

Pursuit of the ineffable: perceptual and motor reversals during the tracking of apparent motion

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Pursuit can be guided by perceived rather than physical motion, but the temporal relationship between motion perception and pursuit is unknown. We used an apparent motion stimulus consisting of a horizontal row of evenly spaced Kanizsa illusory squares (1.44 deg^2): the illusory contours appeared at the midpoints of the illusory squares presented in the previous frame, producing bi-directional apparent motion of the illusory contours (21.5 deg/s) that could be reversed at will. We measured eye movements in five subjects asked to (1) track the motion of the illusory squares, and (2) reverse the perceived direction while continuing to track the squares. We measured the timing of the voluntary perceptual reversals and compared this to the time course of the reversal in tracking direction. We found that subjects could smoothly track the apparent motion of illusory squares and also produce saccade-free reversals in pursuit velocity. The time course of these motor reversals closely followed the measurements of the perceptual reversal and, on average, the perceptual reversals preceded the pursuit reversals by 53 ms, a delay shorter than when the perceptual reversal was visually guided. Smooth pursuit and the perception of motion direction were in temporal register and highly correlated, suggesting that pursuit can provide a real-time readout for the state of motion perception.

Keywords: eye movements, smooth pursuit, motion perception, apparent motion.

Introduction

When viewing moving objects in their visual environment, primates are able to produce tracking eye movements that compensate for the motion of the retinal image of the object of interest. This response provides crucial support for vision by maintaining the retinal image of the object close to the fovea and by minimizing blur that would otherwise undermine visual perception. Because in simple visual situations the perceived motion and the physical motion of the target's retinal image are the same, computational models of pursuit typically assume that the raw retinal-image motion is the driving stimulus for the pursuit response. However, experiments using more complex stimuli have demonstrated that pursuit can be driven by the perceived rather than the retinal motion. For instance, Steinbach (1976) demonstrated that the pursuit system can respond to visual motion that has ambiguous retinal counterparts: subjects tracked a perceived horizontal motion signal resulting from the cycloidal motion of targets attached to the circumference of a rolling wagon wheel. More recently, researchers have used line-figure objects viewed through vertical apertures to disentangle the retinal image motion from the perceived object motion: changing the coherence of the perceived motion affected the pursuit responses even though the retinal image motion remained the same (Beutter & Stone, 2000; Stone, Beutter, & Lorenceau, 1996, 2000). Using a plaid stimulus that produces systematic perceptual errors, it has been demonstrated that pursuit and perception can be

biased in the same way and to the same degree (Beutter & Stone, 1998). Furthermore, it has been shown that cognitive expectations about visual motion can bias both pursuit and perception (Kowler, 1989; Krauzlis & Adler, 2001).

These studies provide evidence that pursuit can be guided by the perceived rather than the physical motion. However, the temporal relationship between motion perception and pursuit eye movements remains largely unknown; such information is critical for understanding the dynamical relationship between perception and action (Masson, Rybarczyk, Castet, & Mestre, 2000). One strategy for studying the time course of motion perception takes advantage of the multi-stability of apparent motion patterns. Multi-stability refers to the situation in which a single visual stimulus can evoke two or more stable percepts (Kelso, 1995). For instance, in the "quartet motion" paradigm, two points of light located at diagonally opposite corners of an unseen square are presented in alternation with two points corresponding to the other diagonal, inducing two distinct percepts: the dots are perceived to move either horizontally or vertically (Ramachandran & Anstis, 1985). A multi-stable directional signal can be generated by alternately presenting two rows of dots with counterphase locations: over a succession of frames, the horizontal position of a row of dots is shifted such that the dots fall in the exact midpoints of the dots presented during the preceding frame (Hock & Balz, 1994). Leftward and rightward motions are equally specified by the stimulus, but only one direction of motion is perceived at a time, making it

possible to study perceptual reversals without changing the visual stimulus (Hock, Schoner, & Voss, 1997).

The ability to smoothly track the apparent motion of an object has been demonstrated in humans (van der Steen, Tamminga, & Collewijn, 1983; Lamontagne, Gosselin, & Pivik, 2002). These studies indicate that if the spatial and temporal separations used to produce the apparent motion are correctly adjusted, the pursuit response is similar to that observed with real motion. Therefore, one could use the apparent motion produced by a counterphase row-of-elements stimulus to test for the relationship between movement perception and pursuit eye movements.

In this study, we report the pursuit responses evoked by a directionally ambiguous apparent motion stimulus made of objects defined by illusory contours (Kanizsa, 1976). We used psychophysical measurements and eye movement recordings to compare the timing of perceptual reversals in motion direction to the timing of pursuit reversals in eye velocity while tracking a directionally bi-stable stimulus. Our results reveal that perception of motion direction and pursuit are in temporal register. Finally, we show that the pursuit motor response can provide a real-time readout for the state of motion perception.

Methods

Subjects

Five human subjects (three female and two male, aged 27–38 years) participated in the experiment. Two of the subjects (R and L) were authors of the study, whereas the other three subjects were naïve as to the experimental conditions and hypotheses. One subject (S) had no previous experience of ocular motor testing. All experimental procedures were reviewed and approved by the Institutional Review Board, and each subject gave informed consent. Subjects were paid a fixed amount of money for their participation.

Stimuli

Stimuli were generated on a Power Mac G4 using the Psychophysics Toolbox extensions for Matlab (Brainard, 1997; Pelli, 1997), and displayed on a video monitor (Eizo FX-E7, 120 Hz) at a viewing distance of 41 cm. To minimize measurement errors, the subject's head movements were restrained using a bite bar so that the eyes in central position were directed toward the center of the screen. Stimuli were presented in discrete trials that required the subject to fixate and pursue a target for about 3 s.

