has independently acquired a mechanism for repressing stem cell division. Because isolated stem cells can proliferate in the absence of exogenous growth factors and the size of the stem cell population may be regulated in vivo by the number of NR progenitor cells during development, this quiescence is likely due to an inhibitory environment in the adult eye. Once freed from the inhibition (or if inhibitory factors can be overcome in vivo), the stem cells have the potential to generate new retinal cells.

References and Notes

1. C. L. Cepko, C. P. Austen, X. Yang, M. Alexiades, D. Ezzeddine, *Proc. Natl. Acad. Sci. U.S.A.* **93**, 589 (1996); C. Pittack, G. B. Grunwald, T. A. Reh, *Development* **124**, 805 (1997).
2. A. Feijen, M. J. Goumans, A. J. M. van den Eijnden-van Raaij, *Development* **120**, 3621 (1994).
3. L. Bodenstein and R. L. Sidman, *Dev. Biol.* **121**, 192 (1987).
4. P. R. Johns, *J. Comp. Neurol.* **176**, 343 (1977); R. Wetts, G. N. Serbedzija, S. E. Fraser, *Dev. Biol.* **136**, 254 (1989).
5. J. L. Coulombre and A. J. Coulombre, *Dev. Biol.* **12**, 79 (1965); C. M. Park and M. J. Hollenberg, *Dev. Biol.* **134**, 201 (1989).
6. B. A. Reynolds and S. Weiss, *Science* **255**, 1707 (1992); C. Lois and A. Alvarez-Buylla, *Proc. Natl. Acad. Sci. U.S.A.* **90**, 2074 (1993); C. M. Morshead *et al.*, *Neuron* **13**, 1071 (1994); C. G. Craig *et al.*, *J. Neurosci.* **16**, 2649 (1996); H. G. Kuhn, H. Dickinson-Anson, F. H. Gage, *J. Neurosci.* **16**, 2027 (1996); J. O. Suhonen, D. A. Peterson, J. Ray, F. H. Gage, *Nature* **383**, 624 (1996).
7. S. Weiss *et al.*, *Trends Neurosci.* **19**, 387 (1996); R. D. McKay, *Science* **276**, 66 (1997).
8. For details of experimental procedures, see supplementary Web material, available at www.sciencemag.org/feature/data/1046592.shl.
9. Web figures 1 and 2 are available at www.sciencemag.org/feature/data/1046592.shl.
10. V. Tropepe *et al.*, *Dev. Biol.* **208**, 166 (1999).
11. C. M. Morshead, V. Tropepe, B. J. Chiasson, D. van der Kooy, *Soc. Neurosci. Abstr.* **24**, 1528 (1998).
12. C. S. Potten and M. Loeffler, *Development* **110**, 1001 (1990); S. J. Morrison, N. M. Shah, D. J. Anderson, *Cell* **88**, 287 (1997).
13. G. M. Truslove, *J. Embryol. Exp. Morphol.* **10**, 652 (1962); I. S. C. Liu *et al.*, *Neuron* **13**, 377 (1994); M. Burmeister *et al.*, *Nature Genet.* **12**, 376 (1996); B. V. Konyukhov and M. V. Sazhina, *Folia Biol. (Prague)* **12**, 116 (1966); B. V. Konyukhov and M. V. Sazhina, *Dev. Biol.* **45**, 1 (1975).
14. S. Hockfield and R. McKay, *J. Neurosci.* **5**, 3310 (1985); F. Doetsch, J. M. Garcia-Verdugo, A. Alvarez-Buylla, *J. Neurosci.* **17**, 5046 (1997).
15. D. Hicks and C. J. Barnstable, *J. Histochem. Cytochem.* **35**, 1317 (1987); D. R. Zhang and H. H. Yeh, *Visual Neurosci.* **6**, 429 (1991); M. W. Kelley, J. K. Turner, T. A. Reh, *Development* **120**, 2091 (1994); R. A. Bascom *et al.*, *Neuron* **8**, 1171 (1992).
16. E. M. Levine, H. Roelink, J. Turner, T. A. Reh, *J. Neurosci.* **17**, 6277 (1997).
17. T. Furukawa, E. M. Morrow, C. L. Cepko, *Cell* **91**, 531 (1997); C. L. Freund *et al.*, *Cell* **91**, 543 (1997); S. Chen *et al.*, *Neuron* **19**, 1017 (1997).
18. V. Tropepe, C. G. Craig, C. M. Morshead, D. van der Kooy, *J. Neurosci.* **17**, 7850 (1997).
19. S. Zhao, S. C. Thornquist, C. I. Barnstable, *Brain Res.* **677**, 300 (1995); D. S. Sakaguchi, L. M. Janick, T. A. Reh, *Dev. Dyn.* **209**, 387 (1997).
20. T. A. Reh and T. Nagy, *Dev. Biol.* **122**, 471 (1987); J. G. Hollyfield, *J. Comp. Neurol.* **144**, 373 (1971); C. Straznicky and R. M. Gaze, *J. Embryol. Exp. Morphol.* **27**, 67 (1971); D. H. Beach and M. Jocobson, *J. Comp. Neurol.* **183**, 603 (1979); M. Ilia and G. Jeffery, *Dev. Brain. Res.* **95**, 176 (1996).

