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Ocular tracking responses to background motion gated by feature-based attention

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Souto D, Kerzel D. Ocular tracking responses to background motion gated by feature-based attention. *J Neurophysiol* 112: 1074–1081, 2014. First published June 11, 2014; doi:10.1152/jn.00810.2013.—Involuntary ocular tracking responses to background motion offer a window on the dynamics of motion computations. In contrast to spatial attention, we know little about the role of feature-based attention in determining this ocular response. To probe feature-based effects of background motion on involuntary eye movements, we presented human observers with a balanced background perturbation. Two clouds of dots moved in opposite vertical directions while observers tracked a target moving in horizontal direction. Additionally, they had to discriminate a change in the direction of motion (±10° from vertical) of one of the clouds. A vertical ocular following response occurred in response to the motion of the attended cloud. When motion selection was based on motion direction and color of the dots, the peak velocity of the tracking response was 30% of the tracking response elicited in a single task with only one direction of background motion. In two other experiments, we tested the effect of the perturbation when motion selection was based on color, by having motion direction vary unpredictably, or on motion direction alone. Although the gain of pursuit in the horizontal direction was significantly reduced in all experiments, indicating a trade-off between perceptual and oculomotor tasks, ocular responses to perturbations were only observed when selection was based on both motion direction and color. It appears that selection by motion direction can only be effective for driving ocular tracking when the relevant elements can be segregated before motion onset.

smooth pursuit eye movements; feature-based attention; attention; motion; eye movements

A CENTRAL QUESTION IN UNDERSTANDING how perception and action may be articulated is whether perceptual selection and eye movement control rely on similar filtering mechanisms (for a review Kowler 2007; Schutz et al. 2011). Involuntary ocular tracking eye movements offer a good opportunity for understanding early filtering mechanisms given that their initiation can involve relatively few processing steps (for a review, see Masson and Perrinet 2012).

Among involuntary tracking eye movements, ocular following is a quasireflexive response to motion covering a large part of the visual field (Kawano 1999; Miles et al. 1986), which is believed to reflect the unfolding of visual motion processing, providing a window on the link between neural computation and behavior (Ilg 1997; Lisberger et al. 1987; Masson and Perrinet 2012). Ocular following depends on first-order motion signals, with little input from higher order motion processing (Hayashi et al. 2008), suggesting that attention may have a minor role. However, this latter aspect is poorly understood, especially in relation to feature-based attention, the ability to select a specific feature dimension (e.g., motion, color, and shape), or value (upward vs. downward motion) across the visual field. In the context of voluntary and involuntary tracking eye movements, feature-based attention may have a role in helping integrate motion information across space, as for tracking surfaces occluded by objects in the foreground (e.g., Grossberg 1998; Mestre and Masson 1997; Murasugi et al. 1989).

Feature-based attention has been shown to modulate motion processing. Arman et al. (2006) showed that the motion aftereffect is stronger for motion in an attended direction even when the test appears at a nonattended location, indicating enhancement of motion processing by selection of same-direction motion signals. In a similar vein, Lankheet and Verstraten (1995) elicited a motion aftereffect in a direction opposite to an attended motion layer, even when the stimulus motion was balanced by showing two clouds of dots moving in opposite directions. However, it is unclear whether feature-based attention modulates involuntary eye-movements, since recent research indicates that perception and slow eye movements rely on partially different networks or on information arising from the same networks but read out in different ways (Simoncini et al. 2012; Spering and Carrasco 2012; Spering and Gegenfurtner 2007b; Spering et al. 2011; Tavassoli and Ringach 2010). Recently, Spering and Carrasco (2012) showed that pursuit eye movements spontaneously follow the direction of the attended motion in dichoptic plaids, suggesting that feature-based attention can determine which motion direction is pursued and perceived. However, their paradigm was not suited to assess the importance of feature-based involuntary eye movements, as there was no fixation point and no incentive to maintain fixation.

With respect to involuntary eye movements in response to background motion, we know that the optokinetic nystagmus, whose early phase shares neural substrates with ocular following (Kawano 1999), can be reduced to some extent by paying attention to stationary elements (Mestre and Masson 1997; Murasugi et al. 1989). However, those studies confounded feature-based and spatial attention. We adapted established paradigms (Miura et al. 2009; Suehiro et al. 1999) to investigate the role of feature-based attention in gating motion signals that drive involuntary ocular responses to background motion. When the background moves orthogonally to the pursuit direction, its motion causes a brief involuntary eye movement in the direction of the perturbation. To obtain responses due to feature-based attention, we presented a balanced motion per-

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turbation in a dual task situation. That is, two clouds of dots moved in opposite directions (transparent motion paradigm) and observers had to pay attention to one of the clouds to discriminate a change in direction. Feature-based attention was expected to gate motion signals in the attended direction, creating an imbalance between motion signals that would result in a tracking response. In separate experiments, we manipulated the dimension on which the motion of one of the clouds could be selected. Selection could be based on both color and direction of motion (*experiment 1*), only on the direction of motion because color was uniform (*experiment 2*), or on color because motion direction was unpredictable (*experiment 3*). We finally compared ocular tracking results against a control condition in which there was only one group of dots.