We used a stimulus consisting of 16 evenly spaced Kanizsa-style illusory squares, subtending an angle of 46-deg horizontal. Each illusory square (1.44 deg^2) was defined by illusory contours produced by four circular inducers placed at each corner of a square and separated by 0.29 deg. The inducers were white disks (1.15 deg of diameter, luminance: 73.8 cd/m^2) from which right-angle sectors had been removed, displayed against a dark-gray background (luminance: 0 cd/m^2) (Figure 1a).

In contrast to previous experiments using the apparent motion of illusory squares (Ramachandran, 1985), the circular inducers rotated by $\pm 90 \text{ deg}$ on each consecutive frame, so that the illusory squares appeared at the exact midpoints of the illusory squares presented in the previous frame (Figure 1b). The stimulus, therefore, consisted of two alternating frames, each shown for 66 ms, and presented for a total duration of several seconds. The rapid alternation of frames produced a strong apparent motion of the illusory contours with a velocity of 21.57 deg/s . During preliminary tests, all subjects reported that they saw bi-directional apparent motion and that they could change the perceived direction of motion at will.

Experiment 1

Subjects were asked to smoothly track the apparent motion of the illusory squares. Subjects were first tested in four blocks of 100 trials. Each trial began with a fixation period lasting for 750–1250 ms. During this period, the two frames containing the rows of counterphase illusory squares were displayed in alternation, producing a bi-directional motion perception (Figure 1b). A small (0.46 deg) white box (luminance: 77 cd/m^2) was superimposed on the display to provide a fixation target. At the end of the fixation period, the fixation target was extinguished and the motion stimulus continued for an additional 2800 ms. Subjects were instructed to fixate the white box until it disappeared, and then track the perceived motion of the illusory squares.

Experiment 1 was designed to document the pursuit of the illusory square apparent motion. In the first block of this session, the fixation target appeared at an eccentricity of 20.8 deg on the left from the straight-ahead position, and subjects were asked to produce rightward pursuit. In the second block, the fixation target was set at an eccentricity of 20.8 deg on the right from the straight-ahead position, and subjects were asked to produce leftward pursuit. The remaining two blocks were designed to explore the ability to perform motor reversal. In these “pursuit reversal” trials, the fixation target always appeared on the left, and subjects were asked to start tracking to the right and to smoothly reverse tracking when reaching the center of the screen to come back to the initial fixation location.

Experiment 2

A second experiment was designed to compare the timing of reversals in perceived motion with the timing of reversals in smooth eye velocity. The procedure involved presenting a brief auditory stimulus (a 12-ms sin-wave at 2000 Hz) at randomized times during tracking. At the end of each trial, subjects were asked to report whether the tone occurred before or after they perceived a change in the direction of motion. This two-alternative forced-choice technique allowed us to estimate the time of perceptual reversals without requiring subjects to provide real-time responses; therefore, it allowed us to measure the timing of perception independent of motor reaction time. We simultaneously measured eye movements, allowing the comparison of perceptual and motor responses obtained from the same trials. We applied this general procedure in three distinct situations.

Test Sessions

Test sessions trials were similar to the “pursuit reversal” trials in Experiment 1, except for the delivery of the auditory stimulus. After a fixation period lasting 750–1250 ms, during which the two frames displaying the rows of illusory squares were alternating, the fixation target was extinguished, and the apparent motion of the illusory squares continued for an additional 2800 ms. After a delay of 866–1000 ms following the disappearance of the fixation target, the auditory tone was presented (Figure 1c). Subjects were instructed to initially track the motion of the illusory squares from left to right, to smoothly reverse tracking when reaching the center of the screen, and to then track the motion back toward the initial fixation location. At the end of each trial, subjects were asked to report whether the tone occurred before or after they perceived a change in the direction of motion by pressing the appropriate button on a response box. Each subject performed 6 blocks of 200 of these test trials.

Practice Sessions

To avoid learning effects during the experiment, subjects ran practice sessions with a real motion stimulus prior to the test sessions. The visual stimulus for these practice sessions consisted of one of the previously described rows of illusory squares (frame A, Figure 1b). Each trial started with a fixation period lasting for 750–1250 ms, during which the fixation target was superimposed to the row of illusory squares at an eccentricity of 20.8 deg on the left from the straight-ahead position. Once the fixation target was extinguished, the horizontal position of the row of illusory squares was incremented every 13.3 ms by steps of 0.29 deg to produce a real motion of the entire row at a linear velocity of 21.57 deg/s. After a period lasting 1000–1266 ms, the motion reversed (from rightward to leftward) for the remainder of the trial (1534–1800 ms for a total

