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.

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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

¹Sloan Center for Theoretical Neurobiology, ²Computational Neurobiology Laboratory, ³Howard Hughes Medical Institute, The Salk Institute for Biological Studies, 10010 North Torrey Pines Road, La Jolla, CA 92037, USA. ⁴Department 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

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-

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 are combined over time in the neural tissue (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 $\pm$ 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.
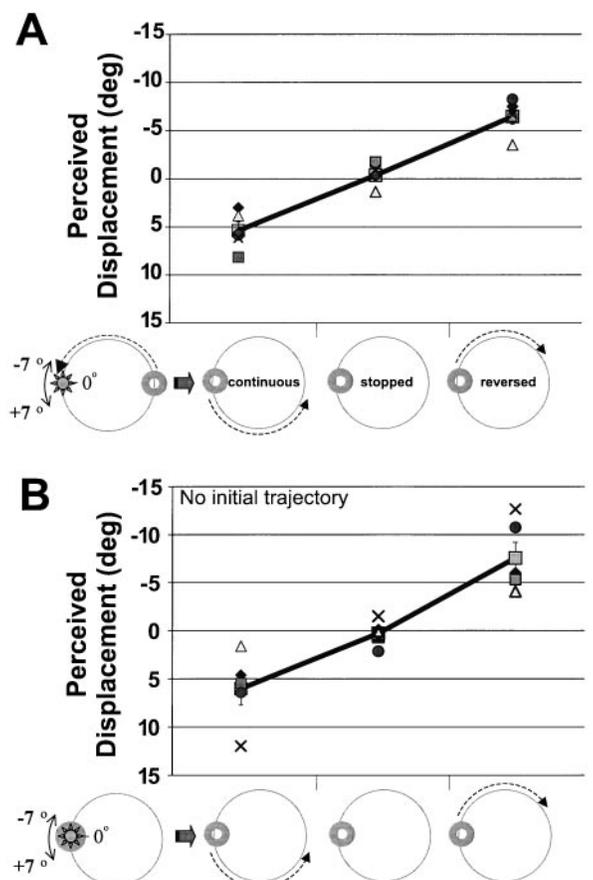

Fig. 2. Determining the time window of influence by means of direction reversals. The paradigm is identical to Fig. 1B, except that after the flash the ring reverses direction after a variable time, t_{rev} (13 to 80 ms) ($n = 6$). The data point at $t_{rev} = 0$ is taken from Fig. 1B and represents the perceived displacement when the ring makes no reversal, e.g., it simply moves counterclockwise instead of starting clockwise and then reversing.
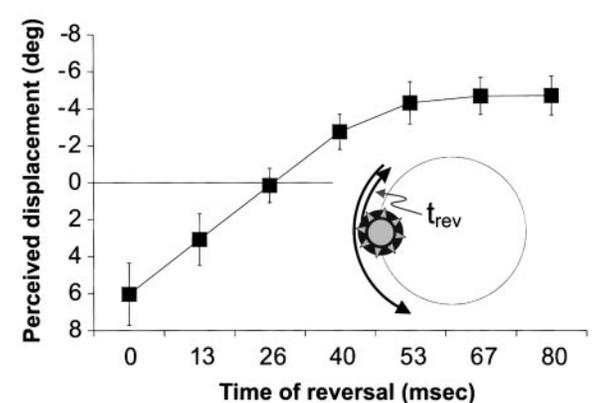
Fig. 3. Separating the flash and moving object in time. Participants were instructed to adjust the radial angle (θ) of a flashed pointer to indicate the starting position of a sudden-onset moving ring. The available range of adjustment was between −18° and 18°, where 0° on the ordinate marks the actual 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 ($\Delta t = 13$, 26, 40, or 53 ms). Bars represent averages from 10 participants ± SEM.
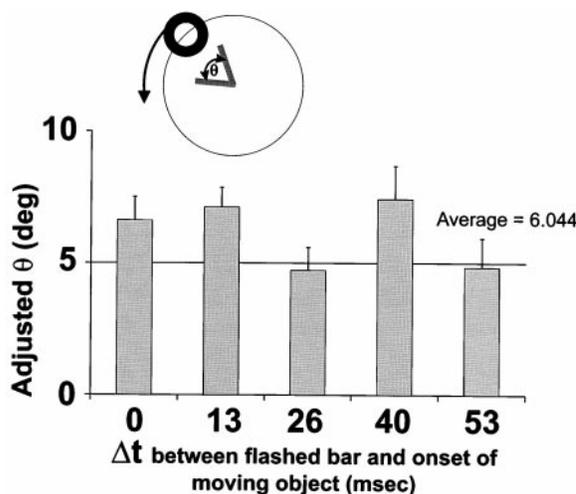
These two stimuli were separated by a stimulus onset asynchrony Δt ranging from 0 to 53 ms. Thus, in one condition, the flash and ring appeared on the same frame ($\Delta t = 0$), but in the remaining four conditions, a variable delay after the single frame with the flash (13 ms < Δt < 53 ms) preceded 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.

