Illusory motion reveals velocity matching, not foveation, drives smooth pursuit of large objects

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When small objects move in a scene, we keep them foveated with smooth pursuit eye movements. Although large objects such as people and animals are common, it is nonetheless unknown how we pursue them since they cannot be foveated. It might be that the brain calculates an object's centroid, and then centers the eyes on it during pursuit as a foveation mechanism might. Alternatively, the brain merely matches the velocity by motion integration. We test these alternatives with an illusory motion stimulus that translates at a speed different from its retinal motion. The stimulus was a Gabor array that translated at a fixed velocity, with component Gabors that drifted with motion consistent or inconsistent with the translation. Velocity matching predicts different pursuit behaviors across drift conditions, while centroid matching predicts no difference. We also tested whether pursuit can segregate and ignore irrelevant local drifts when motion and centroid information are consistent by surrounding the Gabors with solid frames. Finally, observers judged the global translational speed of the Gabors to determine whether smooth pursuit and motion perception share mechanisms. We found that consistent Gabor motion enhanced pursuit gain while inconsistent, opposite motion diminished it, drawing the eyes away from the center of the stimulus and supporting a motion-based pursuit drive. Catch-up saccades tended to counter the position offset, directing the eyes opposite to the deviation caused by the pursuit gain change. Surrounding the Gabors with visible frames canceled both the gain increase and the compensatory saccades. Perceived speed was modulated analogous to pursuit gain. The results suggest that smooth pursuit of large stimuli depends on the magnitude of integrated retinal motion information, not its retinal location, and that the position system might be unnecessary for generating smooth velocity to large pursuit targets.

Introduction

Smooth pursuit is a voluntary eye movement modeled as minimizing the velocity of a moving object's image on the retina (Krauzlis & Lisberger, 1989; Robinson, Gordon, & Gordon, 1986). Minimizing image velocity is essential since sluggish retinal dynamics cause blur when retinal motion exceeds 3°/s (Westheimer & McKee, 1975). Early evidence supported velocity matching models, since the eyes tend to follow motion even when the target is displaced in the opposite direction of its motion (Rashbass, 1961). However, there is evidence that pursuit not only corrects velocity error, but also position error between the target and the fovea to match the position of the target (Blohm, Missal, & Lefevre, 2005; Lisberger & Westbrook, 1985; Pola & Wyatt, 1980). Furthermore, recent work suggests that foveation is the predominant goal of ocular pursuit, since it generates catch-up saccades that place small pursuit targets on the fovea (Heinen, Potapchuk, & Watamaniuk, 2016). Neural pursuit circuitry is consistent with both velocity matching and position matching driving pursuit. Motion processing areas such as the middle temporal area (MT) and medial superior temporal sulcus (MST) are involved in pursuit (Komatsu & Wurtz, 1988, 1989). However, some other pursuit regions are sensitive to position error and are also involved in making saccades, which foveate small targets. These regions include the superior colliculus (SC; Krauzlis, Basso, & Wurtz, 2000), the frontal eye fields (FEF; Bruce & Goldberg, 1985) and the supplementary eye fields (SEF; Heinen, 1995).

Most work implicating velocity and position matching in controlling smooth pursuit was done with

a small spot stimulus (e.g., Keller & Heinen, 1991; Lisberger, Morris, & Tychsen, 1987; Spering & Montagnini, 2011). However, in natural scenes, we often pursue large objects, such as people or animals, and the mechanism that pursues large objects is unknown. Some work suggests they are pursued using a motion signal that is integrated internally (Heinen & Watamaniuk, 1998; Heinen et al., 2016; Watamaniuk & Heinen, 1999). Meanwhile, position information plays a mostly unknown role in large object pursuit. Strictly speaking, large objects cannot be foveated, since they extend beyond the fovea. However, the pursuit system could still calculate the center of mass to minimize centroid position error with respect to the fovea and maintain gaze there during pursuit, as occurs when the saccadic system targets large objects (McGowan, Kowler, Sharma, & Chubb, 1998). Alternatively, the pursuit system could merely stabilize the integrated motion of an object, without regard for absolute stimulus centroid position.

Here, we test whether velocity matching based on motion integration, or centroid matching primarily drives smooth pursuit of large objects. The stimulus consisted of four Gabor patches arranged in a diamond configuration. The Gabors translated together at a constant velocity, but had local drifts that were the same, opposite, or orthogonal to the global translation direction. When a Gabor drifts behind a translating aperture, the perceived motion of the aperture is biased in the drift direction (Lisi & Cavanagh, 2015; Zhang, Yeh, & De Valois, 1993). If the pursuit system merely integrates retinal motion and does velocity matching, it should integrate both the Gabor drift motion and the translational motion of the apertures of the Gabor patches and bias pursuit in the drift direction. However, if the pursuit system corrects position error and matches the centroid, it should discount the local drift motion and center the eyes on the global translating diamond. In a control experiment, we surrounded the Gabors with solid frames to segregate the local drift motion of the apertures from their global translational motion. This was done to test whether the pursuit system can follow a global translational motion signal that is clearly delineated from conflicting motion imposed by the local drifts. Finally, using a staircase procedure, we assessed observers' perception of the translational speed of the Gabors to determine whether pursuit and perception share similar mechanisms.

We found that pursuit gain was higher when the drift was the same as rather than opposite to the global translational motion, suggesting that pursuit was matching the velocity information, and not centroid matching. Interestingly, saccades during pursuit known as "catch-up" saccades did counter the position error caused by the altered gains. Surrounding the Gabors with solid frames cancelled the gain difference across

drift conditions, suggesting that when consistent cues are available, the pursuit system successfully follows the global translation. Similar to smooth pursuit, motion perception in the no-frame experiment was biased by drift condition, while motion perception in the frame experiment was not. The results suggest that the mechanism that modulates pursuit eye velocity is shared with that which underlies motion perception.

Methods

Participants

Based on the effect size obtained in a previous study on the effect of a drifting grating on motion perception (Zhang et al., 1993), for a paired t test between two opposite local drift directions, we needed at least five participants to reach a power of 0.9 at an alpha level of 0.05. We confirmed this with a smooth pursuit study using conflicting local and global motion information (Masson & Stone, 2002). For a paired t test between motion conditions, we required at least three participants to reach a power of 0.9 at an alpha level of 0.05. Although we will mostly use one-way repeated-measure analyses of variance (ANOVA) the logic of comparing dependent measures across different motion conditions is similar to that of previous pairwise comparison studies. Therefore, we used six participants in our study (three males and three females). Four were naïve and two were authors. All observers had normal or corrected-to-normal vision. The protocol for the study was approved by the Institutional Review Board at the Smith-Kettlewell Eye Research Institute. The study also adhered to the Declaration of Helsinki.