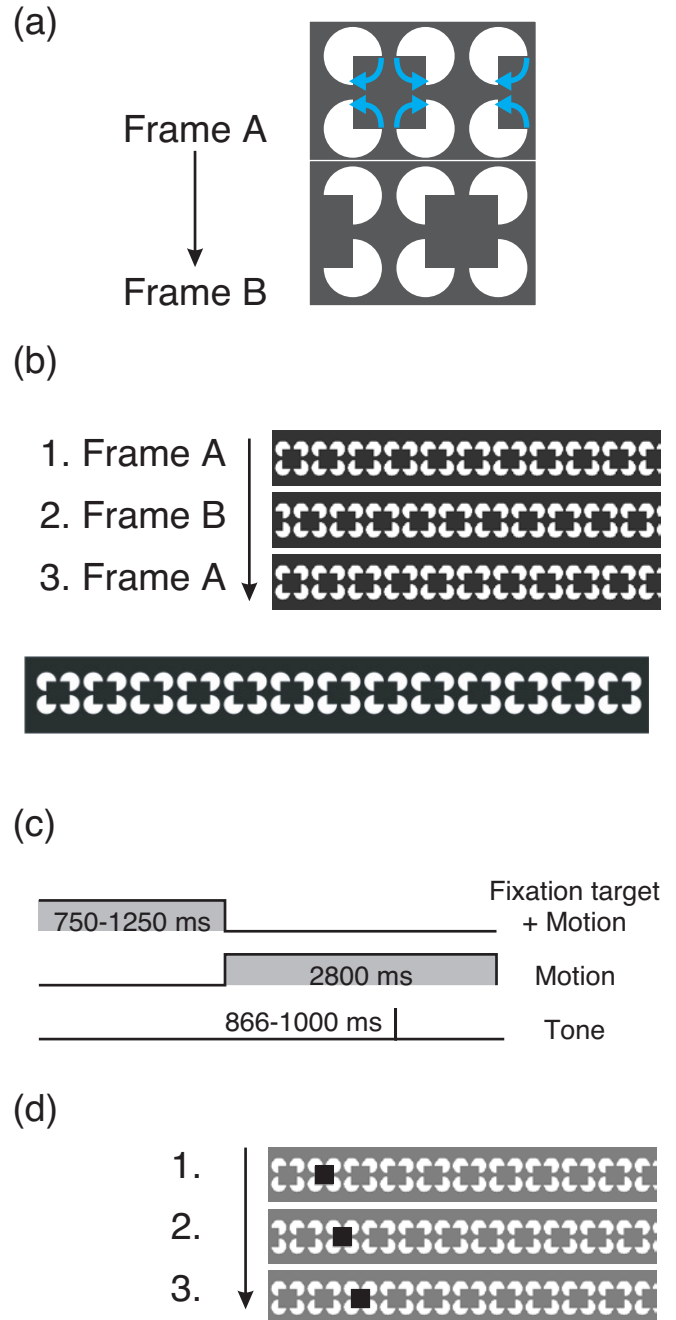


Figure 1. (a) Illustration of the visual stimuli used to induce the apparent motion of an illusory square. The transition from frame A to frame B is accomplished by rotating the circular inducers by ± 90 deg, as illustrated by the blue arrows. (b) Illustration of the stimuli used in test sessions. Only 11 of 16 illusory squares are shown here. (c). Schematic diagram of the temporal sequence of an individual trial used in test sessions of Experiment 2. (d) Illustration of the stimuli used in the control sessions of Experiment 2.

duration of 2800 ms). The delay between the auditory tone onset and the change of direction in motion could assume different durations (-160, -106, -53, 0, 53, 106, and 160, with negative values meaning that the tone occurred before the motion reversal). At the end of each trial, subjects reported whether the tone occurred before or after they perceived a change in direction. They received an auditory feedback following correct answers. For the 0-ms condition (for which there was no correct answer), they received randomized feedback. Each subject performed 6 blocks of 155 of these practice trials.

Control Sessions

To measure the temporal precision of the perceptual reversals, subjects performed control sessions that were identical to the test sessions except that the stimulus included a physical reversal of the tracked square. The visual stimulus consisted of the previously described row of illusory squares, but the background was light gray (luminance: 15.4 cd/m²). After a fixation period lasting for 750–1250 ms, the apparent motion of the illusory squares started as described in Experiment 1. In addition, a black square (luminance: 0 cd/m²) was superimposed to the leftmost illusory square. The black square was then displaced every 66 ms so that its position always coincided with an illusory square, resulting in the apparent motion of a real square (Figure 1d). After a period lasting 1000–1266 ms, the motion reversed (from rightward to leftward) for the remainder of the trial (1534–1800 ms for a total duration of 2800 ms). The delay between the auditory tone onset and the change of direction in motion could assume different duration (-160, -106, -53, 0, 53, 106, and 160, with negative values meaning that the tone occurred before the motion reversal). At the end of each trial, subjects reported whether the tone occurred before or after they perceived a change in direction. No feedback was given during the control sessions. Each subject performed 6 blocks of 155 of these control trials.

Data Acquisition and Analysis

Presentation of stimuli, and the acquisition, display, and storage of data were controlled by a personal computer using the Tempo software package (Reflective Computing). The visual display computer provided feedback signals to the Tempo computer at the onset of each new frame, allowing us to synchronize data collection to stimulus presentation with 1-ms resolution.

Eye movements were measured with an infrared video-based eye tracking system (RK-726, ISCAN Inc.) that reported the horizontal and vertical positions of the pupil with 12-bit resolution using a proprietary algorithm that computes the centroid of the pupil at 240 Hz. Before each block, we calibrated the output from the eye tracker by recording the raw digital values as subjects fixated 19 known locations three times in a pseudorandom

sequence. The mean values during 500-ms fixation intervals at each location were used to generate a smooth function (using cubic spline interpolation) for converting raw eye tracker values to horizontal eye position. We focused our analysis on the horizontal component of eye movements because the stimuli were moving exclusively along the horizontal meridian to minimize measurement errors.

