Improved visual sensitivity during smooth pursuit eye movements

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When we view the world around us, we constantly move our eyes. This brings objects of interest into the fovea and keeps them there, but visual sensitivity has been shown to deteriorate while the eyes are moving. Here we show that human sensitivity for some visual stimuli is improved during smooth pursuit eye movements. Detection thresholds for briefly flashed, colored stimuli were 16% lower during pursuit than during fixation. Similarly, detection thresholds for luminance-defined stimuli of high spatial frequency were lowered. These findings suggest that the pursuit-induced sensitivity increase may have its neuronal origin in the parvocellular retino-thalamic system. This implies that the visual system not only uses feedback connections to improve processing for locations and objects being attended to, but that a whole processing subsystem can be boosted. During pursuit, facilitation of the parvocellular system may reduce motion blur for stationary objects and increase sensitivity to speed changes of the tracked object.

Movements of the eyes directly change the retinal input to the visual system. During fixation, miniature eye movements help to prevent the retinal image from fading[1] and may even increase the sensitivity for certain types of visual targets[2]. Large voluntary eye movements, however, present a challenge to the visual system. During both fast saccadic and slow pursuit eye movements, retinal motion due to the eye movements must be disentangled from retinal motion due to object motion, and object recognition must deal with a changing visual input. For saccadic eye movements, a massive suppression of the magnocellular pathway[3] has been observed around the time of saccade initiation, and it accompanies a compression of visual space[4] and time[5]. Both phenomena imply a strong deterioration of visual performance during saccades. Little is known about similar changes during slow pursuit eye movements. So far, it has been shown that, for accurate pursuit, visual attention must be directed to the pursuit target, which might hamper performance for visual tasks outside the focus of attention[6,7]. Furthermore, retinal image motion during pursuit degrades perceptual performance; this has been confirmed for motion sensitivity[8], localization performance[9] and contrast sensitivity for moving stimuli[10]. Here, we have systematically investigated the influence of smooth pursuit eye movements on contrast sensitivity for chromatic and achromatic stimuli. We found that contrast sensitivity for color as well as for high-spatial-frequency luminance stimuli increased during smooth pursuit eye movements. The magnitude of the enhancement scaled with the pursuit velocity and the increase preceded the onset of the pursuit by around 50 ms. This indicates that the change in sensitivity was triggered actively by an extraretinal signal.

RESULTS

We measured contrast sensitivity for a horizontal line stimulus, which we flashed briefly for 10 ms either during horizontal pursuit or during fixation (**Fig. 1**). The critical feature of the paradigm was that the line was parallel to the path of pursuit and therefore did not produce any net image motion on the retina. Thus, the retinal stimulation was identical for the pursuit and fixation conditions. We modulated the contrast of the line either in color or in luminance[11] and adjusted it by means of an adaptive staircase procedure[12] to determine contrast threshold. Psychometric functions for one representative observer are shown for the detection of red-green color (**Fig. 2a**) and luminance (**Fig. 2b**) stimuli. We observed a leftward shift of the psychometric function for red-green isoluminant stimuli presented during smooth pursuit compared to fixation, indicating an improvement of visual sensitivity to these stimuli during pursuit. Averaged over all 11 observers, the enhancement of sensitivity amounted to 16% (**Fig. 2c**) ($P < 0.001$; two-tailed, paired t-test). At the same time, detection performance decreased for luminance stimuli during pursuit. On average, this attenuation of sensitivity amounted to 5% (**Fig. 2d**) ($P = 0.017$). The decline in performance for luminance-defined stimuli is in line with previous studies that have shown that pursuit requires the allocation of spatial attention to the pursuit target[6,7,10].

We performed several control experiments to rule out some possible explanations for the performance improvement for colored stimuli. The effects were not caused by different temporal uncertainties during pursuit and fixation (**Supplementary Note** and **Supplementary Fig. 1** online). They did not depend on the nature of the pursuit target, as the same results occurred for a chromatic pursuit target (**Supplementary**

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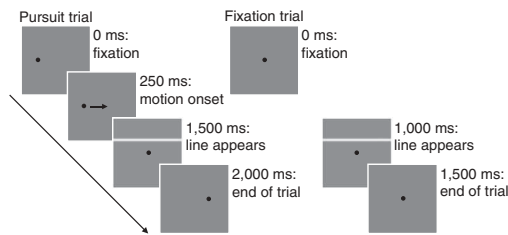
Figure 1 Experimental protocol. Schematic trial sequence in pursuit and fixation trials. Observers had to track a black spot that either moved horizontally across the screen (pursuit) or remained stationary at the screen center (fixation). During each trial we flashed a blurred horizontal line for one refresh cycle of the monitor either above or below the eye-movement target. We varied the nature of the line (color or luminance) and its contrast to measure detection thresholds.