Apparatus and stimuli

Visual stimuli were generated with functions from Psychtoolbox-3 (Brainard, 1997; Kleiner et al., 2007) in MATLAB version R2012a (MathWorks, Natick, MA) on a Macbook Pro computer (Apple Inc., Cupertino, CA), and were presented on a Samsung U28E590D monitor (Samsung, Seoul, South Korea) at a refresh rate of 60 Hz. Observers were stabilized by a chin and forehead rest, which also maintained a constant viewing distance of 57 cm, resulting in the display subtending 51.2° × 33.3° of visual angle. Horizontal and vertical positions of the right eye were sampled at 1000 Hz by an EyeLink 1000 video-based eye tracker (SR Research, Mississauga, ON, Canada). The eye tracker was calibrated and validated with the standard nine-point method included with the system.

The Gabor patches were generated by multiplying a sinusoidal wave (spatial frequency 0.05 c/°, contrast =
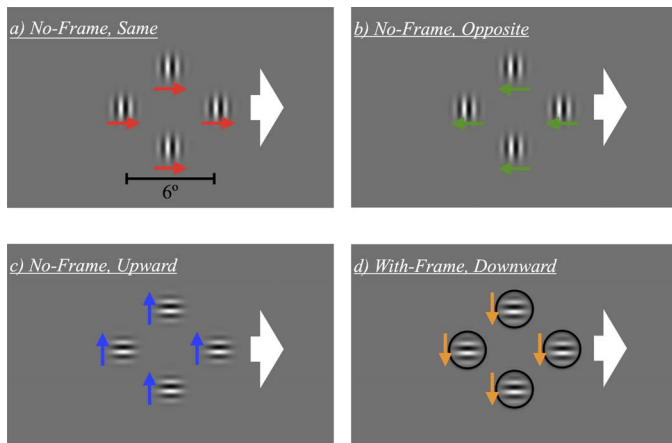
Figure 1. Schematic illustrations of stimuli used in the pursuit experiments. In all conditions, the pursuit target was a diamond configuration consisting of four Gabor patches. (a–c) In the no-frame experiment, in different drift conditions, the Gabors drifted in the same, opposite, upward, or downward (not shown) directions relative to the global translation direction. (d) In the with-frame experiment, solid black frames were added to surround each Gabor patch. All arrows are for illustration purposes and were not present during actual experiments.

95.7%) with a Gaussian aperture (standard deviation = 0.23°). The visible radius was approximately 0.6°. The four Gabors were arranged in a diamond configuration with each aperture centered 3° away from the stimulus center. The Gabors drifted behind the apertures at 0.76°/s in directions that were leftward, rightward, upward, or downward (Figure 1).

Smooth pursuit task

In the smooth pursuit task, observers were instructed to use their eyes to follow the diamond configuration. Each trial started with the diamond centered on the screen for a random duration (0.5 s to 1s). Then, the configuration started to move to the left or right at 10°/s for 2 s. In separate experiments, participants pursued two different variants of the stimuli that comprised the no-frame and the with-frame conditions.

In the no-frame experiment, the stimuli were as described already. The Gabor patches' inner drift could be in the same, opposite, or orthogonal direction to the global translation direction. Since the configuration only translated to the left or right, the orthogonal directions were further divided into upward and downward (see Figure 1a–c for examples of Same, Opposite, and Upward no-frame conditions). Participants completed 30 trials for each of the four drift conditions. All trials were randomly mixed and divided into two blocks of 60 trials.
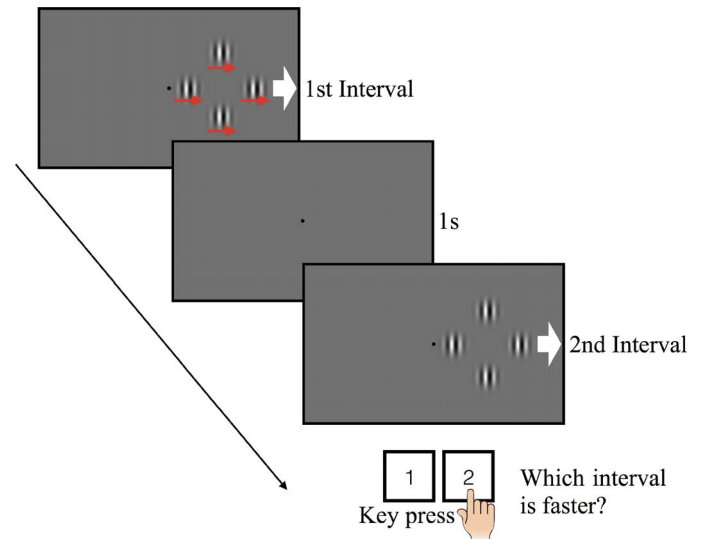

Figure 2. Procedure for the motion perception task. In each trial, observers viewed two intervals in which the diamond configuration translated, and pressed a key to indicate whether the stimulus in the first or second interval moved faster. The speed of the reference interval in the following trial was adjusted based on the response: If the observer reported the reference interval was faster, its speed was decreased on the following trial; otherwise it was increased. Order was counter-balanced across trials; in this example, the test stimulus with drifting Gabors is shown first and the reference stimulus with non-drifting Gabors is shown second.

In the with-frame experiment, stimuli were similar except that a black circular frame (radius = 0.75°) surrounded each Gabor patch (see Figure 1d for an example of the downward with-frame condition). In this case, the translation velocity and position infor-mation of the black frames are consistent with each other, regardless of the local Gabor drift. Again, participants completed 30 trials for each of the four drift conditions randomized and divided into two separate blocks.

Motion perception task

In the motion perception task (Figure 2), performed in separate blocks, we used a staircase procedure to measure the perceived speed of the global translation under the same four drift conditions that were used in the pursuit experiments (Same, Opposite, Upward, Downward). We used 32 trials to determine the per-ceived speed of each drift direction condition. In each trial, observers were first asked to fixate a central dot (radius = 0.1°). Following fixation, the diamond configuration appeared offset 5° to the left or right of the fixation dot and moved toward the same edge of the

screen for 1.0 s, to avoid intersecting the fixation stimulus.

There were two such intervals of global translation, and the stimulus moved in the same direction for each. In one interval, the test stimulus was presented, where the Gabors drifted in either the same, opposite, upward, or downward directions relative to the global translation. The translation speed was always 10°/s. In the other interval, the reference stimulus was presented, where the diamond translated across the screen but the Gabors did not drift. Translation speed was variable, as described in the following material. The test and reference stimuli could appear in either order for all trials.

On the first trial of each block, the reference diamond translated with a speed of 8.3°/s or 11.7°/s. The observer then indicated with a keypress whether the stimulus in the first or second interval moved faster (Figure 2). If the reference diamond was judged to be translating faster than the test, its speed decreased on the next trial. If it was judged to be slower, its speed was increased. The step size of the speed change was always 0.2°/s. With this staircase method, the speed of the reference stimulus becomes successively closer to the perceived speed of test stimulus, thereby yielding the observer's perception of the test stimulus translation speed. The reference stimulus speed was averaged over the last six reversals of a staircase to provide an estimate of the perceived speed of the test stimulus in that block of trials.