All eye movement data and events related to the onset of stimuli were stored on disk during the experiment, and later transferred to a FreeBSD Linux-based system for subsequent offline analysis. An interactive analysis program was used to filter, display, and make measurements from the data. To generate smooth traces free of high frequency noise, we applied a low-pass filter (-3dB at 25 Hz) to the calibrated horizontal eye position signals. Horizontal eye velocities were obtained by applying a finite impulse response (FIR) filter (-3dB at 54 Hz) to the filtered eye position signals. Signals encoding eye acceleration were then obtained by applying the same FIR filter to the signals encoding velocity. We detected the occurrence of saccades by applying a set of amplitude criteria to the eye velocity and eye acceleration signals, as described previously (Krauzlis & Miles 1996). This algorithm permitted us to detect saccades with amplitudes as small as ~0.3 deg. To prevent any contamination of our measurements of smooth eye movements by saccades, we excluded from analysis an additional 5 ms before and after each detected saccade and replaced the corresponding values with NaNs (not a number). Saccade-free eye position, velocity, and acceleration signals were then exported to Matlab for further analysis.

For the motor reversal trials, eye movement signals were aligned on the “time of the motor reversal,” which was identified by (1) defining a 50-ms interval centered on the time at which eye position reached its largest value, and (2) finding the time point in this interval at which eye speed was closest to zero.

To normalize for differences in absolute pursuit gain across subjects, we scaled the velocity signal into a quantity we will refer to as the “percentage of motor reversal,” ranging from 0% (eye velocity during rightward pursuit) to 100% (eye velocity during leftward pursuit). We calculated the “percentage of motor reversal” by subtracting the maximum rightward velocity (V_R) from the velocity signal at each time point ($V(t)$) and dividing this difference by the sum of the absolute maximum velocities in the rightward (V_R) and leftward (V_L) directions (Equation 1).

$$PMR(t) = 100 * (V(t) - V_R) / (|V_R| + |V_L|) \quad (1)$$

We constructed psychometric functions by fitting cumulative Gaussian functions to the tabulated perceptual judgments. We weighted each point by its expected uncertainty (assuming a binomial distribution)

and computed the minimum chi-square fits to the data. The bias and threshold were defined to be the offset and SD of the best-fitting cumulative Gaussian, respectively.

Results

Experiment 1

Subjects tracked the apparent motion of the illusory squares with a smooth continuous movement similar to what one would expect when tracking a real moving object. Figure 2 shows eye position and eye velocity signals for a single trial from subject N (top panels). Following a latent period after the disappearance of the fixation target, eye speed increased smoothly to values close to the stimulus speed (21.57 deg/s) and remained at or near stimulus speed, without saccades, until the final several hundred milliseconds of the trial. Similar patterns were observed in most of the trials for all subjects. Figure 2 (bottom panel) shows the average eye velocity during steady-state tracking for all subjects. Eye velocities were averaged over a 500-ms interval of steady-state tracking for all trials in the rightward and leftward conditions. Despite some variability across subjects, eye speed was close to stimulus speed for both rightward (positive values) and leftward (negative values) trials. Average velocity gain (i.e., the ratio of eye velocity to target velocity) was close to unity (0.99). Only one subject (S) exhibited lower velocity gain (0.91) in the leftward condition. However, it should be noted that such a value is well within the range of normal gain observed in other experimental situations.

On the last blocks of Experiment 1, subjects were asked to reverse tracking when reaching the center of the screen. Eye position and eye velocity signals were aligned on the time of the motor reversal. Figure 3a shows an example of the methods used to realign eye position (top graphs) and eye velocity (bottom graphs) signals in a “pursuit reversal” single trial from subject J. In each trial, the position and velocity signals were then realigned (green arrows) on the time of the motor reversal (right panels).

Figure 3b (left panels) shows the eye position and eye velocity for 11 individual “pursuit reversal” trials (subject N). Because eye position and eye velocity signals are aligned on the motor reversal, the position traces do not always overlap. There were no cues to trigger the motor reversal; subjects were simply instructed to reverse tracking around the center of the screen. The variability in the eye position signals reflects the variability in the timing of the subject’s voluntary reversal. It can be seen that the velocity traces were similar in all trials: eye velocity started at or near the rightward speed associated with the bi-stable stimulus, and then quickly changed to reach the leftward speed associated with the stimulus. In subject N, the transition between leftward and rightward pursuit involved a rapid reversal in eye velocity (lasting

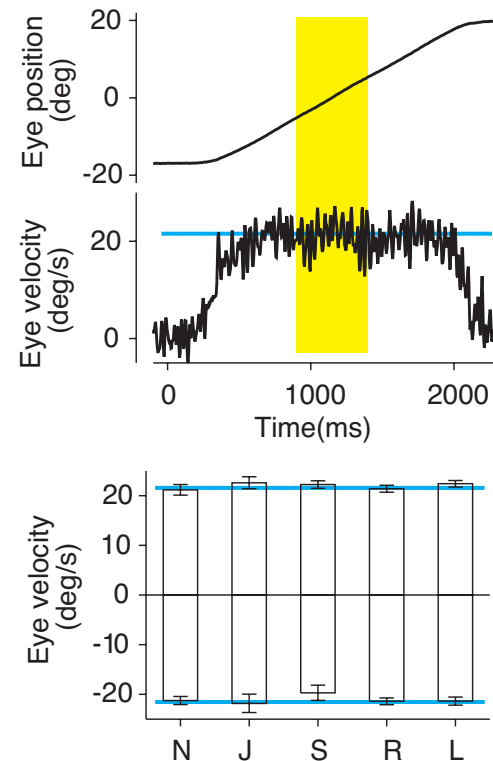


Figure 2. Top panels: example of a single pursuit trial (subject N). Eye position and eye velocity as a function of time aligned with respect to the fixation target disappearance. The yellow area indicates the 500-ms interval used to compute average eye velocity for that trial. The solid blue line indicates the stimulus speed. Bottom panel: average steady-state speeds and corresponding SDs for each subject in the rightward (positive values) and leftward (negative values) trials. The top and bottom solid horizontal blue lines indicate the stimulus speed.

approximately 450 ms) with a peak acceleration reaching about 100 deg/s^2 . An important feature illustrated in the figures is that the motor reversal was made smoothly. First, the reversals in tracking direction did not systematically include saccades, and could occur in the complete absence of saccades. Second, eye speed did not pause at zero before reaccelerating in the new direction. Thus, the pursuit reversal appeared to be made in one continuous, mostly smooth, movement.

