Behavioral/Systems/Cognitive

Similar Effects of Feature-Based Attention on Motion Perception and Pursuit Eye Movements at Different Levels of Awareness

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Feature-based attention enhances visual processing and improves perception, even for visual features that we are not aware of. Does feature-based attention also modulate motor behavior in response to visual information that does or does not reach awareness? Here we compare the effect of feature-based attention on motion perception and smooth-pursuit eye movements in response to moving dichoptic plaids—stimuli composed of two orthogonally drifting gratings, presented separately to each eye—in human observers. Monocular adaptation to one grating before the presentation of both gratings renders the adapted grating perceptually weaker than the unadapted grating and decreases the level of awareness. Feature-based attention was directed to either the adapted or the unadapted grating's motion direction or to both (neutral condition). We show that observers were better at detecting a speed change in the attended than the unattended motion direction, indicating that they had successfully attended to one grating. Speed change detection was also better when the change occurred in the unadapted than the adapted grating, indicating that the adapted grating was perceptually weaker. In neutral conditions, perception and pursuit in response to plaid motion were dissociated: While perception followed one grating's motion direction almost exclusively (component motion), the eyes tracked the average of both gratings (pattern motion). In attention conditions, perception and pursuit were shifted toward the attended component. These results suggest that attention affects perception and pursuit similarly even though only the former reflects awareness. The eyes can track an attended feature even if observers do not perceive it.

Introduction

Selective visual attention enables us to preferentially process visual information that is behaviorally relevant. Feature-based attention (FBA) is important when searching for an object with a specific feature among distracting objects with different features (for a review, see Carrasco, 2011). FBA enhances the detection and discrimination of stimuli with the attended feature (Ling et al., 2009; Liu et al., 2007b; Lu and Itti, 2005; Rossi and Paradiso, 1995; White and Carrasco, 2011) as well as the neuronal representation of the stimulus (Liu et al., 2007a; Maunsell and Treue, 2006; Saenz et al., 2002; Treue and Martinez-Trujillo, 1999; Serences and Boynton, 2007; Greenberg et al., 2010, Stoppel et al., 2011; for reviews, see Bisley, 2011; Carrasco, 2011). FBA can also modulate the processing of visual information that the observer is unaware of (Melcher et al., 2005; Kanai et al., 2006; Schmidt and Schmidt, 2010; for a review, see Koch and Tsuchiya, 2012).

Here we investigate whether FBA affects perception and smooth pursuit eye movements in response to visual motion in a paradigm in which perception and pursuit reflect different levels of awareness. Smooth pursuit eye movements are the type of movement used by primates to center and stabilize the image of an object of interest on the fovea. Spatial attention is usually allocated to the pursuit target (Khurana and Kowler, 1987; Lovejoy et al., 2009). Although motion perception and pursuit are tightly linked in terms of neuronal control (Newsome et al., 1989; Groh et al., 1997; Lisberger and Movshon, 1999) and behavior (for a review, see Spering and Montagnini, 2011) the two responses can differ in direction and sensitivity (Tavassoli and Ringach, 2010; Spering et al., 2011).

In Spering et al. (2011), we compared motion perception and pursuit in response to stimuli that observers were either aware or unaware of. We achieved different levels of awareness through adaptation, effectively manipulating stimulus strength. Generally, visual adaptation, the prolonged viewing of a stimulus, produces a decrease in sensitivity to this stimulus or a similar one during subsequent viewing (for a review, see Kohn, 2007). We used monocular adaptation in Spering et al. (2011) and in the current study: two stimuli moving in different directions—one unadapted and one adapted—were shown separately to the two eyes. Perceptual reports of motion direction followed the unadapted stimulus almost exclusively, indicating that observers were more aware of the unadapted than of the adapted stimulus. Interestingly, pursuit did not follow the perceived direction but
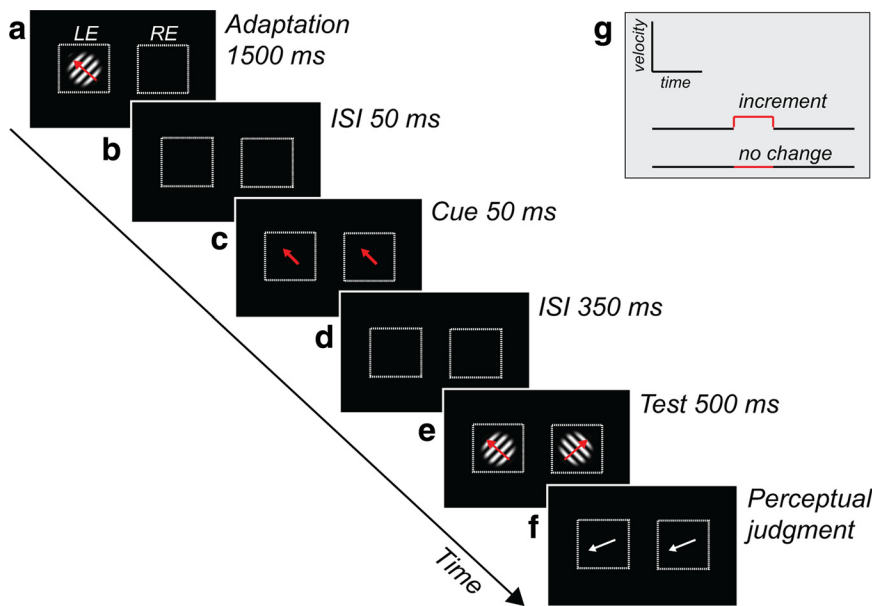
Figure 1. Trial timeline in Experiment 1 and schematic diagram of speed change. *a*, Adaptation phase, following a brief randomized fixation period (50–100 ms): monocular adaptation of either left eye (LE) or right eye (RE) to a moving grating for 1500 ms during fixation (central fixation cross not shown). *b*, 50 ms interstimulus interval (ISI). *c*, Symbolic cue (red arrow) shown for 50 ms to both eyes; cue was either valid and pointed to one motion direction only (up-right or up-left, as shown here) or neutral, i.e., two red arrows pointed to both possible motion directions. *d*, 350 ms ISI. *e*, Test phase: two gratings with opposite orientation and motion direction were shown separately to each eye for 500 ms. The adapted eye received the same stimulus as during the adaptation phase. In 50% of all trials, one of the gratings briefly increased in speed (see *g*). *f*, Observers were prompted to judge whether speed had changed during the test phase (keypress; data not shown) and to indicate motion direction of the stimulus in the test phase by rotating an arrow. *g*, Schematic diagram of speed change. At motion onset, the stimulus moved at 5°/s. In trials with speed change, target speed increased to 8°/s for 100 ms mid-presentation (from 200 to 300 ms after stimulus motion onset).