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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).
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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.

The Position of Moving Objects

Eagleman and Sejnowski (*1*) showed that the flash-lag effect (*2, 3*)—a visual illusion in which two objects physically at the same location appear to be offset because of differing motion trajectories—cannot be explained by latency correction (*4*) or by differential latencies for flashed and moving objects (*5–7*). Our work, like theirs, has found that the flash-lag effect is due to the motion of the moving object after the flash, and we too have proposed that the perceived position of flashed and moving objects is based on temporal integration (*8–10*). We disagree, however, with the statement by Eagleman and Sejnowski that the flash "resets" this integration, and we see no need to "postdict" the perceived offset to the time of stimulus presentation.

To test the temporal-integration hypothesis, we used a stimulus, originally designed by Baldo and Klein (*11*), that involved seven dots,
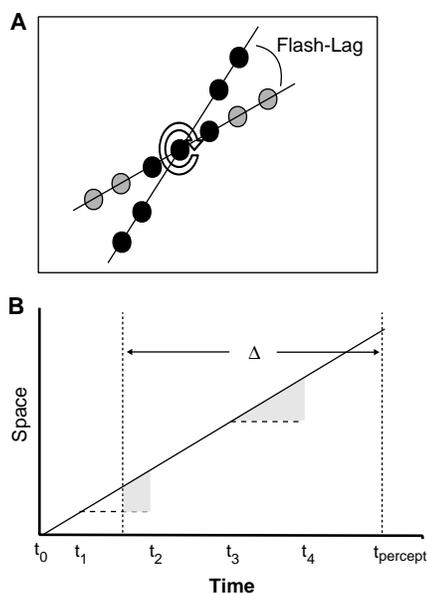

Fig. 1. The flash-lag effect and temporal integration of position signals. (**A**) The flash-lag stimulus. Seven dots in perfect alignment rotate around the central fixation point. The outer dots (gray) are visible only intermittently; the inner dots are continuously visible. Observers perceive a spatial offset between the outer, flashed dots and the inner dots (black dots show the percept). (**B**) The temporal-integration hypothesis as a space-time diagram. The motion trajectory of the inner dots is represented as the solid line; the outer dots are visible only from t_0 to t_1, from t_2 to t_3, and from t_4 onwards. When the outer dots are invisible, we assume that an internal position signal represents their last visible position (dashed line). The percept at time $t_{percept}$ is the average difference of the two position signals (solid and dashed lines) over a temporal-integration window Δ. This average is equivalent to the shaded area divided by Δ.

all of which rotated around the central fixation point (Fig. 1A). The inner three dots were continuously visible; the outer dots could be made visible or invisible at various times. Turning the dots on for only one videoframe at the start of the rotational movement led to a large flash-lag effect. If the dots were switched on again in a later videoframe (again in perfect physical alignment with the inner dots), the flash-lag was much reduced. Thus, the temporal integration did not stop between flashes, nor did the second flash reset the integration. By varying the number of flashes and the time between them, we were able to show that the temporal integration for this particular stimulus configuration extends over approximately half a second (*8–10*).