Each session included one block for each of the four drift conditions. Translation direction and the order of the two intervals were counterbalanced within each block. Similar to the pursuit task, participants completed one session for the no-frame experiment, and another session for the with-frame experiment.

Eye movement data analysis

Horizontal and vertical eye velocities were calculated offline from the recorded position signals by differentiating and filtering (two-pole Butterworth filter, cutoff = 50 Hz). Saccades were detected online by the EyeLink using its built-in algorithm (displacement threshold = 0.1°; velocity threshold = 30°/s; acceleration threshold = 8000°/s^2). Velocity traces were further examined visually, and saccades that were not detected by the EyeLink algorithm were manually identified. All saccades were removed from the velocity traces and replaced by a linear interpolation. Pursuit onset was first detected automatically by computing the mean and standard deviation of eye velocity over a sliding 100 ms window, and determining when eye velocity and eye acceleration exceeded 5°/s and 20°/s^2, respectively. The resulting onset times were subsequently inspected visually and adjusted manually when necessary.

We characterized pursuit initiation and open-loop pursuit by latency and peak acceleration, and steady-state pursuit by pursuit gain, eye position, and catch-up saccades (e.g., Heinen & Watamaniuk, 1998). For the open-loop analysis, we chose the interval from 50 ms to 130 ms after pursuit onset and focused on peak acceleration. For the steady state analysis, we chose the interval from 500 ms to 1500 ms after target motion onset, and focused on horizontal pursuit gain, vertical pursuit gain, and the size and direction of catch-up saccades.

Statistical analysis

For most of the dependent measures, we ran one-way, repeated-measure ANOVAs with drift condition as the within-subject factor to determine whether there was a significant main effect of drift conditions (alpha = 0.05). Post-hoc contrast analyses with Bonferroni correction were performed when the main effect was significant. Greenhouse–Geisser corrections were applied whenever the sphericity assumption was violated.

To assess whether smooth pursuit follows the integrated motion information, we ran repeated-measure ANOVAS to determine if local drift direction had a significant effect on pursuit latency, open-loop peak acceleration, and steady-state pursuit gain. To determine whether eye position was different from that of the stimulus centroid, we directly compared the stimulus centroid to horizontal eye position in the different local drift conditions. To test whether catch-up saccades correct position error between the eyes and the stimulus, we ran repeated-measure ANOVAs to determine if the proportion of forward and backward catch-up saccades differed across local drift conditions. As a validation of those results, we also ran repeated-measure ANOVAs to compare the starting and landing positions of the catch-up saccades. Finally, for the motion perception tasks, we ran repeated-measure ANOVAs to determine whether the perceived speed of the global translation was affected by local drifts. The same analysis was conducted for both the no-frame and with-frame experiments to determine if adding the solid frames produced different results.

Results

Pursuit Task: No-frame experiment
Steady state analysis

We first used the no-frame stimulus to determine whether the pursuit system followed the centroid of a large object, or instead moved the eyes by matching its
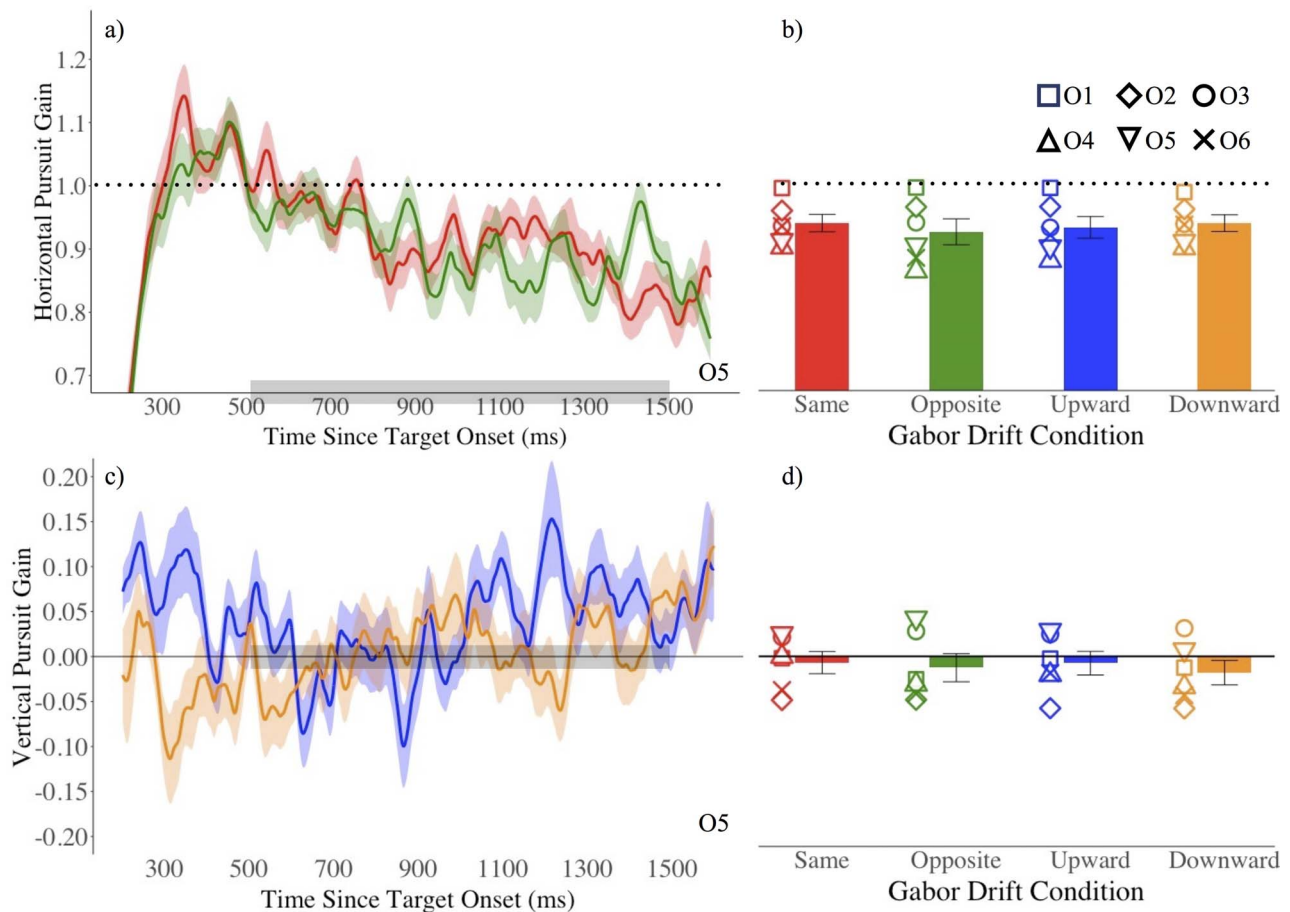
Figure 3. Pursuit gains in the no-frame experiment. (a) Average horizontal pursuit gain from a representative observer (O5), from 200 to 1600 ms after target motion onset. The red trace shows horizontal pursuit gain for the Same condition, and the green trace for the Opposite condition. The shaded region on each trace depicts ±1 *SEM*. The shaded bar on the *x*-axis indicates the analysis interval used for the population data. (b) Average horizontal pursuit gain over the 500–1500 ms interval after target motion onset, for all drift conditions. Symbols show gains of individual observers. Error bars show ±1 *SEM*. (c) Average vertical pursuit gain from O5. The blue line shows vertical pursuit gain for the Upward condition, and the orange line for the Downward condition. Other details as in panel a. (d) Average and individual (symbols) vertical pursuit gain over the 500–1500 ms interval after target motion onset.