tracked the vector average of adapted and unadapted stimuli, disregarding the perceived strength of the individual stimuli. In the present study, we compare the effects of FBA on perception and pursuit in four conditions. We asked observers to either attend to a stimulus (cued) or not (neutral), yielding two attention conditions. The stimulus was either unadapted or adapted, yielding two adaptation conditions, resulting in observers being either aware or almost always unaware of the stimulus, respectively. Similarity of the attention effect on perception and pursuit would indicate that FBA exerts its effects at levels of visual processing responsible for both the control of aware perceptual and unaware pursuit responses to visual motion.

Materials and Methods

We conducted two experiments; Experiment 2 was a variation of Experiment 1 with different stimulus motion directions and different observers.

Observers. Eight observers (mean age 29.3 ± 6.5 years, four females) with normal visual acuity participated, four in Experiment 1 and five in Experiment 2 (one observer participated in both experiments). All observers were graduate students or postdoctoral students at New York University (NYU) Department of Psychology and were naive regarding the purpose of the experiment. The NYU ethics committee approved the study's protocol and all observers participated with informed consent.

Visual stimuli and setup. Stimuli were diagonally (45° or 135°) oriented sine-wave gratings (spatial frequency: 0.5 cycles/degree) drifting orthogonally to their orientation at 5°/s either up-right or up-left (Exp. 1) and down-right or down-left (Exp. 2). Gratings were multiplied with a two-dimensional flat-topped Gaussian window to reduce border artifacts, resulting in a visible stimulus size of 6.7° of visual angle. Stimuli were presented at 100% contrast on a black background (0.01 cd/m²) on a gamma-corrected 21 inch CRT monitor (Sony Trinitron-G520, 100 Hz; 1280 × 1024 pixels; 39.8 × 29.5 cm). Observers viewed the display from

a distance of 48 cm through a four-mirror stereoscope (OptoSigma) that was mounted to a chin rest.

Stereoscope mirror adjustments for each observer were done with great care, using two sets of white nonius lines, one horizontal and one vertical (forming a cross of diameter 1.5°), presented on each side of the visual field. Observers were asked to adjust the mirrors until the two crosses appeared as one and were perfectly fused. To ensure that accurate binocular alignment was maintained throughout the experiment, a texture-framed square (13.4° × 13.4°) was presented on each side of the visual field surrounding the visual stimuli throughout each trial (Fig. 1). At the beginning of each block of trials, during eye tracker calibration, we asked observers to confirm that mirror alignment was still perfect. A nine-dot array had to be fixated and observers had to report whether they were able to see all dots fused and clear.

Procedure and design. We combined a procedure for monocular adaptation to stimulus motion, creating two stimuli with different perceptual strengths (as in Spering et al., 2011; see also Wolfe, 1984), with a procedure to direct visual attention to one stimulus feature (Fig. 1). (1) Monocular adaptation (Fig. 1*a,b,f*): A stimulus moving either up-right or up-left was initially presented to one eye for 1500 ms (adaptation interval, Fig. 1*a*), followed by a time interval containing feature cues. In the subsequent test interval (Fig. 1*e*), both eyes were stimulated for 500 ms. The adapted eye received the same stimulus again, while the other eye received a novel stimulus with orthogonal orientation and motion direction to that of the adapted stimulus. The 500 ms presentation duration was sufficiently long to allow the analysis of pursuit eye movements, elicited by the stimulus motion, while at the same time short enough to prevent fluctuations in perception (as in binocular rivalry); (2) Feature-based attention (Fig. 1*c,d*): A cue to direct attention to either the up-right or up-left motion direction, or a neutral cue pointing in both directions, was presented to both eyes for 50 ms (Fig. 1*c*) during the time interval following adaptation. The cue appeared 50 ms after offset of the adaptation stimulus and was followed by a 350 ms interval (Fig. 1*d*) before onset of the test stimulus to allow sufficient time to allocate attention to the cued feature (Liu et al., 2007a,b). In all conditions, the left and right eye received the unadapted information equally often, i.e., each eye was adapted in 50% of all trials.

