

Visual Form Created Solely from Temporal Structure

Sang-Hun Lee and Randolph Blake*

In several experiments, it was found that global perception of spatial form can arise exclusively from unpredictable but synchronized changes among local features. Within an array of nonoverlapping apertures, contours move in one of two directions, with direction reversing randomly over time. When contours within a region of the array reverse directions in synchrony, they stand out conspicuously from the rest of the array where direction reversals are unsynchronized. Clarity of spatial structure from synchronized change depends on the rate of motion reversal and on the proportion of elements reversing direction in synchrony. Evidently, human vision is sensitive to the rich temporal structure in these stochastic events.

For objects to be seen, they must stand out from their backgrounds. The role of spatial structure in scene segmentation has been exhaustively studied this century, beginning with the landmark work of the Gestalt psychologists. From that work, we know a great deal about how figure/ground segmentation is influenced by spatial factors including proximity, continuity, and symmetry (1). At the same time, we know that vision is dynamic: Objects can move about the visual environment unpredictably, and as observers we are chronically moving our eyes and heads to sample that environment. Consequently, the optical input to vision also contains rich, complex temporal structure. Can the visual system exploit that temporal structure to segregate objects from their backgrounds? Recently this question has attracted growing interest (2), attributable in part to the controversial idea that neural coding of visual objects and events uses temporal fine structure in neural responses (3).

We have created visual displays in which global spatial structure is defined exclusively by temporal fine structure among elements undergoing rapid, irregular change. In our animation displays, individual, static frames contain no information whatsoever about spatial structure. Our displays can be construed as a temporal analog to the random-dot stereogram in which disparity alone defines global form (4). Using these displays, we have discovered that human vision is remarkably sensitive to temporal fine structure contained in stochastic events.

Consider an array of many small circular patches, each containing contours of a given orientation (Gabor elements); throughout the array, contour orientation varies randomly among patches (Fig. 1A). Although the cir-

cular patches themselves are stationary, the contours within each patch move in one of two directions orthogonal to their orientation, with motion direction reversing irregularly over time according to a Poisson process. With no constraints on when individual elements reverse their directions of motion, the display lacks any hint of spatial structure. But suppose we specify that all Gabor elements within a virtual "figure" region reverse their directions of motion simultaneously while, at the same time, Gabor elements outside of this region change direction independently of one another. Now, the "figure" region defined by temporal synchrony stands out conspicuously from the background. Note that grouping of those Gabor elements defining the figure is impossible on the basis of direction of motion, contour orientation, or any other luminance-based cue. Even comparing two successive, static frames of the animation would provide no information about the figure, for all contours move from frame to frame. Only synchronized changes in direction of motion distinguish figure from background.

To quantify and manipulate the information contained in these stochastic displays, we derived several indices of the temporal structure embodied by changes in motion direction. First, the predictability of motion direction within individual Gabor elements can be expressed in terms of entropy (5). Each element moves in either of two directions, a or b ; thus, each Gabor conveys one of two "messages" with associated probabilities P_a and P_b . The average information conveyed by a single Gabor element, then, is given by

$$H_{av} = -[P_a \log_2(P_a) + P_b \log_2(P_b)] \quad (1)$$

Figure 1B shows how entropy varies with P_a in these displays. For each Gabor patch we define the time series of motion reversals using the concept of the point process (6), a sequence of points denoting when events occur (Fig. 1C).

We created an array of Gabor patches, each of which has its own point process, and we specified the extent to which all possible pairs of point processes within given spatial regions of the array were correlated (7). Here, "correlation" refers to the likelihood that a subset of Gabor elements reverses their directions of motion simultaneously. All Gabor elements were always moving, and the individual directions of motion varied randomly over the entire array. The only source of information for grouping a subset of Gabor elements was the temporal synchrony of their reversals in direction of motion. In the language of Gestalt psychology, this information represents a form of common fate (8), with temporal synchrony providing the sole cue for spatial grouping.

How accurately can human vision register the fine temporal structure in these stochastic displays, and how efficiently can that structure be used for spatial grouping? To answer these questions, we systematically varied the entropy of the entire display and the average correlation among Gabor elements within a rectangular region of the display. Using a two-alternative forced-choice procedure, we required observers to judge over a series of 1-s trials whether that rectangular region was vertically or horizontally oriented. Holding area constant, we manipulated the aspect ratio of this rectangular region to vary the difficulty of the task; the location of the rectangular region varied from trial to trial, preventing observers from attending to a subset of Gabor elements.