METHODS

Participants

Undergraduate psychology students at the University of Geneva participated in the experiments for class credit (ages 18–42 yr, mean age 24 yr). The procedure was approved by the local ethics committee. All subjects reported normal or corrected to normal vision. The number of subjects per experiment is given in Table 1. No participant ran more than one experiment.

Apparatus and Stimuli

The stimuli were presented on a 21-in. (diagonal) CRT with a resolution of 1,280 (H) × 1,024 (V) pixels at a refresh rate of 85 Hz. The participants' head position was stabilized with a chin rest at 50 cm from the screen center. Eye movements were recorded with a desktop-mounted, video-based eye tracker (EyeLink 1000; SR-Research, Ontario, Canada) at a sample frequency of 1,000 Hz. The experiment was run in a dimly lit room.

A sketch of the stimuli and procedure is shown in Fig. 1. All stimuli had a luminance of 20.5 cd/m^2 and were presented on a black background. The pursuit target, a light gray bull's eye with a diameter 0.7°, moved horizontally at 11.2°/s for 1 s. The trajectory was centered on the midpoint of the screen. The background consisted of 80 dots (squares, side length of 0.2°) that moved at the same horizontal velocity as the target. For placing dots, the screen was divided in a matrix of 10 columns and 8 lines, and a dot was placed within each cell. The dot position within the cell was randomly jittered. Half of the dots were green, and the other half was red. Dot lifetime was only limited by the borders of the screen. The temporal structure of each trial is illustrated in Fig. 1*C*. The dots started moving vertically 306 ms after target motion onset at 33.6°/s for 200 ms. The vertical motion was added to the horizontal motion, resulting in diagonal motion on the screen. However, dot motion was experienced as vertical because the eye moved at the same horizontal velocity as the dots. The two clouds of dots moved in opposite directions in a retinal reference frame centered on the horizontally moving pursuit target. Dots that left the screen at the edges reappeared on the other side. One cloud slightly changed its vertical direction of motion 94 ms after onset of vertical motion. Instead of moving vertically all along, the motion path deviated by ±10° from vertical. Dots that were closer than 2° to the pursuit target were not presented.

Task and Procedure

Experiment 1: selection by motion and color. The experiment started with two single task blocks, in which observers were asked to pursue the target and to ignore the background. No mention of a change in motion direction during the vertical motion pulse was made. The two single task blocks, our control condition, were run before the two dual task blocks to avoid carry-over effects of attentional set. In two dual task blocks, observers were asked to pursue the target and to report whether the vertical motion of dots in a designated color deviated to the left or to the right. The color of the attended dots was fixed for each participant. The vertical direction of the attended color changed between blocks, while the horizontal direction of target motion varied randomly from trial to trial. The attended color and the vertical direction of motion of the attended dots in the first block were counterbalanced across participants. There were 64 control trials in the control condition (2 × 32) and 96 trials in the attention condition (2 × 48). The control condition had a third less trials than the attention condition because less eye movement variability was expected when participants' eye movements are driven exogenously as opposed to when they need to shift attention according to instructions.

An error message was displayed when the participant blinked during pursuit target motion, when a vertical saccade $>1°$ occurred, or when the distance covered by the eye from motion onset to offset was $<70\%$ of the target's trajectory.

Experiment 2: selection by motion. The methods were as in *experiment 1* with the following exceptions. All dots had the same color, which did not change in the course of the experiment for individual observers but was counterbalanced between red and green across observers. In dual task blocks, observers were instructed to report the horizontal deviation of the cloud of dots moving in a specified direction. The relevant vertical direction was indicated before each of the two dual task blocks. The order of vertical motion directions was counterbalanced across participants. The experiment started with two single task blocks using the same stimuli as the dual task blocks.

Table 1. *Number of excluded participants, excluded trials, and perceptual performance among participants included in the analyses*

	Experiment 1	*Experiment 2*	*Experiment 3*	*Experiment 4*
N participants				
Included	13	13	8	15
Excluded: eye movement criteria	1 of 15	7 of 21	6 of 16	5 of 20
Excluded: perceptual criterion	1 of 15	1 of 21	3 of 16	–
Trials				
Valid: attention	74 (49–89)	67 (46–89)	66 (34–91)	39 (15–57)
Valid: control	37 (14–51)	34 (13–57)	34 (15–55)	25 (12–41)
Pursuit error	4% (1–11%)	6% (0–23%)	5% (1–19%)	2% (0–8%)
Saccade error	25% (13–40%)	31% (9–49%)	30% (16–38)	50% (33–76%)
Perceptual task				
Percent correct	91% (76–98%)	86% (63–98%)	79% (65–93%)	–

Participants were excluded if there were <12 valid trials in any condition (eye movement criteria), or if perceptual performance was <60% correct, to ensure that observers were paying attention to the perceptual task target. Blinks during the critical interval were very rare (0–1%) and are therefore not detailed in the table.