To test whether observers directed attention to the cued feature, in half of the trials, one of the two stimuli, either the adapted or the unadapted stimulus, briefly changed speed during the 500 ms test phase. The speed change was a 100 ms step change from 5°/s to 8°/s occurring mid-presentation during the test phase (Fig. 1*g*). In 50% of the trials with speed change we used a neutral cue; in the other half of the trials we used a cue which was 100% valid and always pointed to the stimulus with the speed change. At the end of each trial, observers gave two judgments: (1) whether the stimulus had changed in speed by pressing assigned keys for "yes" or "no," and (2) the perceived motion direction of the dichoptic plaid by rotating an arrow, presented in the center of the screen, via a trackball mouse between 1 and 360°. Observers were asked to report the overall (most dominant) motion direction they saw, either that of a single grating or of a combination of both gratings. In Spering et al. (2011), we compared this method to an alternative method in which observers were asked to move rectangular markers along interval judgment scales via key presses to indicate one or more perceived motion directions. Although in some trials observers indicated perceiving two motion directions, one

strong and one very faint, they never reported seeing the intermediate (average) motion direction.

Here, we were interested in whether responses followed the motion direction of one grating (component motion) or the combined motion direction of both gratings (pattern motion). When two gratings that drift in different directions are superimposed—either in the same eye, or by fusing images presented separately to each eye—the resulting plaid can be perceived as drifting either in two component motion directions or in a single, intermediate pattern motion direction (Adelson and Movshon, 1982; Tailby et al., 2010; Spering et al., 2011). After one block of 64 practice trials, observers completed eight blocks of 64 trials each.

Eye-movement recordings and preprocessing. Observers were instructed to fixate during the adaptation interval, and received no explicit instruction regarding eye movements for the test interval. In our previous study, observers tracked the moving stimulus reflexively when given no instruction, and voluntarily when asked to track (Spering et al., 2011). In both cases, the characteristics of the elicited eye movements resembled a smooth pursuit tracking response with an average latency of ~150 ms. Here we recorded eye position signals from the left eye with a video-based eye tracker (EyeLink 1000, SR Research) to evaluate eye movements during the test interval. Although we did not document whether the recorded eye was the dominant eye, we would not expect to see any differences in results depending on eye dominance, given that type of information received by the recorded eye—adapted or unadapted—did not affect results with this paradigm in a previous study (Spering et al., 2011). In all conditions in the present study, the left and right eye received the unadapted information equally often, i.e., each eye was adapted in 50% of all trials.

Eye movements were analyzed off-line using Matlab. Eye velocity was obtained by differentiation of eye position signals over time, and smoothed with a low-pass filter (40 Hz cutoff). Saccade onset and offset detection was based on jerk (Wyatt, 1998), the third derivative of eye position over time, obtained by differentiating unfiltered eye acceleration. Four consecutive samples had to exceed a fixed criterion of 95,000°/s^3 to be counted as saccade samples. We found this method to be more sensitive to small saccades than alternative detection algorithms based on acceleration only, or on a combination of velocity and acceleration (such as the Eyelink algorithm). All traces were visually inspected to confirm that the algorithm missed no saccades. Smooth eye movement onset was detected in the initial 500 ms interval of the test phase using a piecewise linear fit to 2D position traces. The least-squares error of the fitted model was minimized iteratively until a fixed criterion was reached, indicating the time of pursuit onset. We excluded traces with blinks (<0.5% trials in any experiment) and those with fixation breaks (eye position outside a 1° fixation window and eye velocity >1°/s) in a 500 ms time interval before the start of the test interval (1.3% excluded in Exp. 1, 1.7% in Exp. 2). This was done to prevent any systematic influence of larger eye movements that might have occurred during the adaptation interval.

Analysis of pursuit and perceptual responses. To determine pursuit direction, we computed the mean point (center of gravity) of the 2D eye position trace from eye movement onset to the end of the trial or the first saccade, whichever occurred earlier, effectively excluding saccades from this analysis; the minimum length of the time interval used for this analysis was 300 ms. Catch-up saccades during the test interval occurred in <1% of trials in either experiment and truncation of the analysis interval was therefore not a concern. Pursuit direction was defined as the angle of the single *x,y*-vector connecting eye position at pursuit onset (fixation) and mean point. We excluded pursuit eye movements in which no onset could be determined (6.2% in Exp. 1 and 4.6% in Exp. 2); this was usually due to low eye velocity. Pursuit direction was classified as component when it fell within ±22.5° of a given diagonal direction (e.g., up-right or up-left), and classified as pattern when it fell within ±22.5° of a cardinal direction (horizontal or vertical).