A similar pattern was observed in all subjects. However, we observed some variability in the time necessary to complete the pursuit reversal. For instance, in subject L (Figure 3b right panels), the motor reversal spanned almost 600 ms, indicating a slower change in velocity. This was also apparent in the position traces. Saccades were also observed more frequently around the time of the motor reversal in subject L than in subject N, although on some trials subject L also accomplished the reversal without any saccades.

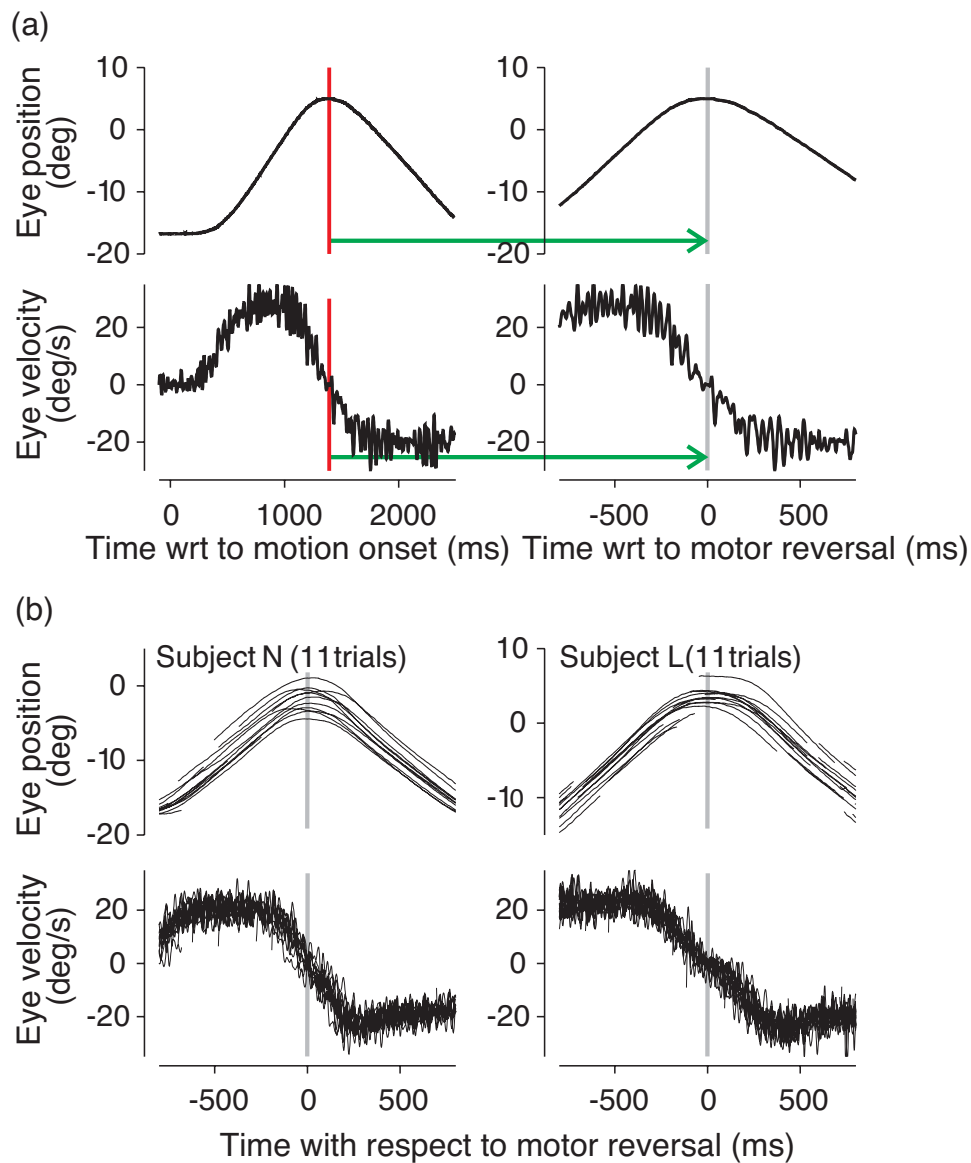


Figure 3. (a) Illustration of realignment of the eye position (top graphs) and eye velocity (bottom graphs) in a single “pursuit reversal” trial (subject J). The solid vertical red lines mark the time of the motor reversal used to realign the signals on the new time base (green arrows). (b) Examples of single “pursuit reversal” trials. Eye position and eye velocity as a function of time aligned with respect to the motor reversal. Left panels: subject N. Right panels: subject L. The solid vertical gray lines mark the time of the motor reversal.

Experiment 2

Control Sessions

In the control sessions of the second experiment, we measured eye movements while subjects tracked the apparent motion of a real square. Subjects were asked to report whether a tone occurred before or after the real square reversed its direction of motion. Based on the reports in each trial, we computed the cumulative probability of reporting a change in direction with respect to the delay between the occurrence of the tone and the reversal in stimulus motion.