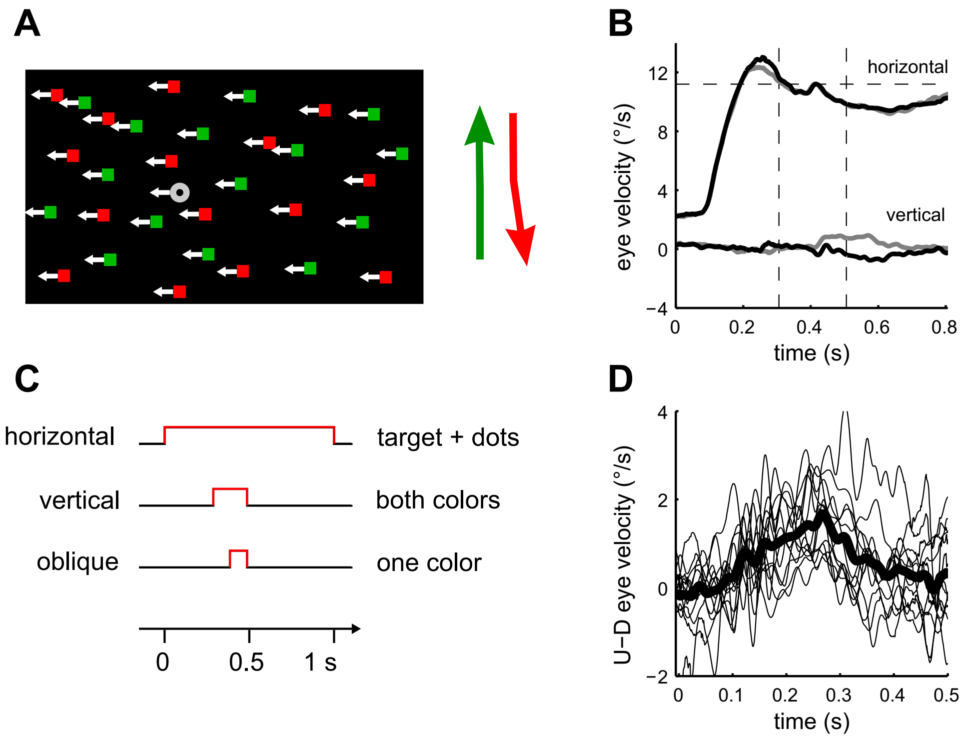

Fig. 1. Experimental procedure and results from *experiment 1*. *A* and *C*: target and background dots moved horizontally for 1 s (first line in *C*). After 306 ms, the dots moved vertically for 200 ms (second line in *C*). Dots of different colors moved in opposite vertical directions at 33.6°/s. The to-be-attended dots moved to the left or right from vertical relative to a reference centered on the pursuit target (oblique motion, third line in *C*). The pictogram to the right of the stimulus indicates the vertical trajectory of red and green dots in 1 particular condition. *B*: mean horizontal and vertical eye movement velocity (group averages) locked to pursuit target motion onset. Gray lines indicate upward dot motion, and black lines indicate downward dot motion. Vertical broken lines delimitate background motion duration. Note that there is a horizontal eye movement of ~2°/s at the start of the target motion, since target onset and trajectory could be anticipated. *D*: U-D eye velocity in the first 500 ms after the onset of vertical motion, obtained by subtracting vertical eye velocity with attention to the downward (D) moving dots from vertical eye velocity with attention to the upward (U) moving dots. A positive value indicates ocular tracking in the direction of background motion. Thin lines represent individual average traces and the thick line the group average.

Experiment 3: selection by color. The methods were as in *experiment 1* with the following exceptions. The vertical direction of motion of each cloud (red or green) changed randomly from trial to trial. In dual task blocks, observers were instructed to focus on the color indicated at the start of each block. As in *experiment 1*, this color did not change for a given observer but was counterbalanced between green and red across observers. The same stimuli were used in the initial single task blocks.

Because of the brevity of the motion signal, it is unlikely that feature-based attention could be voluntarily deployed in time to enhance motion signals if selection was based on motion direction; therefore, we consider that selection was based on color in this experiment.

Experiment 4: classic response. The first two blocks of the experiment were as in *experiment 1*. That is, the direction of motion of each color stayed the same in a block of trials and dots of two colors were overlaid. In the following two blocks, only half of the dots were shown with a single color and direction of motion. For instance, observers saw the red dots moving upward in block three and downwards in block four. There was always a horizontal deviation in the vertical motion pulse of one cloud (as in *experiment 1*), but the change was task irrelevant. As there was no opposite motion, this experiment should reveal the maximal response to the stimulus that was attended in *experiments 1–3*.

Data Analysis

To identify saccades we used the output of the EyeLink 1000 eye movement parser. The criterion used to detect saccade onset was acceleration $>4{,}000°/s^2$ and velocity $>22°/s$. Trials with errors detected online (blinks, vertical saccades, low gain horizontal pursuit, see above) were discarded from further analysis (see eye movement criteria in Table 1). A large number of ocular errors indicated that the participant was unable to maintain smooth pursuit in the presence of distracting stimuli or that the position signal was poor. Observers whose perceptual task performance was <60% were excluded from analysis to ensure that all subjects were paying attention to the stimulus. For offline analysis, we also removed trials in which a saccade was detected during a temporal window going from vertical cloud motion onset to 500 ms after that, ensuring that this most informative period was not contaminated by a saccadic component. Our only criterion to exclude subjects was that there were >12 trials per condition (motion direction × attention task).