Note and **Supplementary Fig. 2** online). It is also very unlikely that the increase in sensitivity for colored stimuli was due to a luminance-based mechanism, as performance for luminance stimuli actually decreased. However, to confirm the chromatic nature of the underlying mechanism, we asked observers to indicate the color of the stimuli (red, green, black or white) rather than their locations in a second experiment (**Supplementary Fig. 3** online). As in the detection experiment, the color-naming sensitivity for chromatic stimuli was enhanced by 18% during pursuit relative to fixation ($n = 11$, $P < 0.001$), whereas performance for luminance stimuli was attenuated by 28% ($P < 0.001$).

The increase in sensitivity for color stimuli was unexpected, because visual motion is the primary signal driving pursuit eye movements[13,14], and color is known to make no or only a modest contribution to the areas of the dorsal stream thought to control pursuit[15,16]. Our further experiments were therefore aimed at finding the link between pursuit and color by investigating (i) whether the results differ for foveally presented stimuli, (ii) where in the visual pathways the pursuit-induced increase in performance emerges, (iii) how the enhancement is accomplished, (iv) whether the effect depends on pursuit velocity and (v) what the dynamics of the effect are.

Foveal sensitivity

As previous studies on the distribution of spatial attention during smooth pursuit suggest a difference between foveal and peripheral performance[6,7,10], we wanted to test whether the observed effects also occur for foveal stimuli. This is especially critical for color stimuli because chromatic sensitivity in the fovea is highly optimized[17]. To measure foveal performance, we flashed a horizontal line modulated in isoluminant red-green contrast on the pursuit trajectory and asked observers to judge the hue of the line. Averaged over ten observers, color discrimination improved by 13% ($P = 0.001$) during pursuit, showing that this enhanced sensitivity for chromatic stimuli also held for foveal stimuli (**Fig. 3a**). Therefore, the enhancement for color during pursuit seemed to be unrelated to the distribution of spatial

attention focused on the pursuit target. For luminance stimuli presented in the fovea (**Fig. 3b**), we found no significant difference between pursuit and fixation ($P > 0.1$). As the attenuation of sensitivity occurred for luminance stimuli in the periphery but not in the fovea, it was most likely caused by the allocation of spatial attention to the (foveal) pursuit target.

Visual pathways

The earliest processing stage in the visual system that receives feedback connections is the lateral geniculate nucleus (LGN) in the thalamus. There are three roughly independent pathways from the retina to the LGN and on to the visual cortex. The parvocellular pathway is sensitive to red and green color and to luminance and has a higher spatial resolution than the color-blind[18,19] magnocellular pathway. Signals concerning blue and yellow colors are mainly processed in the koniocellular pathway[20]. As our red-green stimuli very likely cannot be identified through the magnocellular pathway, the performance increase could be due to a general boost of the parvo- or koniocellular pathways.