21. We thank D. Vidgen and L. Ploder for excellent technical assistance; R. McKay for the antibody to nestin; C. Barnstable, R. Molday, and G. Travis for retinal-specific antibodies; K. Hadjantonakis and A. Nagy for GFP mice; and C. Cepko for the Crx plasmid. This work was supported by the Medical Research Council of Canada, the Canadian Network of Centres of Excellence Genetics and Neuroscience Networks, and University Medical Discoveries. R.R.M. is an International Research Scholar of the Howard Hughes Medical Institute.

26 October 1999; accepted 4 February 2000

Motion Integration and Postdiction in Visual Awareness

David M. Eagleman[1,2,4]* and Terrence J. Sejnowski[2,3,4]

In the flash-lag illusion, a flash and a moving object in the same location appear to be offset. A series of psychophysical experiments yields data inconsistent with two previously proposed explanations: motion extrapolation (a predictive model) and latency difference (an online model). We propose an alternative in which visual awareness is neither predictive nor online but is postdictive, so that the percept attributed to the time of the flash is a function of events that happen in the ~80 milliseconds after the flash. The results here show how interpolation of the past is the only framework of the three models that provides a unified explanation for the flash-lag phenomenon.

The flash-lag effect is a robust visual illusion wherein a flash and a moving object that appear in the same location are perceived to be displaced from one another (*1*, *2*). Two explanations have been suggested in recent years: The first proposal is that the visual system is predictive, accounting for neural delays by extrapolating the trajectory of a moving stimulus into the future (*2*). The second is that the visual system processes moving objects more quickly than flashed objects. This "latency difference" hypothesis asserts that by the time the flashed object is processed, the moving object has already moved to a new position (*3*, *4*). The latter proposal tacitly rests on the assumption that awareness (what the participant reports) is an online, or real-time, phenomenon, coming about as soon as a stimulus reaches its "perceptual end point" (*5*). We have designed a series of psychophysical experiments to directly test these two frameworks. Our results are inconsistent with both models. Here we propose that visual awareness is postdictive, so that the percept attributed to the time of an event is a function of what happens in the ~80 ms following the event.

To directly test extrapolation into the future against interpolation of the past, we designed a series of psychophysical experiments. Five participants sat in front of a computer screen and were instructed to indicate whether a flashed white disk occurred above or below the center of a moving ring (Fig. 1A) (*6*). Beginning with the frame following the flash, the ring took one of three randomly interleaved trajectories: continuing, stopping, or reversing direction (Fig 1A). The initial trajectory of the ring (up to and including the frame with the flash) was identical in all three conditions; thus, if motion extrapolation were occurring, the predicted trajectory should be the same. Contrary to that hypothesis, the perceived position of the flash relative to the ring was independent of the initial trajectory. In the case of the uninterrupted trajectory, participants perceived the flash to be in the middle of the ring when the flash was physically displaced $5.39° \pm 0.9°$ in front of the moving ring, as expected from previous studies of the flash-lag effect. However, in the presentations wherein the moving ring stopped, participants reported the ring and flash co-localized when there was no displacement ($-0.36° \pm 0.27°$), indicating that movement preceding the flash does not by itself engender the flash-lag illusion. When the ring reversed direction immediately after the flash participants reported colocalization of the ring and the flash only when the flash was physically displaced by an average of $-6.47° \pm 0.8°$. The direction of the flash-lag effect is opposite in the continuous and reversing conditions, but the magnitude of the effect is the same (t test, $P > 0.398$, $t = -0.89$). On the other hand, those two conditions are significantly different from the stopping condition ($P < 0.0017$, $t = 6.11$), wherein no illusion is seen (*7*).