Ocular following is a relatively small response, even though it is enhanced when performing a pursuit eye movement (Miura et al. 2009). Therefore, it is customary to improve the velocity signal by subtracting the average response to an upward motion signal to the response to a downward motion signal, and given it is a slow response, by filtering the velocity data with a low cutoff frequency (e.g., Hayashi et al. 2008; Miura et al. 2009). Velocity traces were filtered with a second-order Butterworth filter with a 20-Hz cutoff frequency. We ensured that no saccades were present in the velocity traces during an interval going from 0 to 0.5 s after onset of vertical motion. Furthermore, we extended the definition of a saccadic episode by adding 40 ms after the end of a saccade and 25 ms before its start. Because the vertical direction of motion was blocked, we also tested whether there was anticipation of the vertical motion pulse by analyzing the interval from vertical motion onset until 80 ms thereafter, which is too early for a visually driven response.

RESULTS

Table 1 summarizes the criteria used for analyzing the data, the number of excluded participants in all experiments, percent discarded trials, and average perceptual performance. The number of discarded trials is rather high (about 30–35% in *experiments 1–3*), especially in *experiment 4* (>50%), due to a large number of saccades executed during the interval of interest where they are more likely to be triggered as retinal slip increases (de Brouwer et al. 2002). Because we wished to focus on the well-described slow eye movements following background motion, we had to exclude saccadic episodes.

Figure 1*D* shows the difference in vertical eye velocity between attending upwards and downwards motion in *experiment 1*, which we refer to as U-D response. Upward and downward movements of the eye were given positive and negative signs, respectively. U-D values result from subtracting attention to downward motion from attention to upward motion. Therefore, positive U-D values indicate responses in the direction of attended background motion.

The individual U-D responses in Fig. 1*D* show a deflection in the direction of the attended motion in *experiment 1*. Figure 2*A* also shows a clear effect of the direction of attended dot motion on the averaged data that peaks at 222 ms [95% confidence interval (CI): 165–280 ms] after motion onset. Figure 2*D* shows that the peak occurred earlier when only a single cloud was shown in *experiment 4* (135 ms, 95% CI: 125–144 ms). The U-D peak amplitude was 1.67°/s in *experiment 1* (95% CI: 1.21–2.14°/s). With only a single cloud in *experiment 4*, the peak amplitude was 4.82°/s (95% CI: 3.67–5.97°/s). That is, the feature-based response was 34% of the classical response to unidirectional background motion; over the same time, the U-D response in the control condition without instruction to attend to one of the two clouds was close to zero (*experiment 1*: 0.04°/s; *experiment 4*: −0.28°/s). Statistical significance of the difference between attention and control conditions was evaluated by two-tailed *t*-tests over a large temporal window, going from 80 to 400 ms postvertical motion onset; we had no a priori reason for choosing a narrower temporal window for the effect of feature-based attention. This showed a significantly larger U-D eye velocity in the attend condition compared with the control condition in *experiment 1* (0.87 vs. 0.03°/s), $t(12) = 5.792$, $P < 0.0001$, but not in *experiment 2* (0.19 vs. 0.08°/s) and *experiment 3* (0.30 vs. 0.14°/s), $P > 0.4$. Furthermore, there was a significant difference between attention and control in *experiment 4* (1.08 vs. −0.12°/s), $t(14) = 5.743$, $P < 0.0001$.

It should be noted that observers anticipated the horizontal motion of the target, as the horizontal eye velocity at motion onset was ~2°/s (see Fig. 1*B*). Because the target always moved from an eccentric position toward the center of the screen, target motion was highly predictable and this explains the anticipatory eye movement. There was also evidence of anticipation in the response to the vertical dot motion when they were displayed in a single direction (*experiment 4*; Fig. 2*D*). We tested for an anticipatory component in the vertical ocular response by carrying out paired *t*-tests on the initial 80 ms after motion onset. During this period, only U-D eye movements in *experiment 4* were significantly different from zero, $t(14) = 3.919$, $P = 0.0015$ (other $P > 0.42$), with an average of 0.62°/s (95% CI: 0.31–0.93°/s).

