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Ongoing eye movements constrain visual perception

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Eye movements markedly change the pattern of retinal stimulation. To maintain stable vision, the brain possesses a variety of mechanisms that compensate for the retinal consequences of eye movements. However, eye movements may also be important for resolving the ambiguities often posed by visual inputs, because motor commands contain additional spatial information that is necessarily absent from retinal signals. To test this possibility, we used a perceptually ambiguous stimulus composed of four line segments, consistent with a shape whose vertices were occluded. In a passive condition, subjects fixated a spot while the shape translated along a certain trajectory. In several active conditions, the spot, occluder and shape translated such that when subjects tracked the spot, they experienced the same retinal stimulus as during fixation. We found that eye movements significantly promoted perceptual coherence compared to fixation. These results indicate that eye movement information constrains the perceptual interpretation of visual inputs.

Due to the nonuniform sampling resolution of the human retina, high acuity vision requires eye movements to place the images of objects of interest in our environment on the fovea. There are two classes of voluntary eye movements: saccades, which rapidly foveate peripheral objects, and smooth pursuit, which maintains the images of moving objects close to the fovea. These two classes of eye movements occur so frequently that they have provided quite a conundrum for vision scientists: on the one hand, they serve vision by allocating the high-resolution fovea to objects of interest in the environment, and on the other, they cause major and frequent disruptions to the flow of visual information from the retina to the brain.

The question of how the brain achieves perceptual stability in the face of disruptive eye movements has been debated for a long time, and theories of varying complexity have been proposed to answer it. Some theories suggest that vision is 'paused' during eye movements. This view is supported by the visual suppression of image displacements during saccades[1] and by the phenomenon of change blindness in complex, natural scenes[2–4]. However, vision is not entirely suppressed during eye movements. In fact, only the magnocellular system is suppressed during saccades[5,6]—if at all[7]. More elaborate theories of perceptual stability involve mechanisms that require prediction of the sensory consequences of eye movements and subsequent compensation for these consequences[4,8–12]. All of these mechanisms involve active handling of the effects of eye movements by perception, which might be why eye movement–related activity appears in almost all stages of visual processing in the brain[10,13,14].

Conversely, visual perception can also drive eye movements[15]. For example, spots of light that undergo cycloidal motion, as if attached to the perimeter of an invisible rolling wheel, can elicit smooth pursuit of the center of the 'perceived' wheel[16], even though there is never an image of a wheel or its center on the retina. A recent study[17] using stimuli consisting of partially occluded, translating figures[18] demonstrated that eye movements are directly correlated with visual percepts. Subjects tracked such figures almost flawlessly when they perceived them as coherent objects, but not when they perceived them as incoherent.

Here, we tested for a new interaction between visual perception and eye movements: that eye movements provide information that can constrain visual perception. It is known that the efference copy of any eye movement command contains information that is important for maintaining perceptual stability[11,19,20]. Such information may also be important for resolving the otherwise ambiguous spatial relationships that exist between parts of objects, which are often fragmented because of occlusion by other objects. If efference copy information were used in this manner, then eye movements might be expected to influence the ways in which we segment and analyze visual scenes.

RESULTS

Using a perceptually ambiguous stimulus, we designed a set of experiments in which we kept the retinal input constant and varied the eye movement requirement. In our most basic manipulation, subjects viewed a chevron translating along a circular trajectory behind an occluder having two apertures (**Fig. 1a**). Under fixation, such a stimulus typically results in the perception of two unconnected groups of lines translating vertically[21]. We then introduced different eye movement conditions without changing this stimulus, by making use of the fact that, with the head fixed, retinal motion is determined by eye motion in the orbit as well as by object motion in space. That is, if $\dot{\mathbf{r}}(t)$ is the retinal velocity of the chevron, $\dot{\mathbf{e}}(t)$ is the velocity of the eye in the orbit and $\dot{\mathbf{o}}(t)$ is the world-centered velocity of the same chevron, then $\dot{\mathbf{r}}(t)$ is given by

$$\dot{\mathbf{r}}(t) = \dot{\mathbf{o}}(t) - \dot{\mathbf{e}}(t). \quad (1)$$

Different combinations of $\dot{\mathbf{o}}(t)$ and $\dot{\mathbf{e}}(t)$ can give rise to the same $\dot{\mathbf{r}}(t)$.

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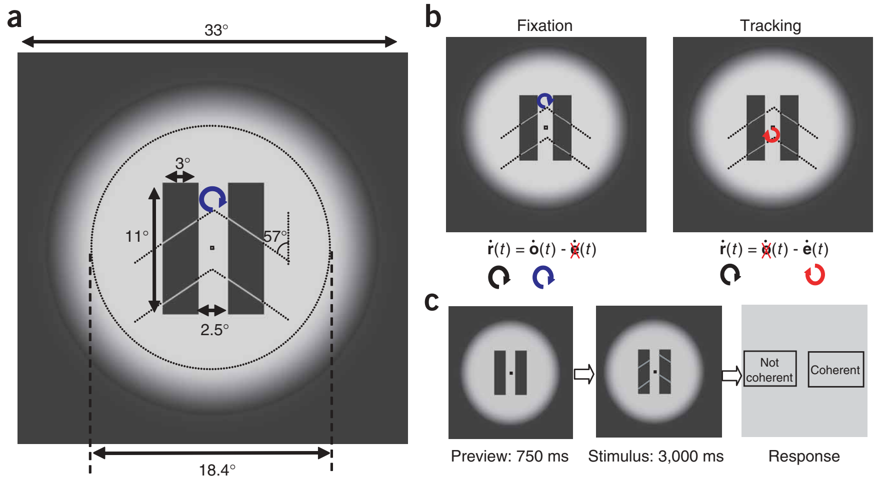

Figure 1 Stimulus and methods. (**a**) The stimulus consisted of a partially occluded outline chevron. The chevron translated behind an occluder along a circular trajectory around a central fixation spot. The vertices of the chevron were never revealed by the two vertical apertures in the occluder, and the occluder luminance decreased gradually toward the background luminance in the periphery. (**b**) Two eye movement conditions were initially tested. With maintained fixation, the motion of the chevron in retinal coordinates was accounted for by its motion in space, as in **a**. Similar retinal motion was accounted for by eye movements in tracking when the chevron was fixed in space and the fixation spot and occluder moved along a circular trajectory. $\dot{\mathbf{r}}(t)$ is retinal slip of the chevron, $\dot{\mathbf{e}}(t)$ is eye velocity, and $\dot{\mathbf{o}}(t)$ is chevron velocity in space. (**c**) Every trial of each experiment started with a preview period of 750 ms. During this period, the occluder and fixation spot appeared without the chevron, stationary in fixation trials and moving in tracking trials. By the end of this period, subjects were in steady-state fixation or pursuit, at which time they were presented with the chevron for 3,000 ms and then with a response screen until they responded. Depending on the particular experiment, the chevron and response screens differed slightly.