Figure 1B explains our temporal-integration hypothesis. The offset between two objects that is perceived at time *t* is given by the average of the difference of the two position signals over a time window Δ that precedes the moment of perception. In that time window, the moving object occupies multiple visible positions, but the flashed object is hidden. We suggest that the integration mechanism will, in the absence of an updated position signal, resort to using the last visible position of the flashed object. A temporal integration on the order of half a second quantitatively agrees with the data. Moreover, the model predicts that as more of the motion trajectory of the flashed object becomes visible, less flash-lag should remain, and that is indeed the case (*8, 9, 12*). Another prediction of the model is that it should be possible to abolish the flash-lag effect by halting the moving object after the flash or between multiple flashes. We confirmed that prediction for multiple flashes (*10*), and Eagleman and Sejnowski showed it to hold for single flashes [figure 1 of (*1*)].

Our work suggests that there is no need to postdict the perceived offset to the time of the flash. The causal chain of events is unambiguous: light hits the retina, neural mechanisms start processing the stimulus, and after some time a decision is reached to answer the question the experimenter asked. The observer need not relate this decision time to the time at which the light from the stimulus hit the retina, which only the experimenter knows. That motion after the flash influences the percept generated by that flash merely shows that visual processing takes time. That should be uncontroversial.

Bart Krekelberg
Markus Lappe
Department of Neurobiology
Ruhr University Bochum
Bochum 44780, Germany
E-mail: bart@neurobiologie.
ruhr-uni-bochum.de

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Eagleman and Sejnowski (*1*) recently proposed a "postdiction" model of the so-called flash-lag effect, in which a moving stimulus appears spatially to lead a flash, even though both stimuli are actually precisely aligned (*2*). According to postdiction, the moving object appears ahead of the flash because at each moment the object's position is estimated by integrating forward in time; the flash resets all the integrals so that only those starting immediately after the flash will produce a position estimate, and the forward average is necessarily in advance of the position of the flash.

Eagleman and Sejnowski suggested that this flash-reset mechanism also explains why a moving object that abruptly appears and starts to move is initially invisible for some distance, a phenomenon known as the Fröhlich effect (*3*). In the postdiction model, the abrupt onset of a moving object acts as a flash, so the first perceived position of the object, integrated during the following ~80 ms, is again well ahead of the object's actual first position. Alternative explanations for the flash-lag effect (*4−7*), by contrast, including our model of differential latencies for flashed and moving objects (*5*), are unable to account for the Fröhlich effect. Eagleman and Sejnowski conclude that if the flash-lag effect and the Fröhlich effect are caused by the same mechanism, and our differential-latency model fails to explain the Fröhlich effect, then our model must also be rejected as an explanation of the flash-lag phenomenon (*1*).

A closer examination, however, shows that postdiction explains neither the flash-lag effect nor the Fröhlich effect, and that our differential-latency model remains a viable account of the flash-lag phenomenon. According to postdiction, the flash resets all the ongoing motion integrals. That should render any nearby moving object invisible for the 80 ms before the flash's appearance, as occurs at the onset of motion in the Fröhlich effect. Thus, a series of flashes, each of them aligned with a moving object (within <80 ms of each

other), should continually reset all the integrals before any value is determined, completely masking the moving stimulus. When a series of aligned flashes is presented sequentially (7), however, the visibility of the motion is unaffected, and an undiminished flash-lag effect is seen for each individual flash.

In addition, contrary to the hypothesis of Eagleman and Sejnowski, we find that a single mechanism cannot account for both the flash-lag and Fröhlich effects (Fig. 1). When a stationary object was presented for 2500 ms ("stationary cue" in Fig. 1A), removed for 30 ms, and then presented again in immediate motion, the extent of the initial trajectory over which the object remained invisible was greatly reduced or eliminated (blue symbols in Fig. 1B). According to postdiction, the invisibility of motion initiation should not depend on events before the onset of motion, because the motion onset itself resets all ongoing integrals. Our data show that this is not

the case. The cue overrode the initial invisibility of the moving object and, thus, effectively abolished the Fröhlich effect; yet, regardless of whether the cue was presented, an adjacent flash (15 ms) aligned with the motion initiation appeared to lag behind the moving object, and the flash-lag effect remained (red symbols in Fig. 1B).