Focusing on the attention condition, multiple comparisons between experiments over the same critical interval (80–400 ms postmotion onset) gave statistically significant differences between *experiments 1* and *2*, $t(24) = 3.369$, $P = 0.0025$; between *experiments 1* and *3*, $t(19) = 2.771$, $P = 0.0122$; but not between *experiments 1* and *4*, $t(26) = 1.273$, $P = 0.214$. *Experiment 4* was also significantly different from *experiment 2*, $t(26) = 4.287$, $P = 0.0002$, and from *experiment 3*, $t(21) = 3.437$, $P = 0.0025$. There was no statistical difference between *experiments 2* and *3*, $P = 0.806$. *Experiment 4* yielded an early peak and then a response opposite to the attended motion. Hence, the comparison of average U-D velocity over a large temporal interval does underestimate the strength of the response, which prompts us to compare *experiments 1* and *4* by their peak response. Peak responses in *experiments 1* and *4*

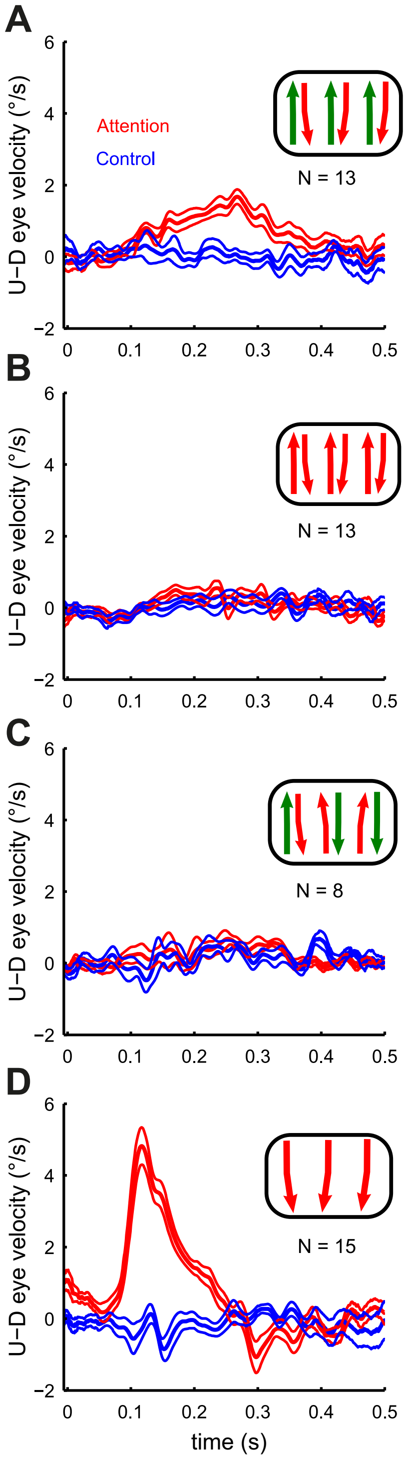

Fig. 2. Vertical eye velocity in *experiments 1–4* locked to vertical motion onset. *Insets*: experimental condition by showing the direction of the clouds of dots and how they change from trial to trial. *A*: both color and direction of the motion to discriminate are kept constant within a block (color + direction selection). *B*: direction is kept constant (direction selection). *C*: color is kept constant (color selection). *D*: only 1 cloud of dots is displayed (classic effect). Note that in this experiment the "attention condition" is an exogenous attention condition in which there is only 1 cloud of dots that is task irrelevant. *A–D*: thick lines represent the group average. Thin lines represent means ± SE.

were significantly different (1.67 vs. 4.82°/s), $t(26) = 4.287$, $P < 0.0001$. Statistical significance levels was also reached when comparing open-loop responses from 90–180 ms post-vertical motion onset (0.62 vs. 3.27°/s), $t(26) = 11.144$, $P <$ .0001.

We were also interested in testing whether there was a significant response during the open-loop response phase. The fastest open-loop responses may occur within a time window going from 90–180 ms (following Hayashi et al. 2010). Measured over this time window we obtained significantly larger responses in the attended compared with the unattended conditions (0.67 vs. 0.16°/s) in *experiment 1*, $t(12) = 2.521$, $P =$ 0.0268, and in *experiment 4* (3.32 vs. −0.35°/s), $t(14) =$ 11.298, $P < 0.0001$. Other experiments yielded no significant differences, $P > 0.2$.

Perceptual performance between groups was compared as an indication of task difficulty (see Table 1). Perceptual performance between *experiments 1* to *3* was compared by running multiple comparisons using a nonparametric test, the Wilcoxon rank sum test. Perceptual performance was higher with direction and color being constant (*experiment 1*: 91%) than with direction alone (*experiment 2*: 86%) or color alone (*experiment 3*: 79%) defining the target cloud. The difference between *experiments 1* and *3* was statistically significant, $z = 2.609$, $P < 0.01$, but neither between *experiments 1* and *2*, $z = 0.822$, $P = 0.4108$, nor between *experiments 2* and *3*, $z = 1.340$, $P =$ 0.1800. This suggests that the task was either easier in *experiment 1* compared with *experiment 3* or that observers may have engaged less in the perceptual task in *experiment 3*, which would explain the lower perceptual accuracy and the absence of attentional modulation of the vertical tracking response. If there was less engagement in the perceptual task in *experiment 3* than in *experiment 1*, horizontal smooth pursuit gain should have suffered less from the dual task situation.