These results indicate that the perceived position of the flash relative to the ring is not dictated by the initial trajectory because if visual awareness were predictive, the same initial trajectory would lead to the same extrapolation Our results are consistent with a recent demonstration by Whitney and Murakami in which the perceived displacement of a flash was influ-

[1]Sloan Center for Theoretical Neurobiology, [2]Computational Neurobiology Laboratory, [3]Howard Hughes Medical Institute, The Salk Institute for Biological Studies, 10010 North Torrey Pines Road, La Jolla, CA 92037, USA. [4]Department of Biology, University of California at San Diego, 9500 Gilman Drive, La Jolla, CA 92093, USA.

*To whom correspondence should be addressed. E-mail: eagleman@salk.edu

enced by a motion change that occurred after the flash (*4*). In our experiment, by directly comparing stimuli with an identical pre-flash trajectory to three different post-flash trajectories, we demonstrated that the perceived displacement of the flashed and moving stimuli is a function of the movement after the flash. (In the stopped case there is no flash-lag effect at all.) Thus, we suggest that the perception attributed to an event at time t_0 depends on what happens in $t_0 < t < t_0 + h$, where h is a window of time whose magnitude serves as a lower bound on the length of the delay before visual awareness.

To verify that the pre-flash trajectory plays no role in the flash-lag effect, we made another test in which the flash and ring appeared on the screen at the same time and the ring's movement began in the next video frame (*8*). Thus, there is no trajectory (no previous motion) from which to extrapolate. The results (Fig. 1B) are essentially unchanged from Fig. 1A ($P > 0.75$, $P > 0.35$, $P > 0.55$, for the continuous, stopped, and reversed cases, respectively), supporting the conclusion that motion extrapolation is untenable and that only events after the flash determine the perception. The similarity of results in Fig. 1, A and B, suggests that the flash resets motion integration in the visual system, making motion after the flash effectively like motion that starts de novo (Fig. 1B). One explanation may be that the flash temporarily redirects attention (*9*).

To determine how much information the brain integrates after the flash for its decision, we designed stimuli analogous to those in Fig. 1B but included a direction reversal. Immediately after the flash, the ring moves in one direction and then it reverses direction after a variable number of video frames (Fig. 2). If the visual system only uses information from the 10 to 20 ms after the flash (as might be predicted from Fig. 1, and from the latency difference hypothesis), then the trajectory of the ring after that time window should not affect the percept. Contrary to that hypothesis, movement up to 80 ms after the flash influences the percept. We find that 67 to 80 ms of unidirectional movement is necessary to approach the illusory displacement measured in Fig. 1. As the amount of time before the reversal is reduced, the illusory displacement is lessened, and with only 26 ms before reversal, the flash-lag effect is effectively canceled out (as though the ring were stopped). With only one video frame remaining before reversal, the perceived displacement changes direction (*10*). These data are consistent with a temporally weighted spatial averaging that takes place during the ~80 ms after the flash. Physiological mechanisms for the spatiotemporal filtering may involve a form of temporal recruitment, the process by which motion signals in the neural tissue are combined over time (*11*). However, most of the available literature implicitly assumes that motion integration would occur over the time before the flash, i.e., the visual system would collect information until the time of the stimulus, with perceptual processing following online. Our data indicate instead that the visual system integrates information after the flash, which necessitates that perception be delayed. The direction reversal experiment indicates that the position of the moving object is interpolated as a point within the integrated path, and given the results of Fig. 1, A and B, our interpretation is that the flash serves to reset the motion integration.

To further examine our interpretation, we next separated the temporal coincidence of the flash and the moving object. A latency difference model assumes a "race" between a flash and a moving object to a perceptual end point; thus, we reasoned that giving the flash a temporal advance should change the outcome of such a race. Participants were instructed to adjust the angle of a "pointer" line (flashed for 13 ms) to point to the beginning of the trajectory of the moving ring (Fig. 3). The pointer was flashed and then the moving ring appeared.