Our results show that the Fröhlich effect—the delayed onset of visibility of a target set abruptly in motion—is not a flash-lag effect. When Eagleman and Sejnowski claimed, in their third experiment, to have disproved the differential-latency model, they based their claim on the onset of visibility, that is, on the Fröhlich effect. That is not a test of our model. Our results with the stationary cue are consistent with previous suggestions that the Fröhlich effect involves attention and possibly metacontrast masking (8).

Postdiction thus is unable to account for the flash-lag and Fröhlich effects, because the two phenomena are actually caused by distinct mechanisms. Our differential latency model (5) remains a viable explanation of flash-lag data.

David Whitney
Patrick Cavanagh
Vision Sciences Laboratory
Harvard University
33 Kirkland Street
Cambridge, MA 02138, USA
E-mail: whitney@wjh.harvard.edu

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Response: Both the comment of Krekelberg and Lappe and that of Whitney and Cavanagh question our interpretation of the flash-lag effect and propose different explanatory models. However, both their results (*1–5*) and ours (*6*) can be explained within the postdictive framework we have proposed.

Specifically, the authors of both comments disagree with our hypothesis that the flash resets motion integration (i.e., previously collected information). We assume that the visual system has an internal model of external visual stimuli and that this internal model is compared continuously with new external measurements (*7*). If an unpredicted transient (such as a flash) occurs, it may be advantageous to temporarily devalue the internal

model and to rely more heavily on subsequent measurements. This need not be an all-or-none switch, however, as the authors of the comments apparently assume. Instead, the amount of information discarded will likely be graded and will depend on the salience of the transient stimulus: The greater the surprise, the less the internal model is relied upon. We hypothesize further that visual awareness requires a match between the internal model and external measurements, which is disrupted by the transient stimulus.

In the flash-lag effect, the internal model of the moving object is strongly discounted (i.e., reset) by the flash, and a new internal model of the moving stimulus is generated de novo; this situation yields the Fröhlich effect. Whitney and Cavanagh argue that the flash-lag effect is not an expression of the Fröhlich effect. In the experiments that they report to establish that argument, however, more than one parameter was changed between conditions. In one condition (stationary cue, no flash), the brief offset of the cue was only moderately salient, and thus the illusory displacement that followed was small. The other three conditions, by contrast, contained a flash, or the sudden, unpredicted onset of the square, or both; under those conditions, the salience of the stimulus was higher and the illusory displacement was larger, as we would predict. The experiments of Whitney and Cavanagh thus do not rule out the relationship between the flash-lag effect and the Fröhlich effect, but rather serve to illustrate
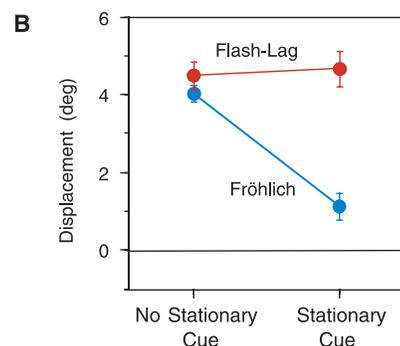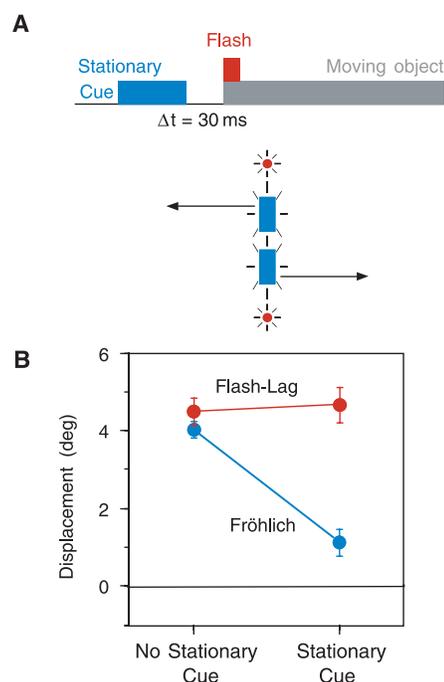