apparent velocity. During steady state pursuit, eye velocity gain was higher when the component Gabors drifted in the same direction as the diamond's translation than when they drifted in the opposite direction (Figure 3a, b). The result suggests that the pursuit system spatially integrated the motion of the Gabor drifts with the translational motion of the apertures. Hence, pursuit appeared to preferentially follow the velocity signal, allowing differences in pursuit gain for same and different Gabor drifts to shift the eyes to different positions on the large stimulus, away from the diamond's centroid.

A one-way repeated-measures ANOVA showed a main effect of drift condition on average steady state horizontal pursuit gain, $F(3, 15) = 44.15$, $p < 0.001$, $\eta_G^2 = 0.898$. Post-hoc contrasts showed that the horizontal pursuit gain under the Same condition was significantly higher than the Opposite, $t(5) = 9.21$, $p < 0.001$); Upward, $t(5) = 6.57$, $p = 0.001$; and Downward, $t(5) =$ 5.38, $p = 0.003$, conditions. The horizontal pursuit gain under the Opposite condition was significantly lower than the Upward, $t(5) = 4.57$, $p = 0.006$; and Downward, $t(5) = 6.17$, $p = 0.002$, conditions. There was no significant difference between the Upward and Downward conditions, $t(5) = 1.10$, $p = 0.32$. The results suggest that the pursuit system integrated the motion information from the Gabors and apertures to generate eye velocity instead of matching the centroid of the target.

We also assessed vertical pursuit gain to further test the motion integration versus centroid matching hypotheses. When the Gabors drifted vertically, orthogonal to the translational direction, we found evidence that motion integration dominated in those conditions as well. As occurred with horizontal gain, the gain of vertical eye velocity, normally close to zero during horizontal pursuit, was biased in the direction of the Gabor drift (Figure 3c, d). A one-way repeated-
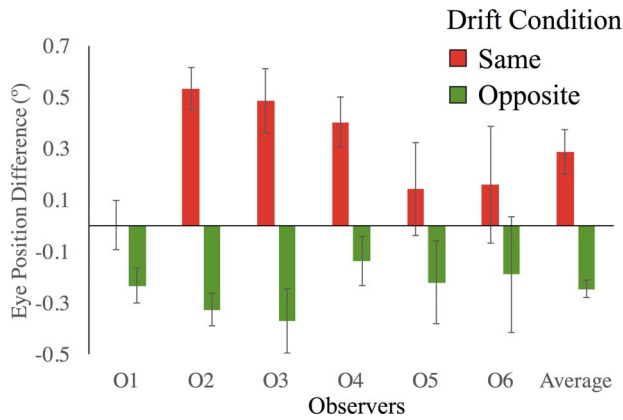
Figure 4. Horizontal eye position difference between the same or opposite conditions and the mean of the two orthogonal conditions in the no-frame experiment. Positive values indicate that relative to the orthogonal conditions, eye positions are more ahead of the stimulus centroid; negative values indicate the opposite. Error bars show ±1 *SEM*.
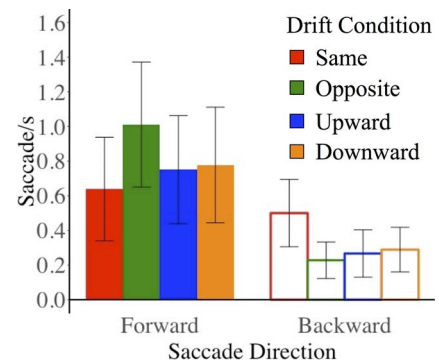

Figure 5. Saccade frequency of forward and backward saccades in the no-frame experiment, during the 500–1500 ms interval after target motion onset, for different drift conditions. Error bars show ±1 *SEM*.

measures ANOVA showed a significant main effect of drift direction on average steady state vertical pursuit gain, $F(3, 15) = 23.66$, $p < 0.001$, $\eta_G^2 = 0.826$. Post-hoc contrasts showed that the vertical pursuit gain was significantly higher for the Upward than the Down-ward $t(5) = 5.26$, $p = 0.003$; Same, $t(5) = 4.06$, $p = 0.01$; and Opposite, $t(5) = 5.22$, $p = 0.003$, conditions. The pursuit gain for the Downward condition was signif-icantly lower than the Same, $t(5) = 4.73$, $p = 0.005$, and the Opposite, $t(5) = 4.96$, $p = 0.004$, conditions. There was no significant difference between the Same and Opposite conditions, $t(5) = 0.34$, $p = 0.75$. The results further support the idea that the pursuit system integrates local motion signals to drive smooth eye velocity, despite that by doing so, it moves the eyes away from the stimulus centroid.

The results to this point demonstrate that the pursuit system was using the integrated velocity of the Gabor drift and aperture translation as a drive. But when the pursuit system was following the motion, was it truly ignoring the centroid of the stimulus? To test this, we compared relative eye position when the Gabors were drifting in the same and opposite directions (Figure 4). Because there can be individual differences in eye position between observers and within a trial, we compared eye position of each observer in the same and opposite drift conditions to that observed with orthogonal drifts, since orthogonal drifting Gabors did not affect horizontal pursuit gain. When we did this, we found that horizontal eye position was different for the same and opposite drift conditions (Figure 4). Here, positive values indicate that compared with the orthogonal conditions, the eyes were farther ahead of the target's centroid and negative values indicate the eyes were farther behind. All observers show a similar

pattern: The eyes were more ahead in the Same condition, and more behind in the Opposite condition, evidence that the pursuit system was not following the centroid of the large target.

