Coherent global motion in the absence of coherent velocity signals

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It is widely believed that form and motion are analysed separately in mammalian visual systems. Form is confined within a stream that projects ventrally from V1 to the inferotemporal cortex, and motion within a stream that projects more dorsally, to the posterior parietal cortex [1–7]. Current descriptions suggest that there is little contact between the two streams until the products of their separate analyses are bound together at a late (and still unidentified) stage in perception [3,8–10]. There are, however, indications that form and motion signals may interact [11], and that form signals, streaks derived from motion, may assist in the analysis of its direction [12]. Lennie [13] proposes that all image attributes, form and motion included, remain intimately coupled within the same retinotopic map at all stages of visual analysis. Here we show that form, independent of motion, can give coherence to incoherent motion. Sequences of Glass patterns [14] built to a common global rule are devoid of coherent motion signals, but they produce motion consistent with the global rule for form, not with the random velocity components of the pattern sequence.

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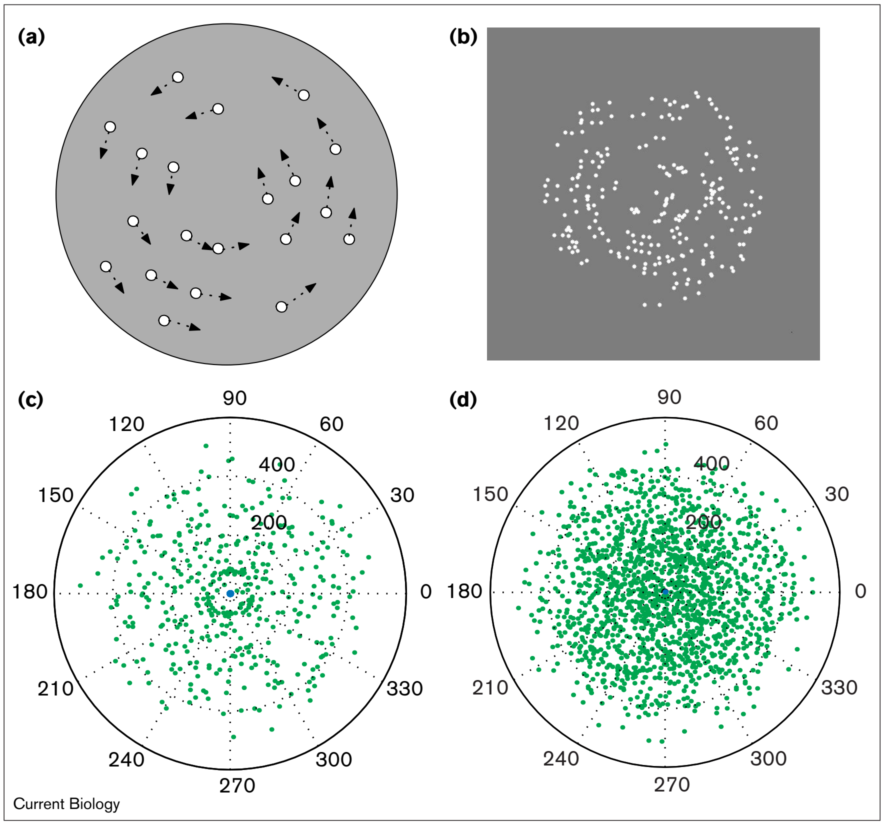
Results and discussion

The motion that is perceived when spatially and temporally distributed local-motion signals are combined is referred to as 'global motion'. A much-used stimulus for global-motion studies is a sequence of random-dot displays in which some dots from each frame are displaced coherently (for example translated or rotated) on succeeding frames. Because the dots that carry the coherent motion signal may differ from frame to frame, and because the threshold proportion of coherently moving dots is commonly less than 10%, observers must integrate these local signals. They are capable of doing so over large spatial areas and over eight or nine frame-transitions [15]. Summation of global motion (translational, rotational or radial) has been measured in circular fields up to 70° in diameter [16]. Cells that respond to global motion, with receptive fields of at least 10° diameter, have been found in the dorsal segment of the medial superior temporal (MST) cortex of monkeys [17–19]. If a sufficient number of dots are rotated during a frame transition (Figure 1a), observers see spin in the direction of rotation. Motion captures the whole field, including dots that are not displaced in the direction of rotation, and this capture occurs even when the dots displaced are confined to sectors interleaved with sectors of purely random motion [16].

