7. Distribution of pursuit latencies (*y* axis) of 3 observers for step ramps with isoluminant targets (●) and luminance targets of low (△), medium (□), and high contrast (○) as a function of acceleration (*x* axis). For isoluminant targets pursuit latencies are higher and accelerations are lower than for all achromatic targets of different contrasts.

Effects of smooth pursuit eye movements on perceived speed

Our results of the effect of isoluminance on pursuit eye movements are somewhat similar to psychophysical results obtained under fixation conditions. As shown in Fig. 1, perceived speed for slowly moving isoluminant grating stimuli is severely impaired at isoluminance (Cavanagh et al. 1984). Pursuit as judged by acceleration and latency of slow isoluminant targets is severely affected at isoluminance, whereas pursuit steady-state eye gain is not or only weakly impaired. These results imply that signals about stimulus speed of isoluminant targets become available during pursuit. We tested whether the perceptual system can use these signals for speed estimates. To achieve this, we compared psychometric functions of speed judgments of luminance and isoluminant gratings under two conditions: central fixation and active pursuit.

When observers were instructed to maintain fixation during stimulus presentation, we found a rightward shift of the psychometric curves of the speed judgments toward higher velocities for isoluminant gratings during fixation. An example of the psychometric functions is shown for one observer in Fig. 8*A.* When the observer judged the speed of the luminance test grating relative to the remembered standard grating (moving at 2.57°/s), the point of subjective equality was very close at 2.61°/s (Fig. 8*A,* black curve). Under the same fixation condition and with a luminance grating as the standard, the isoluminant test grating was required to move at ~3.66°/s to match the speed of the luminance grating (Fig. 8*A,* hatched curve).

When the observer was instructed to pursue the test and the standard grating and to make a judgment during pursuit, the speed judgments were veridical for both luminance and isoluminant test gratings (Fig. 8*B,* black curve: luminance grating; dashed curve: isoluminant grating). The speed judgments for luminance and isoluminant gratings for all four observers followed the pattern shown for the single observer in Fig. 8 and are plotted as perceived speed of the isoluminant gratings relative to the perceived speed of the luminance gratings for all three standard speeds in Fig. 9.

It is apparent, that under fixation (□), isoluminant stimuli are consistently perceived to move slower, while during pursuit (●) isoluminant stimuli are seen to move at the same speed or even faster than luminance stimuli. In principle, observers could use the distance traveled by the stimulus or by the eyes to make accurate judgments about speed because these two quantities were confounded in the preceding experiments. While it is known that observers do not use cues such as time or distance for speed judgments during fixation (Henning and Derrington 1994; McKee et al. 1986), the situation is unclear for speed judgments during pursuit. Therefore we ran an addition control experiment where stimulus duration was randomized to decorrelate distance and speed. The results for two naïve observers at two speeds (2.57 and 5.15°/s) indicated accurate judgments of speed for isoluminant targets during pursuit, just as observed in the preceding text. Perceived speed for isoluminant gratings during pursuit was not significantly different from that for luminance gratings, while it was still affected during fixation (between 15 and 34%). The slope of the psychometric functions in these control experiments was not different from the experiments using constant durations, indicating that all observers indeed used speed to make their judgments.