Two combinations of $\dot{\mathbf{o}}(t)$ and $\dot{\mathbf{e}}(t)$ were initially compared: one with $\dot{\mathbf{e}}(t)$ being zero and $\dot{\mathbf{o}}(t)$ being circular motion (fixation), and the other with $\dot{\mathbf{o}}(t)$ being zero and $\dot{\mathbf{e}}(t)$ being circular smooth pursuit (tracking). With the phase of $\dot{\mathbf{e}}(t)$ in tracking being 180° relative to that of $\dot{\mathbf{o}}(t)$ in fixation, the retinal motion of the chevron was the same in both conditions. Such motion was accounted for entirely by motion of the chevron in space in the fixation condition but by ongoing eye movements in the tracking condition (**Fig. 1b**).

We first show, using both subjective and objective methods, that perceptual coherence was markedly improved during tracking compared to fixation. We then clarify the likely mechanisms underlying this phenomenon, by reporting how it was affected by variations in object shape, by moving versus stationary objects, and by changes in the salience of the line terminators in the apertures. The results from this series of experiments, all run with naïve subjects, support the conclusion that eye movements provide an important constraint for perceptual integration.

Perceptual coherence during tracking versus fixation

We made our basic observation on the influence of eye movements on perceptual coherence by using equation (1) above (**Fig. 1b,c**). In this experiment, and all others, we maximized the similarity of retinal events across the different eye movement conditions by including a preview period of 750 ms during which subjects achieved steady-state pursuit or fixation before the object appeared (**Fig. 1c**). Also, during tracking, the occluder translated with a trajectory identical to that of the spot that subjects pursued; it was therefore stationary in retinal coordinates just as during fixation.

We assessed whether the retinal inputs were indeed similar in fixation and tracking by analyzing subjects' eye movements during this task and all others in this paper. Specifically, we used eye velocity measurements to compare the retinal slip (equation (1)) of the chevron (diamond in later experiments) during fixation to that during tracking for the entire duration that the chevron was visible in a trial (illustrated in **Fig. 2a** for one of our subjects). To evaluate whether the eye movement condition significantly affected the retinal slip of the chevron, we determined the *P*-value of the eye movement factor in a two-way analysis of variance (ANOVA; factors: trial type and time) of our measured retinal slips. There was no significant difference in retinal slips between fixation and tracking for our subjects (average *P*-values for horizontal and vertical slips across subjects in the experiments shown in **Figs. 1–5**: 0.56 ± 0.29 s.d., and 0.39 ± 0.31 s.d.). We also

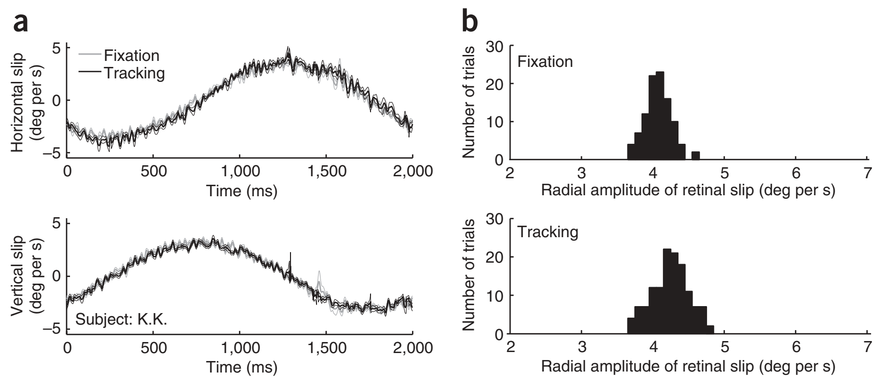

Figure 2 Comparison of retinal slips across eye movement conditions that we performed in this study. (**a**) Because our tasks involved motion integration, we compared the retinal motion or slip (equation (1)) of the perceived shape under fixation to that under the various eye movement conditions we tested—with the particular example shown being that of tracking as in **Figure 1b**. The retinal motion of the shape was circular and similar for both conditions even though one condition involved fixation with a moving shape and the other involved pursuit with a stationary shape. Thick lines show mean traces, thin lines show s.e.m. Data from one session are shown as one cycle of eye and shape oscillation according to the procedure described in Methods. (**b**) Trial-to-trial variability of retinal motion of the shape in fixation and tracking was assessed by obtaining an average radial amplitude of this motion for each trial that was accepted. The distributions of such amplitudes are shown for the same subject and session as in **a**. Tracking involved slightly greater variability in retinal slip. However, most trials fell within the range of variability observed in fixation. This held for all subjects and experiments.