We classified observers' perceptual judgments of motion direction in the same way as pursuit responses and averaged them across trials. We present perceptual and pursuit responses to motion direction as mean proportions of responses in a given motion direction. In cued conditions, we normalized responses to the right (as if down-right was cued) and
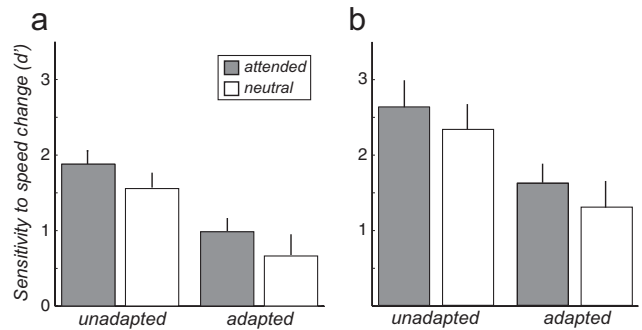

Figure 2. Mean sensitivity (*d′*) to the speed change. *a*, Experiment 1, four observers. *b*, Experiment 2, five observers. Error bars indicate SEM.

compared them against responses in neutral conditions with Bonferroni-corrected two-tailed paired *t* tests. For perception, we compared mean proportions of responses; for pursuit, we compared mean direction. We used the sensitivity measure *d prime* (*d′*), defined as

$$d' = z(H) - z(F) \qquad (1)$$

where $z(H)$ and $z(F)$ are experimentally determined z-transformed hit and false alarm rates, respectively, to quantify perceptual judgments of the speed change. We compared *d′* values using a repeated-measures ANOVA.

Results

Experiment 1: Upward motion

We first tested whether observers successfully allocated attention to the cued motion direction. A 3-way repeated-measures ANOVA with factors attention (attended vs neutral), adaptation (adapted vs unadapted) and cueing direction (up-right vs up-left) yielded significant main effects of attention ($F_{(1,3)} = 9.36$, $p = 0.05$) and adaptation ($F_{(1,3)} = 51.39$, $p = 0.001$), indicating that observers were more sensitive to the speed change when it occurred in the attended versus the unattended feature and in the unadapted versus adapted feature (Fig. 2a), as adaptation results in a weakening of perceptual responses. The effect of cueing direction was not significant, $F_{(1,3)} = 6.51$, $p = 0.09$. None of the interactions were significant (all *F* values <1). These findings indicate that both attention, regardless of cueing direction, and adaptation modulated observers' sensitivity to the speed change.

The following analysis of perceptual and pursuit judgments of motion direction is based on trials with and without speed change (distributed evenly across conditions). Although potential effects of the speed change itself should be constant across conditions, we tested whether the speed change had an effect on the pursuit response, as reported in Spering and Gegenfurtner (2007). These authors found a transient increase or decrease in pursuit velocity starting at ~150 ms after the onset of a 100 or 200 ms target speed perturbation. Here, we found no such effect of the speed change on pursuit; pursuit peak velocity and number of catch-up saccades in the time interval following the perturbation were not increased (both *t* < 1, n.s.). The difference between the previous study and the present results is most likely due to different levels of scrutiny: whereas observers in that study were instructed to accurately track the target and discriminate its speed, observers in the present study received instructions on speed change detection but not for pursuit.

Next, we report pursuit eye movements and perceived motion directions for neutral conditions, in which both motion directions were simultaneously cued. Results show the expected dissociation between perception and pursuit (Fig. 3a–c and Fig. 4a,b
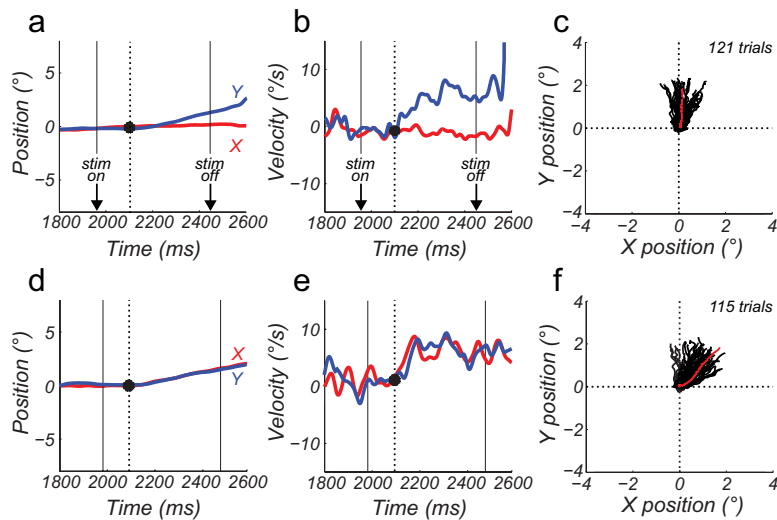
Figure 3. Individual eye movement traces for observer MR in Experiment 1. Top row: responses to motion in a neutral condition with up-leftward motion adapted and up-rightward motion unadapted. **a**, Horizontal (red) and vertical (blue) eye position over time relative to trial begin; solid vertical lines mark onset and offset of plaid motion during the test phase, dotted vertical line denotes pursuit onset. **b**, Horizontal and vertical eye velocity. **c**, 2D eye position in 121 valid pursuit trials plotted from plaid motion onset to offset; red trace is the same as the trace in **a** and **b**. Pursuit responses follow the vector average of adapted and unadapted motion directions. Bottom row: responses to motion in an attention condition with up-leftward motion adapted and uncued (unattended) and up-rightward motion unadapted and cued (attended). **d**, Eye position. **e**, Eye velocity. **f**, 2D eye position in 115 valid pursuit trials. Eye movements are shifted away from the vector average toward the attended direction.