The method used to construct global-motion sequences may also be used to produce static Glass patterns [14] (Figure 1a,b). Static Glass patterns may be considered to be static equivalents, or limiting cases, of the motion sequences described above, where the length of the sequence is two, and the frames are simultaneous. These patterns have a global grainy appearance that has been aptly described as 'static flow' [20]. Figure 1b shows a rotational Glass pattern in which the second dot of the randomly placed pair is consistent with the original dot being rotated about the centre of the figure. The motion-signal vectors in a global-motion sequence are themselves organized. Figure 1c depicts the distribution of velocities obtained by connecting all dots in one frame with all dots in the next. The dense ring near the centre of the plot corresponds to dots that move with a constant speed and thus represent a coherent motion signal. There is no corresponding organization in the motion vectors from a sequence of independent Glass patterns (Figure 1d), and thus a percept of coherent motion is not predicted. Yet, as we report here, a sequence of independent rotational Glass patterns can give rise to coherent global motion: an apparent full-field spin that is unambiguously rotational but ambiguous in direction (either clockwise or anticlockwise). It is otherwise indistinguishable from real motion, and quite different from the incoherent motion produced by a sequence of random dot fields. Because coherence cannot come from the motion signals delivered by a sequence of Glass patterns, it can only come from their internal static structure.

To establish the limits for seeing spin, observers were presented with a sequence of ten independent Glass patterns of the rotational type (Figure 1b). Each pattern was composed of 100 pairs of small round dots and was set within a 10° display area. Observers were asked to rate the quality of spin they observed on a scale from 0 (no rotation) to 9 (very vivid) as pair separation and frame duration varied. Figure 2 presents a contour plot of the results for each observer and shows that spin was strong

Figure 1



Rotary motion, rotational Glass patterns and motion vectors. **(a)** Schematic illustration of a stimulus sequence for global rotary motion (spin). The sequence starts with dots placed at random with uniform density within a circular display area. On each succeeding frame a proportion of dots from the previous frame is moved as indicated by the arrows. **(b)** A rotational (100%) Glass pattern of the type used for the experiments reported. Initial dots are placed at random. All are provided with partners in positions as illustrated for motion. **(c)** Polar plot of all motion vectors generated when a field of 20 random dots is displayed in a disc of radius 256 on one frame, the dots rotated as illustrated in (a) and all displayed on a second frame. Vectors arising from pairings of the original dots and their displaced partners fall in a ring. The spin that is seen is consistent with this ring of motion vectors, and motion consistent with other vectors is suppressed. **(d)** Polar plot of motion vectors from a pair of successively displayed independent Glass patterns each containing 20 dot pairs. The expected vector mean is zero, independent of Glass pattern type or pair separation. There is no ring of vectors like that in (c).

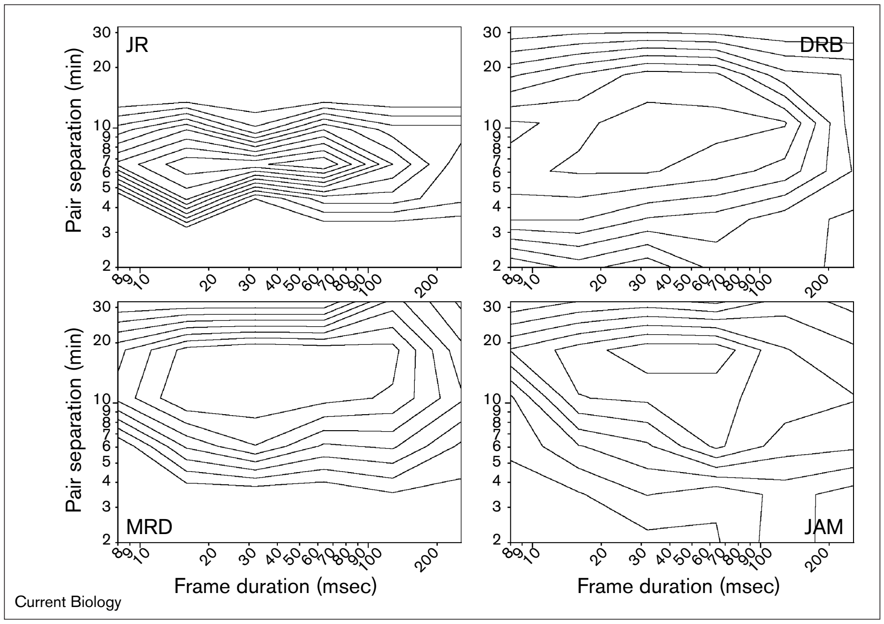
in the pair separation range 6–15 arc min, and in the frame duration range 16–128 msec. These parameter values are similar to those found to be optimal for seeing global motion [21–23] and for seeing Glass patterns [24,25]. To check that observers did see global spin, they were required to distinguish a sequence of four independent Glass patterns from a sequence of four Glass patterns linked by real bidirectional motion signals at a speed of 22° sec^{-1}. The speed was needed to match the apparent speed of rotation of the independent Glass pattern sequence. All observers performed at chance levels. When required to distinguish real uniform clockwise motion from real anticlockwise motion at the same speed (22° sec^{-1}), the performance of all four observers was nearly perfect, however. These results show that under conditions where observers can easily use motion signals to distinguish the direction of spin, they cannot distinguish true spin from the apparent spin of sequences containing no coherent motion signals.