The pursuit system appears insensitive to the centroid of the diamond. However, it might be that catch-up saccades, which correct position error to small objects (de Brouwer, Missal, Barnes, & Lefèvre, 2002), compensate for the position error introduced by the pursuit system's response to the integrated motion signal. To determine if saccades corrected for position error introduced by the altered gain during pursuit of the diamond, we compared the metrics of catch-up saccades that occurred in different drift conditions during the same interval in which we analyzed pursuit gain. We first grouped catch-up saccades into three categories: Forward (angular difference within $\pm45°$ to the direction of target motion), Backward (angular difference within $\pm45°$ to the opposite direction of target motion), and Orthogonal. We found that there were more forward catch-up saccades in the Opposite than in the Same condition, and more backward catch-up saccades in the Same than in the Opposite condition (Figure 5). A four (Drift Condition) $\times$ two (Saccade Type) repeated-measures ANOVA showed no main effect of drift condition, $F(3, 15) = 2.78$, $p = 0.08$, $\eta_G^2 = 0.005$, nor of saccade type, $F(1, 5) = 5.27$, $p = 0.07$, $\eta_G^2 = 0.149$, but a significant interaction, $F(3, 15) = 7.58$, $p = 0.003$, $\eta_G^2 = 0.039$). Post-hoc simple main effect analysis showed that while more Forward saccades happened in the Opposite condition than the Same condition, $t(5) = 3.20$, $p = 0.024$, more Backward saccades happened in the Same than the Opposite condition, $t(5) = 2.58$, $p = 0.049$. The results suggest that the saccadic system corrected for position error caused by the augmented or diminished pursuit gains.

We further tested if catch-up saccades started and landed at different positions under different drift conditions by calculating position error at the start and

end positions of each saccade relative to the computed centroid. We found that the starting position of saccades under the Same condition were more ahead of the target than under the Opposite condition, $t(5) = 3.56$, $p = 0.016$, Cohen's d = 1.45). However, there was no significant difference between the ending positions under the two conditions, $t(5) = 0.35$, $p = 0.74$, Cohen's d = 0.14). These results show that under the Same and Opposite drift conditions, catch-up saccades ended at approximately the same horizontal location. Therefore, the saccadic system appeared to be unaffected by the drifting Gabors and generally returned the eyes to similar locations on the stimulus.

Pursuit initiation and open-loop analysis

The drifting Gabors within the translating apertures produced systematic changes in pursuit gain and catch-up saccades during steady state pursuit, so we sought to determine if they also affected pursuit initiation. To this end, we analyzed pursuit latency and open-loop peak acceleration (horizontal), and found no difference in these variables as a function of the different directions of Gabor drift. There were no difference among different drift conditions for pursuit latency, $F(3, 15) = 2.38$, $p = 0.16$, $\eta_G^2 = 0.322$, and no significant difference among different drift conditions for open-loop peak acceleration, $F(3, 15) = 1.32$, $p = 0.28$, $\eta_G^2 = 0.209$. The results suggest that the effect of illusory motion is limited to steady-state pursuit.

Pursuit Task: With-frame experiment

Steady state analysis

In this experiment, we surrounded each Gabor patch with a solid black frame (see Methods) to determine if the pursuit system could follow the global translation of the diamond configuration when its motion and position information was segregated from the drifting component Gabors. We found that the frames completely nullified the horizontal and vertical steady-state gain changes caused by the drifting Gabors observed in the previous experiment (Figure 6). One-way repeated-measure ANOVAs showed no significant difference for average steady state horizontal pursuit gain, $F(3, 15) = 1.81$, $p = 0.237$, $\eta_G^2 = 0.266$, and no significant difference for average steady state vertical pursuit gain, $F(3, 15) = 1.41$, $p = 0.278$, $\eta_G^2 = 0.220$, across the four drift conditions.

We also analyzed catch-up saccade direction and position correction as we did for the no-frame experiment. As opposed to the no-frame experiment, direction, and position of the catch-up saccades in the with-frame experiment were unaffected by the Gabor drift direction (Figure 7). For saccades, a four (Drift Condition) × two (Saccade Type) repeated-measures ANOVA showed that there was no main effect of drift condition, $F(3, 15) = 0.76$, $p = 0.45$, $\eta_G^2 = 0.003$, a significant main effect of saccade type, $F(1, 5) = 19.6$, $p = 0.007$, $\eta_G^2 = 0.252$, and no significant interaction, $F(3,15) = 2.08$, $p = 0.16$, $\eta_G^2 = 0.005$. Overall, there were more forward than backward catch-up saccades in all conditions. For the position analysis for the catch-up saccades, there was no significant difference between the starting and ending positions under the Same and Opposite conditions [Start: $t(5) = 1.30$, $p = 0.25$, Cohen's d = 0.59; End: $t(5) = 0.56$, $p = 0.60$, Cohen's d = 0.25].

Pursuit initiation and open-loop analysis

We also analyzed pursuit latency and peak open-loop acceleration, and found no effects of the drifting Gabors in the with-frame experiment, mirroring the no-frame experiment results. There were no significant differences among different drift conditions for pursuit latency, $F(3, 15) = 0.85$, $p = 0.39$, $\eta_G^2 = 0.145$, and no significant difference for open-loop peak acceleration, $F(3, 15) = 0.45$, $p = 0.53$, $\eta_G^2 = 0.083$.

Together, the results suggest that adding frames to the Gabor apertures completely nullified the effect that the Gabor drift had on smooth pursuit. When motion and position signals from the drifts are clearly segmented from the overall object translation, it appears the pursuit system can ignore them.