For stimuli modulated in isoluminant blue-yellow color, our observers ($n = 9$) also showed an improved sensitivity (11%) during pursuit compared to fixation (**Fig. 3c**) ($P = 0.050$). Therefore, the enhanced sensitivity for color found during the execution of pursuit would be consistent with a facilitation of the signals conveyed through the parvo- and koniocellular pathways. A further possibility for differentiating between the parvo- and koniocellular pathways and the magnocellular pathway is through stimuli of high spatial frequency[18], as shown by lesion studies of the parvocellular layers of the LGN[19]. If processing along the parvocellular pathway is indeed facilitated during pursuit, the sensitivity for high-spatial-frequency patterns should be enhanced too. We tested this hypothesis by measuring the contrast sensitivity to a high-spatial-frequency, square-wave pattern stimulus composed of thin horizontal lines with a vertical spatial frequency of 14 cycles per degree (c.p.d.). We flashed the square-wave pattern either just above or just below the horizontal midline and asked observers to judge its location. Relative to that during fixation, sensitivity to these high-spatial-frequency stimuli was improved by 16% during pursuit (**Fig. 3d**) ($n = 9$, $P = 0.009$). In line with the results using foveal blurred lines above, there was no change in sensitivity to foveally presented, low-spatial-frequency Gabor patches (**Supplementary Note** and **Supplementary Fig. 4** online). Combined with the improved sensitivity to chromatic stimuli,
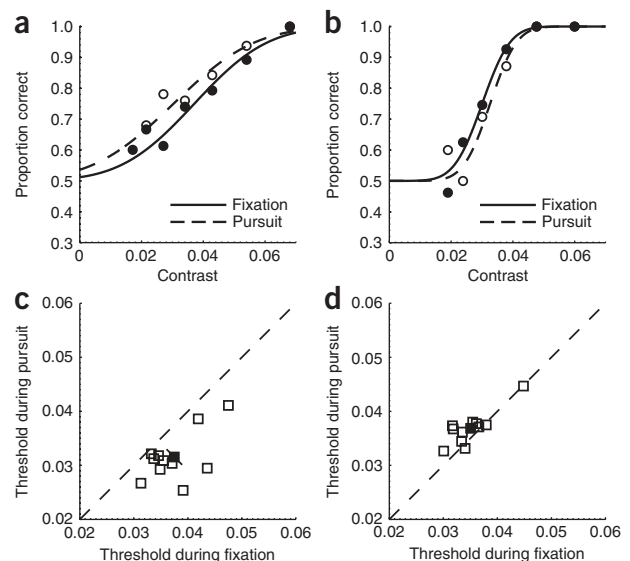
Figure 2 Contrast thresholds during pursuit and fixation for red-green color and luminance stimuli. (**a–d**) Data for stimulus detection, with stimuli presented either 2° above or 2° below the pursuit/fixation target. Data are for isoluminant red and green stimuli (**a,c**) or for achromatic black and white stimuli (**b,d**). Psychometric functions of one representative observer are shown in **a** and **b**. Dashed line and open circles, pursuit; solid line and filled circles, fixation. Only data points with at least ten observations are shown. Detection thresholds for all observers are shown in **c** and **d**. Open squares, individual data; filled squares, mean over all observers. Diagonal error bars, 95% confidence intervals of the mean difference between the thresholds during fixation and pursuit.
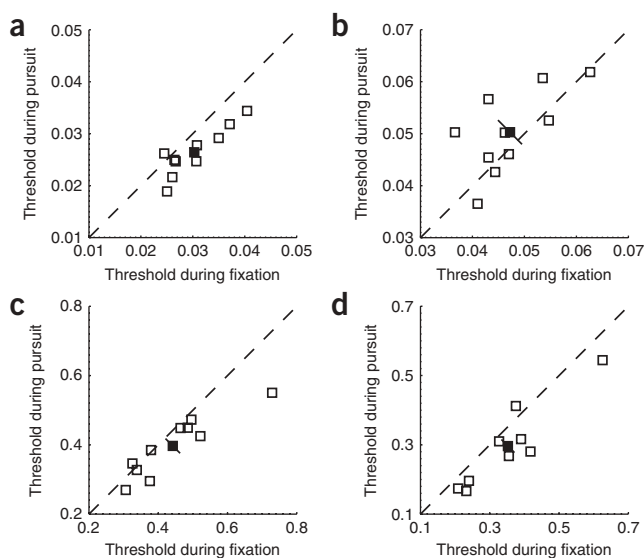
Figure 3 Influence of spatial location and stimulus type. (**a**) Foveal discrimination thresholds for isoluminant red and green stimuli. (**b**) Foveal discrimination thresholds for achromatic black and white stimuli. (**c**) Peripheral detection thresholds for isoluminant blue and yellow stimuli. (**d**) Foveal detection thresholds for 14 c.p.d. achromatic square-wave stimuli. Conventions are the same as in **Figure 2c,d**.

this result presents strong evidence for a general enhancement during smooth pursuit eye movements of the signals conveyed by the parvocellular pathway.