With high entropy and high correlation, the "figure" region stood out conspicuously, resulting in flawless performance (Fig. 2). Indeed, the accuracy of shape discrimination rivals that measured using motion- and contrast-defined rectangles (9). At lower values of correlation, the shape of the rectangular figure was ill-defined and thus performance suffered. This is predictable because lowering the average correlation among point processes within the figure region reduces the signal-to-noise ratio of the relevant cue. Discrimination performance also fell with decreased entropy, which stands to reason because the rate of information (bits per second) relevant to the task was reduced. It is noteworthy that performance was best at the highest entropy level, which implies that the visual system can register fine temporal structure with high fidelity. Of course, there must be an upper limit to the effectiveness of entropy, imposed by the limited temporal resolution of the visual system. At the 100-Hz frame rate of our display, the highest value of entropy produced, on average, 50 changes per second in direction of motion. Earlier work using repetitively flickering elements suggests that this value could represent an upper limit to entropy's effectiveness (2).

Local motion was produced by small spa-

Vanderbilt Vision Research Center, Vanderbilt University, Nashville, TN 37240, USA.

*To whom correspondence should be addressed. E-mail: randolph.blake@vanderbilt.edu

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tial phase shifts of the grating within its aperture. Thus, when a grating reversed direction of motion, it very briefly returned to the same spatial position it occupied two frames earlier in the animation sequence. In principle, this spatial coincidence could produce a momentary enhancement in apparent contrast owing to local luminance summation. Of course, these enhancements in local contrast would occur throughout the entire array, but they would occur simultaneously among figure elements but not simultaneously among background elements. If contrast signals were pooled within subregions of the display, observers might get an overall impression of larger net changes in apparent contrast within the figure compared to the background. If an observer's performance were based on such an impression, shape discrimination should suffer when comparable net changes in apparent contrast are introduced into the background as well. This is easily accomplished by specifying that all background elements follow a single point process uncorrelated with the point process defining the figural elements. All background elements would change directions of motion simultaneously and therefore would be subject to the same pooled contrast-enhancement effect as elements defining the figure. But if figure/ground segmentation depends on temporal synchrony, shape discrimination should be enhanced when all background elements obey a single point process: Now the background region too is unambiguously defined, albeit by a point process unrelated to the one defining the figure.

With this in mind, we retested three observers on the shape discrimination task, using Gabor arrays in which the point processes for background elements were either uncorrelated or perfectly correlated. In both conditions, point processes for elements within the figural region were perfectly correlated. Performance was consistently superior for the latter condition (Fig. 2B), ruling out contrast enhancement as the cue for shape discrimination.

Rotational motion also provides a potent messenger for temporal synchrony. We created an array of "windmills," each of which rotated either clockwise or anticlockwise about its center (10). The direction of rotation of each windmill reversed over time probabilistically (Fig. 3). Again we specified that all windmills within a "figural" region of the array reversed their directions of rotation simultaneously, whereas those in the "background" region did not. In both regions some windmills rotated clockwise and others rotated anticlockwise, so direction of rotation itself provided no cue for segmentation. The figural region defined solely by correlated change in direction of rotation stood out conspicuously from its background. It will be informative to learn whether other "messengers" of temporal structure besides motion

can be deployed in the interest of spatial group (11).

In a final experiment, we used windmill arrays to determine whether shape from temporal synchrony provides input to stereoscopic

depth. Two windmill arrays were created as stereo half-images, each portraying two small squares above and below a central fixation point; these squares were defined by synchronized reversals in direction of rota-