We therefore analyzed the eye movement gain for the horizontal component of smooth pursuit eye movements within the first 500 ms after the onset of vertical motion. Figure 3 shows that horizontal eye movement gain is lower in the attention condition compared with the control condition across experiments (0.95 and 1.04, respectively). An ANOVA taking experiment as a between-subjects factor (*experiments 1–4*) and task as a within-subjects factor (attend to cloud, control) confirmed that there was no effect of experiment, $F(3,45) =$ 0.316, $P = 0.814$, or an interaction between experiment and task condition, $F(3,45) = 0.993$, $P = 0.405$, but an effect of task, $F(1,45) = 32.827$, $P = 0.001$. Hence, there was no evidence that attentional engagement was reduced in *experiment 3*. It must be noted that there was no explicit instruction to attend background motion in *experiment 4*, but it is likely that attention was engaged exogenously in that experiment, resulting in a similar reduction in gain.

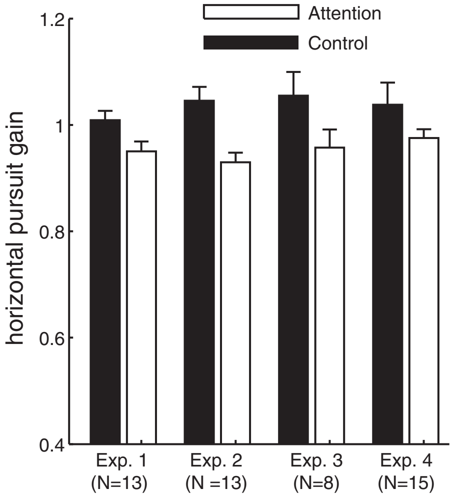

Fig. 3. Horizontal eye movement gain averaged across subjects in the 4 experiments (time window: 0–500 ms after vertical motion onset). Error bars represent means ± SE.

Finally, we sought to characterize eye movement velocity on a trial-by-trial basis in *experiment 1*. This analysis is relevant to distinguish between rival conceptions of feature-based attention effects. A priming account predicts a buildup of effects across trials due to the repetition of the attended feature. Therefore, feature-based effects are expected to be absent at the beginning of the experiment and to increase over trials. A feed-forward selection account claims that feature-based attention selects the relevant feature before stimulus onset. Therefore, the effects should be present from the first trial onward without any changes over trials. Since signal variability did not allow for an accurate calculation of velocity profiles in every trial (this can be appreciated in Fig. 4*A*), we took the peak velocity latency of the group as a reference for comparing velocity across trials (i.e., the peak of the thick line in Fig. 1*D*). Therefore, velocity was averaged over a 50-ms time window centered on the group peak latency. On the first trial, the attention condition yielded statistically significant larger responses compared with the control condition, $t(12) = 2.845$, $P = 0.0148$. The subsequent analysis was restricted to the first 30 trials to avoid missing data in the attention condition. We observed that the U-D eye velocity fluctuated around a constant level across trials, as indicated by the slopes of the best-fitting least-squares linear regression in attention and control conditions (see Fig. 4*B*). Individually, regression lines in the attention condition had a negative slope in five subjects (from −0.001 to −0.09), indicating decreasing U-D velocity across trials; in 8 of them slopes were positive (from 0.025 to 0.23). The slope of the group average was 0.04, which was not statistically different from zero (Wilcoxon rank sum test, $z =$ 1.041, $P = 0.1677$). The fact that feature-based effects were present on the first trial and did not increase over the course of the experiment is inconsistent with the priming account and favors feed-forward selection.

To sum up, when moving dots are displayed alone (*experiment 4*) or when one of the two clouds of dots is selected by its color and direction of motion (*experiment 1*), observers involuntarily track the attended motion direction. This effect depends on feature-based attention since vertical motion is otherwise balanced, as indicated by the absence of differences when the dots are unattended (i.e., single task condition), and that selection by location is unlikely because presentation time was short, the dots were relatively dense and not shown in the fovea. Trial-by-trial analysis indicates that performance fluctuates around a constant level in the first 30 trials.

DISCUSSION

We asked whether background motion signals generate an ocular tracking response depending on feature-based attention.

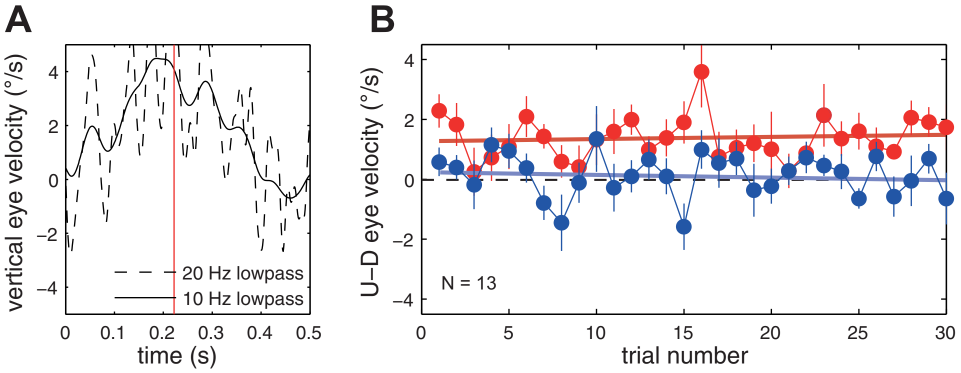

Fig. 4. Trial-by-trial analysis of ocular response in *experiment 1*. *A*: Vertical eye velocity in response to a target moving upwards on the 1st trial in 1 observer. A 10-Hz low-pass filtered version is shown with the original trace (20-Hz low pass) for clarity. The latency of the group peak velocity is shown as a vertical red line. This was the reference for comparing U-D vertical eye velocity across trials in *B*, showing control (blue) and attention conditions (red) and respective regression lines. Error bars represent means ± SE.