Perception task

Although controversial, there is evidence that smooth pursuit shares motion signals with the motion perception system (Gegenfurtner, Xing, Scott, & Hawken, 2003; Stone & Krauzlis, 2003; Watamaniuk & Heinen, 1999). Thus we tested if the perceived motion of the translating diamond stimulus was biased by the drifting Gabors in a similar fashion as was pursuit. We used the same stimuli to test perception that we used in the pursuit experiment, except now the perceived translation of the test stimulus with drifting Gabors was compared with that of a reference stimulus in which no drift was present. The perceived translation speed was obtained using a staircase method in which the speed of the reference was varied systematically until its perceived speed matched the fixed speed of the test stimulus (see Methods). Trials during which the eyes deviated more than 1° from the fixation dot were excluded from analysis (n = 88, 5.7% of total collected trials). On average, there were 14 staircase reversals in each block, ranging from eight to 19.
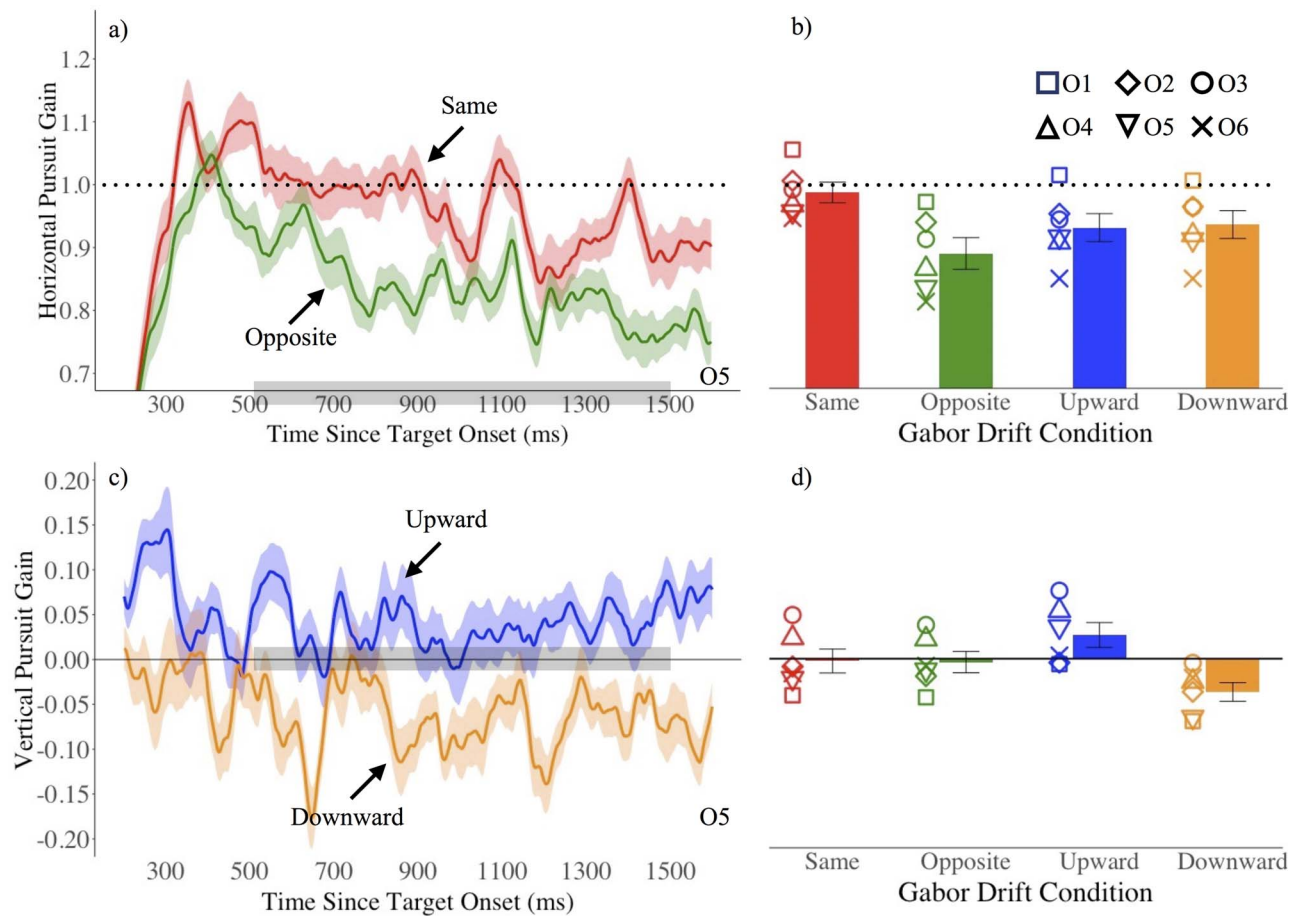
Figure 6. Pursuit gains in the with-frame experiment. (a) Average horizontal pursuit gain from a representative observer (O5), from 200 to 1600 ms after target motion onset. The red trace shows horizontal pursuit gain for the Same condition, and the green trace for the Opposite condition. The shaded region on each trace depicts ±1 *SEM*. The shaded bar on the *x*-axis indicates the analysis interval used for the population data. (b) Average horizontal pursuit gain over the 500–1500 ms interval after target motion onset, for all drift conditions. Symbols show gains of individual observers. Error bars show ±1 *SEM*. (c) Average vertical pursuit gain from O5. The blue line shows vertical pursuit gain for the Upward condition, and the orange line for the Downward condition. Other details as in panel a. (d) Average and individual (symbols) vertical pursuit gain over the 500–1500 ms interval after target motion onset.
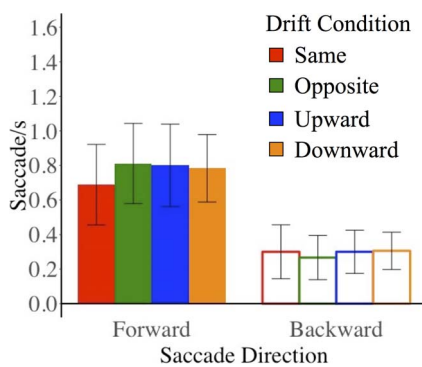

Figure 7. Saccade frequency of Forward and Backward saccades in the with-frame experiment, during the 500–1500 ms interval after target motion onset, for different drift conditions. Error bars show ±1 *SEM*.

Results from the no-frame perceptual experiment

We found that the perceived horizontal translation speed was biased by the inner drift direction, such that the Same condition was perceived as moving faster than the Opposite one. A one-way repeated measures ANOVA showed a marginal significant main effect of drift condition on the perceived speed of the configuration, $F(3, 15) = 5.60$, $p = 0.049$, $\eta_G^2 = 0.528$; Figure 8a). Post-hoc contrasts showed that the perceived speed in the Same condition was significantly higher than the Opposite condition, $t(5) = 7.32$, $p < 0.001$, and no other contrast reached significance.

Results from the with-frame perceptual experiment

In the pursuit experiment, surrounding the Gabor patches with frames eliminated the gain biases introduced by the inner drifts. Here, we tested whether
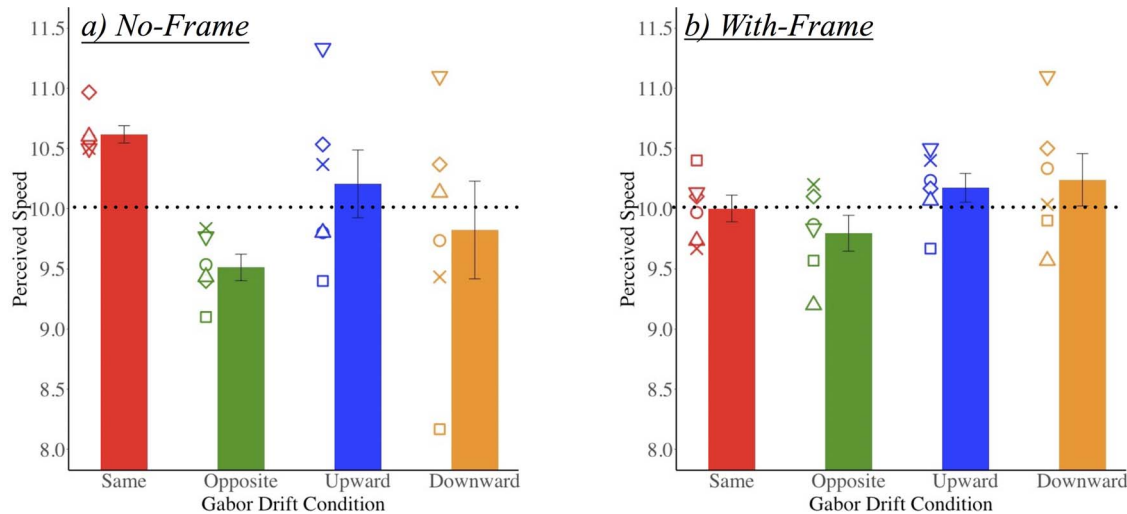
Figure 8. Average perceived speed of different drift conditions in the (a) no-frame and (b) with-frame experiments. The dotted line indicates the speed of the test stimulus. Error bars show the ±1 SEM.

frames analogously removed the motion perception bias, and found that they did (Figure 8b). A one-way repeated-measures ANOVA showed that there was no significant main effect of drift conditions on the perceived speed of the configuration, $F(3, 15) = 2.32$, $p = 0.12$, $\eta_G^2 = 0.317$.