Figure 4 shows the cumulative probability of reporting a reversal in stimulus motion (filled blue circles) as a function of delay, for each subject. Data were fit with a probit function (blue lines). The psychometric functions are centered near the time of physical motion reversal (time zero), verifying that the procedure used to measure the perceptual changes was accurate. At the time of stimulus motion reversal (delay = 0 ms), the average cumulative probability was 52.6 % and reached 89.7% after 106 ms.

For each trial, we also measured the time of the motor reversal (defined in “Methods”). We then computed the time interval between the occurrence of the auditory tone and the motor reversals. Based on these

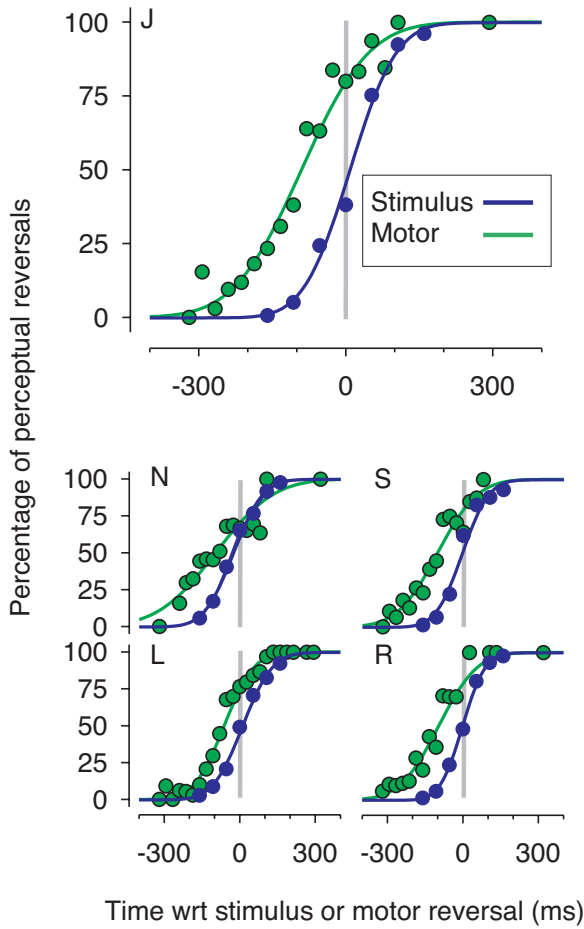


Figure 4. Psychometric functions of the cumulative probability of perceptual reversal of direction during tracking the apparent motion of a real square for each subject. Data were aligned on the reversal in stimulus motion (filled blue circles) and fitted with a probit function (solid blue lines). The green circles plot the same data aligned with respect to the motor reversal and the green lines are the corresponding fitted functions. The solid vertical gray lines mark the time of the motor reversal.

measurements, we constructed psychometric functions, again showing the percentage of perceptual reversals as a function of time, but now with respect to the time of the motor reversals. We choose intervals of 26.67 ms (i.e., two refresh rates) to compute the cumulative probabilities and discarded intervals with less than 10 psychometric measures. These data and the corresponding fitted functions are shown in Figure 4 (green circles and green lines). It can be seen that the psychometric functions aligned on the motor reversal are shifted to the left compared to the data aligned on the stimulus reversal. These shifts reveal the delay in processing visual inputs for pursuit: it is commonly estimated that it takes about 100 ms for the pursuit system to exhibit a response to change in visual motion. To analyze the temporal properties of the perceptual reversal, we computed the

point in time at which the cumulative probability reached 50%. On average, the 50% probability was reached 89 ms (SD: 16) before the motor reversal (90, 96, 97, 102, and 62 ms, respectively, for subjects J, N, R, S, and L). These values are delays attributable to the pursuit system.

Test Sessions

In the test sessions, subjects were instructed to reverse tracking around the midpoint of the screen. To compensate for the variability in the timing of these voluntary reversals, we aligned the eye position and velocity data on the motor reversal. We also discarded trials in which a saccade occurred in a 600-ms interval, starting 500 ms before the motor reversal and ending 100 ms after the motor reversal. Saccade frequency for the interval around the motor reversal was highly variable across subjects.

Figure 5 plots the proportion of trials with saccade-free reversals. In some subjects (J and N), nearly all of the motor reversals were accomplished without saccades; the frequency of saccades was very low (5.22% and 19.78%, respectively). In other subjects (R and L), only half of the trials were saccade-free (saccade frequency: 47.15% and 45.81%, respectively). In one subject (S), the saccade frequency was high (74.04%). However, each subject performed a large number of test trials ($n=1200$), so that even after discarding trials because of saccades, the remainder was high enough to ensure accurate measurements, even for subject S ($n=305$ saccade-free trials). Average eye velocity was then measured on a millisecond-by-millisecond basis for a 1000-ms interval around the “turning point” and transformed into percentage of motor reversal from rightward to leftward motion, using the previously described procedure.

Psychometric functions were then computed for each subject as previously described for the control sessions.