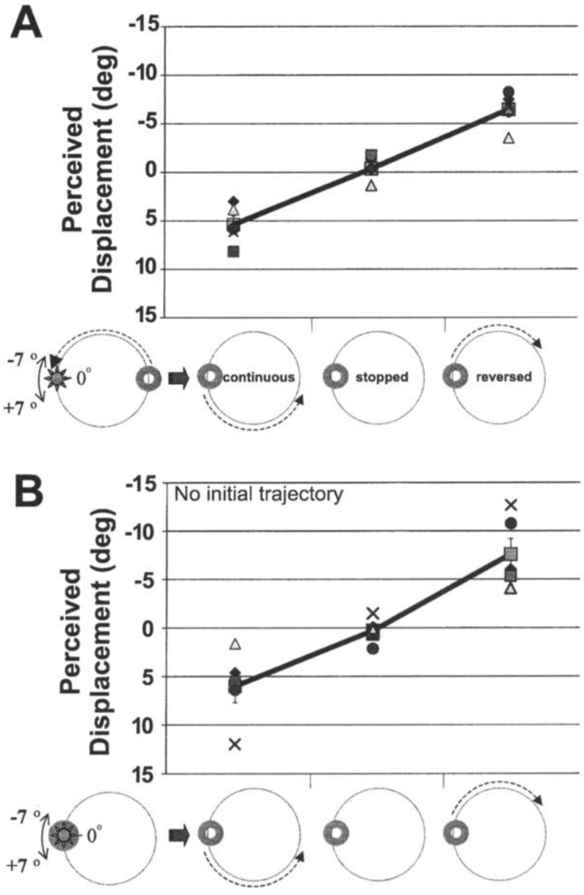

Fig. 1. The flash-lag illusion with variable outcomes after the flash. (**A**) Participants reported whether they perceived a flash above or below the center of a moving ring (forced choice). The ring moved in a circular trajectory at a speed of 360° s^{-1}. When the ring reached the opposite side, a flash (bright white disk) appeared in a range that extended above and below the ring on its trajectory, in 7° each direction. After the flash, one of three conditions followed: The ring continued, stopped, or reversed. Participants were instructed to fixate on a small square 1° to the right of the flash location; however, eye fixation was not monitored, as the three conditions were randomly interleaved to obviate any predictive effects. The initial trajectory of the ring was mirrored in half the trials. The same results were found with repeated presentations of the same trajectory (*18*), indicating that prediction does not appear to enhance or diminish the perceptual effect. Symbols represent the average displacement at which participants' psychometric curves crossed 50% (the point of perceived alignment of flash and ring). The thick line marks the average for five participants ± SE (*19*). (**B**) Same paradigm as in (A), but here the ring and flash appear simultaneously on a blank screen. Results are not significantly different from (A). The illusion is unchanged even if the ring is initially present and set in motion after the flash, as opposed to simultaneous onset here.

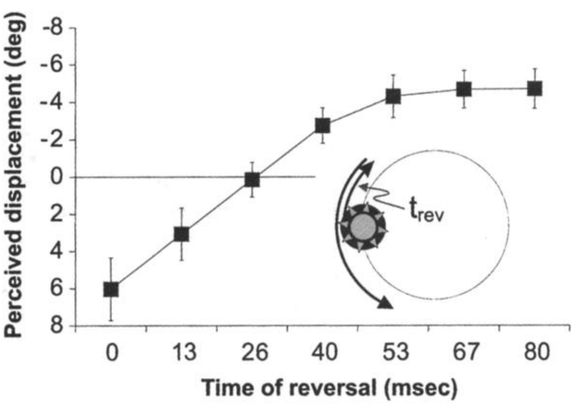

Fig. 2. Determining the time window of influence by means of direction reversals. The paradigm is identical to Fig. 1B, except that after the flash the ring reverses direction after a variable time, t_{rev} (13 to 80 ms) ($n = 6$). The data point at $t_{rev} = 0$ is taken from Fig. 1B and represents the perceived displacement when the ring makes no reversal, e.g., it simply moves counterclockwise instead of starting clockwise and then reversing.