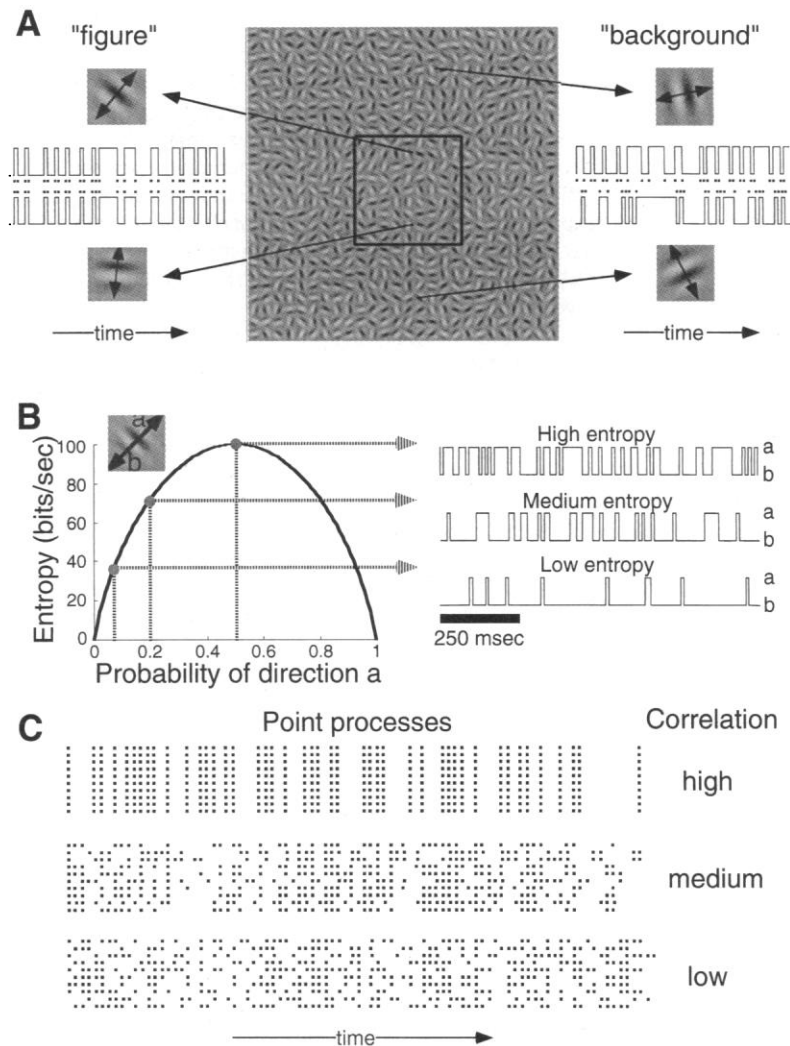


Fig. 1. Spatial structure from correlated changes in direction of motion. (A) Each frame of the animation sequence consisted of an array of small Gabor patches within which contours moved in one of two directions orthogonal to their orientation, and motion direction changed irregularly over time. Shown schematically on either side of the square array of Gabor patches are enlarged pictures of several Gabor patches with double-headed arrows indicating the two possible directions of motion. The time series indicate direction of motion, and the small dots associated with each time series denote that time series' point process (points in time at which direction changed). Gabor patches within a virtual region of the array (shown in outline) had point processes that were correlated, whereas Gabor patches outside this virtual area were uncorrelated. Time scale is dependent on entropy level. (B) Informational content of each Gabor element was specified in terms of entropy, the amount of information about direction conveyed per unit time. Entropy is determined by the complementary probabilities that motion will be in one direction (p_a) or the other direction (p_b) of motion. When the probability of either direction is equal, direction of motion is highly unpredictable over time: Entropy is maximum. When the probability of one direction is much less likely, direction is more predictable: Entropy is low. (C) Average correlation among point processes within a "virtual" figure region could range from zero to unity. To manipulate correlation, we generated sets of point processes whose average pairwise correlations corresponded to the value desired; these point processes were then assigned to the Gabor elements within the target region. When all Gabor elements within a given region follow the same point process, correlation is 1.0. When each Gabor patch follows its own, independently determined point process, average correlation is zero. (With zero correlation, point processes may be partially correlated by chance alone, some with positive correlation and some with negative correlation. All possible pairwise correlations among point processes constitute a normal distribution with mean of zero.) Time scale is dependent on entropy level.

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tion (10). We introduced a small crossed disparity in either the upper or the lower pair of squares. The two "squares" in the two stereo half-images do not exist in individual frames of the animation, so depth cannot possibly be seen when two static half-images are fused: The individual windmills on corresponding retinal areas do not even match (except by chance) and are, therefore, rivalrous throughout the array. With the dynamic display, both squares were conspicuously visible, and one of the two appeared clearly nearer than the other. Over a series of 100 trials, each 750 ms in duration, observers judged which square appeared nearer in depth. Performance on this two-alternative, forced-choice task averaged 91% correct for

the four observers (scores ranged from 84 to 96% correct), indicating that shape from temporal synchrony is registered before binocular combination and disparity computation.