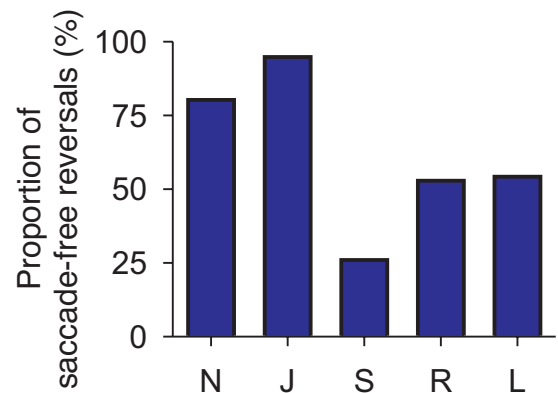


Figure 5. Proportion of saccade-free pursuit reversals (percent of trials in which no saccade was detected in a 600-ms interval starting 500 ms before the motor reversal) for each subject in the test sessions.

Data were aligned on the motor reversal. To obtain values directly comparable to the oculometric analysis, perceptual reports from trials in which a saccade occurred in the 600-ms interval starting 500 ms before the motor reversal were excluded from the psychometric analysis.

Figure 6 plots the percentage of motor reversals, the psychometric measurements of perceptual reversals, and corresponding fits to the data, for each subject in the test sessions. For subject J (Figure 6, top panel), the motor and perceptual reversals began at about the same time. About 200 ms before the motor reversal, the cumulative probability of perceiving a leftward motion was close to zero. The probability then rapidly increased to reach 50%

70 ms before the turning point (50% of motor reversal) and 100% about 100 ms after the eye velocity crossed zero (50% of motor reversal). The change in eye velocity from rightward to leftward started 200 ms before the turning point and spanned about 400 ms. The change in perceptual reports preceded and occurred over a shorter time span than the motor reversal. A similar pattern with some variability was observed in all subjects. In subjects N and R, the motor and perceptual reversal spanned a similar time interval, resulting in parallel psychometric and oculometric functions. However, in subject R, perceptual reversal preceded motor reversal by 70 ms, whereas in subject N this delay was reduced to 20 ms. For

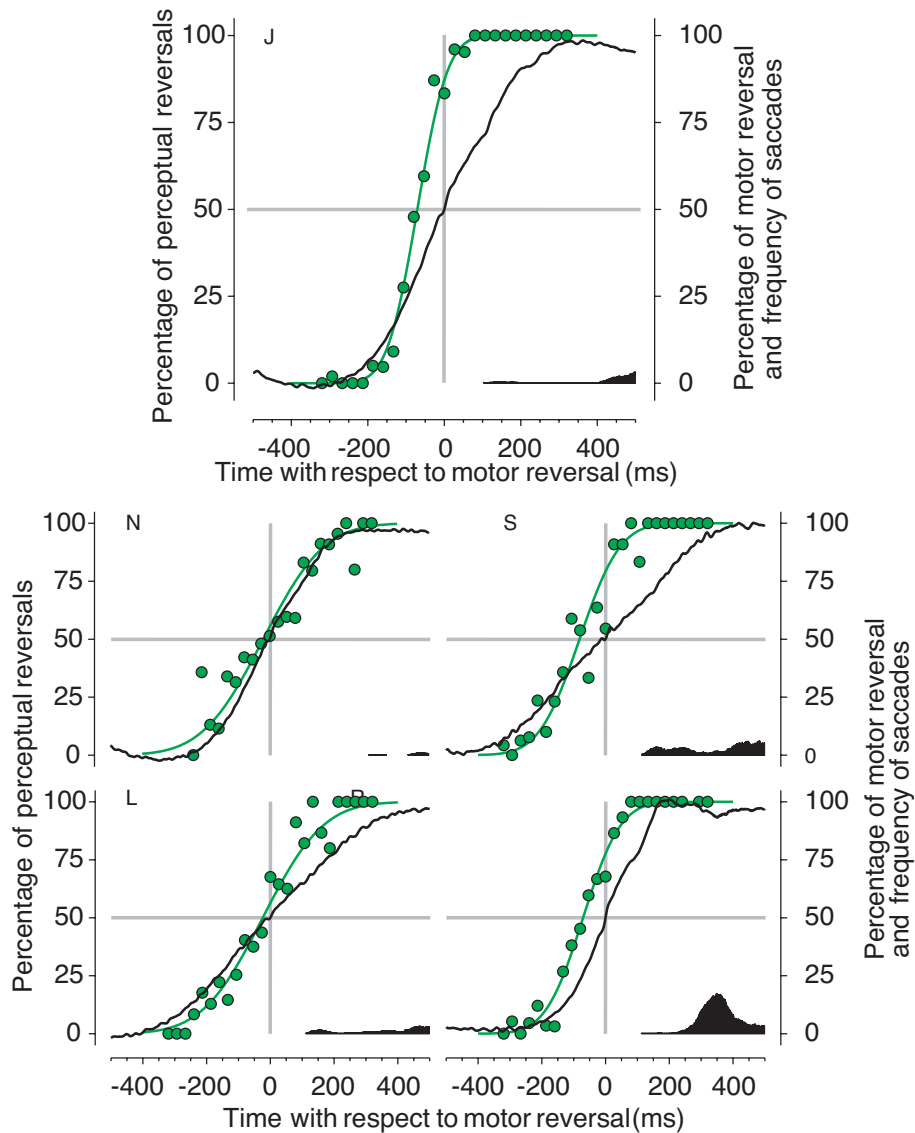


Figure 6. Percentage of motor reversal (black lines), percentage of perceptual reversals (green circles), and corresponding fitted functions (green lines) with respect to the motor reversal for each subject. The histogram at the bottom of each panel indicates the frequency of saccades for each point of time. The horizontal gray lines indicate 50% in perceptual and motor reversals, and the solid vertical gray lines mark the time of the motor reversal.