Next, slower motion signals, clockwise on some trials and anticlockwise on others, at a speed just above 4° sec^{-1}, were added to a sequence of ten Glass patterns. The proportion of pairs that moved from frame to frame to provide real motion signals was varied, and two observers were asked to judge the speed of spin on a five-point scale from 1 (slowest) to 5 (fastest). The results (Figure 3) show that as the proportion of motion signals increased, average rated speed dropped linearly from each observer's independently determined threshold for discriminating direction of spin (4% and 8% coherent motion) to 48%. When the motion signals were radial—but the Glass patterns rotational—the speed of apparent spin again dropped with increasing signal proportion, but spin ceased completely at signal proportions above 40%. Thus, when coherent motion signals are present within the motion signal ensemble, they have an increasingly dominant role in global analysis as their number increases.

Observers indicate that they perceive strong coherent motion in sequences of rotational Glass patterns, even though the distribution of local motion vectors is random on each frame transition. Sequences of other types of Glass patterns (radial, spiral and, to a lesser extent, translational) also give rise to coherent global motion that is ambiguous in direction, but always in accordance with the pattern's structure. Furthermore, that motion is indistinguishable from coherent motion, which contains a relatively strong motion signal. Static form must therefore have an input to global-motion analysis.

Geisler [12] has proposed that sufficiently fast object motion leaves behind it a record of spatial signals, or

Figure 2



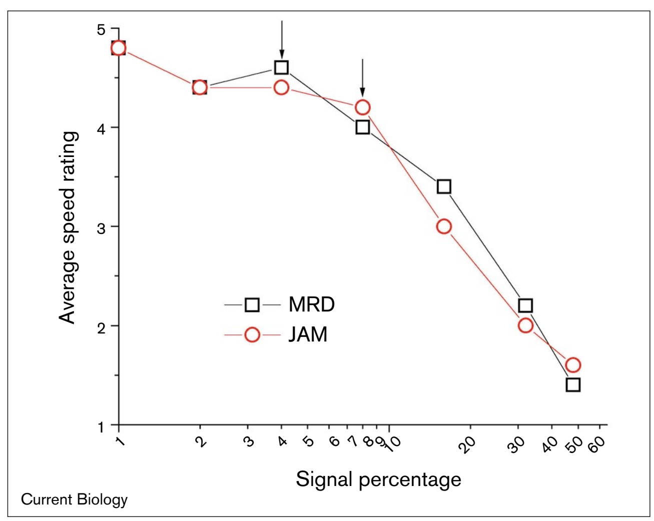
Contour mounds (central areas high) for four observers showing averages of three ratings of quality of spin, on a scale from 0 (no spin) to 9 (vivid spin), of a sequence of ten independent Glass patterns. Frame duration varied from 8–256 msec, and pair separation from 2–32 arc min. The high and low average ratings of the four observers were: JR, 0 and 9; DRB, 0 and 8.3; MRD, 0 and 9; JAM, 0 and 8.7. Variances of ratings (within and between observers) were low at all combinations of frame duration and pair separation, suggesting that each produced a consistent appearance of spin and that judgements were easy to make.

streaks, which are helpful in the estimation of its direction, by stimulating neurons in primate area V1 whose preferred orientation is parallel to its direction. Dot pairs within individual Glass patterns within a sequence will also stimulate orientation-tuned neurons in V1. The fact that random motion from a sequence of independent Glass patterns is perceived as orderly confirms Geisler's hypothesis that spatial-orientation signals may contribute to the visual analysis of motion. But it also implies that they can do more than help in the estimation of direction.