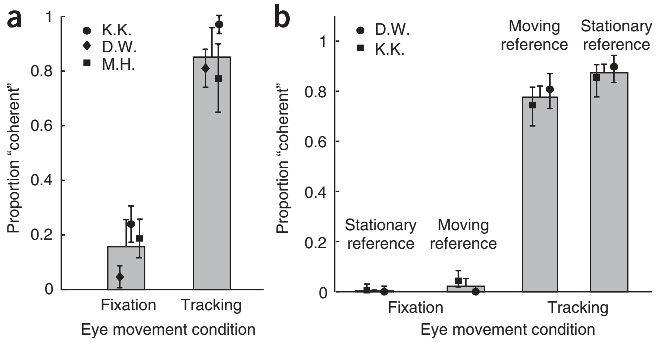

Figure 3 Despite similar retinal stimulation, tracking promoted perceptual coherence over fixation. (**a**) With maintained fixation, subjects experienced substantial difficulty in perceiving the chevron[21]. However, with the same retinal stimulus during tracking, subjects reported perceiving a coherent chevron for most trials. (**b**) Fixation and tracking, again with similar retinal stimulation, were compared with the addition of an explicit reference outline square around the apertures. The square either moved with the occluder or with the chevron in all conditions—that is, it either moved or was stationary in space (as labeled in the figure). The eye movement conditions were a much stronger factor in influencing perceptual coherence—as measured by the proportion of trials resulting in coherent responses—than the square movement patterns, ruling out external reference cues as the determinants of the results in **a**. Data from individual subjects are shown with individual symbols and their own 95% confidence intervals. Bars showing the means and s.d. of the individual subject means are also shown for easy visualization.

computed the mean radial amplitude of the retinal slip for each trial in a session and grouped trials according to eye movement condition (**Fig. 2b**). Tracking often involved slightly greater trial-to-trial variability in retinal slip than fixation. However, there was a great deal of overlap between the distributions (**Fig. 2b**) (average percentage of tracking trials falling within the range of variability of fixation trials across subjects in the experiments of **Figs. 1–5**: 89% ± 8% s.d.), again suggesting that the retinal motion of the chevron was similar across eye movement conditions. As for systematic position errors, the periodic nature of our stimuli meant that subjects were able to track the motion of the occluder with minimal phase lag (average across subjects in the experiments of **Figs. 1–5**: 40 ms ± 29 ms s.d.).

We then compared subjective reports of perceptual coherence between fixation and tracking and found that, despite the similar retinal inputs, subjects saw a coherent chevron more frequently during tracking than during fixation (**Fig. 3a**). In fact, subjects had difficulty seeing a chevron during fixation, consistent with earlier results[21].

One explanation for these results is that external reference cues in our subjects' environment may have allowed them to infer the chevron's stability during tracking, and therefore its high coherence. Even though we performed our experiments in the dark and designed the occluder to avoid the occurrence of a visible display frame (Methods), it is conceivable that subjects could see trace outlines of stable objects in their environment. To investigate this issue, we added a black outline square around the apertures; this square either moved or was stationary. Specifically, we had two pairs of fixation and tracking conditions that each had similar retinal stimulation across eye movement conditions and that introduced an external reference frame for either the chevron or the occluder. We found that eye, rather than square, movements were the main modulator of coherence (**Fig. 3b**), ruling out external references as a confound in our original experiment (**Fig. 3a**).

We also validated the results of the subjective report with a more objective measure of changes in stimulus appearance. Guided by evidence that perceptual coherence facilitates the processing of spatially disparate features[22], we added oscillating sinewave gratings to the visible chevron edges (**Fig. 4a**) and predicted that perceptual coherence should improve our subjects' ability to discriminate the spatial phase of the oscillating gratings. We asked subjects to compare the oscillation phase of the gratings in the right aperture to that of the gratings in the left aperture, and to report whether the phases were identical or different. We again compared performance in fixation and tracking, but now by tallying the percentage of trials in which subjects correctly discriminated the gratings' phase. All subjects showed better performance during tracking than during fixation (**Fig. 4b**), confirming our earlier findings and demonstrating that the increased perceptual coherence observed during tracking was not simply the result of a change in response bias relative to fixation.

Effects of object shape and added noise

Because form provides an important constraint to perceptual integration[21], we investigated whether the effects observed above were specific to the chevron, by using a diamond instead. However, as coherence of the diamond is almost perfect during fixation[21], we needed to reduce it enough to allow seeing an improvement with tracking. One way to do this is to introduce varying amounts of noise to the motions of the visible diamond segments (**Fig. 5a**). In each trial, we added a 'noise' sinusoid of pseudorandom phase and variable amplitude to the vertical position of each diamond segment independently.

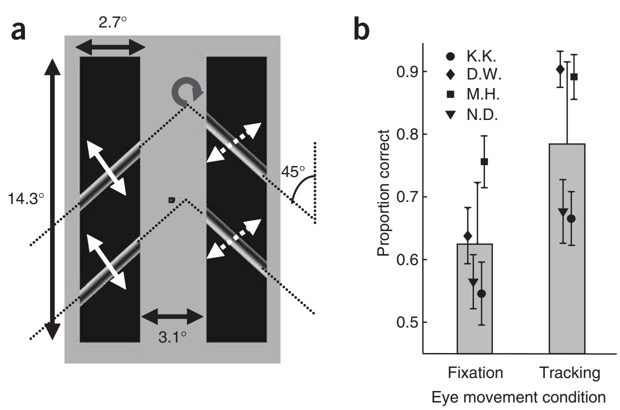

Figure 4 Variant of our stimulus used to obtain an objective measure of perceptual coherence, and results using this measure. (**a**) Expanded view of the central portion of the stimulus highlighting the apertures and sinusoidal gratings on the chevron edges. The remainder of the stimulus (the occluder at larger eccentricities) was identical to that in **Figure 1**. The gratings had a spatial phase that oscillated sinusoidally with a frequency of 1 Hz and an amplitude of π radians. In some trials, the oscillations in the right aperture were in phase with those in the left; in others they were out of phase. At the end of a trial (**Fig. 1c**), subjects made a same/different judgment on the oscillation phase across the apertures as opposed to a subjective coherent/incoherent judgment on the chevron. (**b**) Phase discrimination performance improved with tracking over fixation for all of our subjects. Data from individual subjects are shown with individual symbols and their own 95% confidence intervals. Bars showing the means and s.d. of the individual subject means are also shown for easy visualization.