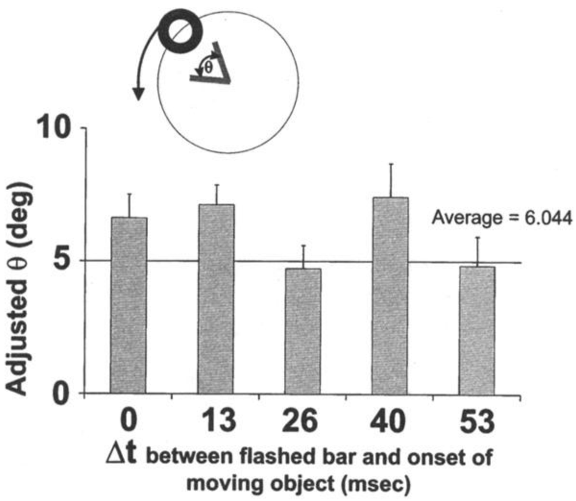

Fig. 3. Separating the flash and moving object in time. Participants were instructed to adjust the radial angle (θ) of a flashed pointer to indicate the starting position of a sudden-onset moving ring. The available range of adjustment was between −18° and 18°, where 0° on the ordinate marks the actual starting position of the ring. At $\Delta t = 0$, the flash and ring appeared in the same frame; in the remaining four conditions, the ring did not appear until some delay after the 13 ms with the flash (Δt = 13, 26, 40, or 53 ms). Bars represent averages from 10 participants ± SEM.

These two stimuli were separated by a stimulus onset asynchrony Δt ranging from 0 to 53 ms. Thus, in one condition, the flash and ring appeared on the same frame ($\Delta t = 0$), but in the remaining four conditions, a variable delay after the single frame with the flash (13 ms $< \Delta t <$ 53 ms) preceded the appearance of the ring. The sequence was repeated after a 1 s delay and participants were allowed to see a condition as many times as they wished before committing to an answer. Regardless of the length of the delay, participants adjusted the pointer to indicate a position an average of ~6° ahead of the actual starting position of the ring (this is the same magnitude as the displacements in Figs. 1 and 2). These results do not support the latency difference model because giving the flash a head start does not change the perceptual outcome. Instead, this demonstrates that participants do not correctly perceive the starting position of a newly moving object—a long-known observation called the Frohlich effect (*12*)—but instead perceive an interpolation of its past positions. Thus, the entirety of the flash-lag effect in Fig. 1B can be explained by the fact that the starting point of a newly moving object is interpolated (misperceived). Further, it seems the traditional flash-lag effect (Fig. 1A) is well explained by our suggestion that a flash resets motion integration.

The evidence presented here does not support the two frameworks previously proposed to explain the flash-lag illusion. First, we demonstrated that the illusory displacement between moving and flashed stimuli is independent of the pre-flash trajectory of the moving object and depends entirely on movement after the flash. Many previous experiments appeared to be consistent with motion extrapolation (*2, 13*) only because the movement after the flash happened to be continuous with the movement before. For an action such as catching a ball, it is unnecessary for extrapolation to take place in visual perception because neural delays can be compensated for in the training of the motor systems. Second, we demonstrated that even when the flash occurs at various times before the moving object appears, the degree of misperception of the moving object is the same. The latency difference model is unsupported by the result in Fig. 3 and cannot explain the results in Fig. 1B, wherein the "moving" object does not begin to move until after the flash. In this case, the newly appearing moving object should initially suffer the same processing delays as the flashed stimulus. We suggest that although latency differences may apply to other phenomena (for example, the Pulfrich effect wherein one retina is dark-adapted), they are not relevant to the flash-lag effect.

We have proposed an alternative hypothesis: The flash resets motion integration, and motion is newly calculated and postdicted to the time of the flash. This hypothesis requires visual awareness to be postdictive, a conclusion already supported elsewhere (*14*). For example, in backward masking (*15*) the perception of a stimulus can be blocked or modified if it is followed in rapid succession by a second stimulus. Another example is the color phi phenomenon (*16*), wherein two colored dots, presented sequentially within small amounts of time and distance, will appear to have changed color in the middle of their apparent trajectory. Because the viewer cannot know the color of the second dot until having seen the second dot, the conscious percept attributed to the time of the trajectory must be formed in retrospect. Overall, these experiments indicate that the visual system consults the ongoing input of information from the near future of an event before committing to a percept (*17*). This postdictive framework has implications for interpreting physiological data related to visual perception.