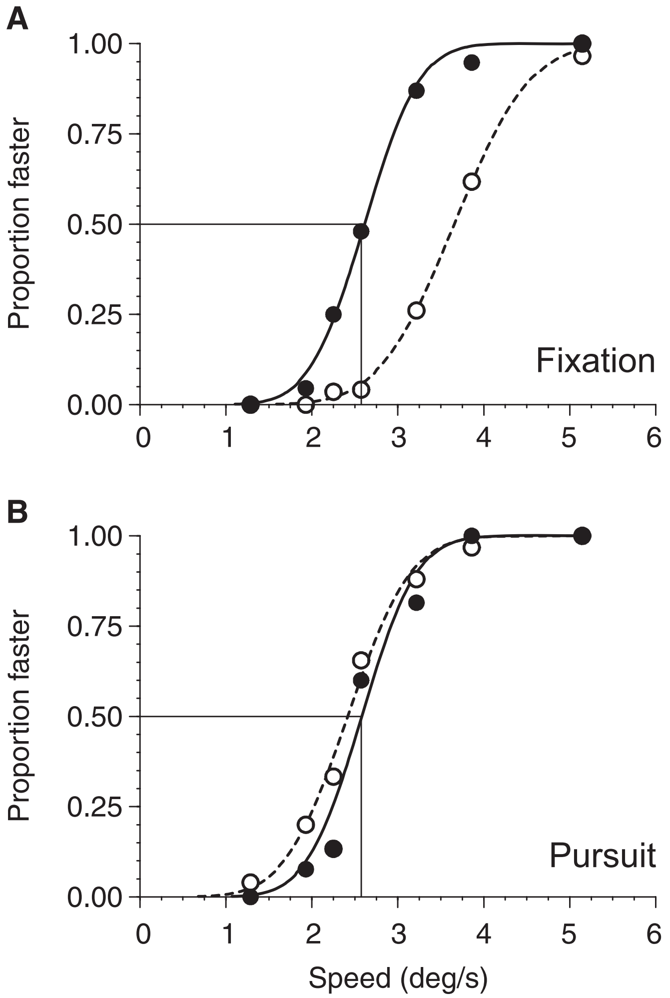

FIG. 8. Psychometric functions of the speed comparisons for a single naïve observer (*MS*) for a standard speed of 2.57°/s. *A*: data obtained under fixation conditions. *B*: data obtained during pursuit. The open symbols and dashed line indicate isoluminant stimuli, the filled symbols and solid line luminance stimuli. The *x*-axis plots the physical speed of the comparison stimuli. The *y* axis shows the proportion of trials in which the comparison stimuli were judged to be faster as the memorized standard stimulus.

DISCUSSION

We compared psychophysical speed judgments and smooth pursuit eye movements to different moving stimuli to investigate whether motion cued by pure color or luminance contrast affects motion perception and the execution of pursuit eye movements in the same way. Similar to the slowing of chromatic stimuli close to isoluminance that occurs perceptually (~25%) for slow speeds during fixation, we found that the same chromatic stimuli had an effect on pursuit eye movement at all speeds. For both, fast and slow target speeds, the strong effects of isoluminance are present during the phase of initiation: latencies for pursuit onset show a substantial delay in the order of 40–50 ms, and eye accelerations are slowed down by ~10–20% compared with luminance stimuli. This effect of isoluminance seems to be specific for pursuit initiation because no latency difference was found for saccadic eye movements to isoluminant targets. Compared with pursuit initiation only a small reduction of ~5% was found for the steady-state eye velocities for small and large isoluminant stimuli.

Interestingly, speed judgments made during pursuit were veridical for all isoluminant stimuli at all speeds compared with judgments during fixation. Therefore when pursuing a target, valuable information about its speed seems to be available for perceptual judgments that is not or cannot be used for pursuit initiation.

Comparison to psychophysical studies

There is an extensive literature on the visual processing of motion stimuli defined by color only. While some of the earlier studies indicated that motion perception might be nearly abolished at isoluminance (Cavanagh et al. 1984; Ramachandran and Gregory 1978), later work showed that any differences between luminance and chromatic motion depend on the exact stimulus parameters (for a recent review, see Cropper and Würger 2005). While chromatic motion perception is severely attenuated when stimuli are presented briefly or in the peripheral visual field (Derrington and Henning 1993; Lu et al. 1999; Teller and Lindsay 1993), sensitivity to chromatic motion is quite exquisite when stimuli are presented foveally (Gegenfurtner and Hawken 1995a; Stromeyer et al. 1995). However, despite the high sensitivity to chromatic motion at or near the fovea, chromatic stimuli appear to move slower than luminance stimuli (Cavanagh et al. 1984; Hawken et al. 1994), especially when they are presented at low temporal frequencies (Gegenfurtner and Hawken 1996).

We found notable differences between pursuit behavior and psychophysical judgments to the same stimuli. Most importantly, while the perceptual effects are present only at slow speeds, eye movements are affected at all speeds, and the effects are present at high speeds. At isoluminance, pursuit initiation is massively delayed, acceleration is slower, and the steady-state gain is slightly lower as well. Because of the

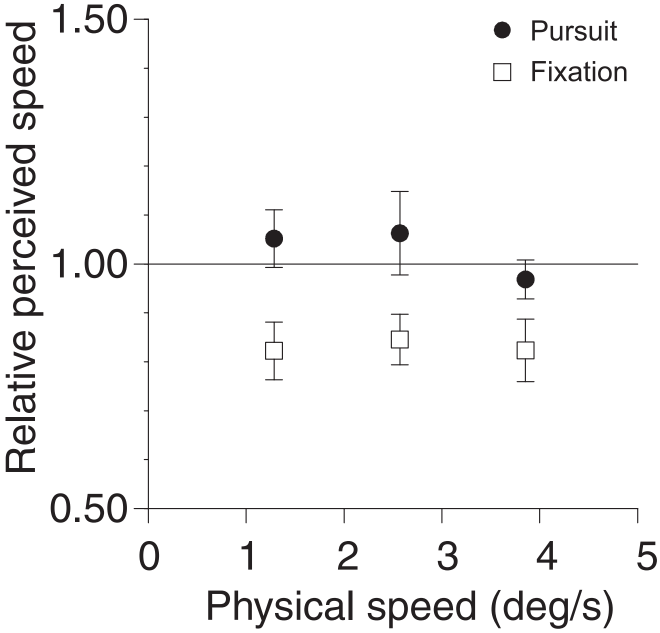

FIG. 9. Perceived speed of isoluminant gratings relative to the perceived speed of luminance gratings during fixation and pursuit for base speeds of 1.29, 2.57, and 5.15°/s. □, data obtained during fixation; ●, data obtained during pursuit. The *x* axis indicates speed of the standard stimulus. The average of 4 observers is plotted. Error bars denote ±1 SE.

differences with which the perceptual and pursuit effects occur at slow and fast speeds, we think that the two phenomena are not directly related.