illustrate individual responses and Fig. 5a–d indicates mean proportions of perceptual and pursuit responses in a particular motion direction; see Materials and Methods, Analysis of pursuit and perceptual responses): whereas perception was strongly biased toward the unadapted component's motion direction (winner-take-all; Figs. 4a, 5a,b), pursuit followed pattern motion, i.e., the vector average of unadapted and adapted motion direction, indicating that monocular adaptation had no effect on pursuit eye movements (Figs. 3a–c, 4b, 5c,d). These results replicate our previous findings (Spering et al., 2011).

Attention biased both winner-take-all perceptual responses and vector-averaging eye-movement responses toward the attended motion direction (Figs. 3d–f, 6a–d). Cueing the adapted direction shifted both perceptual reports (Fig. 6a) and pursuit directions (Fig. 6c) toward the attended direction (see also corresponding single responses in upper halves of Fig. 4c,d). This finding is reflected in significant differences between responses in the attended = adapted versus the pooled neutral conditions (normalized to the right, as if rightward motion was unadapted) for both perception ($t_{(3)} = 18.77, p < 0.002$) and pursuit ($t_{(3)} = 8.14, p = 0.005$; compare mean eye movement angles between Fig. 4b,d). Cueing the unadapted direction (Fig. 6b,d; see Fig. 3d–f and upper halves of Fig. 4e,f) enhanced the pursuit response to the unadapted direction compared with neutral (pursuit: $t_{(3)} = 11.10$, $p = 0.007$; perception: $t < 1$, n.s.).

Experiment 2: Downward motion
Experiment 1 tested perception and pursuit in response to upward motion. In Experiment 2, we investigate whether findings generalize to downward motion directions. Behavioral studies have reported asymmetries in performance for downward (preferred) versus upward motion in pursuit (Grasse and Lisberger, 1992). We repeated Experiment 1 with down-left and down-right motion directions in five observers (one had participated in Exp.

1), all experienced in psychophysics studies but naive regarding the purpose of the experiment.

As in Experiment 1, results for the speed change detection task were analyzed via a 3-way repeated-measures ANOVA, and we found the same main effects of attention ($F_{(1,4)} = 9.15, p = 0.03$) and adaptation ($F_{(1,4)} = 14.16, p < 0.02$; see Fig. 2b), but no main effect of cueing direction ($F_{(1,4)} = 1.68, p = 0.26$). None of the interactions was significant (all F values <1). These results indicate that observers were more sensitive to the speed change when it occurred in the attended than in the unattended and in the unadapted than in the adapted motion direction. As in Experiment 1, there were no effects of the speed change on pursuit peak velocity and catch-up saccades (both $t < 1$, n.s.). Results for perception and eye movements in the neutral condition were similar to those in Experiment 1 and confirm the dissociation between perception and eye movements: perception followed component motion, eye movements followed pattern motion (Figs. 4a,b, 5e–h). Figure 6e–h shows a shift in perceptual and pursuit responses toward the attended motion direction. As in Experiment 1, cueing the adapted motion direction counteracted responses to the unadapted (perceptually stronger) direction (Fig. 6e,g; see also Fig. 4c,d; perception: $t_{(4)} = 35.24, p = 0.001$, pursuit: $t_{(4)} = 5.6, p = 0.005$). Cueing the unadapted motion direction enhanced pursuit responses compared with neutral (Fig. 6f,h; see also Fig. 4e,f; pursuit: $t_{(4)} = 8.55$, $p = 0.001$; perception: $t < 1$, n.s.).

Discussion
In this study, we present two results: (1) For neutral conditions, a dissociation between perception and pursuit eye movements in response to adapted visual motion information. Observers reported the motion direction of the adapted component much less frequently, indicating that observers were less aware of the adapted than the unadapted motion component, although pursuit reacted sensitively to the adapted (unaware) information (see also Spering et al., 2011); (2) For attention conditions, a shift of responses toward the attended motion direction in both perception and pursuit, regardless of whether the attended stimulus was adapted or unadapted. These findings indicate that FBA affects perception and pursuit similarly even though the former reflects awareness whereas the latter does not necessarily do so (Spering et al., 2011; Tavassoli and Ringach, 2010).