The results from the perception task matched what we observed in the pursuit task: Without a frame surrounding the drifting Gabors, observers perceived the Same stimuli to move significantly faster than the Opposite ones. However, when solid frames were added to segregate the local motion signals from the global ones, participants were able to perceive the global target translation speed accurately. The results suggest that the bias in translation speed in the pursuit task caused by the drifting Gabors could arise in a similar way as in the motion perception system.

Discussion

The current study investigated whether the dominant drive for smooth pursuit of large stimuli relies on velocity matching or centroid matching. We used motion stimuli with local motion information that either conflicted with or was consistent with the global translation. Across conditions, the stimuli had different combinations of motion and position information, allowing us to contrast their relative contributions. We found that the pursuit system corrected for the motion rather than tracking the centroid of the stimulus. Pursuit gain was enhanced when local Gabors drifted in the same direction as the global translation, and diminished when they drifted opposite to it, consistent with observers' perception of the translational speed.

Furthermore, orthogonal drifts yielded corresponding changes in vertical pursuit gain. In all cases, catch-up saccades corrected for position errors introduced by the altered pursuit gains. Therefore, smooth pursuit of large stimuli appears predominantly driven by an integrated motion signal.

Contributions of motion and position to smooth pursuit

Dominant pursuit models posit that the pursuit system matches eye velocity to target velocity (Krauzlis & Lisberger, 1988; Robinson et al., 1986). Rashbass (1961) directly investigated the relative contribution of motion and position inputs. The target was stepped away from center, and immediately moved in the opposite direction. In this step-ramp paradigm, position matching and velocity matching predict different eye movements. It was found that pursuit eye movements followed the motion direction, and a subsequent catch-up saccade corrected the position error. The results were interpreted as evidence that motion contributes more than position to pursuit initiation. However, a growing body of evidence suggests that pursuit also corrects position error between the fovea and a small target's retinal image, resulting in foveation (Blohm et al., 2005; Heinen et al., 2016; Pola & Wyatt, 1980).

The data supporting the view that pursuit corrects for motion and position errors was largely acquired with a small, spot stimulus (for reviews: Keller & Heinen, 1991; Lisberger et al., 1987; Spering & Montagnini, 2011). However, many natural pursuit objects are much larger than the spot, and the large-object pursuit mechanism is unknown. Some work

suggests that pursuit of large stimuli follows an internally generated motion signal arising from motion integration (Heinen & Watamaniuk, 1998; Jin, Watamaniuk, Khan, Potapchuk, & Heinen, 2014). What's more, the retinal image of a large object may extend beyond the fovea, making a foveating mechanism untenable. However, pursuit might instead follow the centroid of a large object, as occurs with saccades (McGowan et al., 1998).

During normal pursuit, motion and position signals are usually confounded since they are both generated in the moving target's direction. Smooth eye velocity and catch-up saccades are also normally generated in the same direction. In the current study, we employed a stimulus designed to oppose motion and position information, and to evaluate the contribution of position and motion to steady-state pursuit. The stimulus was a diamond configuration of four Gabor patches that translated horizontally across the screen, while the Gabors drifted behind Gaussian apertures in either the same or different directions to the translation. Integrating the translational and drift motions produces a net motion that is different across Gabor drift conditions, and velocity matching predicts different pursuit gains. However, the translating diamond's centroid is the same across conditions. Therefore, centroid matching predicts equal pursuit gains across drift directions. We found that during steady-state, the pursuit system followed the integrated stimulus velocity despite that the eyes were displaced from the stimulus's centroid. Therefore, an integrated motion signal appears to be the dominant drive of large-object pursuit.

Smooth pursuit is thought to rely on a network of motion processing structures, but also on those that correct position error and generate saccades. Motion processing in primates begins in primary visual cortex (V1), and motion is spatially integrated in MT in macaques and hMT in humans to generate global motion perception (Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996; Furlan & Smith, 2016; Tootell et al., 1995). Motion processing proceeds from MT to a sensorimotor interface at MST to produce smooth eye velocity (Komatsu & Wurtz, 1988; Lisberger & Movshon, 1999; Newsome, Wurtz, & Komatsu, 1988). Other structures that are thought to generate smooth pursuit also either encode position error or make saccades. The SC encodes position error (Munoz & Guitton, 1985), and neurons in the SC pursuit region are active during small saccades (Hafed, Goffart, & Krauzlis, 2009). The pursuit region in the FEF (MacAvoy, Gottlieb, & Bruce, 1991) is adjacent to the small saccade zone (Bruce, Goldberg, Bushnell, & Stanton, 1985). In the SEF, the regions that generate saccades (Schlag & Schlag-Rey, 1985) and pursuit (Heinen, 1995) overlap. We found that eye velocity was

directed opposite to catch-up saccades, evidencing that, while pursuing large objects, position structures might function independently from motion structures, and therefore might not contribute to smooth pursuit.

Motion perception and smooth pursuit

There is evidence that the pursuit and perceptual systems receive similar motion input (Gegenfurtner et al., 2003; Stone & Krauzlis, 2003; Watamaniuk & Heinen, 1999), though the topic remains controversial (for a review, see Spering & Montagnini, 2011). We found similar behavior for both pursuit and perception, and therefore our results support the notion that similar motion inputs drive motion perception and pursuit.