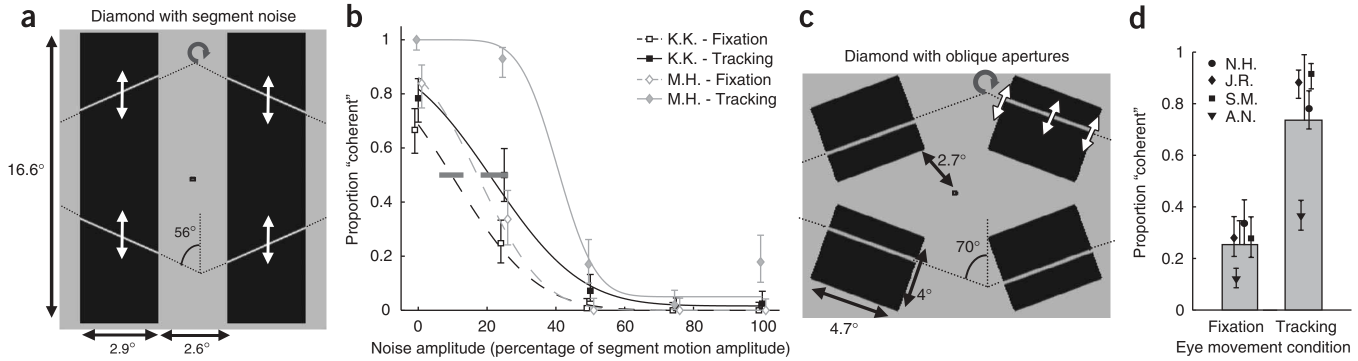

Figure 5 Our effects did not depend on shape. (**a**) We again compared fixation to tracking (**Fig. 1**), but with a diamond. Each diamond segment received an added 'noise' sinusoid to its vertical position (random phase, 1 Hz frequency, and variable amplitude—shown in **b** as percentage of true vertical amplitude of segment motion). The occluder at larger eccentricities was identical to that in **Figure 1**. (**b**) Data and fitted cumulative Gaussian psychometric curves[47,48] for two subjects who viewed **a**. Error bars show 95% confidence intervals. Gray horizontal bars show 95% confidence intervals for the 50% threshold points in fixation and tracking (not shown for subject M.H. to reduce clutter). Both subjects had higher psychometric curves of coherence during tracking than during fixation. (**c**) We repeated the experiment of **Figure 1** identically but with the diamond. Apertures were such that the line terminators (at the junctions with the apertures) moved identically to the orthogonal components of the lines' motions (white arrows). (**d**) We observed higher perceptual coherence during tracking than during fixation for the stimulus in **c**. Data from individual subjects are shown with individual symbols and their own 95% confidence intervals. Bars showing the means and s.d. of the individual subject means are also shown for easy visualization. All remaining experiments used the same set of subjects.

We then measured subjective experience of coherence as a function of noise amplitude.

For both subjects tested, the fixation psychometric curves obtained had high levels of coherence that dropped rapidly with noise. During tracking, however, perceptual coherence was less sensitive to the noise (**Fig. 5b**). For each of the subjects, the psychometric curve for tracking was higher than that for fixation ($P < 0.05$), supporting the conclusion that improvements in coherence associated with tracking are not specific to the chevron.

Another way to reduce the coherence of the diamond is to change the scene context. Specifically, oblique apertures—for which the line terminators of the visible diamond segments move identically to the orthogonal components of these segments' motions (**Fig. 5c**)—result in an incoherent percept of the diamond[23,24]. We observed this in our data (**Fig. 5d**, fixation). However, when the same diamond was viewed through the same apertures during tracking, its coherence increased. This particular stimulus is interesting because it eliminates retinal line-terminator motion as a possible source of information for perceptual integration; we therefore used it to further investigate the influences of eye movements on the ambiguous orthogonal motion signals seen through the apertures.

Effects with moving objects

Because our chevron/diamond was stationary during tracking but not during fixation in the above experiments, our results so far can be attributed to a stable-world assumption by the visual system in interpreting visual inputs during self-motion[25]. To address this issue, we compared our fixation condition to two tracking conditions in which the eye moved sinusoidally along a horizontal or vertical direction. To produce the same retinal motion for these two conditions as during fixation, we also sinusoidally translated the object along the complementary axis. In addition to avoiding a stable object, this arrangement allowed us to compare perceptual reports when the eye translated either in a direction of retinal ambiguity[18,26–28] of edge motions or in another direction. Initial 'pilot' data using subjective reports indicated that there was a benefit for tracking in a direction of retinal ambiguity (**Supplementary Note** and **Supplementary Figs. 1–4** online), so we investigated this possibility fully here and with the same set of subjects as used for our latest diamond experiments (illustrated in **Fig. 5d** and **Supplementary Fig. 4**).

Our approach was to require subjects to make a direction judgment on the world-centered motion of a diamond, which was either fully visible (unambiguous control) or partially occluded (**Fig. 6a**), while they maintained fixation, tracked horizontally or tracked vertically. There were two reasons for choosing direction judgments. First, as we now had a moving object in all conditions, it was possible to ask about its motion and therefore more explicitly investigate how eye movements influence motion integration. Second, it is established that incoherent percepts bias direction judgments away from the true solutions toward those that represent the vector-average solutions of the orthogonal components of all visible motions[29–32]. Therefore, for directions of motion for which the two solutions are sufficiently different, direction judgment constitutes a suitable objective measure of perceptual coherence.

We had eight retinal axes of motion along which the diamond could move (**Fig. 6b**). In fixation, these axes were identical to the true motion axes for the diamond; during tracking, they were achieved by having the fixation spot and occluder move horizontally or vertically with a constant-amplitude sinusoidal motion while the diamond moved along an axis determined by equation (1). For example, a retinal axis of $+45°$ was achieved in horizontal tracking by having the diamond move along an axis of $+90°$. This example raises a potential problem: to achieve similar retinal stimulation across conditions, fixation involved directions that were predominantly oblique whereas tracking involved ones that were predominantly cardinal. Thus, benefits observed during tracking could be due to an oblique effect during fixation[33–36]. To address this concern, we included a second fixation condition in which the entire stimulus was rotated by 45° (**Fig. 6c**). Motion axes were now centered on the cardinal directions. Even though this condition does not match retinal stimulation to that in the remaining three, it does test whether any differences in results between fixation and tracking are due to the differences in the axes of motion.