Participants pursued a target moving horizontally, while attending to a designated cloud of dots in the background. A vertical ocular tracking response occurred in response to the attended dot motion when selection could be based on specific feature values along two feature dimensions: motion and color. The amplitude of the attention-based tracking response was ~30% of the tracking response elicited in a single task with only one direction of background motion and ~20% if we consider not the peak response but an estimate of the open-loop response.

In two other experiments, we tested the effect of the perturbation when selection was based on color while motion direction varied unpredictably (color selection, see *experiment 3*) or when selection was based on motion direction because all dots had the same color (direction selection, see *experiment 2*). Although the decrease of horizontal pursuit gain indicated that observers across experiments were equally engaged in the perceptual task, ocular responses to perturbations depended on the combination of color and motion selection. In *experiment 3*, we assumed that selection of one of the clouds is too slow when its motion direction is unpredictable. Previous research has shown that it takes at least 300 ms to see the perceptual benefits of selecting a layer of dots based on direction of motion (Andersen and Muller 2010; Liu et al. 2007), but vertical motion only lasted 200 ms in our experiments.

We noted no significant feature-based response when selection was based on the color of the dot layer or when selection could only be made by attending to a given motion direction. We may think of this pattern of results as a multiplicative effect of combining selection by color with selection by motion. We take this as an indication that selection by motion direction can only be effective for driving involuntary ocular tracking when the relevant layer can be segregated before the motion starts, on the basis of any object feature, such as color, or depth plane (Mestre and Masson 1997).

The ocular responses that we recorded were always in the direction of the motion perturbation. Regarding the direction of the response, we note that there is a discrepancy in the literature. Some studies report an ocular response opposite to the background perturbation whereas others report an ocular response in the same direction. However, there is an essential difference in those studies. Studies that present background motion orthogonal to the pursuit direction show a response in the same direction (Lindner et al. 2001; Miura et al. 2009; Suehiro et al. 1999), with the exception of Spering and Gegenfurtner (2007a), probably because of their relative low background velocity (Miura et al. 2009).

Our results indicate that although ocular tracking responses are often characterized as low-level responses to motion energy, they can nonetheless be modulated by feature-based attention. At the same time, we show that this effect is limited to specific conditions. Next, we consider a number of alternative interpretations to our results. Is the response we recorded in *experiment 1* due to the gating (or enhancement) of motion signals by feature-based attention or is it secondary to attentional tracking? Short presentation times and high velocities were supposed to discourage attentional tracking as an efficient way of performing the direction discrimination task. Latencies can help disentangle those two interpretations. Although we observed longer peak response latencies in *experiment 1* compared with the classical effect in *experiment 4*, the most informative analysis concerns the early, open-loop response. Because of high variability on single trials (see Fig. 4*A*), we could not estimate response onsets reliably. However, we can analyze early average responses. The *feature-based tracking hypothesis* would state the ocular response was initiated by tracking a particular feature by a covert movement of attention, rather than by the gating of first-order motion signals by feature-based attentional selection (*gating hypothesis*). It was shown that feature-based tracking and luminance-based motion are independent (Cavanagh 1992; Lu and Sperling 1995). Feature-based tracking implies that the eye movement will start after attentional tracking starts, which can only happen with some delay after onset of first-order motion. Consequently, the earliest response to feature-based tracking is necessarily delayed relative to the response to first-order motion. In contrast, the gating hypothesis allows for preemptive selection of motion signals according to a particular defining feature, for instance, by enhancing the weight given to responses coming from a subset of motion detectors. Further, studies indicate that the open-loop response of tracking eye movements is a response to first-order motion (Wilmer and Nakayama 2007), as is initial ocular following (Sheliga et al. 2005). Our data showed a response during the open-loop period in the attention compared with the control condition in *experiments 1* and *4*, favoring the gating hypothesis. A caveat of this analysis is that the motion direction of the relevant cloud of dots could be anticipated, contaminating the supposedly open-loop response. However, our analysis indicated no anticipatory component in *experiment 1*. An anticipatory component is only observed in *experiment 4* (Fig. 2). A further argument against feature-based tracking is that when motion direction was constant and there was no color cue, we did not observe a feature-based attention based response. To sum up, we suggest that the ocular tracking response reflects preemptive feature-based selection rather than attentional tracking.

The idea that selection could be based on motion when target motion direction is held constant within a block presupposes that we can deploy "preparatory attention" to motion. However, this is a contentious issue in the literature (e.g., Fannon et al. 2007). Recently, Theeuwes (2013) made a case for distinguishing between postselection and feed-forward selection processes in feature cueing effects. He proposed that features can be primed in a bottom-up manner when there is a match with the target on previous trials but that features cannot be voluntarily selected by directing attentional resources towards a target feature. Our data do not lend support to the bottom-up (priming) account, since this would predict a buildup of the tracking response across trials. Not only did some observers show a strong response in the attended direction on the first trial, but on average, the best fitting linear trend indicated a constant response across trials.