Mechanisms

There is a limited number of possible ways the visual system can increase its sensitivity. It may happen either by increasing integration across space and time or by increasing the contrast gain. If the enhancement is accomplished by an increased temporal integration, we would expect temporal resolution to decrease, and sensitivity for stimuli flickering at high temporal frequencies should also decrease. Therefore, we measured sensitivity for red-green stimuli flickering for 120 ms at 16.6 Hz. For such high-temporal-frequency stimuli (**Fig. 4a**), sensitivity was 13% higher during pursuit than during fixation ($n = 11$, $P = 0.003$). This result ultimately rules out the possibility that the enhancement is achieved by increasing the temporal integration time.

Instead of temporal integration, the enhancement could be accomplished by spatial integration. Indeed, a recent study reports an increased spatial integration along a motion trajectory for colored stimuli[21]. A similar spatial integration along the pursuit trajectory could account for the sensitivity increase during pursuit. If this is the case, the enhancement should depend on the spatial extent of the detection target and should disappear for stimuli smaller than the integration area. Thus, we flashed chromatic lines with four different horizontal widths (0.15, 0.225, 0.375 and 0.675°) during pursuit and during fixation ($n = 9$). To compensate for the lower sensitivity to these stimuli, we presented the lines for 40 ms. To ensure a constant retinal input in the pursuit condition, we moved the lines parallel to the pursuit target. The results (**Fig. 4b**) indicate that the performance difference between fixation and pursuit was independent of stimulus size and occurred even for the smallest size. At the same time, thresholds improved for larger stimuli, indicating that these stimuli were indeed smaller than the critical area of integration. A two-way, repeated-measures analysis of variance (ANOVA) on individual

thresholds (stimulus width × eye movement condition) revealed a significant main effect of stimulus width ($F_{3,24} = 124.91$, $P < 0.001$) and a significant main effect of eye movement condition ($F_{1,24} = 25.74$, $P = 0.001$). There was no significant interaction between stimulus width and eye movement condition ($F_{3,24} = 2.08$, $P = 0.129$). We calculated t-tests for all stimulus widths to compare sensitivities between pursuit and fixation. For all stimulus widths, sensitivities were significantly higher during pursuit than during fixation (0.15°, $P = 0.020$; 0.225°, $P = 0.001$; 0.375°, $P = 0.015$; 0.675°, $P = 0.001$). Thus, the enhancement seems to be accomplished neither by integration over time nor by spatial integration along the pursuit trajectory.

This leaves a gain mechanism as the most likely possibility. Attention is one example of such a gain mechanism. Another example has actually been observed during smooth pursuit. Small perturbations in the speed of the pursuit target result in stronger eye-movement responses during pursuit than during fixation, which is due to an increased sensori-motor transformation gain[22], most likely in frontal brain areas controlling pursuit[23].

Pursuit velocity

It is known that the sensori-motor transformation gain increases with increasing pursuit velocity[22]. To test whether the enhancement of color sensitivity depends on pursuit velocity as well, we measured contrast sensitivity for chromatic and luminance stimuli during fixation and at three different pursuit velocities (3.52, 10.57 and 14.10° s⁻¹, $n = 11$). In **Figure 5a**, thresholds are plotted relative to the threshold during fixation. We used linear regression to model the dependence of luminance and color thresholds on pursuit velocity (**Fig. 5b**). The regression slopes for luminance were significantly above zero ($P < 0.001$), indicating an increase in threshold for higher pursuit velocities. This is in line with previous studies showing increasing attentional demands with increasing pursuit velocity[24]. The regression slopes for color were significantly below zero ($P = 0.004$), indicating a decrease in threshold for higher pursuit velocities. A two-way, repeated-measures ANOVA (target velocity × stimulus condition) revealed a significant main effect of target velocity ($F_{3,30} = 8.38$, $P < 0.001$) and a significant main effect of stimulus condition ($F_{1,30} = 89.80$, $P < 0.001$). The interaction between target velocity and stimulus condition was also significant ($F_{3,30} = 37.06$, $P < 0.001$). Thus, the increase of the enhancement effect with pursuit velocity mimics the increase of the sensori-motor transformation gain with higher pursuit velocity[22].