We again analyzed eye movements to verify that retinal stimulation was closely matched between fixation and tracking. Specifically, we

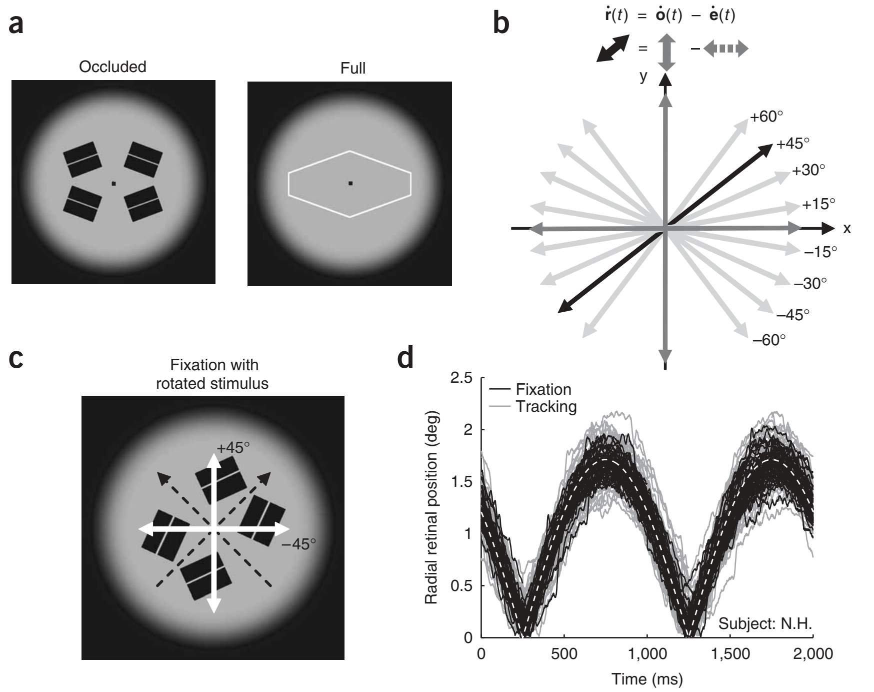

Figure 6 Investigating how eye movements influence coherence with moving objects. (**a**) We used the diamond of **Figure 5c** and included it in full or occluded form. Trial sequence was identical to that shown in **Figure 1c** (Methods). (**b**) The diamond moved along one of eight retinal axes (shown in light gray with numbers indicating angle). In fixation, true diamond motion was identical to one of these axes. In horizontal or vertical tracking, equation (1) was used to deduce proper diamond motion. For example, a retinal axis of +45° (black axis) was achieved during horizontal tracking (dashed gray axis) with the diamond moving along an axis of +90° (solid gray axis). (**c**) We also included a condition in which the stimulus and all possible axes were rotated by 45°. This allowed having fixation with motion axes around cardinal directions. For example, +45° and −45° from **b** now involved horizontal and vertical object motion (white axes). We also had a full shape that was also rotated. (**d**) Example of how well retinal stimulation in **a** and **b** was matched between fixation and tracking. Radial retinal positions of the diamond are shown for individual fixation and horizontal tracking trials from a sample session (one composite period shown). The range of amplitudes of the curves largely overlapped. All angles for the retinal diamond motion as well as both occlusion conditions were combined. White dashed line shows the ideal radial retinal position of the diamond.

computed the radial retinal position of the diamond experienced by our subjects in individual fixation and tracking trials, and found that most of the trials overlapped (illustrated in **Fig. 6d** for one of our subjects). We assessed this further by fitting rectified sinusoids to individual-trial radial retinal position curves. We then performed *t*-tests on the amplitudes of these sinusoids in fixation and tracking (average *P*-values across subjects in the experiments of **Figs. 6–8**: 0.32 ± 0.15 s.d.). We also measured the percentage of tracking trials that fell within the range of variability of fixation trials and found it to be large (average across subjects in the experiments of **Figs. 6–8**: 89% ± 5% s.d.). Finally, we established that there were minimal systematic position errors by measuring phase lags during tracking (average across subjects in the experiments of **Figs. 6–8**: 4 ms ± 15 ms s.d.). One subject (J.R.) occasionally had sessions in which she exhibited a difference in average retinal positions between tracking and fixation ($P < 0.05$). Even though this did not happen for every session, it prompted us to repeat all behavioral analyses from this and the next experiments for all subjects but keeping only tracking trials that fell within the range of trial-to-trial variability of the retinal position of the object in fixation. Our results (data not shown) did not change, meaning that the effects we describe below cannot be explained by the extremes in the distributions of retinal stimulation parameters between fixation and tracking.

We studied each subject's behavior by measuring the error in the direction-of-motion judgment made across conditions (**Fig. 7a**). The main effects of eye movement condition and occlusion condition were highly significant for all subjects ($P < 0.01$, two-way ANOVA). Pairwise comparisons using Tukey's HSD test revealed that in fixation, errors were always higher for the occluded shape than for the full one ($P < 0.05$). This is consistent with an incoherent percept associated with the occluded shape (refs. 23,24,29–32, **Fig. 5d** and **Supplementary Fig. 4**). This was also true for vertical tracking. For horizontal tracking, however, there were remarkably no differences between the full and occluded shapes ($P > 0.05$), suggesting that any misjudgments of direction associated with misperception of the diamond disappeared in this condition. This result cannot be attributed to having the axes of motion closer to a cardinal direction in horizontal tracking, because vertical tracking also involved the object moving close to one. Furthermore, the fixation deficit was itself not due to the oblique effect[33–36], because it persisted for fixation with the rotated stimulus.

These results validate the results of the subjective report obtained with a similar task and using the same subjects (**Supplementary Note** and **Supplementary Figs. 3** and **4**). Moreover, they suggest that with horizontal tracking, motion signals across the apertures were integrated well enough to match the performance supported by the full, unambiguous shape. Because of the shallow segment slopes for our diamond, horizontal movements were in the direction of the most ambiguous component of the true segment motions, implying that eye movements promoted perceptual coherence in our experiments by constraining the ambiguous retinal motion signals.

If the above interpretation is correct, then using a diamond with steep lines should result in vertical tracking being the condition for which direction judgment errors disappear relative to the full shape, because for such a diamond, the most ambiguous component of true retinal motion would be vertical. This is exactly what we observed when we transposed our stimuli (**Fig. 6**) by 90° (**Fig. 7b**). We again obtained significant main effects of eye movement condition and occlusion condition for each subject ($P < 0.01$). Moreover, pairwise comparisons revealed direction judgment deficits in fixation ($P < 0.05$), fixation with rotated stimulus ($P < 0.05$, except subject S.M.), and horizontal tracking ($P < 0.05$). For vertical tracking, direction judgment deficits disappeared, affirming the interpretation that eye movements promote perceptual coherence by constraining the interpretation of ambiguous retinal motion signals.