Balz, & Eastman, 1996; Ramachandran & Anstis, 1985), from coherent motion to flicker (Hock, Park, & Schoner, 2002) or in direction (Hock & Balz, 1994). However, these previous studies differ from ours in that they manipulated the visual stimulus to test for effects on spontaneous changes in perception. The effects we report here involve a voluntarily controlled switch in perception, independent of the stimulus itself. This raises the question of how a perceptual reversal may occur in the absence of changes in the visual signal. It could be possible that saccades transiently disrupted the motion signal at the time of perceptual switch. However, we carefully controlled for the occurrence of saccades, and all the perceptual reversals we report here occurred during saccade-free tracking. Most subjects exhibited a large proportion of these saccade-free reversals (up to 94%), ruling out the possible need of a saccade to reverse motion perception at will. Selective attention is a likely candidate to account for the observed perceptual reversals. Attentional modulation in V5/MT has been demonstrated in humans (Friston & Buchel, 2000) and in monkeys (Treue & Maunsell, 1996), revealing early influence of attention on motion processing. Moreover, it has been suggested that attention is necessary to perceive apparent motion when large spatial separations are used (Horowitz & Treisman, 1994). In our experiments, subjects reported the subjective feeling that they had to let the rightward motion go before engaging in leftward pursuit. Some subjects also acknowledged a short period of time during which no clear percept was seen. One possible explanation is that a delay exists between the disengagement of attention to one direction of motion and the selection of the other. This would result in a lag between the two percepts during which perception remains in an intermediate state. The consequence in the motor counterpart would be a delay between disengaging rightward pursuit and engaging leftward pursuit. Preliminary data from our laboratory suggest that a 100-ms delay may be observed during a pursuit reversal with our stimulus. However, further studies are required to test for that possibility. One could therefore postulate that using a voluntary controlled instead of a visually guided perceptual reversal is not appropriate to measure the timing of motion perception and pursuit. However, the time course of the perceptual reversals in both conditions was very similar (compare Figures 4 and 6).

Pursuit Provides a Real-Time Readout for Motion Perception

Our data revealed a tight link between perceived and pursuit reversals. In particular, they exhibited similar temporal dynamics: Figure 6 reveals that the perceptual and motor reversals tended to start at the same time. In some subjects, the motor reversal took a little more time to complete than the perceptual reversal. This is not surprising because the motor processing required to

reverse the physical motion of the eyes likely adds additional delays and temporal variability. In fact, pursuit and perception may not always provide the same answer. As pointed out in previous studies (Beutter & Stone, 2000; Krauzlis & Adler, 2001), in addition to shared visual noise (Watamaniuk & Heinen, 1999), there may be downstream sources of noise in the processing for pursuit that are different from those for perception, and these independent noise sources can reduce or eliminate the agreement between perception and pursuit. However, with the perceptually bi-stable stimuli we have used, it appears that the signals shared between pursuit and perception dominate the two responses. In fact, the delay between the perceptual reversal and the motor reversal (i.e., null eye velocity and 50% of cumulated probability to see a reversal, respectively) appeared on average to be shorter when using a voluntarily controlled reversal (53 ms in the test sessions, Experiment 2) than when using a visually guided reversal (89 ms in the control sessions, Experiment 2). What is the reason for this difference? Because this delay is a relative measurement comparing pursuit and perception, we cannot unambiguously identify whether the difference is due to changes in the timing for pursuit, perception, or both.

One possibility is that the delay associated with pursuit is relatively constant, and that during voluntary reversals, the perceptual estimate is systematically biased toward later times, resulting in a shorter delay between pursuit and perception. Perceptual estimates were very close to veridical in the case of a physical reversal (Figure 4), suggesting that accurate perceptual estimates of timing might depend on the full complement of visual information.

Alternatively, perceptual estimates might remain veridical even in the case of voluntary reversals, and the difference might be due to changes in the timing for pursuit. In the case of a physical reversal, changing the direction of pursuit involves a sequence of visual and motor processes requiring about 90 ms. When the change in pursuit is caused by a voluntary reversal, the drive signals for pursuit may bypass early visual processing which, based on our data, would take ~40 ms.

Finally, the difference could be caused by interactions between pursuit and perception. Pursuit can improve the perception of motion (Greenlee, Schira, & Kimmig, 2002; Haarmeier, Bunjes, Lindner, Berret, & Thie, 2001). In our experiment, the reduction of perceptual ambiguity by pursuit might have resulted in better agreement between pursuit and perception during voluntary than during visually induced reversals.

In general, perceptual reversals preceded the pursuit motor reversals by only a short delay (averaging 53 ms), again supporting our general conclusion that smooth pursuit and perception were in temporal register. Moreover, and despite inter-subject differences, it appears that the correlation between perception and pursuit eye velocity during the transition from rightward to leftward

pursuit is very high. This indicates that pursuit can provide a real-time readout of the state of motion perception, albeit with a 50–100 ms temporal delay. A related conclusion has been drawn from studies of the optokinetic system (Masson & Mestre, 1998), but to our knowledge, this is the first attempt to directly compare the timing of perception to the timing of pursuit eye movements.

Conclusions

Extending previous findings suggesting that pursuit may be controlled by perceived rather than physical motion, we show that the pursuit system can be driven by the perceived motion of illusory objects. Using a bi-stable motion stimulus, we show that the reversal of perception and pursuit eye movements follows a very similar time course, with perception preceding pursuit by 50–100 ms. The delay between pursuit and perception is longer when the reversal is visually guided than when voluntarily initiated. We suggest that pursuit eye movements can provide an accurate real-time readout for the state of motion perception.

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