Dynamics of the enhancement

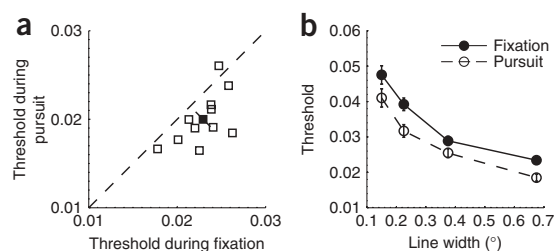Because neurons at the early stages of the visual system cannot discriminate between eye movement and object motion[25], the

Figure 4 Influence of temporal and spatial integration. (**a**) Peripheral detection thresholds for 16 Hz red-green flicker. Conventions are the same as in **Figure 2c,d**. (**b**) Average peripheral detection thresholds during fixation and pursuit for chromatic stimuli with different spatial widths. Error bars, 95% confidence intervals of the mean difference between the thresholds during fixation and pursuit.
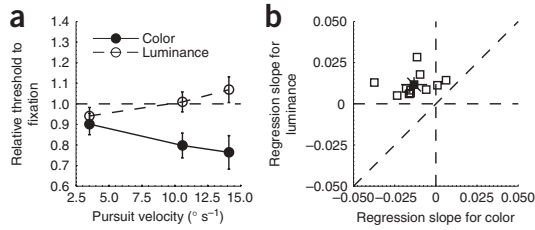
Figure 5 Influence of pursuit velocity. (**a**) Average peripheral detection thresholds for chromatic and achromatic stimuli during pursuit of different target velocities. Relative threshold values compared to the threshold during fixation are shown. Dashed line and open circles, achromatic stimuli; solid line and filled circles, chromatic stimuli. Error bars, 95% confidence interval. Horizontal dashed line, the threshold during fixation. (**b**) Slopes of regression lines. The thresholds for each individual observer were fitted by regression lines, separately for achromatic and chromatic stimuli. Open squares, individual data; filled squares, mean over all observers. Horizontal and vertical error bars, 95% confidence intervals of the slope means. Diagonal error bar, 95% confidence interval of the mean difference between the slopes for achromatic and chromatic stimuli.

performance enhancement must be conveyed by active feedback signals from cortical regions that have information about eye movements. Therefore, we investigated the time course of the enhancement during the initiation of smooth pursuit. If the enhancement occurred at later stages as a result of passive, feed-forward processes caused by retinal changes contingent on eye movement onset, then the earliest improvement would occur at the onset of the eye movement plus some extra time for retinal processing. If, however, the enhancement is an active, feedback-based process, triggered by an extraretinal signal[26], changes could occur even before the onset of the eye movement. Because of the sluggishness of the motor system, extraretinal signals controlling eye movement may precede the actual onset of eye movement. To differentiate between these two alternatives, we measured the detection performance for a red horizontal line with a fixed contrast presented at various times before and after pursuit initiation (**Fig. 6a**). We determined the onset of the increase in perceptual enhancement by the interception of two regression lines fitted to the detection rate (**Fig. 6b,c**). The perceptual enhancement was evident from about 100 ms after target motion onset and 50 ms before the eyes started to move (**Fig. 6d**), supporting the hypothesis that there is an extraretinal source. These dynamics, together with the dissociation between the sensitivities for luminance and color stimuli, effectively also rule out the possibility that the enhancement is due to any artifacts of the experimental setup. These dynamics indicate also that the perceptual improvements reported here are the result of an active process, serving to adjust early visual processing to the requirements of pursuit eye movements. This is also
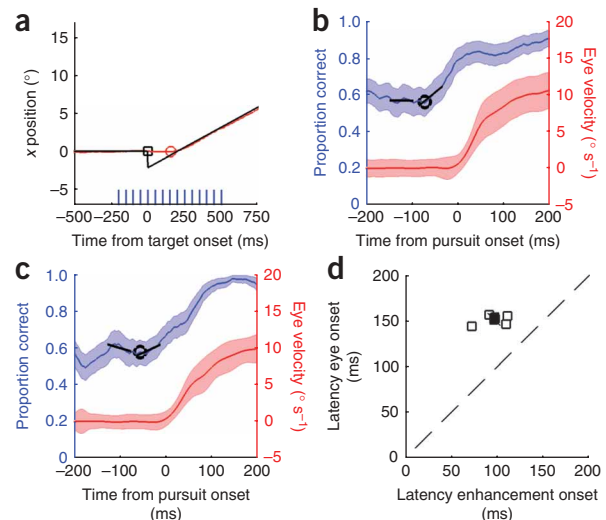
quite different from an enhancement for colored stimuli that has been reported for some observers at the end of saccadic eye movements[3,27].

