



Attention-Based Motion Perception

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folding of the nucleation cluster, formation of the helix 4 would induce a "hydrophobic collapse" (24) in the subdomain on the right of Fig. 4, resulting in a more extensive hydrophobic core around the nucleation cluster (Fig. 3). In further steps, hydrophobic contacts with the first subdomain mediated by the apolar side chains of Leu⁴⁸, Leu⁵², and Leu⁵⁹ would lead to further growth of the hydrophobic core and proper spatial positioning of the two subdomains (Fig. 4). Although this selection of distinct folding events derived from combined inspection of the structures of folded and urea-unfolded 434-repressor(1-63) is largely hypothetical, it may provide a platform for additional experiments to investigate spatial and temporal patterns of the order in which distinct, individual folding events take place.

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21. In this context, one should also recall that only a short lifetime of ~1 ns is needed for a protein conformation to give rise to negative NOEs [G. Otting, E. Liepinish, K. Wüthrich, *Science* **254**, 974 (1991)], as observed in the urea-unfolded 434-repressor(1-63) and 434-repressor(44-64). In contrast, chemical shift averaging is typically observed between different conformers even when they have a life time of the order of 1 ms.
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25. Abbreviations for the amino acid residues are: A, Ala; C, Cys; D, Asp; E, Glu; F, Phe; G, Gly; H, His; I, Ile; K, Lys; L, Leu; M, Met; N, Asn; P, Pro; Q, Gln; R, Arg; S, Ser; T, Thr; V, Val; W, Trp; and Y, Tyr.
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Two "attentive" tracking tasks reveal the existence of an attention-based motion process. In the first task, oppositely rotating luminance and color gratings were superimposed. Because of masking from the color grating, the bars of the luminance grating were not visible; nevertheless, their motion was visible and it determined the perceived direction of the stimulus rotation. On the other hand, the bars of the color grating were visible but they could only be seen to move (in the opposite direction to the overall stimulus rotation) when they were tracked with attention. In a second task, the perceived velocity of a color grating, typically slow at equiluminance, speeded up when individual bars were attentively tracked. These findings demonstrate two independent motion processes: one that is "low-level" or automatic in that it signals motion even in the absence of attention to the stimulus, and one that is mediated by attention to visible features and provides accurate velocity judgments independently of the features being tracked.

Attention often plays a crucial role in motion perception. For example, when a stimulus contains two components moving in opposite directions, attentive tracking of either one can reveal its motion independently of the other (1, 2). Many neurons in primary visual cortex are sensitive to the direction of motion (3) and attention might act by selecting one or the other of these low-level motion responses. However, the experiments described here demonstrate that the perception of motion during attentive tracking can arise independently of low-level motion responses and may be derived from the internal signals that move the focus of attention (4).

In the first experiment, the stimulus was constructed by superimposing color and luminance gratings that moved in opposite directions around an annulus (Fig. 1A) in order to eliminate the possibility of tracking eye movements (5). Measurements of detection and motion thresholds, motion strength, and tracking performance were made. An unexpected feature of the results is that the superimposed color grating greatly increased the separation between the pattern and motion thresholds (6) for the luminance grating. Without the superimposed color grating, the thresholds for seeing the luminance component and seeing it move were very close, replicating earlier findings (7). With the superimposed color grating, both detection and direction thresholds rose by a factor of 4 or 5, again replicating earlier findings (8). However, as will be seen, an additional order of magni-

tude of contrast was necessary before the luminance grating could be tracked, implying that the features that mediated the detection of the grating and its motion do not support its localization or tracking.

The relative strengths of the color and luminance contributions to the apparent global rotation of the combined stimulus were determined with a nulling procedure. The color contrast was set at 40% of the maximum available contrast between the red and green phosphors (9), and the relative modulations of red and green were set to approximate equiluminance with the use of a minimum apparent speed criterion (10). The observers then adjusted the contrast of the luminance grating to null the global motion seen in the annulus without paying attention to the individual features of the two gratings. At low values of luminance contrast, the combined stimulus appeared as a red-green grating rotating smoothly in the direction of the color component. At high values of luminance contrast, the stimulus appeared to be a flickering red-green grating rotating with a jerky motion in the direction of the luminance grating. At some intermediate value between 5 to 10% contrast (depending on the observer), the global motion was nulled and its direction became ambiguous.

The same combined stimulus was used in the tracking task; however, the contrast of the luminance grating was set to one of eight values uniformly spaced from 5% to an upper value of 25 to 45% (11), whereas the color contrast remained fixed at 40%. For each trial, the observer carefully fixated the central bull's-eye. To begin the trial, an inner pointer appeared beside the pair of

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stimulus bars to be attentively tracked and rotated along with that pair for 1.0 s. The pointer was then extinguished and the observer continued tracking these two bars with attention for an additional 1.5 s, after which a test pointer appeared for 240 ms pointing to the tracked bars or to the adjacent pair (on either side) with the same contrast polarity. The observer pressed a key to report whether the test pointer was aimed at the bars that they had been tracking. Each observer participated in at least four sessions. For half the sessions, the pointers indicated color bars as targets for tracking; for the other half, the pointers indicated luminance bars, and the direction of rotation was set randomly for each trial.