Testing the role of line terminators

Our results so far suggest that ongoing eye movements improve perceptual coherence relative to fixation. Such improvement seems to

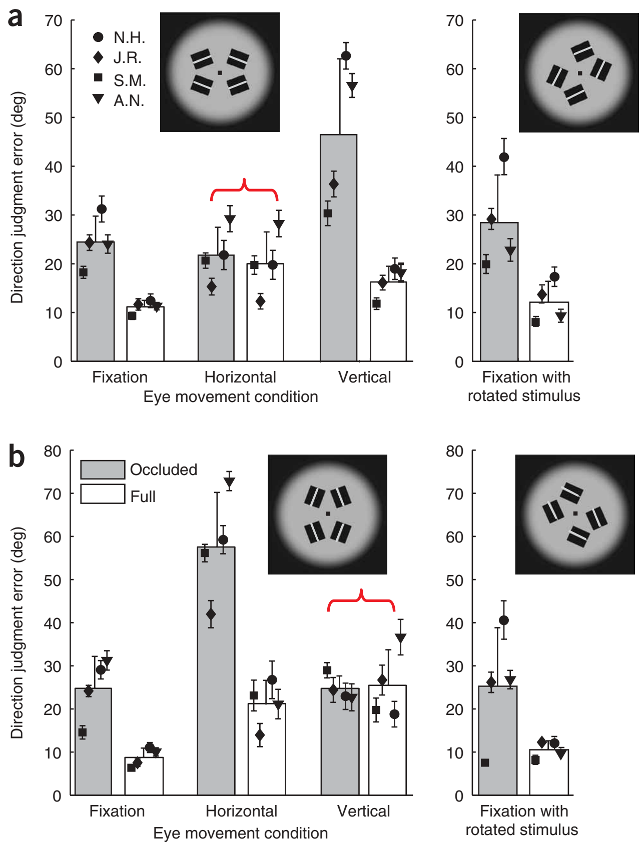

Figure 7 Direction judgment, a measure of perceptual coherence, was highly dependent on eye movement direction. (**a**) Each data point shows the mean and s.e.m. for the direction judgment error exhibited by a subject in the different conditions of **Figure 6**. For each eye movement condition (fixation, horizontal tracking, vertical tracking, and fixation with rotated stimulus), the left data point is for the occluded shape and the right data point is for the full, unambiguous shape. For all conditions except horizontal tracking, subjects were significantly worse in judging the direction of the axis of motion of the occluded diamond than that of the full, unambiguous diamond ($P < 0.05$). (**b**) When we transposed our stimuli by 90°, effectively having a diamond with steep edges rather than shallow ones (see insets), the same observations were made except that horizontal and vertical tracking now swapped roles. Bars show the means and s.d. of the individual subject means for easy visualization. Gray bars correspond to the occluded condition, and white ones to the full condition.

be relatively immune to noise, robust to variations in object shape, and highly dependent on the relative direction between the eye movement and the ambiguous retinal motion. However, the fact that the occluder moved during tracking suggests another possible explanation. Specifically, subjects may have deduced motion cues that were related to the occluder rather than to the actual perceived shape. Even though the occluder was stationary in retinal coordinates, it did move in space during tracking. This means that the line terminators at the junctions between the visible object segments and the apertures had unambiguous world-centered motion signals that could have promoted the sensation of coherence.

To investigate this possibility, we repeated our direction judgment experiment (**Fig. 6a,b**) on the same subjects but using invisible occluders for the occluded shape condition (inset in **Fig. 8**). Without occlusion cues, the visual system is forced to rely much more heavily on the endpoints of the visible line segments[18,27]. If the primary reason for our earlier results was the use of unambiguous world-centered motion signals associated with the motion of the occluder, then this experiment should have produced results similar to those seen previously (**Fig. 7a**). In contrast, we found that, for all subjects and all eye movement conditions, performance with the occluded shape was worse regardless of tracking direction (**Fig. 8**; $P < 0.05$ for all pairwise comparisons between occluded and unoccluded shapes per eye movement condition, using Tukey's HSD test). Therefore, the eye movement effects we observed earlier were not an artifact of the unambiguous world-centered motions of the visible diamond segment terminators at the junctions with the apertures. Instead, these effects occurred because integration was facilitated through the presence of occlusion cues. Moreover, when this facilitation did occur, it occurred through the use of eye movement direction as an informative constraint—giving rise to differential benefits across tracking directions.

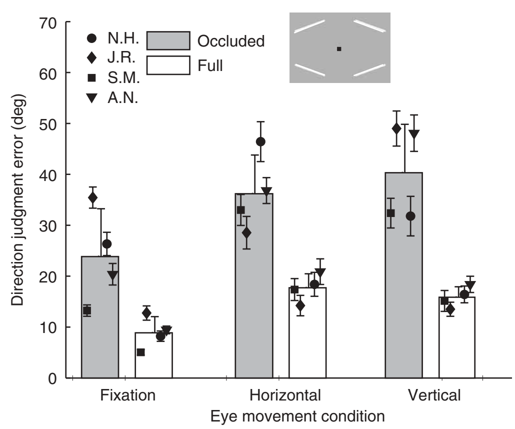

Figure 8 Our effects in **Figure 7** could not be explained by the mere presence of world-centered and/or retinal motion. When we removed occlusion cues from the occluded conditions of **Figure 6a,b** by having the apertures reveal a background of the same luminance as the occluder (see inset), we did not see a differential benefit to horizontal tracking as we saw in **Figure 7a**, even though the world-centered and retinal motions experienced (by the same set of subjects) were identical. Subjects were always worse in the occluded condition than in the full condition ($P < 0.05$), suggesting strong misperceptions in all conditions.