DISCUSSION

Our results show a substantial improvement in the sensitivity to colored or high-spatial-frequency luminance targets during smooth pursuit eye movements. Because these two types of stimuli effectively isolate the parvocellular pathway or, for the blue-yellow colored targets, the koniocellular pathway, the facilitation emerges most likely in the lateral geniculate nucleus (LGN) of the thalamus, which is the earliest stage of visual processing that receives feedback connections. Feedback plays several important roles in visual processing. Through attentional modulation, processing of particular locations or objects can be enhanced as though shining a spotlight on them. Certain types of stimuli can be disambiguated[28], or knowledge about the world can be used to guide low-level, bottom-up processing[29]. Finally, some processing subsystems can be suppressed, such as the magnocellular system during saccadic eye movements[3]. Our results show that the opposite can occur as well—a boost of the parvo- and koniocellular systems that is not spatially constrained. Notably, this boost is not accompanied by a general suppression of the magnocellular pathway, as the sensitivity attenuation for luminance stimuli is spatially selective for peripheral stimuli and therefore more in line with an attentional modulation. The enhancement of the parvocellular and koniocellular pathways seems to be realized by a contrast gain mechanism, as other possibilities such as increased temporal or spatial integration can be ruled out effectively. Thus, the enhancement seems to reflect an increased sensory gain during pursuit, which may be similar to the previously reported increased motor gain during pursuit. This view is supported by the fact that both gain mechanisms scale in a similar manner with pursuit velocity.

The source of the enhancement is a bit more unclear than its site and its realization. Measuring the dynamics of the effect, we were able to restrict the possible candidates. First, the visually evoked response latency must be below 100 ms and activation must be present 50 ms before the onset of pursuit. Second, the activation has to sustain during pursuit, even when the target is essentially stabilized on the retina. At least two regions match these criteria: the medial superior temporal area (MST) and the frontal pursuit area (FPA), which is a pursuit-specialized subregion of the frontal eye fields. Activation in MST and the frontal eye fields builds up with a latency of around 75 ms (ref. 30), which is in line with our results. Visual tracking neurons in MST encode target motion in world coordinates and are active even when the pursuit target is

Figure 6 Dynamics of the enhancement. Peripheral detection performance for chromatic stimuli during the initiation of smooth pursuit eye movements. (**a**) Example eye position (red) and pursuit target position (black) in one trial. We presented a red horizontal line with a fixed contrast at different points in time (blue vertical lines) relative to target onset (black square) of a step-ramp motion. For the analysis, the data are aligned to eye movement onset (red circle). (**b,c**) Detection performance for two representative observers. Data are aligned to pursuit onset. Proportion correct is plotted in blue on the left *y* axis, mean eye velocity in red on the right *y* axis. Blue shaded area, s.e.m. of the detection rate; red shaded area, s.d. of the eye velocity. Black lines, regression lines for determining the onset of the rise in detection rate (black circle). (**d**) Latency of enhancement rise and pursuit onset relative to target onset. Open squares, individual data; filled squares, mean over all observers. Diagonal error bar, 95% confidence interval of the mean latency difference between enhancement and pursuit onsets.

blanked[31,32]. Recently, tracking neurons in MST have been shown to be active exclusively during voluntary gaze shifts—irrespective of whether gaze is redirected by head or eye rotation—but not during reflexive gaze stabilization[33,34]. The second plausible candidate, the FPA, has been shown to be involved in smooth pursuit gain control[23]. Activation in the FPA correlates with pursuit velocity, which is consistent with our velocity-dependent enhancement. However, latency measurements in the FPA yield only a slight advance of 25 ms relative to pursuit initiation[35], which is not fully compatible with our data.

Our results raise the question of the functional role of an enhanced parvocellular system during pursuit. There are basically three possibilities for why and how visual processing could be improved during pursuit: (i) improved recognition of the pursuit target, (ii) improved perception of other stationary and moving objects and (iii) improved tracking of the pursuit target.

Very little is known about the recognition of tracked, moving targets. Certainly one of the functional roles of pursuit is to bring the pursuit target to the fovea for closer inspection. Because the residual eye speeds during pursuit are higher than during fixation[36], recognition is more difficult owing to this additional jitter. Improving sensitivity of the visual pathway that is predominantly concerned with medium and high spatial frequencies could certainly benefit object recognition.