Local elements can be spatially grouped on the basis of a variety of cues including luminance, color, disparity, texture density, contour orientation, or common motion vectors (12). None of these cues, however, can contribute to the global spatial structure perceived in our displays; shape from temporal synchrony must involve computation of high-order statistics. Specifically, the visual system must (i) compute changes in velocity in each of a number of spatially distributed motion vectors, (ii) register with high fidelity the points in time at which those changes occur,

(iii) correlate the times at which those changes occur over neighboring local elements throughout the array, and (iv) identify boundaries associated with abrupt transitions in correlation values among local elements. These requisite computations are not ingredients within contemporary models of shape perception (13) or models of structure from motion (14). Nor can spatial structure from temporal synchrony be explained by models in which higher order motion signals are extracted by nonlinear mechanisms (15). Any successful theoretical account of our results will require spatially interacting mechanisms exquisitely sensitive to the rich temporal structure contained in these high-order stochastic events.

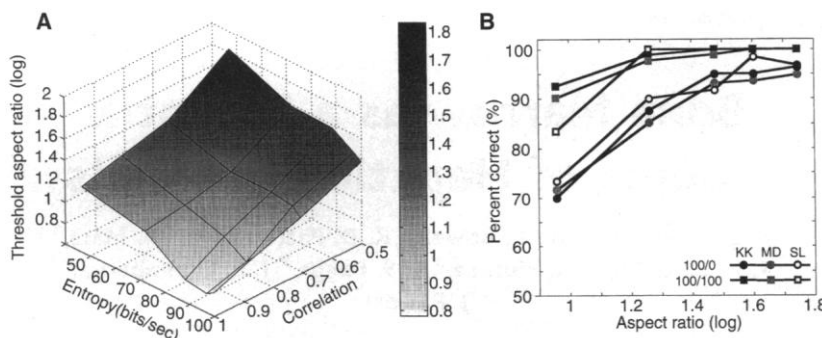


Fig. 2. Shape discrimination from temporal structure. (A) Aspect ratio—expressed as $\log [(l_l - l_s)/l_s] \times 100$, where l_l and l_s give the length of the longer and shorter borders, respectively—yielding 75% correct performance on a two-alternative, forced-choice task. These threshold values were estimated from probit analysis applied to the psychometric curves for the individual conditions; each data point on those curves is based on 50 trials. Performance is shown as a function of (i) correlation among Gabor patches defining the target and (ii) entropy of all Gabor patches within the array. For this experiment, the average correlation among point processes for Gabor patches in the background region was zero. In this graph, light gray denotes good performance and dark gray denotes poorer performance. Entropy is expressed as bits per second. (B) Percent-correct performance on the shape discrimination task where point processes of Gabor patches defining the figure were identical (1.00 correlation) and point processes of elements defining the background were either uncorrelated (circles) or perfectly correlated (squares) among themselves but uncorrelated with those in the figure. Symbols indicate each of three observers tested, with each data point based on 60 two-alternative, forced-choice trials.

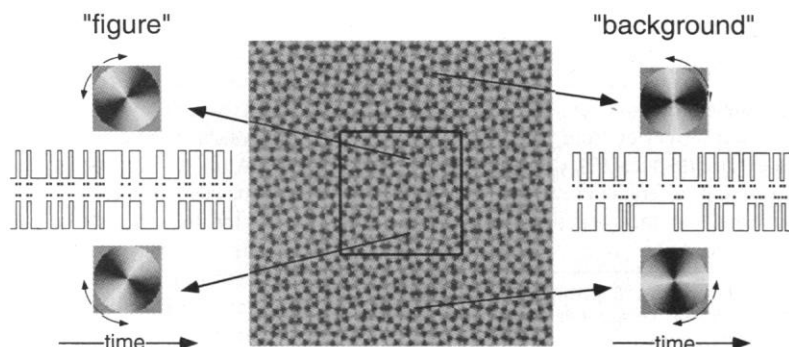


Fig. 3. Schematic of one frame of a rotational motion display in which an array of windmills rotates either clockwise or anticlockwise (indicated by double-headed arrows), with reversals in direction of rotation occurring randomly over time (indicated by time series and point processes). The initial rotational position of each windmill is random, providing no spatial structure in single frames of the animation. Points in time when reversals occur constitute a point process, and the correlation among point processes within a "figure" area and the remaining "background" area can be manipulated. Time scale is arbitrary.