Observers had normal or corrected-to-normal visual acuity and normal color vision.

The data for all three observers showed that colored bars could be tracked with surprising accuracy well beyond the point at which the global rotation of the stimulus was opposite to the direction of the colored bars. In marked contrast, the luminance bars were difficult to track even when they were moving in the same direction as the global rotation. Tracking performance for the luminance bars did not reach the 75% threshold value until the luminance contrast was two to four times the contrast at which the global motion was dominated by the luminance grating.

This dissociation between the direction

seen for the overall motion and the direction in which individual bars could be tracked shows that tracking cannot be based on motion signals from low-level detectors alone; if it were, then the luminance bars that were producing the dominant motion signal in the striped range of Fig. 1C could have been tracked at least as easily as the color bars. If tracking is not based on low-level signals alone, what is the source of the motion impressions during tracking? One possibility is that the signals that keep attention positioned over the tracked target provide information on either location or displacement that leads to impressions of motion (12). Within the striped zone of Fig. 1C, the opposing motion stimulus therefore dissociates the two levels of motion processes that typically operate in tandem: The motion of the luminance grating is available only as a global, low-level response and the motion of the color grating is available only through attentive tracking of local features.

The data show that tracking is not based on low-level motion signals alone. However, it could be claimed that, once a feature is sufficiently visible to be tracked, then the sensations of motion for the feature are based on low-level signals. The second experiment therefore measured the effect of attention on the apparent velocity of features that were always visible (Fig. 2).

The stimulus was again a rotating grating; however, this time only a color grating was present in the outer ring. To indicate the apparent rate of rotation, the observer adjusted the speed of rotation of a luminance grating that rotated in the opposite direction in the inner ring. The luminance contrast of the color grating was varied in the experiment in order to measure the variation of apparent speed. Both gratings reversed direction occasionally to avoid motion aftereffects. The motion judgment was made in two different ways.

In the global match, the observer equated the overall motion impression from the outer and inner ring. In the tracking match, the observer had to pick a pair of bars on opposite sides of the center and track them with attention as they rotated. The observer made an estimate of the rotation rate during this tracking and then switched his attention to the inner ring and tracked a pair of bars there, adjusting their rotation rate to match the remembered rate of the outer ring. The observer could switch attention back and forth between the rings as often as necessary to make an acceptable match.

The results show that the global motion judgment varied considerably with the luminance contrast of the color grating, dropping to a minimum at a particular value. This replicates the well-known loss of speed

Fig. 1. (A) Superimposed radial grating stimulus. An eight-cycle sinusoidal red-green grating was superimposed additively on an eight-cycle sinusoidal luminance grating, and the two rotated in opposite directions at 2.0 Hz (0.25 revolutions per second). The annulus had inner and outer radii of 4.0° and 8.4°, respectively. At the center was a high-contrast, black and white bull's-eye with a radius of 1°. The luminance grating was produced by modulating both the red and green phosphors in phase about the mean combined value of 45 cd/m², whereas the color grating was produced by modulating the two phosphors out of phase. The CIE x- and y-coordinates of the phosphors were 0.608 and 0.348 for red and 0.249 and 0.602 for green. The mean chromaticity within the annulus was yellow, with CIE x- and y-coordinates of 0.409 and 0.488. (B) Percentage of trials for which test bars were correctly identified as a function of the contrast of the luminance grating for observer T.W. The data for the two other observers were similar. The point at which the two gratings contributed equally to the global rotation seen in the annulus is given by the motion null point shown by the vertical arrow. (C) Thresholds for detecting presence of the luminance grating and identifying its direction of motion for observer T.W., both for isolated gratings and with a superimposed color grating of 40% color contrast. The data for the two other observers were similar. The motion null point and the tracking threshold are also replotted from (B). In the range of contrasts filled by stripes between these two points, the overall motion was in the direction of the luminance grating; however, the luminance bars could not be tracked.