Second, an improvement of visual sensitivity to medium and high spatial frequencies would have an immediate benefit for peri-pursuit perception. As pursuit eye movements can be maintained for extended periods of time, perception during pursuit is important. Smooth pursuit induces a constant retinal motion of the whole scene, so that all physically stationary objects move on the retina. As a result, these movements might cause motion blur. Increasing contrast sensitivity would alleviate this effect, and it seems that there are indeed some corrective mechanisms in place that cause less motion blur during pursuit than what would be expected based on the retinal motion alone[37,38]. This hypothesis agrees very well with our finding that the increased sensitivity is not caused by increased spatial or temporal summation, which would actually increase motion smear.

The last possibility—improved tracking—might seem far-fetched, because pursuit is associated with visual motion, and visual motion in turn with the middle temporal area (MT), which receives predominantly magnocellular inputs. However, during pursuit the pursuit target is close to stationary on the retina and moves across the retina rather slowly. Although the ongoing pursuit is driven mainly by an internal signal[14], small errors in speed and position are used to make corrections if necessary[39,40]; for example, when the tracked object changes its speed. In this situation, a high sensitivity to these speed or position errors would be beneficial. Neurons in brain areas associated with the fast, first-order motion energy mechanism are typically tuned to higher speeds[41,42]. Even lesions of area MT do not adversely affect the maintenance of pursuit[43]. Alternatively, a high-level motion mechanism based on position tracking[44] has been suggested as the basis for precise pursuit. This position-tracking mechanism seems to be more efficient at low speeds and is also capable of detecting the motion of low-contrast, isoluminant stimuli[16,45]. However, such position-based input to pursuit might not depend on cortical motion processing at all[46]. There are neurons in the rostral part of the superior colliculus that encode position error, which can be used to guide saccades or smooth pursuit[47].

Most likely, the enhancement of the parvocellular system would benefit all three of these functions. It could aim at a facilitation of the position tracking for pursuit maintenance, and at the same time lead to an improvement in sensitivity to all other stimuli being processed through the same system. In this way, the improved sensory gain described here goes hand in hand with the improved motor gain described earlier to optimize sensori-motor processing for smooth pursuit eye movements.

METHODS

Observers. Twenty-one observers (mean age 28 ± 8 years), including authors A.C.S., D.I.B. and K.R.G., participated in these experiments. Informed consent was obtained according to the Declaration of Helsinki. Methods and procedures followed the guidelines of the Deutsche Gesellschaft für Psychologie. Each experiment was completed by at least six observers.

Visual stimuli. The observers were seated in a dimly lit room facing a gamma-corrected 21-inch CRT monitor (ELO Touchsystems) driven by an Nivida Quadro NVS 28 graphics board with a refresh rate of 100 Hz non-interlaced. At a viewing distance of 47 cm, the active screen area subtended 45° horizontally and 36° vertically on the subject's retina. With a spatial resolution of 1,280 × 1,024 pixels, this results in 28 pixels per degree. We used a black bull's-eye with an outer radius of 0.3° and an inner radius of 0.15° as a pursuit or fixation target. To measure contrast sensitivity, we used different stimuli. The basic stimulus was a horizontal line that spanned the whole screen horizontally and was modulated vertically by a gaussian distribution with a s.d. of 0.15°. We flashed this stimulus for one refresh cycle of the monitor, nominally 10 ms. Because on CRT screens all pixels are drawn sequentially line by line, the effective stimulus duration depends on the refresh rate and the decay times of the monitor phosphors. Measurement of the stimulus intensity with a photodiode showed that our phosphors decayed to 50% of peak in less than 1 ms and to 5% of peak in less than 2 ms. The gaussian bar contains mostly low spatial frequencies, because the Fourier transform of a gaussian distribution is gaussian again. In our case, the s.d. in the frequency domain was 1.06 c.p.d., which means that about 70% of its energy is below 1 c.p.d. and about 95% below 2 c.p.d. To measure the contrast sensitivity for high spatial frequencies, we used a horizontally aligned square-wave pattern with a vertical spatial frequency of 14 c.p.d. and an overall height of 1.2°. To measure the influence of temporal integration, we flickered the basic line with a temporal frequency of 16.6 Hz in red-green isoluminant color for 120 ms and asked the observers to indicate the position. To measure the influence of spatial integration, we used gaussian patches with a vertical s.d. of 0.15° and four different horizontal s.d. values: 0.15, 0.225, 0.375 and 0.675°. We presented the gaussian patches for 40 ms at the same horizontal position as the pursuit target.