References and Notes

1. K. Koffka, *Principles of Gestalt Psychology* (Harcourt Brace Jovanovich, New York, 1935); I. Rock, in *Handbook of Perception and Human Performance*, K. R. Boff, L. Kaufman, J. P. Thomas, Eds. (Wiley, New York, 1986), vol. 2, pp. 33-1-33-71; S. E. Palmer, *Cognit. Psych.* **24**, 436 (1992).
2. A few recent studies have examined whether temporal coincidence of spatially distributed features can promote figure/ground segregation, but with mixed results. Several found that small temporal offsets, on the order of a few milliseconds, between features defining figure and ground could promote perceptual grouping [U. Leonards, W. Singer, M. Fahle, *Vision Res.* **36**, 2689 (1996); M. Fahle, *Proc. R. Soc. London Ser. B* **254**, 199 (1993); V. S. Ramachandran and D. C. Rogers-Ramachandran, *Bull. Psychon. Soc.* **29**, 391 (1991); M. Usher and N. Donnelly, *Nature* **394**, 179 (1998)]. In these studies, individual, static frames from the flicker sequence contain visible luminance discontinuities that clearly differentiate figure from background. When rapidly flickered in antiphase, the two regions of the display blend into one and figure/ground segmentation becomes impossible. These experiments thus measured the temporal limits to figure/ground segregation. Other studies using flickering elements failed altogether to find evidence for spatial grouping from temporal synchrony [D. C. Kiper, K. R. Gegenfurtner, J. A. Movshon, *Vision Res.* **36**, 539 (1996); M. Fahle and C. Koch, *ibid.* **35**, 491 (1995)]. All of these studies—successes and failures—used figure and ground elements that flickered periodically, with only the rates and phases of flicker varying. Periodic flicker represents a highly predictable, deterministic signal, which, from an ecological perspective, constitutes a rather artificial event. In the natural environment, there exists considerable irregularity in the temporal structure of the optical input to vision. From an information-theoretical perspective, repetitively flashed elements convey little information and, in fact, may be relatively poor stimuli in terms of revealing the temporal resolving power of visual neurons [G. T. Buracas, A. M. Zador, M. R. DeWeese, T. D. Albright, *Neuron* **20**, 959 (1998)].
3. Neurophysiologists vigorously debate the role of temporal fine structure in neural coding. Some propose that sensory information may be represented in single neurons by temporal patterning among trains of action potentials [W. Bialek and F. Rieke, *Trends Neurosci.* **15**, 428 (1992); B. Richmond, L. Optican, H. Spitzer, *J. Neurophysiol.* **64**, 351 (1990); R. K. Snider, J. F. Kabara, B. R. Roig, A. B. Bonds, *ibid.* **80**, 730 (1998)]. In an extension of this idea, some believe that ensembles of neurons carry information about spatial coherence within the temporal coherence of those neurons' spike discharges [R. Eckhorn, R. Bauer, W. Jordan, M. Brosch, W. Kruse, *Biol. Cybern.* **60**, 121 (1988); W. Singer and C. M. Gray, *Annu. Rev. Neurosci.* **18**, 555 (1995)]. In contrast, others [M. N. Shadlen and W. T. Newsome, *J. Neurosci.* **18**, 3870 (1998)] believe that neurons are inherently too noisy for temporal patterning to carry useful information.

4. B. Julesz, *Foundations of Cyclopean Perception* (Univ. of Chicago Press, Chicago, 1971).
5. Borrowing ideas from information theory [C. E. Shannon and W. Weaver, *The Mathematical Theory of Communication* (Univ. of Illinois Press, Urbana, IL, 1949); W. R. Garner, *Uncertainty and Structure as Psychological Concepts* (Wiley, New York, 1962)], we can characterize a series of signals over time as an ensemble of n distinct messages $\{m_1, m_2, \dots, m_n\}$, whose individual probabilities $\{p_1, p_2, \dots, p_n\}$ sum to unity. Then the information (expressed in binary units: bits) conveyed by each message is given by

$$H_i = -\log_2(p_i)$$
 and the average information associated with the entire ensemble of messages is given by

