Coherent motion pops out during smooth pursuit

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Stimulus motion is a prominent feature that is used by the visual system to segment figure from ground and perceptually bind widely separated objects. Pursuit eye movements can be influenced by such perceptual grouping processes. We have examined the subjects' ability to detect small amounts of coherent motion in random dot kinematograms during pursuit. We compared performance on tests of coherent motion perception while subjects fixated a stationary spot or while they tracked a moving target. The results indicate that smooth pursuit can improve subjects' ability to detect the presence of coherent motion. We tentatively propose that an efference copy of the eye movement signal can enhance the ability of the visual system to detect correlations between sparsely placed targets among noisy distractors. *NeuroReport* 13:1313–1316 © 2002 Lippincott Williams & Wilkins.

Key words: Coherent motion; Eye-movement recording; Motion detection; Perceptual pop-out; Saccades; Smooth pursuit eye-movements; Vision

INTRODUCTION

Vision helps us to move through a world full of moving objects (usually) without bumping into things. While in motion ourselves, another moving object may catch our eye and we may decide to track it. Despite the inherit complexity of this task, we experience little difficulty in tracking such moving targets although they are embedded in a complex scene containing both stationary and moving objects. While some forms of illusory distortions of vision during pursuit have been reported [1,2], for the most part perception remains stable during eye movements, and we appear to be able to move our eyes at the correct speed and direction to keep up with a pursued target, even when it is presented on top of a cluttered background [3,4]. Various explanations have been put forth to explain our ability to separate image motion introduced by self movements *vs* those introduced by object movements [5,6]. Whereas vision in the brief moments prior to saccade onset appears to be suppressed or distorted [7], we demonstrate here that motion perception can actually benefit from on-going pursuit eye movements. Using the paradigm of coherent motion detection [8,9] we show that thresholds drop to values as low as 2% during smooth pursuit, which corresponds to as few as six to eight dots moving coherently among 400 random dots. This form of pursuit-induced pop-out of motion detection challenges simple theories of motion perception [10], requiring the need to incorporate extra-retinal information into an early stage of visual processing [11,12].

MATERIALS AND METHODS

The visual stimuli were generated on a PC and a Cambridge Research Systems VSG-Card using programs written in C. The stimuli were back-projected on a semi-translucent screen (60×40 cm) using a Panasonic SVGA-Projector (800×600 pixels). They were viewed from a distance of 130 cm, resulting in a pixel resolution of 0.03° with a display range from $\pm 12.5°$ horizontally and $\pm 9.5°$ vertically. The internal precision of the pixel position was 16 times higher than that produced by the projector, thereby insuring smooth dot motion.

The visual stimuli consisted of a fixation target dot (7×7 pixels = 0.23°) and 400 background dots (5×5 pixels = 0.17°). The fixation dot was either stationary or it moved horizontally. The background dots moved along random trajectories creating a random dot kinematogram (see Fig. 1). In half of the trials 0.5–16% of the random dots were replaced by dots that moved coherently along the horizontal axis with a sinusoidal velocity profile.

The speed of the random dot trajectories was distributed over the same range and they had the same mean velocity as those of the coherent dots. The overall distribution of directions was carefully balanced to prevent net drifts. To mask any possible cues owing to speed-dependent perceived brightness, the luminance of all dots was jittered (within $\pm 5\%$ of the luminance of the fixation dot). The half-life of each dot (coherent or random) was 840 ms, after which time it changed speed and direction. These transition periods were randomised over time, such that a steady migration of dots from random to coherent or vice versa occurred.

The subjects judged the presence or absence of coherent motion in the random-dot displays. They were instructed to press one of two buttons depending on whether they thought the stimulus contained any dots that move in a coherent direction. They were also instructed that half of the trials would contain stimuli with coherent motion, whereas