The present study advances previous psychophysical studies demonstrating effects of spatial attention on the processing of unaware visual information in patients with blindsight (Kentridge et al., 1999) and effects of FBA and spatial attention on processing unaware visual information in healthy observers (Melcher et al., 2005; Kanai et al., 2006; Schmidt and Schmidt, 2010). Notably, here we show that these effects transfer to the motor domain: attending to adapted, unaware visual motion direction causes a shift in both motion perception and pursuit to the attended motion direction. Moreover, previous studies have shown that other motor responses, such as saccades or reaching
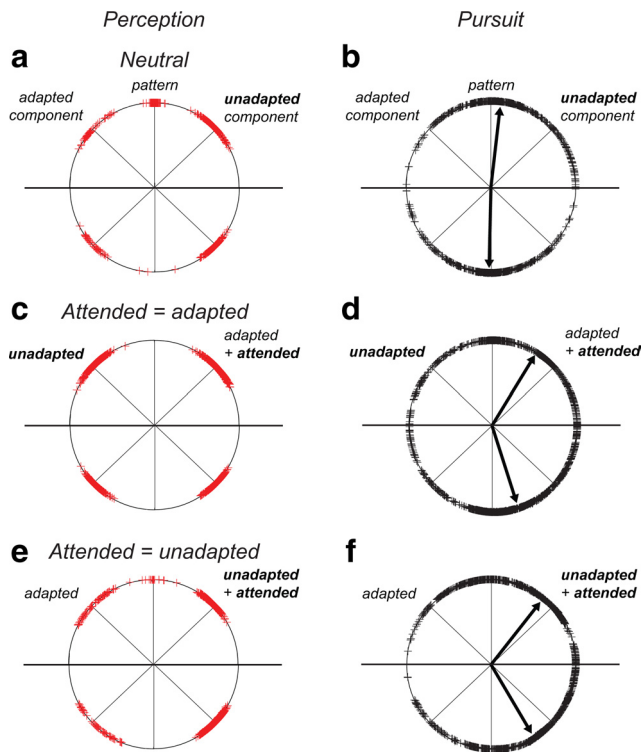
Figure 4. Individual perceptual (red) and pursuit responses (black); each cross represents one trial. Top halves: upward motion in Experiment 1 (perception: 2048 trials, pursuit: 1884 trials). Bottom halves: downward motion in Experiment 2 (2560/2387 trials). Black arrows denote mean pursuit angles. ***a***, Pooled perceptual responses in neutral conditions normalized to the right (as if up-rightward or down-rightward motion was unadapted and therefore perceptually stronger). ***b***, Pooled and normalized pursuit responses in neutral conditions. ***c***, Perceptual responses in cued conditions in which attended = adapted direction, all data normalized to the right (as if rightward motion direction was cued). ***d***, Pursuit responses for same conditions as in ***c***. ***e***, Perceptual responses in cued conditions in which attended = unadapted, data normalized to the right. ***f***, Pursuit responses for same conditions as in ***e***.

movements, can be performed in the absence of conscious perception of the target in both patients (Isa and Yoshida, 2009; Weiskrantz et al., 1974) and healthy observers (Goodale et al., 1986; Roseboom and Arnold, 2011). Remarkably, here we show that pursuit to unperceived visual features can be modulated by attention.

Interaction of attention and adaptation
We used monocular adaptation (see Materials and Methods, Procedure and design, and Fig. 1) to vary the perceptual strength of two images, presented to each eye separately but simultaneously. This paradigm resembles binocular flash suppression (Wolfe, 1984). The reduced sensitivity generally brought about by adaptation has been linked to a contrast gain control mechanism through which the gain of neuronal responses, tuned to the adapter stimulus, is decreased (Kohn, 2007; Ohzawa et al., 1982). Our perceptual results in the neutral condition (no directed attention) match these general effects of adaptation: observers' perceptual reports were almost exclusively driven by the unadapted stimulus' motion direction; we did not observe binocular rivalry, indicating that adaptation effectively weakened one stimulus. This finding is consistent with our previous study (Spering et al., 2011).

In attention conditions, we asked observers to attend to the motion direction of one of the two images—the adapted or the unadapted stimulus—and tested the effects of FBA and adapta-

tion on motion perception and pursuit. Studies that paired visual adaptation with visual spatial attention showed that attention modulates responses to adapted stimuli by strengthening the effect of adaptation (Chaudhuri, 1990; Ling and Carrasco, 2006; Rezec et al., 2004) and that attention affects perception regardless of adaptation state (Pestilli et al., 2007). Previous studies on feature-based attention and adaptation used aftereffects and showed that FBA enhances the process of adaptation to stimuli with attended features, thereby strengthening the aftereffect (Alais and Blake, 1999; Kanai et al., 2006; Liu et al., 2007a; Zirnsak and Hamker, 2010; for a review, see Carrasco, 2011). The present study shows that FBA not only affects the perceptual responses but also the pursuit responses to adapted stimuli: attention enhanced adaptation when the attended stimulus was unadapted and therefore novel and counteracted adaptation when the attended stimulus was adapted and therefore perceptually weaker, in both cases rendering the stimulus perceptually stronger.

FBA modulates vector-averaging responses
Pursuit in neutral conditions revealed a vector-averaging response pattern, equally weighting unadapted and adapted plaid components (see also Spering et al., 2011; Tailby et al., 2010 found a similar perceptual response to dichoptic plaids). Vector averaging is an important processing mechanism for the integration of multiple motion signals in the primate's middle temporal area (MT; Groh et al., 1997; Lisberger and Ferrera, 1997; Lisberger, 2010) and for the guidance of pursuit (Ferrera and Lisberger, 1995; Lisberger and Ferrera, 1997), especially when the observer (monkey or human) is uncertain about which motion direction to track.