Eye movement recording and analysis. Observers viewed the display binocularly and their heads were fixed using a chin rest. We recorded eye position signals with a head-mounted, video-based eye tracker (EyeLink II; SR Research Ltd.) sampled at 250 Hz. By digital differentiation of eye position signals over time, we obtained eye velocity signals. The eye position and velocity signals were filtered by a Butterworth filter with cut-off frequencies of 30 and 20 Hz, respectively. To determine smooth pursuit onset, we analyzed an interval between 80 ms and 300 ms after target onset. We defined the interception of the best-fitting regression line to the velocity trace and the x axis as pursuit onset[48]. To determine smooth pursuit gain, we divided the eye velocity by the pursuit target velocity in a 150 ms interval 1,250 ms after pursuit target motion onset. To detect saccades, we used a cut-off criterion ($75,000° \text{ s}^{-3}$) on the third derivate of eye position[49]. Data from trials containing saccades in an interval of 100 ms centered on stimulus presentation and trials with a pursuit gain lower than 0.7 were discarded and the trials repeated.

Psychophysical data analysis. We adjusted the contrast of the stimuli according to a staircase procedure[12] and obtained thresholds by fitting the percentage of correct answers for the different contrast levels with a cumulative gaussian function. We used the Psignifit toolbox[50] in Matlab to fit the psychometric function. To investigate the time course of the enhancement, we flashed a red line with a fixed contrast at various points in time around the pursuit target onset. We calculated the time course of the detection rate by means of a sliding weighted average[49]. Then we determined the onset of the rise in detection rate by the interception of two sliding regression lines. The regression intervals were 50 ms long and were separated by a 10-ms gap. As soon as the difference of the slopes exceeded a criterion of 1.5, their intercept was defined as onset of the enhancement.

Statistical analysis. If not stated otherwise, we used two-sided *t*-tests to check for threshold differences between fixation and pursuit. In the case of a second independent variable or more than two eye-movement conditions, we used a repeated-measures ANOVA to test the influence of the independent variables. We performed all tests at a 0.05 significance level.

Experimental procedure. In fixation trials we presented the bull's-eye for 1,500 ms at the center of the screen, where observers had to keep fixation. One thousand milliseconds after the beginning of the trial, we flashed the line stimulus for 10 ms, 2° above or below the bull's-eye. In pursuit trials, we presented the bull's-eye 13° left or right of the center of the screen. After 250 ms, the bull's-eye moved toward the screen center at a velocity of 10.6° s^{-1}; observers were instructed to track it as accurately as possible. When the bull's-eye reached the screen center, we flashed the line, resulting in the same physical and retinal stimulation as in fixation trials. Motion continued for another 500 ms. At the end of the trial, we collected the perceptual judgment. Depending on the task, observers were asked whether the stimulus appeared above or below the fixation target or what the hue of the stimulus was. Feedback was provided. In the experiment with varying pursuit velocity, we kept the time course constant but adjusted the starting point of the pursuit target, so that the pursuit target always reached the screen center 1,250 ms after motion onset.

Experimental protocols. We varied the tasks of the observers and the nature or position of the visual stimuli. In the basic protocol, we used stimuli that were modulated in luminance or in isoluminant red-green or blue-yellow color and asked observers to indicate the stimulus position. If not stated otherwise, the stimuli were presented either 2° above or 2° below the pursuit/fixation target. To determine the sensitivity of color naming, we asked observers to indicate the hue of the stimulus. To test the influence of spatial location, we flashed the horizontal line at the vertical screen center (that is, on the target's trajectory in pursuit trials) and asked observers to indicate the hue of the stimuli. The sensitivity for high spatial frequency in the fovea was assessed by presenting the square-wave pattern either above or below the vertical screen center and asking observers to indicate its location. Finally, we investigated the time course of color enhancement during the initiation of smooth pursuit[48]. In this case, we flashed a red line with a fixed contrast at various points in time around the initiation of smooth pursuit and asked the observers to indicate its location.

Note: Supplementary information is available on the Nature Neuroscience website.

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