Orientation-tuned neurons could provide indications of the local orientation of motion produced by a sequence of Glass patterns, but not its direction, because whereas the velocity components of a moving object have a consistent local direction, those from a sequence of independent Glass patterns do not. Hence, if signals from orientation-tuned neurons are the basis of the global motion seen when Glass patterns are shown in sequence, the direction of motion must be ambiguous, as we observe it to be.

Most current descriptions of the dorsal and ventral visual-processing streams show a link between V4 and MT (V5) that is thought to provide only a chromatic input to motion processing. One interpretation of our results is that there is a more powerful input to MT of V4's analysis of global form. A recent functional magnetic resonance image (fMRI) study by Braddick *et al.* [26] supports the anatomical plausibility of such input. A more natural interpretation is that the analysis of form and motion is tightly coupled at all stages of visual analysis, as Lennie [13] has suggested. If it were, information about form could contribute to the analysis of motion, just as information about motion can to the analysis of form [27].

Figure 3



Rated speed of motion of a sequence of ten Glass patterns with slow motion signals added by moving a proportion of pairs by 8 arc min (the same as pair separation in the Glass patterns) from frame to frame and replacing the remainder with fresh pairs, placed at random. Motion signals were all in the same direction on any trial, but randomly assigned either clockwise or anticlockwise. The proportion of pairs moved ranged from 1–48%. The threshold signal proportions at which the observers could discriminate between clockwise signals in one interval, and anticlockwise signals in another, are shown by arrows. Each observer's speed rating drops after threshold is reached.

Materials and methods

Equipment and stimuli

The stimuli were displayed within a circular region of 10° diameter on the screen of an Hitachi Accuvue 4821 monitor at a frame rate of 120 Hz and a resolution of 800 × 600 pixels. Background luminance was 21.5 cd m^{-2} and the luminance of each circular dot (diameter 5′) was 93 cd m^{-2}. Viewing distance was 114 cm. The four observers all had normal or corrected-to-normal vision and were experienced in psychophysical tasks. Rotational Glass patterns (Figure 1), composed of 100 pairs of dots of constant separation, were used in the experiments reported. Other types were used for less formal observations. Each pattern, composed of, usually, 100 pairs of small round dots set within a 10° display area, was drawn to a separate page on a Cambridge Research System VSG2/4 graphics card, then all pages were displayed in sequence. Each sequence was composed of ten different patterns. The individual patterns were produced by randomly positioning the first dot of the pair and then placing the partner according to the chosen global rule. It is easy to show, by numerical and analytic means, that this procedure produces uncorrelated velocity signals.

Procedure

Experiment 1: Performance was measured as a function of dot-pair separation, which ranged from 2–32 arc min, and frame duration, which ranged from 8–256 msec. A rating procedure was used to obtain estimates of the salience of the appearance of motion. Observers used a nine-point scale where 0 indicated random motion and 9 indicated 100% coherent motion. All observers were shown examples of coherent motion sequences corresponding to the end points of the scale and were then asked to rate the dynamic Glass sequences, which lack coherent motion signals, relative to these examples.

Experiment 2: Glass pattern sequences were dosed with coherent motion signals; pair separation was 8 arc min and frame duration 32 msec – values at which quality of spin is high in the absence of coherent motion signals. The dot-pairs that were shifted from frame to frame to produce coherent motion signals were also moved by 8 arc min, giving a linear motion speed of just over 4° sec^{-1}. A rating procedure was used to obtain estimates of the apparent speed of the Glass pattern sequence. Observers used a five-point scale where 0 indicated slow coherent motion at 4° sec^{-1} and 5 corresponded to a speed of 22° sec^{-1}. All observers were shown examples of coherent-motion sequences corresponding to the end points of the scale and were then asked to rate the dynamic glass sequences relative to these examples.

Experiment 3: Observers attempted to discriminate a sequence of independent Glass patterns from a sequence in which half of all pairs were moved coherently on each frame transition; pair separation was again 8 arc min and frame duration 32 msec. Linear speed of coherent motion signals was set at 22° sec^{-1} to match the apparent speed of Glass pattern spin and, in order to mimic the ambiguity in the direction of Glass pattern spin, the circular display area was divided into four annuli of equal width, the direction of motion within annuli being alternately clockwise and anticlockwise. Observers were presented with two 128 msec sequences in succession. One sequence was composed of four independent Glass patterns. The other was composed of patterns in which half of the dot pairs moved in a coherent manner from frame to frame. The observer's task was to indicate which sequence contained the coherent motion.

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