$$H_{av} = -\sum_{i=1}^n p_i \log_2(p_i)$$
 Although not widely used in work in visual perception, the concept of entropy has been successfully applied in the study of human stereopsis [B. Julesz and C. W. Tyler, *Biol. Cybern.* **23**, 25 (1976)] and motion perception [D. Gilden, E. Hiris, R. Blake, *Psychol. Sci.* **6**, 235 (1995)].
6. D. R. Brillinger, *Can. J. Stat.* **22**, 177 (1994); R.-D. Reiss, *A Course on Point Process* (Springer-Verlag, New York, 1993).
7. Gray-scale animations were created on a NEC 21-inch monitor (frame rate 100 Hz; pixel resolution 1024 vertical by 768 horizontal; P104 phosphor) using Matlab in conjunction with the Psychophysics toolbox [D. Brainard, *Spat. Vision* **10**, 443 (1997)]; all display and trial-related events were programmed on a Macintosh Power PC computer. Luminance nonlinearities were corrected using a calibrated look-up table. The display consisted of 676 Gabor elements regularly arrayed within a 6.7° by 6.7° square (average luminance 24.5 cd/m^2). Individual Gabor elements did not overlap visually within the array. Each Gabor patch was the product of a sinusoidal grating and a circular Gaussian envelope with a standard deviation of ± 4.5 arc min. The peak spatial frequency of every grating was 5.8 cycles per degree (bandwidth 1.2 octaves), the contrast of every grating was 0.80, and the orientation of each grating was randomly set. Each grating moved at 3.45° per second in one of two directions orthogonal to its orientation, with smooth apparent motion being produced by phase-shifting the grating from frame to frame of the animation by one-fifth of the grating cycle synchronized to the monitor frame rate. The direction of motion of each grating within the stationary window reversed over time unpredictably according to the Poisson distribution. New animations were created and stored on hard disk before each test session. Demonstrations of these displays can be seen at <http://www.psy.vanderbilt.edu/faculty/blake/Demos/TS/TS.html>.
8. One of the principles of perceptual organization identified by Gestalt psychologists was common fate, a form of temporal structure in which visual elements moving in the same direction appear to group into a single object. Birds flying in the same direction, for example, perceptually form a global unit called a flock.
9. D. Regan and S. Hamstra, *Perception* **20**, 315 (1991).
10. Each stimulus element in this display consisted of a radial grating 19 arc min in diameter. Each grating resembled a circular "windmill" divided into four equal-sized wedges, two black and two white. The starting phase of each windmill was random. When animated, each windmill rotated 45° ($1/2$ wedge size) from frame to frame, producing smooth apparent rotation whose direction was unambiguous. Average luminance of the display was 24.5 cd/m^2 . For the stereoscopic experiment involving presentation of two windmill arrays, each array consisted of 324 windmills within a 5.8° by 5.8° square. Each array contained two virtual "figure" regions, each 1.9° (horizontal) by 1.3° (vertical) on a side, located immediately above and below a small, central fixation mark. Crossed disparity was introduced into the upper pair of figures or the lower pair of figures by shifting the corresponding "figure" regions 1 windmill diameter to the left in one eye and 1 diameter to the right in the other eye; this produced an effective

disparity of 38.6 arc min. For this experiment, rotational reversals of windmills defining the background region of the two half-images followed one point process, reversals of windmills defining the upper pair of "figures" in the two half-images followed another point process, and the reversals for the lower pair of "figures" followed a third point process.

11. In preliminary work we also found that synchronized, irregular changes in luminance can promote spatial grouping [S.-H. Lee and R. Blake, *Invest. Ophthalmol. Visual Sci.* **40**, S45 (1999)]; S. E. Palmer (paper presented at the 39th annual meeting of the Psychonomic Society, Dallas, TX, 21 November 1998) found that periodic, synchronized changes in size, shape, or color can bias perceptual organization.
12. D. Regan, *Vision Res.* **29**, 1389 (1989); S. Anstis and V. S. Ramachandran, in *The Artful Eye*, R. Gregory, J. Harris, P. Heard, D. Rose, Eds. (Oxford Univ. Press, New York, 1995), p. 232; M. Bravo and R. Blake, *Vision Res.* **32**, 1793 (1992); D. J. Field, A. Hayes, R. F. Hess, *ibid.* **33**, 173 (1993).
13. I. Biederman, *Psychol. Rev.* **94**, 115 (1987); M. C. Mozer, *The Perception of Multiple Objects: A Connectionist Approach* (MIT Press, Cambridge, MA, 1991); S. Grossberg, *Neural Networks* **6**, 463 (1993); S. P.