When monkeys or humans are asked to select one of two stimuli moving into different directions, and track the selected target, initial pursuit follows the vector average of the two motion directions (Lisberger and Ferrera, 1997; Spering et al., 2006). Vector averaging is a transient response and the pursuit direction usually shifts toward one selected stimulus (winner-take-all response) during later pursuit stages. If one of the stimuli is cued by either a direction or a color cue (Garbutt and Lisberger, 2006) or by a spatial cue (Ferrera and Lisberger, 1995; Recanzone and Wurtz, 1999), responses are biased toward the cued stimulus, shifting initial pursuit responses from vector averaging toward winner-take-all behavior. Thus, both FBA and spatial attention influence pursuit target selection. Here, we observe a similar shift in pursuit eye movement responses: when FBA was directed to one of two motion directions, vector-averaging responses were shifted toward the attended stimulus feature.

FBA affects subcortical motion processing
Similar early visual areas, most notably area MT, process visual information for motion perception (Newsome et al., 1989; Salzman et al., 1992) and pursuit (Komatsu and Wurtz, 1988; Groh et al., 1997; Lisberger and Movshon, 1999; for a review see Lisberger, 2010). Psychophysical studies suggest similar processing mechanisms for motion perception and pursuit (Pack and Born, 2001; Gegenfurtner et al., 2003; Stone and Krauzlis, 2003; for a review see Spering and Montagnini, 2011).

Our results suggest that adapted visual motion information is processed more readily for pursuit than for explicit motion perception. This perception-action dissociation indicates that either processing pathways or mechanisms somehow have to differ. One candidate for a more sensitive processing of unaware information for pursuit is the retino-tectal or pulvinar pathway, which directly connects the retina to superior colliculus (SC) and brain-
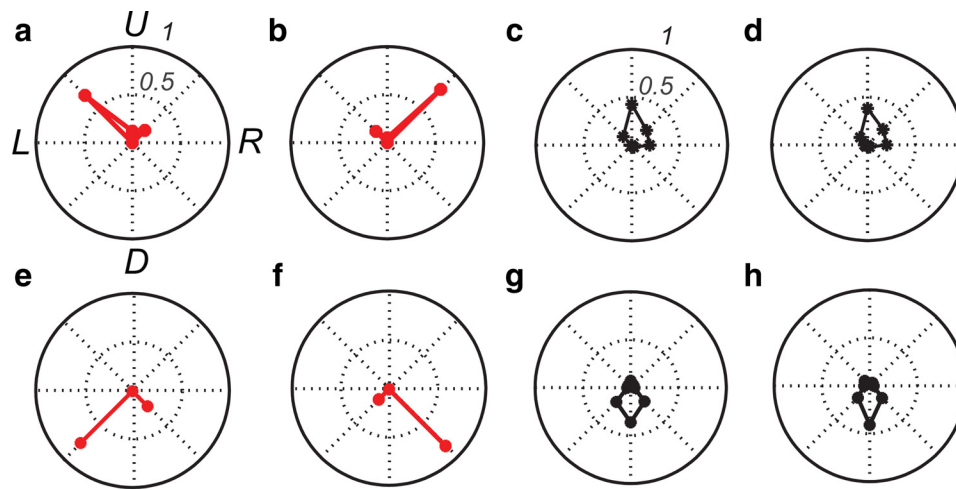
Figure 5. Mean proportion of perceptual (red) and pursuit responses (black) in neutral conditions (data not normalized). Top row, **a– d**: Upward motion in Experiment 1. **a**, Perceptual responses and **c**, pursuit responses in conditions with up-left motion direction unadapted; **b**, perceptual responses and **d**, pursuit responses in up-right motion direction unadapted. Bottom row, **e– h**: Downward motion in Experiment 2. **e**, **g**: down-right unadapted; **f**, **h**: down-left unadapted.
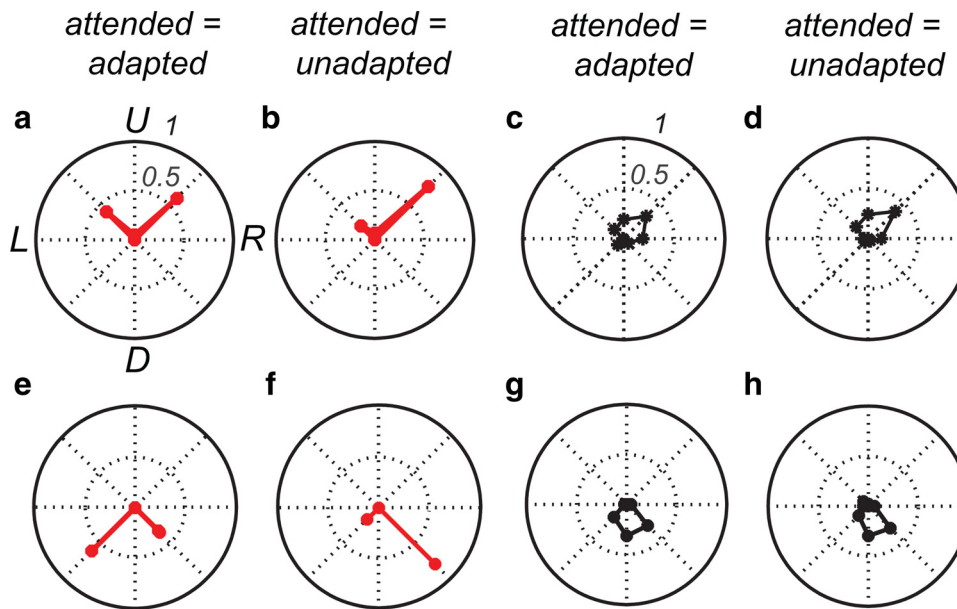