DISCUSSION

Perception involves a process of integration of information from a set of local features into global constructs, such as figure versus ground or object versus occluder. In this paper, we investigated the hypothesis that information about an ongoing eye movement contributes to such integration. We started out with an ambiguous stimulus under passive fixation and showed, using both subjective and objective methods, that this stimulus becomes perceptually coherent in the presence of ongoing smooth pursuit. This result held even when eye movements did not fully account for the entire retinal motion of the object, in which case eye movement information was most effective when it involved a direction that would resolve the inherent ambiguity in the retinal image. In all experiments, subjects experienced similar retinal stimulation across eye movement conditions. These results argue that information about ongoing eye movements is used to constrain the perceptual interpretation of retinal inputs.

The task of segmenting and analyzing retinal images is rendered particularly challenging by two facts: images of single objects are fragmented into disparate features because of occlusion, and images on the retina undergo dramatic changes because of eye movements. While not precluding the existence of other mechanisms for handling these two sources of complexity, our results suggest that the same type of process that compensates for the disruption of vision by eye movements may help resolve the ambiguities presented by retinal images. This process involves the use of corollary discharge information about ongoing eye movements and gives rise to dynamic remapping of spatially organized sensory and motor maps[10–12], thus allowing us to correctly perceive the world as spatially stable[10–14,19,20]. Our results suggest that another function of corollary discharge information is to provide a reference frame that, when coupled with retinal images, can help disambiguate the relationships that exist among disparate retinal features.

Consistent with the classic role of corollary discharge information, some of our results may be explained by the use of a stable-world assumption during self-motion[25]. Specifically, eye movement information may have been used to construct an allocentric coordinate system for the scene. In such a system, stationary objects are perceived more effectively than moving ones[25], which can explain our basic chevron and diamond results (**Figs. 3–5**). However, other parts of our results cannot be explained by assuming a stable world. In particular, we found increased perceptual coherence during tracking over fixation even with moving objects (**Fig. 7**, **Supplementary Note** and **Supplementary Figs. 2** and **4**), indicating that stationarity or stability in the world *per se* was not the primary determinant of our results.

We also found that the increased coherence we observed with moving objects (**Fig. 7** and **Supplementary Figs. 2** and **4**) was not because the world-centered motions of stimuli were different in fixation and tracking (despite their retinal similarity) (**Fig. 8**). Instead, our results (**Figs. 7,8**) suggest that eye movement direction provides a constraint on the ambiguous components of visible motions and that the effects of this constraint emerge when contextual cues induce perceptual integration. These results argue that in addition to its classic role of ensuring the perception of a stable world across eye movements[10–14,19,20,37–40], corollary discharge information also helps guarantee the perceptual stability (that is, coherence) of visual objects, even when these objects are moving, rather than stationary, in the world.

One seeming caveat to this interpretation is that we found relatively large direction judgment errors for the full, unambiguous shape during tracking (**Fig. 7a,b**)—these tended to be bigger than the fixation errors (but were similar to previous reports[41,42]). Such direction misjudgments are often taken as evidence for an imperfect corollary discharge signal[41,42] and a reason to dismiss eye movements as disrupting perception rather than aiding it[41–43]. However, note that for perception in general, and perceptual integration of occluded shapes in particular, the mere presence of a corollary discharge signal may be much more important than its quality. When faced with four visible lines having ambiguous retinal motion, a single, albeit imperfect, eye movement vector that applies equally well to all four lines may be just enough of a constraint to allow them to be properly grouped and represented as parts of one rigid object. In fact, this may be why the full shapes in our experiments (and indeed shapes in everyday life) never get distorted during tracking (casual observation). As for direction judgments, these happen following perceptual integration[29–32] and clearly depend on the quality of the corollary discharge signals provided by the motor system. For both the full and occluded shapes, this signal is the same, explaining the similar direction judgment errors observed between the two conditions when the occluded shape became perceptually coherent (**Fig. 7**). Thus, whereas ongoing eye movements are known to influence, among other things, direction judgments[41,42], what we seem to have identified here is an earlier, and positive, effect on perceptual integration, without which such judgments would not be possible in the first place.

METHODS

General. Depending on the experiment, 1–4 sessions were required. Subjects, all naïve, were well-practiced in pursuit. Subjects gave informed consent, and all procedures were approved by our institutional review board.

Subjects sat in a dark room 41 cm from a computer monitor displaying stimuli at a 75-Hz frame rate. Head movements were minimized by using a bite bar, and eye movements were sampled at 240 Hz using a video-based eye tracker (Iscan). Experimental control and data acquisition were performed by the Tempo software package (Reflective Computing), and stimuli were generated using Matlab's (MathWorks) Psychophysics Toolbox[44,45].

Stimuli and tasks. Subjects viewed a chevron translating behind an occluder along a circular trajectory at a 0.5-Hz rate. The occluder had two apertures on either side of a central spot (**Fig. 1a**). The chevron's trajectory radius was 1.1°, and aperture width and height were 3° and 11°, respectively. The apertures were centered around ±2.75° from the central spot horizontally and 0° from it vertically. The occluder was bright (65.6 cd m^{-2}), and the chevron (86 cd m^{-2}) translated over a black background. At eccentricities larger than 9.2° from the spot, the luminance of the occluder decreased smoothly with a profile of a normal cumulative distribution function having a s.d. of 1.16°. Occluder luminance reached the black background luminance at 15.8° eccentricity.

The stimulus shown in **Figure 1a** constituted our fixation condition. We compared this to a tracking condition in which the occluder and fixation spot translated together along a circle and the chevron was stationary, such that when subjects tracked the spot, equation (1) resulted in similar $\dot{\mathbf{r}}(t)$ to fixation (**Fig. 1b**). Directions of motion for the chevron and central spot (with occluder) were chosen to give clockwise/counterclockwise retinal translation of the chevron. These motions started at one of eight phases. Fixation and tracking were randomly interleaved.

Trials started with a preview of the occluder for 750 ms (**Fig. 1c**). Then, a full stimulus containing the chevron and occluder appeared for 3,000 ms, after which subjects reported on the coherence of the chevron by button press—coherent meaning that they saw a chevron, and incoherent meaning they saw unconnected, moving lines. In tracking, the fixation spot and occluder translated together during both the stimulus and preview periods. Subjects were told to maintain gaze on the spot and that they were viewing a chevron translating along a circle behind an occluder with two apertures. Subjects performed one session of this experiment.