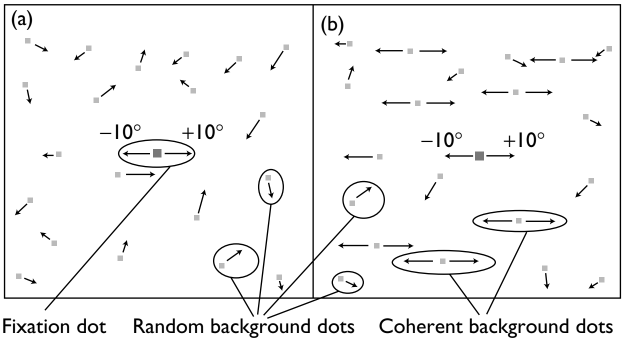

Fig. 1. Schematic illustration of the experimental paradigm and the subject's task. Subjects were instructed to pursue a moving illuminant target (encircled in (**a**)), which drifted (signified by arrows) with a sinusoidal velocity profile on a dark background along the horizontal meridian. The subjects' eye movements were recorded using infrared light reflection and limbus tracking (see Materials and Methods). Within the visual field 400 illuminant dots moved along random trajectories (encircled random background dots). On half of all trials all dot trajectories were random, while on the other half of trials, 0.5–16% of the random dots were replaced by dots that moved in a synchronized fashion with the fixation dot (encircled coherent background dots, in (**b**)). During pursuit, the subjects were requested to judge whether the random dot kinetograms contained any dots that moved coherently with the fixation dot. In a further condition, the same subjects fixated a stationary target and judged whether the random dot kinetograms contained any coherent dot motion. In the in-phase-pursuit condition, the fixation dot moved horizontally with a sinusoidal velocity profile (see Materials and Methods). In the counter-phase-pursuit, condition the stimuli were similar, but now the coherent dots moved in counter-phase to the movement of the fixation dot. In the fixation condition the fixation dot remained stationary throughout and subjects were instructed to maintain steady fixation.

the other half would contain stimuli without coherent motion. They were further instructed to maintain steady fixation during the condition with a stationary fixation spot. In the conditions with smooth pursuit, they were instructed to pursue the moving fixation spot as accurately as possible while they judged the presence or absence of coherent motion in the background motion.

Three conditions were tested. (1) Fixation: the fixation dot was stationary throughout the run, and subjects were instructed to maintain steady gaze at the center of the screen. (2) In-phase coherent motion: The fixation dot moved with a sinusoidal velocity profile on the horizontal meridian from -10° to $+10^\circ$ (with 0° in the center of the screen), and the maximum speed of 12.6°/s occurred when it passed the center of the screen. This yielded a frequency of ~ 0.2 Hz. The coherent dots of the random dot kinetograms were synchronized with the fixation dot so their relative position to the fixation dot was stable over the 840 ms refresh period. (3) Anti-phase coherent motion: the fixation dot moved as in the in-phase condition but now the fixation dot and the coherent background dots were out-of-phase. Each subject performed three blocks, one for each of the main conditions. Each block contained 60 trials of 10 seconds duration. Subjects knew in advance whether the coherent motion trials would contain dots that were in-phase or in anti-phase with the fixation dot.

Eye movements were recorded using an infrared corneal reflection device (IRIS, Skalar Medical, Delft, The Netherlands) with a best spatial resolution of 2 min of arc. The system is linear within 3% for horizontal eye displacements of $\pm 20^\circ$ and derives eye velocity by on-line differentiation of the eye position signal. Position and velocity signals of the left eye, as well as the computer-generated position signal of the pursuit stimulus were sampled at 1000 Hz and stored in a laboratory computer for off-line analysis. Calibration of eye position was performed prior to and after each run. For calibration, subjects made saccades from the central fixation point to targets at lateral locations of $\pm 12^\circ$. For the analysis of the pursuit eye movement recordings, smooth eye movements were separated from saccades by identifying, under visual control, the saccades and replacing them by linear segments, joining the corresponding beginning and end points of the eye traces. This was performed with the help of an interactive computer program. The smooth eye movement signal and the stimulus time course were Fourier transformed and expressed in terms of gain and phase. Gain was defined as the ratio between eye and stimulus amplitudes. Phase was defined by the phase difference between eye and stimulus traces. These values were calculated for ≥ 2 cycles of the sinusoidal stimulation, and a mean of these estimates was taken. No significant differences were found between leftward and rightward eye movements. The data were therefore pooled across both directions.

Saccade detection was performed by a velocity threshold algorithm.The program yielded estimates of duration, peak velocity and amplitude of each saccade. We then calculated the mean amplitude of saccades as well as the total number of saccades that occurred during the stimulation period (saccade frequency). The product of the two parameters, mean amplitude and frequency, gives an estimate of saccadic activity (mean saccade amplitude per time interval). Twelve healthy subjects with normal acuity participated in the experiments.