A

Flash

Stationary Cue   Moving object

Δt = 30 ms

B

Fig. 1. Stimulus time course and data distinguishing the flash-lag effect from the Fröhlich effect. (**A**) Two stationary objects were presented for 2.5 sec (stationary cue), then removed for 30 ms. After that Δt, the objects were presented again and immediately began to move in opposite directions (to avoid eye movements). In a second experimental condition, no stationary cue was presented. (**B**) Blue symbols refer to the perceived Fröhlich effect, the degree to which the initial position of the moving objects appeared shifted in the direction of their motion. Red symbols refer to the perceived flash-lag effect, the degree to which the flashes appeared to trail behind the position of the moving objects. The flash-lag effect was constant whether the cue was presented or not; the Fröhlich effect was reduced dramatically when the cue was presented.
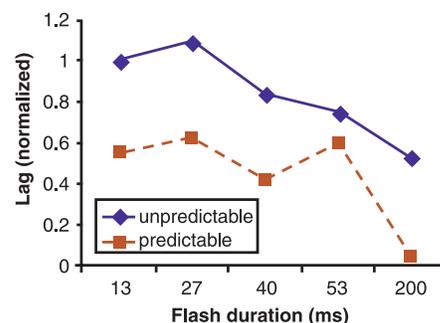

Fig. 1. Role of predictability in the flash-lag effect. Experimental conditions replicate those of (*5*): three central dots spin at 0.5 Hz; two pairs of flanking dots are flashed with an offset angle. Illusory displacement is quantified by a method of adjustment at five flash durations (six trials each duration). Each trial reflects of one of two randomly interleaved conditions: the flashes appear once every 2000 msec at the same location each time (predictable, squares), or they appear randomly from 1500 to 2500 ms after the last flash and, thus, at random locations (unpredictable, diamonds). Data on each subject are normalized to the magnitude of the lag angle in the unpredictable condition at 13 ms (absolute lag angles for that condition, $n = 6$ subjects: 9.2°, 10°, 6.7°, 8.3°, 19.2°, and 17.5°). Demonstrations of stimuli can be found at www.cnl.salk.edu/~eagleman/flashlag.

our hypothesis that differentially salient stimuli will engender differential amounts of perceived displacement.

As a further test of our hypothesis, we replicated the multiple-flash experiment of Krekelberg and Lappe (*3, 5*), but with a new condition: Instead of the outer dots flashing periodically and predictably, on half the trials the outer dots were flashed at unpredictable times but at the same average rate. The degree of perceived displacement in the unpredictable case was approximately twice as large (Fig. 1). Our interpretation is that the internal model is less able to predict the next appearance of the flash for the aperiodic stimuli, and as a consequence suffers more devaluation due to surprise. The Krekelberg and Lappe model does not predict these results because it does not take into account the salience of a signal, but only its positional difference within a fixed temporal window.

A detailed discussion of the possible neural mechanisms underlying the flash-lag effect is beyond the scope of this discussion. Ultimately, however, the difference between our explanation and those of the comment authors is that, whereas they propose purely "feed-forward" models, our framework requires feedback, an important architectural feature of the cerebral cortex. The term "postdiction" captures this simple but crucial idea. Additional support for postdiction is seen in well-established phenomena such as backward masking and apparent motion, and our hypothesis has found support in recent experiments (*8, 9*).

David M. Eagleman
Sloan Center for Theoretical Neurobiology
The Salk Institute for Biological Studies
10010 North Torrey Pines Road
La Jolla, CA 92037, USA
E-mail: eagleman@salk.edu

Terrence J. Sejnowski
Howard Hughes Medical Institute
The Salk Institute for Biological Studies
and Department of Biology
University of California at San Diego
La Jolla, CA 92093, USA

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