We also repeated this experiment but adding a black square (17.1° wide × 17.1° high, each side 0.06° thick) that surrounded the apertures. We compared two fixation and two tracking conditions. In each condition, the square either moved or was stationary in space, with motion identical to either eye or chevron. Subjects performed two sessions of this experiment.

To objectively measure coherence, we used the stimulus shown in **Figure 4a**. The chevron edges were 0.83° thick and consisted of sinusoidal gratings having a spatial frequency of 1.21 cycles per deg and a contrast of 80%. The gratings had a spatial phase that oscillated sinusoidally as a function of time with an amplitude of π radians and a frequency of 1 Hz independently from the motion of the eye or chevron. The gratings in the right aperture oscillated in phase with those in the left aperture or with a phase offset of 0.4π radians. At trial end, subjects indicated whether the gratings in the right and left apertures were in phase or not. Subjects performed three sessions of this experiment.

For **Figure 5a**, each segment of the diamond had vertical aperture motion that was the superposition of true retinal motion expected from circular translation (0.5 Hz) behind the occluder, and a 'noise' sinusoid with 1 Hz frequency and variable amplitude (five levels between 0% and 100% of the vertical amplitude of the true aperture motion). 'Noise' phase was chosen pseudorandomly for each individual segment independently (25 possible random phase combinations for the four segments). No two phases could be within 36° of each other. Other details were as in **Figure 1**. Subjects performed four sessions of this experiment. As for **Figure 5c**, the experiment was identical to that illustrated in **Figure 1**. However, the diamond's trajectory radius was 1.71°. Subjects performed one session of this experiment.

We then compared a fixation condition to two tracking conditions: one involving sinusoidal pursuit (of the fixation spot and occluder) in a horizontal direction and one in a vertical direction (1.21° amplitude; 0.5 Hz frequency; random starting phase from eight equally spaced values). The diamond, either occluded or full (**Fig. 6a**), also translated sinusoidally subject to the constraint that equation (1) yielded an $\dot{\mathbf{r}}(t)$ similar to that obtained in the fixation condition. There were eight possible $\dot{\mathbf{r}}(t)$ vectors for each eye movement condition (**Fig. 6b**). These were all sinusoids with 0.5 Hz frequency and 1.71° radial amplitude, and they were chosen such that the vector-average solution to the retinal segment motions was sufficiently different from the true diamond motion[17,29–32]. We also added another fixation condition for which the stimulus (occluded or not) and all motion axes were rotated by 45° (**Fig. 6c**).

Trial sequence was identical to that shown in **Figure 1c**. However, at trial end, subjects reported the perceived world-centered axis of motion of the diamond. They saw a thin line (10° long) centered on the display. Pressing one button rotated this line clockwise; pressing another rotated it counterclockwise. When satisfied with the orientation of the line, subjects pressed a third button indicating that this was their perceived axis of motion. Subjects performed three sessions of this experiment.

We also repeated this experiment after transposing all stimuli by 90° clockwise (**Fig. 7b**). We repeated it again for **Figure 8** except that there was no fixation condition with rotated stimulus and, for the occluded condition, the apertures now revealed a background of the exact same luminance as the occluder (inset of **Fig. 8**). Subjects performed two sessions of this experiment.

Data analysis. We analyzed subjects' eye movements in order to establish that retinal stimulation was similar in tracking and fixation for a given session. We computed eye velocity traces by differentiating eye position signals with a 19-point FIR filter (cut-off frequency, 54 Hz). We then inspected eye position and velocity and eliminated trials in which subjects did not align their gaze with the fixation spot by 750 ms, did not properly track the spot for the entire duration of the stimulus after the 750 ms preview (whether in fixation or tracking), or blinked. This resulted in the elimination of 10–30% of the trials, depending on the subject. We then computed the retinal slip of the object for every trial (equation (1)).

The slip calculation was made for the entire 3,000-ms period in which the object was visible. We then aligned our data in phase and duration onto one composite period of oscillation (2,000 ms) by wrapping around traces in an appropriate fashion, and we down-sampled our traces to 83 Hz before running ANOVAs (factors: eye movement condition and time). Comparison of slips across conditions in this manner took into account variability of tracking due to catch-up saccades and small tracking errors as well as variability of fixation due to microsaccades and drifts[46]. We also computed the average radial amplitude of retinal slip in each trial and compared all such amplitudes in fixation to those in tracking. This allowed us to assess trial-to-trial variability of slip across conditions. Finally, we estimated systematic position errors in tracking by measuring pursuit lags. This was done by fitting sinusoids to eye position traces using a least-squares algorithm and measuring the phase of these sinusoids relative to the tracked spot.

For the experiments of **Figures 6–8**, we also fit a rectified sinusoid of appropriate frequency to the realigned radial retinal position curve for each trial. The amplitude distributions obtained were compared (fixation versus horizontal or vertical tracking) using *t*-tests. Because subjects only tracked along cardinal directions, angular deviations from the eight $\dot{\mathbf{r}}(t)$ axes were minimal[34]. So, all angles of motion were combined in this analysis (as well as both occlusion conditions). We did not analyze eye movements in fixation with the rotated stimulus (**Fig. 6c**), except for manual inspection to verify that subjects maintained fixation.

We measured either the proportions of trials in which subjects reported coherent/correct responses (**Figs. 1–5**) or the absolute values of the errors in the subjects' direction judgments (**Figs. 6–8**). Data was shown for individual subjects, always in the form of measured proportions and associated 95% confidence intervals, or measured mean direction judgment errors and s.e.m. We also showed average population data. For the data in **Figure 5b**, we fit cumulative Gaussian psychometric curves to the data of each eye movement condition and estimated 95% confidence intervals for the 50% threshold point using a bootstrapping algorithm[47,48]. For the data in **Figure 7**, we performed ANOVAs with eye movement condition (fixation, horizontal tracking, vertical tracking, and fixation with rotated stimulus) and occlusion condition (full and occluded) as the factors. This was also done for the data in **Figure 8**, except that there was no fixation with rotated stimulus condition. For individual subject data, each shown data point was based on at least 100 trials (**Figs. 1–4**), 80 trials (**Fig. 5**), or 40 trials (**Figs. 6–8**).

Note: Supplementary information is available on the Nature Neuroscience website.

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COMPETING INTERESTS STATEMENT
The authors declare that they have no competing financial interests.

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