Vecera and R. C. O'Reilly, *J. Exp. Psychol. Hum. Percept. Perform.* **24**, 441 (1998).

14. Models of structure from motion extract discontinuities—boundaries—within a field of local motion vectors, with grouping based on common directions or speeds of motion [N. M. Grzywacz, S. N. J. Watamaniuk, S. McKee, *Vision Res.* **35**, 3183 (1995); W. B. Thompson, D. Kersten, W. R. Knecht, *Biol. Cybern.* **66**, 327 (1992); J. Chey, S. Grossberg, E. Mingolla, *J. Opt. Soc. Am. A* **14**, 2570 (1997)]. In our displays, motion direction is completely random throughout the array of elements. Speed too is constant except at the moment of reversal. It is conceivable that reversals in motion direction create brief transients in speed-selective neurons, which could constitute the neural embodiment of the point processes defining temporal structure (Fig. 1C).
15. C. Chubb and G. Sperling, *J. Opt. Soc. Am. A* **5**, 1986 (1988); H. R. Wilson and J. Kim, *Vis. Neurosci.* **11**, 1205 (1994); P. Cavanagh, *Science* **257**, 1563 (1992); Z.-L. Lu and G. Sperling, *Nature* **377**, 237 (1995).
16. Supported by NIH grants EY07760 and EY01826. We thank J. Schall, A. B. Bonds, M. Donnelly, S. Grossberg, W. Newsome, and J. Lappin for helpful discussions.

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Bone Marrow as a Potential Source of Hepatic Oval Cells

B. E. Petersen,^{1*} W. C. Bowen,¹ K. D. Patrene,² W. M. Mars,¹ A. K. Sullivan,^{4†} N. Murase,³ S. S. Boggs,² J. S. Greenberger,² J. P. Goff²

Bone marrow stem cells develop into hematopoietic and mesenchymal lineages but have not been known to participate in production of hepatocytes, biliary cells, or oval cells during liver regeneration. Cross-sex or cross-strain bone marrow and whole liver transplantation were used to trace the origin of the repopulating liver cells. Transplanted rats were treated with 2-acetylaminofluorene, to block hepatocyte proliferation, and then hepatic injury, to induce oval cell proliferation. Markers for Y chromosome, dipeptidyl peptidase IV enzyme, and L21-6 antigen were used to identify liver cells of bone marrow origin. From these cells, a proportion of the regenerated hepatic cells were shown to be donor-derived. Thus, a stem cell associated with the bone marrow has epithelial cell lineage capability.

Hepatic oval cells proliferate under certain conditions, mainly when hepatocytes are prevented from proliferating in response to liver damage, and may be stem cells for hepatocytes and bile duct cells or the intermediate progeny of a hepatic stem cell. Oval cells may originate either from cells present in the canals of Herring (1) or from blastlike cells located next to bile ducts (2). Oval cells have been shown to proliferate in certain pathological conditions, in which hepatocyte prolifer-

ation is inhibited before severe hepatic injury. In experimental models, hepatocyte proliferation is suppressed by exposure of the animal to 2-acetylaminofluorene (2-AAF), and hepatic injury can be induced by partial hepatectomy or by administration of carbon tetrachloride (CCl_4) (3, 4). Oval cells express CD34, Thy-1, and c-kit mRNAs and proteins (5–7) and flt-3 receptor mRNA (8), all of which are also found in hematopoietic stem cells (HSC).

We tested the hypothesis that oval cells and other liver cells may arise from a cell population originating in, or associated with, the bone marrow (BM). This hypothesis was tested by three approaches: (i) bone marrow transplantation (BMTx) from male rats into lethally irradiated syngeneic females and detection of donor cells in the recipients by means of DNA probes to the Y chromosome *sry* region; (ii) BMTx from dipeptidyl peptidase IV-positive (DPPIV⁺) male rats into DPPIV[−] syngeneic females and detection of

¹Department of Pathology, ²Department of Radiation Oncology, ³Division of Transplant Pathology, Department of Pathology, School of Medicine, University of Pittsburgh, Pittsburgh, PA 15261, USA. ⁴Department of Hematology/Oncology, McGill University, Quebec H3A 2T5, Canada.

*To whom correspondence should be addressed. E-mail: bryon+@pitt.edu

†Present address: Department of Oncology, King Faisal Specialist Hospital and Research Centre, Post Office Box 3354, Riyadh, Kingdom of Saudi Arabia.