RESULTS

Performance was compared under conditions demanding the steady fixation of a centrally projected stationary dot, to that requiring the pursuit of a moving target. The latter moved at the same speed as the dots with coherent motion and its cyclic motion was either in- or out-of-phase of the coherent background motion. Figure 2 presents the results with respect to the subjects' ability to detect coherent motion. During steady fixation, subjects required on average 6% coherent motion for detection level performance of 75%, which is comparable with published values for similar conditions [13,14]. During pursuit and in-phase coherent motion, the threshold for coherent motion detection dropped to $\leq 2\%$. This shift in the threshold curve cannot be explained by a change in the subjects' response bias, since their willingness to report the presence of coherent motion in its absence (i.e. the false alarm rate) did not significantly differ across conditions. An ANOVA revealed a significant effect of the motion condition (in-phase with pursuit, anti-phase to pursuit, fixation; $F(2,84) = 4.3$, $p < 0.02$) and the motion coherence level ($F(6,84) = 29.3$, $p > 0.0001$). The interaction term between these main effects is also significant ($F(12,84) = 2.2$, $p < 0.02$), which is reflected in the steeper slope of the fitted Weibull function (Fig. 2). Inspection of the individual threshold functions indicated

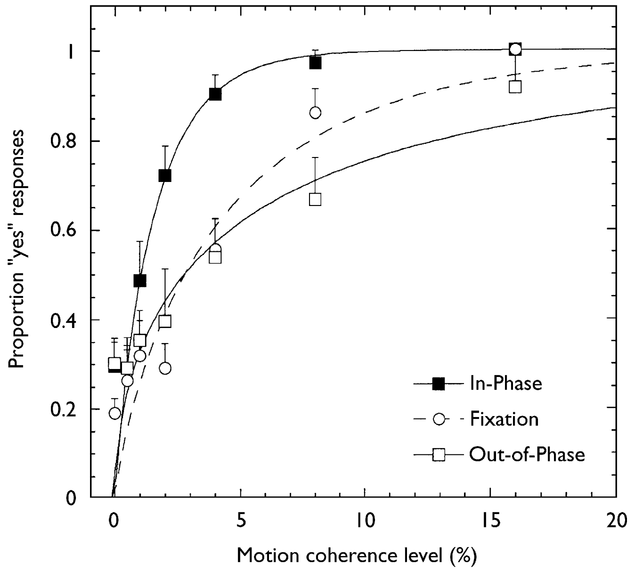

Fig. 2. Results of the coherence motion detection experiment. The proportion of 'yes' responses (i.e. subject responds that coherent motion was present) is shown as a function of the level of motion coherence for the conditions with steady fixation (open circles), with smooth in-phase pursuit (filled squares), or with out-of-phase pursuit (open squares). The curves are best-fitting Weibull functions. The data points show the results of 12 subjects.

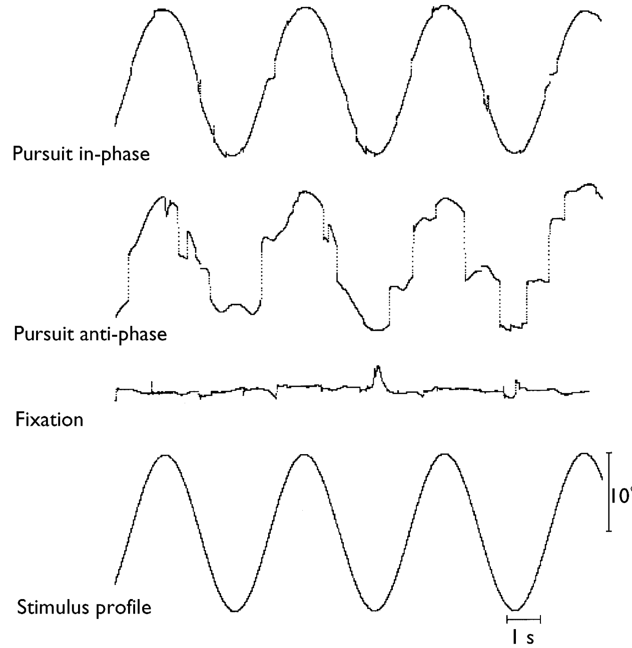

Fig. 3. Typical eye movement traces recorded for one subject. Eye position traces are shown during the conditions of in-phase and anti-phase (out-of-phase) coherent motion, as well as during the steady fixation of a stationary spot. Vertical and horizontal bars represent the amplitude and time scales. Note the degradation of the pursuit signal during trials with coherent motion (16% for this example), moving in the opposite direction of the eyes.

that 83% of the subjects showed a significant effect, with only 2 of the 12 subjects showing functions that were not statistically different across these conditions. Pursuit in a direction opposite to that of the coherent motion (i.e. the out-of-phase condition) led to an overall drop in performance (Fig. 2). These differences were most pronounced for trials with high coherence levels.