Was task difficulty a factor explaining the absence of ocular tracking in some conditions? The perceptual task was easier when the target was defined by two rather than by one constant feature, as indicated by the percentage of correct trials, at least when comparing *experiments 1* and *3*. We also observed that involuntary tracking was absent when there was only one constant feature, opening the possibility that the task might have been too difficult in those conditions or that observers were less engaged in the task. However, performance in the oculomotor task (horizontal tracking) does not support the idea of differential attentional engagement. The availability of attention to a secondary task trades-off with ocular performance, especially when the perceptual task requires a motion judgment (Kerzel et al. 2008, 2009; Kowler and Zingale 1985). If observers engaged in the secondary task similarly across experiments, we should see that the pursuit task performance was reduced equally across experiments in the attention condition compared with the control condition. The analysis of smooth pursuit gain confirms an equal reduction of gain in all attention conditions, suggesting that the absence of involuntary ocular tracking was not due to a lack of engagement in the perceptual task. Overall, however, it remains possible that the pattern of eye movements was explained by task difficulty, at least when comparing *experiment 1* (constant motion and color) and *experiment 3* (constant color). That is, perceptual performance suggests that it was easier in *experiment 1* to selectively attend to a specific dot-field despite that the velocity of horizontal eye movements confirms the same level of engagement as in the other experiments.

Finally, did anticipatory pursuit contaminate our estimation of open-loop ocular following since motion direction was predictable? Since the predictability of motion direction across trials was a precondition for observing an effect, we cannot exclude this possibility; however, there is no indication that this is the case. There was no significant response that would have been clearly anticipatory (0–80 ms postmotion onset) in *experiment 1*. Also, the ocular tracking response in *experiment 1* showed no discontinuity that would characterize the presence of anticipatory pursuit together with a visually driven response, as both responses have different accelerations (Kao and Morrow 1994). The anticipatory component observed in *experiment 4* was actually clearly separated from the visual response (Fig. 2*D*). Furthermore, in *experiment 2* the ocular effect was not observed even though motion direction was held constant, ruling out anticipation of motion as a sufficient factor.

Neural Mechanisms

Electrophysiological evidence points to the implication of cortical motion processing (MST, V1) in driving ocular following, the dorsolateral pontine nucleus (DLPN) acting as a relay passing motion information to the cerebellum, where the motor command is elaborated (Kawano 1999; Masson and Perrinet 2012; Miles et al. 1986).

The maximal magnitude of the ocular tracking effect (color and motion selection) that we observed was 30% of the effect with a single dot layer. This number can represent the bias towards the attended layer resulting from enhancement of the attended surface and from suppression of the unattended surface. Feature-based attention modulation of neural responses in MT when motion is attended was found to be 13%, by comparing attention towards a same direction of motion outside the receptive field to the null direction response (Masson and Perrinet 2012; Treue and Martinez Trujillo 1999); 20% increment for blood oxygen level-dependent signal in hMT+ (Beauchamp et al. 1997). We also note that attentional modulation appears stronger from lower to higher level visual areas, in the order of 10% in V1 to about 30–40% in hMT+ when motion (or color) matched the direction at the attended location (Saenz et al. 2002). Modulation by spatial attention was stronger in MST than in MT (40 vs. 20%, respectively) (Treue and Maunsell 1996). Taking into account differences between paradigms and measures, our results are roughly compatible with how feature-based attention gates motion information in MT-MST.

Functional Role

Mestre and Masson (1997) have pointed out the significance of feature-based attention in singling out a depth plane for controlling the optokinetic nystagmus. In their study attention to a given flow field was sufficient to segregate signals for perception and for tracking. Our present contribution adds that under some conditions feature-based attention can help in segregating motion signals lying on the same depth plane for driving ocular tracking, but this has to be qualified by the weakness of the feature-based response compared with a single direction response. The question of why we are unable to selectively enhance a motion direction for driving ocular tracking without the help of another cue (color) requires further investigation, as it might reveal the involvement of attention in form and motion interactions whose major function could be segregating an object from its background (Grossberg 1998) and especially a dissociation between ocular and perceptual tasks. Finally, we would like to point out that the relatively weak effect of feature-based attention on smooth pursuit is matched by relatively weak effects on perception during saccadic eye movements (Born et al. 2012, 2013; Jonikaitis and Theeuwes, 2013). However, it remains to be proven that spatial attention has a larger effect than feature-based attention on ocular tracking responses.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: D.S. and D.K. conception and design of research; D.S. performed experiments; D.S. and D.K. analyzed data; D.S. and D.K. interpreted results of experiments; D.S. and D.K. prepared figures; D.S. and D.K. drafted manuscript; D.S. and D.K. edited and revised manuscript; D.S. and D.K. approved final version of manuscript.

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