Figure 6. Mean proportion of perceptual (red) and pursuit responses (black) for attended direction = adapted direction and attended direction = unadapted direction. Top row, **a– d**: Upward motion in Experiment 1. **a**, Perceptual responses and **c**, pursuit responses in conditions with up-left motion direction unadapted; **b**, perceptual responses and **d**, pursuit responses in up-right motion direction unadapted. Bottom row, **e– h**: Downward motion in Experiment 2. **e**, **g**: down-right unadapted; **f**, **h**: down-left unadapted. All responses are normalized to the right (as if rightward motion direction was cued).

stem through the nucleus of the optic tract (NOT), as well as through the pulvinar nucleus of the thalamus. Direct evidence for an involvement of the pulvinar pathway in pursuit control comes from lesion and inactivation studies, showing that rostral lesions of the NOT can cause impairments in pursuit gain (Yakushin et al., 2000), and that the inactivation of the rostral SC can modulate pursuit metrics (Basso et al., 2000). Further, the SC is known to play an important role in pursuit target selection (Carello and Krauzlis, 2004; for a review, see Krauzlis, 2005) and in determining the weights for motion signal integration, as shown in pursuit vector average responses following SC inactivation (Nummela and Krauzlis, 2011). Moreover, both NOT and pulvinar have direct connections to area MT (Distler and Hoffmann, 2008; Berman and Wurtz, 2010, 2011). Interestingly, this pathway has recently been associated with the processing of invisible informa-

tion (Wilke et al., 2009), with residual visual abilities in blindsight patients (Huxlin et al., 2009), and with the translation of unperceived visual signals into motor outputs (Tamietto et al., 2010).

Given that FBA equally biases perceived direction and pursuit responses toward the cued motion direction, this type of attention seems to exert its influence both at cortical and subcortical processing levels. In line with this hypothesis, FBA enhances neuronal responses in multiple cortical areas, such as area MT (Treue and Martinez-Trujillo, 1999; Maunsell and Treue, 2006; Liu et al., 2007a; Stoppel et al., 2011), and subcortical areas (e.g., the pulvinar) show attention-related activity (Wilke et al., 2010; for a review see Wurtz et al., 2011). Cavanaugh and Wurtz (2004) showed that electrical stimulation of the SC mimics effects of attentional cueing on visibility of a moving stimulus; more importantly, both SC stimulation and attentional cueing counteract effects of change blindness. This evi-

dence links effects of FBA and awareness to a subcortical pathway, and provides a possible neurophysiological correlate for the shift of responses due to FBA in our study.

In the same vein, a human functional imaging study showed that FBA can operate at subcortical levels of the visual system. Schneider (2011) reported enhanced activity following FBA in some subcortical visual regions, such as the pulvinar and magnocellular layers of the lateral geniculate nucleus, but not in others, such as the SC. These neuroimaging findings are consistent with direction selectivity in pulvinar neurons (Merabet et al., 1998) and with lack in selectivity in most SC neurons (Schiller and Koerner, 1971).

Comparing perception and pursuit

Differences in response modality are a crucial methodological issue to consider when comparing perception and pursuit (for a review, see Spering and Montagnini, 2011). Pursuit responses are updated continuously; they are fast and potentially inaccurate. They provide an orienting response averaging global motion and may be based on information that observers do not consciously perceive. Perceptual decisions are discrete; they may be based on motion signals at a specific moment in time or averaged across the whole presentation time and beyond. The perceptual system has to classify, i.e., detect or discriminate, particular visual features and must therefore provide an accurate analysis of visual signals. However, even if we assume different time windows for the integration of motion signals for perception and pursuit, this is unlikely to explain the dissociation in response direction observed here.

Perceptual and pursuit responses are also given through different effectors, implying a necessary separation of the information streams toward the motor-output end. An alternative explanation for the perception-pursuit dissociation could be that it arises from differences at the motor output stage, rather than from an early separation of pathways or from differences in motion processing within the same pathway. Whereas this explanation may work for differences in response magnitude, it is unlikely that identical motion processing can result in pursuing an unperceived (average) motion direction, as observed in the present study.

To conclude, we found a dissociation of perception and pursuit, and that FBA affects both responses similarly. The eyes can track an attended feature even if observers do not perceive it.

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