Neural substrate

In humans, imaging studies have shown that color-defined motion stimuli activate the MT/V5 complex but often with a reduced magnitude when compared with luminance stimuli (PET: Ffytche et al. 1995; fMRI: Chawla et al. 1998, 1999; Tootell et al. 1995; Wandell et al. 1999). Consequently, the MT/V5 complex can analyze the movement of a pattern composed of pure color contours, but the strength of the output is considerably weaker than that for the movement of a pattern composed of contours defined by luminance contrast. Areas V3 and V4 give relatively strong responses to both motion and color (Ferrera et al. 1994ç Gegenfurtner et al. 1997; Tolias et al. 2001). Thus it is possible that signals for slowly moving pure chromatic stimuli are routed via these ventral extrastriate areas before reaching area MT. Additional signal processing in these areas might explain the increase in pursuit latencies for isoluminant stimuli, which we found for pursuit latencies of both, slow and fast speeds.

In monkey, neurophysiology several studies have compared the response behavior of MT neurons to moving luminance and chromatic stimuli of different contrast and speeds (Gegenfurtner et al. 1994; Riečanský et al. 2005; Saito et al. 1989; Thiele et al. 1999). Depending on the stimulus characteristics, the response behavior of MT neurons to moving achromatic and chromatic stimuli show important differences (Gegenfurtner et al. 1994; Saito et al. 1989; Seidemann et al. 1999). Saito et al. (1989) reported that the average MT directional response to isoluminant magenta/cyan stimuli was reduced to ~35% of the maximal cell response. In half of the MT cells, the direction selective response to chromatic motion stimuli decrease considerately and sometimes even disappeared at a luminance ratio close to the human isoluminance. In the other half, responses persisted at any contrast ratio but were reduced to a different extent (30–90%) for chromatic stimuli close to isoluminance. Only few neurons responded robustly to isoluminant stimuli. These authors therefore concluded that area MT could still detect the movement direction of pure chromatic contours in spite of the reduced directional sensitivity for these stimuli. Also Gegenfurtner et al. (1994) found a strong attenuation of directionally selective responses of MT neurons when the moving gratings were spatially modulated only in chromaticity. However, for one-third of the MT neurons, no chromatic stimulus was found in which the directional response was completely abolished. These MT cells had their null elevation slightly tilted away from the isoluminant plane and gave reliable responses only to intensely modulated isoluminant stimuli. However, because the contrast thresholds of MT neurons for isoluminant targets were much higher than the behavioral measurements for direction identification of the same motion stimuli, these authors concluded that area MT does not provide the chromatic motion signals used for the detection of slowly moving isoluminant targets.

Effects of isoluminance on pursuit

This study shows that isoluminance causes a consistent delay of ≤50 ms for pursuit initiation for small and large stimuli at all target speeds. It is important to note that this latency increase for isoluminant stimuli is specific to the initiation of pursuit eye movements because no latency effect was found for saccadic eye movements as has been reported in a previous study where saccades to chromatic and luminance stimuli with matched cone contrasts were compared (White et al. 2006). A delay of the early suppressed ocular response to chromatic gratings and plaids by 20% compared with luminance stimuli was reported for monkeys by Guo and Benson (1999).

Latency differences of the same order of magnitude have been observed for changes in MT responses and pursuit behavior. Pack and Born (2001) showed that MT neurons solve the "aperture problem" dynamically over time by refining their initial estimates of motion direction. Initially MT neurons respond to the component of motion perpendicular to the contour orientation of moving bars. However, over a period of ~60 ms, their response behavior shifts to encode the true stimulus direction independent of the contour orientation. This shift in directional responses might be caused by the integration of local motion and terminator signals over a larger spatial scale. Furthermore, Smith et al (2005) found a latency difference in the response behavior of component and pattern direction-selective MT neurons. Pattern direction selective neurons responded only 6 ms later, but their computations proceeded at a slower rate and reached the fully selective state ~50–75 ms after the response of component cells. This early direction-tuned response of MT neurons seems also to be present in the orientation-dependent bias in the initial deviation of pursuit eye movements in the direction perpendicular to the orientation of contours (Beutter and Stone 1998). During pursuit initiation of a perceptually ambiguous stimulus described by two motion vectors, the eyes initially follow the simple vector average. After ~50 ms, a change of pursuit direction toward the "correct" intersection of constraints is observed (Beutter and Stone 1998; Born et al. 2006; Masson et al. 2000). This dynamic behavior in the response properties of neurons in area MT suggests that the visual system seems to redefine the initial estimates of the movement direction and signals the true direction of motion after a certain time for signal integration.