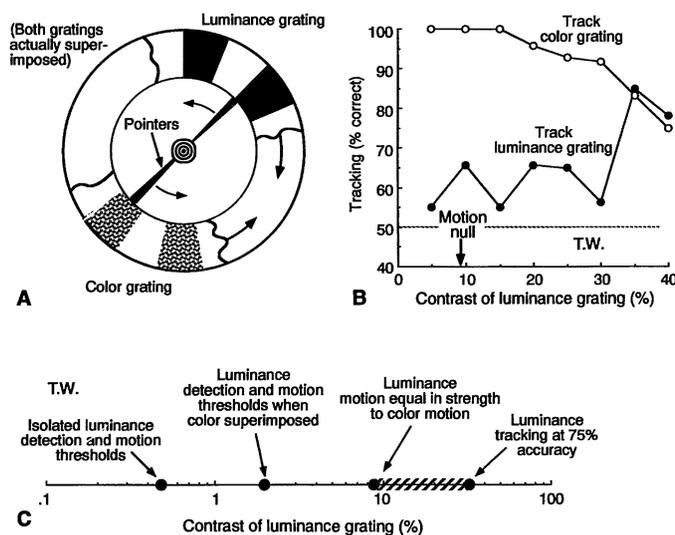
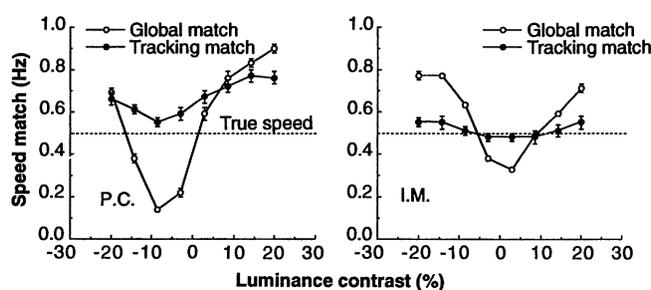


Fig. 2. Apparent speed of the rotating color grating as a function of its luminance contrast and the type of judgment for two observers P.C. and I.M. Positive contrast values indicate red more luminous than green; negative values indicate green more luminous than red. The stimulus was identical to that of the first experiment except that the outer ring contained only a color grating, which itself varied in luminance contrast from trial to trial, and the rotation rate was 0.5 Hz. The inner ring contained a luminance comparison grating of 15% contrast rotating at an adjustable rate.



for equiluminous stimuli (10). The tracking judgments, on the other hand, varied much less as a function of the luminance contrast of the color grating.

There are therefore dissociations between performance in global and tracking motion tasks even when low-level signals can easily be attached to the tracked features. Thus, both experiments indicate that low-level signals alone are not responsible for the perceived motion of tracked objects.

This finding adds a second, attention-based motion process to the passive motion-specific detectors that are thought to cover the visual field with several arrays of spatiotemporal comparators (13). Attention-based tracking has been studied in other contexts in which it appears to be mediated by a limited number of object-specific processes (14). This attention-based motion process provides a mechanism for some of the phenomena previously grouped together as long-range motion effects (15). However, many long-range stimuli undoubtedly engage both the attention-based motion process and low-level processes, confounding the interpretation of the phenomena. The experiments described here demonstrate that the two processes can be studied separately and imply that their individual contributions to "long-range" phenomena may eventually be disentangled.

The thresholds for performing the tracking task clearly link this process to the visibility of the forms to be tracked, as opposed to the visibility of the low-level, global motion that they produce. The visibility of luminance-defined forms measured in this fashion was strongly masked in the presence of superimposed color gratings, implying that previous detection threshold measures for luminance stimuli (including those with color masks) were not indicative of the visibility that is required for spatial localization. Tracking of spatial features

depends on identifying form boundaries, and it appears that the form signal from luminance is especially susceptible to masking by color. This might be expected because any object traveling through a shadowed environment will have many luminance boundaries drifting across it that are unrelated to the object and need to be discounted, whereas color boundaries are more reliably tied to object borders.

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5. Although the eye can rotate about the axis of gaze, it is unlikely that this cyclotorsion would be any greater than about 6° for the radial gratings used here [B. S. K. Cheung and I. P. Howard, *Vision Res.* **31**, 1327 (1991)]—quite insufficient to follow the large rotations in the tracking task (for example, 135°). One observer's eye movements were monitored during attentive tracking to determine whether the eye might be tracking in a small orbit around the fixation point in synchrony with the target. However, the excursions from the central fixation were random, unsynchronized drifts that never exceeded 0.3°.
6. The drifting (2.0 Hz) luminance grating was first presented alone. Each observer adjusted the luminance contrast of the grating to the threshold for noticing the presence of the grating, starting twice from suprathreshold values and twice from subthreshold values. The average of these four values was taken as the approximate detection threshold. The procedure was then repeated for the threshold for seeing the direction of motion of the grating. These two threshold tasks for the luminance grating were then repeated with the color grating (at 40% contrast, drifting at 2 Hz) superimposed on the luminance grating.
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9. This value is about 20 times the detection threshold. The color detection thresholds were measured with the drifting (2.0 Hz) color grating presented alone. Each observer adjusted the color contrast of the grating to the threshold of visibility, starting twice from suprathreshold values and twice from subthreshold values. The average of these four values was taken as the approximate detection threshold.
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11. The upper limit of the contrast range was determined individually for each observer so that it would at least extend beyond his or her tracking threshold value.
12. The other possibility is a process—for example, either a position readout or specialized motion detector—that operates on retinal features selected by attention. A supplemental observation is suggestive although not decisive here. If the annulus of Fig. 1A is masked down to a small window (45°, covering one cycle of the gratings), and observers attend to it under the presentation conditions of the striped region of Fig. 1C, the motion of the color bars is still not observed unless the observer actively tracks a bar as it moves through the window. This would argue against a process that operates on the retinal image within an attended region and for one that depends on the position or displacement of attention itself.
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