References and Notes

1. D. MacKay, *Nature* **181**, 507 (1958).
2. R. Nijhawan, *Nature* **370**, 256 (1994).
3. M. V. Baldo and S. A. Klein, *Nature* **378**, 565 (1995); G. Purushothaman, S. S. Patel, H. E. Bedell, H. Ogmen, *Nature* **396**, 424 (1998).
4. D. Whitney and I. Murakami, *Nature Neurosci.* **1**, 656 (1998); expanded upon in D. Whitney, I. Murakami, P. Cavanagh, *Vision Res.* **40**, 137 (2000).
5. S. Zeki and A. Bartels, *Proc. R. Soc. London Ser. B* **265**, 1583 (1998).
6. The rotational speed of the ring was 360° s^{-1}. The trajectory of the stimulus covered 4° of the visual angle; the inner diameter of the moving ring and outer diameter of the flashed disk were 1°. All stimuli were programmed in C on a Silicon Graphics workstation, with a monitor refresh rate of 72 Hz = 13.3 ms/frame.
7. Data was also gathered from several participants at a slower motion speed (rotational ring speed 180° s^{-1}) with proportionally scaled results (displacement for the continuous case, 3.3° ± 1.3°; for the stopped case, −0.3° ± 0.6°; for the reversed case, −4.5° ± 0.6°; $n = 8$).
8. This paradigm is analogous to the "flash-initiated cycle" used by B. Khurana and R. Nijhawan, *Nature* **378**, 566 (1995).
9. S. Yantis and J. Jonides, *J. Exp. Psychol. Hum. Percept. Perform.* **10**, 601 (1984); E. Weichselgartner and G. Sperling, *Science* **238**, 778 (1987); J. Musseler and G. Aschersleben, *Percept. Psychophys.* **60**, 683 (1998); K. Watanabe and S. Shimojo, *Perception* **27**, 1041 (1998).
10. Results are the same when the ring appears for only six frames after the appearance of the flash, as opposed to remaining on screen until the end of the trial ($n = 2$ of the 6 participants).
11. R. J. Snowden and O. J. Braddick, *Vision Res.* **29**, 1621 (1989); *Vision Res.* **31**, 907 (1991); B. Krekelberg and M. Lappe, *Vision Res.* **39**, 2669 (1999).
12. F. W. Frohlich, *Z. Sinnesphysiol.* **54**, 58 (1923).
13. A model for the flash-lag effect based on motion extrapolation from retinal mechanisms has been proposed [M. J. Berry II, I. H. Brivanlou, T. A. Jordan, M. Meister, *Nature* **398**, 334 (1999)]; however, that model does not predict our results (for example, compare predictions from our stopped and reversed conditions). Because we propose that motion extrapolation does not explain the flash-lag effect, we do not interpret the retinal data from Berry *et al.* as directly relevant to the psychophysics. Further, a recent paper shows that the flash-lag illusion is not limited to low-level visual mechanisms but instead integrates other modalities such as the vestibular systems [J. Schlag, R. H. Cai, A. Dorfman, A. Mohempour, M. Schlag-Rey, *Nature* **403**, 38 (2000)]. Such cross-modal interactions may require more processing time, just the sort of need for which a perceptual delay could make allowances.
14. B. Libet, E. W. Wright, B. Feinstein, D. K. Pearl, *Brain* **102**, 193 (1979); D. C. Dennet, *Consciousness Explained* (Little, Brown, Boston, 1992); D. C. Dennet and M. Kinsbourne, *Behav. Brain Sci.* **15**, 183 (1992); M. Kinsbourne, *Ciba Found. Symp.* **174**, 43 (1993); L. Pessoa, E. Thompson, A. Noe, *Behav. Brain Sci.* **21**, 723 (1998).
15. T. Bachmann, *Psychophysiology of Visual Masking* (Nova Science, Commack, NY, 1994).
16. P. Kolers and M. von Grunau, *Vision Res.* **16**, 329 (1976).
17. This method of estimating a value in a time series by using values from the future is known as smoothing in the engineering literature and has recently been appreciated as a useful strategy for many systems (R. P. Rao, D. M. Eagleman, T. J. Sejnowski, in preparation).
18. D. M. Eagleman and T. J. Sejnowski, data not shown.
19. Demonstrations of the stimuli and supplemental information can be found at www.cnl.salk.edu/~eagleman/flashlag.

20. We thank R. Rao, T. Wachtler, F. Crick, O. Braddick, T. Albright, and A. Messinger for helpful discussions. Supported by the Sloan Center for Theoretical Neurobiology and by an National Institute of Mental Health training grant in cognitive neuroscience.

15 November 1999; accepted 27 January 2000