Simultaneous to the acquisition of the psychophysical judgments of coherent motion, we measured the subjects' pursuit eye movements. An example of the pursuit eye movements of one subject is given in Fig. 3 and the results from all 12 subjects are summarized in Fig. 4. During the steady fixation task, subjects were able to maintain fixation, although some eye movements could be detected (Fig. 4, open circles above zero). During the pursuit task, the gain of the pursuit was close to unity for the condition of in-phase pursuit and this was independent of the level of coherent motion. Interestingly, in the out-of-phase condition pursuit gain dropped significantly (ANOVA, $p < 0.001$) and the level of saccadic activity increased. This finding indicates that the subjects had more difficulty to perform the pursuit task even for trials with few coherently moving dots. The differences evident in Fig. 4 reflect the subjective difficulty experienced by the subjects while performing this dual task. Perceptual pop-out in the in-phase condition led to better task performance and subjects reported having little difficulty detecting coherent motion during pursuit.

DISCUSSION

These findings suggest that motion perception and pursuit eye movements are interdependently related: pursuit boosts the ability of the motion perceptual system to extract sparse coherent motion signals from a noisy background and, at the same time, coherent motion aides the pursuit system to guide eye movements while tracking a target moving among distractors. The observation that the coherence motion thresholds and pursuit gain are both dependent on the relative phase of the target and coherently moving background dots suggests that the observed effect is specific to the synchronicity among pursuit target and background. Perceptual pop-out implies that pre-attentive [15,16] early visual mechanisms might be responsible for this phenomenon. It has been shown that the superior colliculus generates a collorary discharge of the eye movement control signal [17] and this signal could be sent back to the cortex. This information may be used pre-attentively to compare incoming motion signals with the on-going efference copy of the pursuit signal [18]. This notion would explain why this form of pop-out only occurs when the eyes are in motion and the coherent motion signal is in-phase with the pursuit signal. Such perceptual pop-out might help to shed light on the complex nature of motion perception [19–21] and heading perception [22,23] during eye movements. Interestingly, damage to the dorsal occipito-parietal pathway leads to an impairment in the ability to discount illusory motion in stationary backgrounds while the eyes move [24,25], suggesting this area's involvement in the analysis of extraretinal signals.

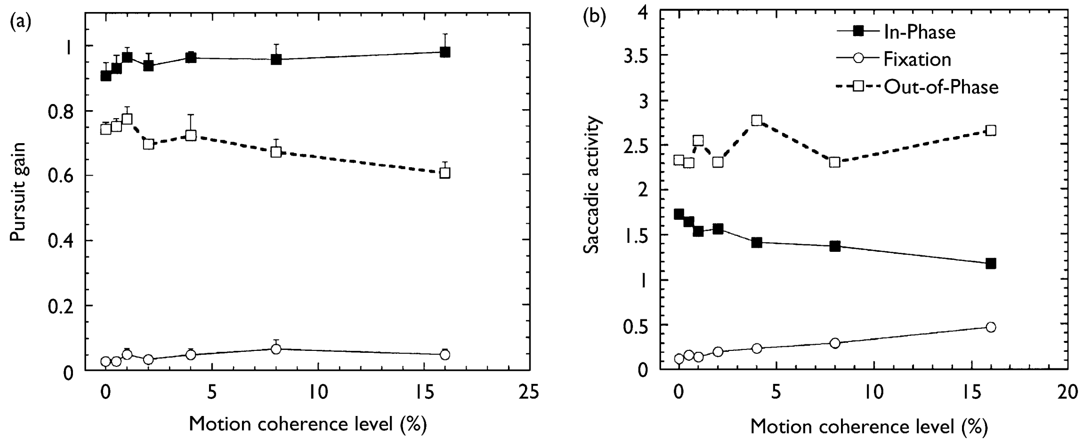

Fig. 4. Summary of the eye movement data. (**a**) Pursuit gain and (**b**) saccadic activity, of the eye movement data (recorded in 12 subjects) are plotted as a function of the motion coherence level. The subject viewed the stimulus with their head resting on a chinrest. Eye movements were recorded with a head mounted Infrared-based Skalar system, recorded at a sampling rate of 1000 Hz, and analyzed with specially designed software. Saccade frequency and amplitude were determined on each trial, and the saccadic activity was defined as saccadic activity = average saccade amplitude × saccade frequency. To determine the gain of the smooth pursuit, the eye-movement data were first screened for the presence of saccades, which were subsequently removed from the traces. The amplitude and phase of the resulting traces were extracted with Fourier analysis. Gain was defined as the ratio between the stimulus and eye trace amplitudes.

CONCLUSION

Our results suggest that smooth pursuit of a moving target improves subjects' ability to detect the presence of coherent motion. This form of pursuit-induced pop-out suggests that an efference copy of the eye movement signal enhances the ability of the visual system to detect correlations among motion signals in noise.

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