These delays could be due to neurons in MT which dynamically refine the initial estimates of the movement direction through lateral interactions within MT as has been suggested by some models (Bayerl and Neumann 2004). However, a recent analysis of local and global motion signals in area MT has shown that MT itself seems to signal local motion only (Ilg and Churan 2004; Majaj et al. 2007). In this case, inputs from the ventral stream would have to be used to solve the aperture problem and maybe also to signal the motion of isoluminant stimuli.

A further argument against the involvement of area MT in initiating smooth pursuit to isoluminant targets is the lower acceleration we observed. In some ways, pursuit initiation to isoluminant targets looks quite similar to the initiation after lesions of area MT. After small punctuate chemical lesions in area MT monkeys are disabled to match the smooth pursuit eye speed to target speeds and can no longer compensate for target motion when making saccades to moving stimuli. In the first 100 ms of pursuit responses postlesional eye speeds were reduced by 50% and reached a normal level only after a corrective saccade (Newsome et al. 1985). Interestingly, we also observed an effect, albeit a small one, on eye gain during steady-state pursuit. It is known that during the phase of steady state, eye velocity is maintained by velocity memory if retinal errors are eliminated by stabilization (Morris and Lisberger 1987). However, even during the steady-state phase of pursuit, visual properties of the stimuli are important determinants of pursuit gain. For example, the pursuit gain of stimuli at low contrast or of stimuli defined by second-order variations is considerately reduced (Hawken and Gegenfurtner 2001; Spering et al. 2005). Changes in contrast affect the gain of pursuit of both, luminance and chromatic stimuli (Gegenfurtner and Hawken 1995b). Here we found that the pursuit gain for small foveal and large isoluminant targets moving at slow to fast speeds is slightly smaller as that for luminance targets with a similar cone contrast. This could be interpreted as evidence that for the sensorimotor system the contrast of all our chromatic stimuli is still smaller than that of luminance stimuli, but that the steady-state phase of pursuit is driven by the same mechanisms.

To summarize, the behavioral and neuronal latency differences mentioned in the preceding text are similar in magnitude to the latency differences we found for pursuit initiation to isoluminant targets. As with the more complex motion stimuli described in the preceding text, the delay of neuronal signals initiating smooth pursuit eye movements to isoluminant stimuli could be due to inputs from areas along the ventral stream or due to additional local computations in area MT or due to feedback connections with earlier visual areas such as V1 or V2.

Perception during smooth pursuit

It is commonly assumed that during pursuit, perception includes a combination of afferent (visual) and efferent (motor) signals and that extra-retinal signals encoding the eye movement are used to compensate for retinal motion caused by the eye rotation (Gregory 1958; von Helmholtz 1909; Von Holst 1954). The compensation allows to achieve spatial constancy and to correct judgments of object movements. Some well-known illusions reveal that during pursuit the actual displacement of the eyes is underestimated by the visual system. Stationary objects are seen to move in the direction opposite to pursuit (Filehne 1922) and the velocity of a pursuit object moving in the fronto-parallel plane is underestimated in comparison to its perceived speed during fixation (Aubert 1886; von Fleischl 1882) by as much as 30% (Dichgans et al. 1975; Gibson et al. 1957). We compared speed judgments of the same stimuli during pursuit and fixation in our last experiment. Different from the above-cited studies, we found a large and positive effect of the execution of pursuit on perceived speed: during pursuit, the veridical speed for isoluminant stimuli is perceived also at slow speeds. This result shows that the visual system is capable of using internal signals about eye speed for speed judgments once smooth pursuit is initiated. During fixation, and presumably also for initiation, these signals are not available. One possible reason could be that during fixation the brain relies on another mechanism for the speed judgments of isoluminant targets; a mechanism with a higher sensitivity to these targets—even though this mechanism bases its computations on position rather than speed (Krauskopf and Li 1999; Seiffert and Cavanagh 1999).

Conclusion

Our results convincingly show that smooth pursuit eye movements can be initiated and maintained even for isoluminant targets despite some restrictions on the latency and the acceleration of the response. Once pursuit is initiated, it supports the veridical perception of the speed of isoluminant stimuli, which are perceived as slowed down or even standing still under fixation conditions. Our psychophysical experiments showed that speed judgments made during pursuit are veridical for all stimuli at all speeds compared with judgments during fixation. Therefore when pursuing a target, information of its speed seems to be available for perceptual judgments that is or cannot be used for judgments during fixation.

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