Previous work investigated the relationship between motion perception and smooth pursuit in the context of the aperture problem. When a moving object is occluded by an aperture, leaving only some of its components visible, a conflict can arise between the local motion of the visible parts and the global motion of the object. In this situation, accurate motion integration is required to successfully reflect the global motion direction. Buetter and Stone (2000) showed that with a clear visible aperture, both perception and pursuit follow the global object motion. However, when the aperture is invisible, both systems follow the local components. This is similar to our results in the with-frame and no-frame conditions. In our study, the with-frame condition also led both pursuit and perception to follow the global motion, and the local motion modulated both systems when no frame was present. Other studies showed that while perception and pursuit initially follow the local motion, they gradually correct to follow the global motion (Born, Pack, Ponce, & Yi, 2006; Masson & Stone, 2002; Montagnini, Spering, & Masson, 2006). These results suggest that perception and pursuit share similar motion integration mechanisms. In the no-frame condition in our study, during steady-state pursuit the eyes fail to follow the global translation velocity, which also occurred with perception. We reasoned that while in the previous aperture-problem studies, successful motion integration led to correct global motion computation, in our study, motion integration led to a miscalculation of the global translation velocity. Therefore, our results are consistent with previous findings that the integrated motion signal dominates during both smooth pursuit and motion perception.

It is worth noting that not every study using similar stimuli found consistent results across perception and eye movement tasks. Zivotofsky (2005) showed that when a target moved on an orthogonally drifting

background, its perceived trajectory was biased opposite the direction of the background motion. On the other hand, smooth pursuit eye movements did not follow the illusory trajectory. Zivotofsky concluded that smooth pursuit and motion perception were controlled by separate pathways. However, in Zivotofsky's study, the pursuit target was very small (0.3°) and easily foveated. Therefore, it might be that pursuit was using the foveation system in this experiment, which overrode the background motion and produced veridical pursuit. Thus the discrepancy between motion perception and smooth pursuit may reflect different weighting of position and motion pathways and not two distinct systems (Kwon, Tadin, & Knill, 2015). Spering and Gegenfurtner (2007) also showed that a drifting background, no matter its motion direction, increased pursuit acceleration and velocity. They reasoned that both absolute and relative motion cues are important for controlling smooth pursuit.

Lisi and Cavanagh (2015) showed a dissociation between perception and saccadic eye movements using diagonally translating Gabors with orthogonal inner drifts. However, while a saccade is a relatively ballistic eye movement that matches target location, smooth pursuit requires observers to continuously follow the motion of the target. Therefore, smooth pursuit might rely more on trajectory information than saccadic eye movements, and that may be why we found similar effects for perception and smooth pursuit.

Our results can also be interpreted in the context of different motion systems. Lu and Sperling (1996, 2001) proposed that three motion systems exist: a first-order system that responds to luminance change (motion energy), a second-order system that detects moving modulations of derived feature types (e.g., contrast, flicker or motion), and a third-order system that uses figure-ground segmentation to track motion based on "object" position. The second- and third-order motion systems are further combined as a higher-level position-based system (Ma, McCloskey, & Flombaum, 2015; Seiffert & Cavanagh, 1998, 1999).

Although our stimuli were not drift-balanced (mean luminance distribution remains constant) and thus not pure second-order stimuli, they are ideal to study the relative contribution of first- and higher-order motion information to smooth pursuit. Each local Gabor stripe has first-order luminance defined motion that is the sum of the local drift velocity of the stripe and the global translation. On the other hand, the higher-level position based systems extract the global translation speed by comparing the position of features and objects across successive frames. Therefore, the motion information provided by the low- and high-level systems is inconsistent. We found that both pursuit and perception interpreted the object as moving faster when the Gabors drifted in the same direction as the

translation, and slower when they drifted opposite. Vertical pursuit was also biased by orthogonal Gabor drifts. Therefore, it appears that first-order motion energy plays a dominant role in guiding pursuit of large targets, and contributing to their perceived speed. The pre-attentive nature of the first-order motion system (Adelson & Bergen, 1985; van Santen & Sperling, 1984) may make it more readily available for use by the pursuit system.

Several other studies found similar perception and pursuit behavior in response to pure second-order motion. Most relevant to our results are those that used "theta" motion, in which a global object's translation is defined by dots that move opposite to the translation (Zanker, 1993). Previous work comparing pursuit to first-order and theta motion showed that while all available motion information (i.e., both first- and second-order motion) is integrated during pursuit initiation, first-order motion is weighted more heavily (Lindner & Ilg, 2000). This is somewhat inconsistent with our result where local drifts do not affect pursuit initiation. This may be because Lindner and Ilg (2000) used a much higher local drift speed (4.6°/s or 9.2°/s, the same as their global translation speed) than the local drift speed of our Gabors (0.76°/s). Since pursuit initiation takes the weighted average of both first- and second-order motion, a slower local drift speed may make a difference in pursuit initiation more difficult to observe. Further work is needed to systematically test the effect of speed on the interaction between first- and second-order motion on both pursuit initiation and steady-state pursuit.

Eye velocity during steady-state pursuit fails to accurately reflect the speed of theta motion (Butzer, Ilg, & Zanker, 1997). Hawken and Gegenfurtner (2001) studied pursuit to theta motion, as well as "first-order +" motion in which a translating object is defined by dots moving in the same direction at twice the translation speed. Such stimuli share properties with our Gabor stimuli that drifted in the same direction as the translating global stimulus and that enhanced pursuit gain. However, Hawken and Gegenfurtner found that for theta and first-order+ motion, steady-state pursuit gain was lower than for first-order motion stimuli, and concluded that pursuit of second-order motion is poorer than pursuit of first-order motion. Because they used a small target (0.5°), a lack of sufficient motion energy might account for why pursuit gain in their experiment did not increase with first-order+ motion stimuli.

No-frame vs. with-frame conditions

We found that adding frames to the Gabors canceled the drift effect for both pursuit and perception.

Previous work demonstrated a similar cancellation of illusory perception. Zhang et al. (1993) showed that when the "soft" Gaussian aperture of a drifting Gabor was made "hard" by rendering it circular, motion integration between the aperture and the grating was disrupted. Other work demonstrated that inner drifts bias saccade landing position when an aperture is soft but not when it is hard (Kosovicheva, Wolfe, & Whitney, 2014). These results are consistent with the claim that a distinct boundary is necessary to segregate local from global motion signals (Zhang et al., 1993). Therefore, we reasoned that when both motion and position signals were clearly defined by the frame in our study, the pursuit system could ignore inconsistent local motion and veridically pursue the translating stimulus. With the frame, the drifting Gabors were perceived as semi-independent component features of the translating object, like the arms and legs of people walking or running, and thus the drifts had less influence on global pursuit and perception.

Conclusions

Smooth pursuit eye movements are critical to prevent moving objects from blurring. Although extensive literature describes pursuit of small objects that are foveated, little is known about pursuing large objects common in natural viewing. We use a large pursuit stimulus with drifting local elements, which creates the illusion that the stimulus moves at a different speed and dissociates stimulus speed from location. We find that pursuit follows the motion of the stimulus, not its centroid, unlike pursuit of small stimuli where a target's position is computed to foveate it. The results provide evidence that mechanisms for pursuing large objects are different from those for pursuing small ones, and suggest a revision of neural pursuit circuitry.

Keywords: eye movements, saccades, MT, superior colliculus, motion perception

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