Review TRENDS in Cognitive Sciences Vol.6 No.9 September 2002 387

Neural delays, visual motion and the flash-lag effect

Romi Nijhawan

In the primate visual system, there is a significant delay in the arrival of photoreceptor signals in visual cortical areas. Since Helmholtz, scientists have pondered over the implications of these delays for human perception. Do visual delays cause the 'perceived' position of a moving object to lag its 'real' position? This question has recently been re-evaluated in the context of the flash-lag phenomenon, in which a flashed object appears to lag behind a moving object, when physically the two objects are co-localized at the instant of the flash. This article critically examines recent accounts of this phenomenon, assesses its biological significance, and offers new hypotheses.

When a flashed stimulus is presented physically aligned with a continuously moving object, the flash is visible in a lagging position relative to the moving object. This is the flash-lag effect and it was first studied some 80 yrs ago [1–3]. A striking form of the effect is seen when a disk is flashed in the center of a moving ring. Observers report that the flashed disk appears to lag relative to the ring so that a gap is seen within the ring (Fig. 1).

Recent studies have widened the scope of this phenomenon. The effect has been used to study color perception (Box 1) and visual attention (Box 2). Other experiments have investigated analogous effects with stimuli that are stationary on the retina (Box 3). The greatest impact on the explanation of the flash-lag effect has come from displays that I will here call half-cycle displays. After introducing these displays, I provide a critical examination of the main accounts.

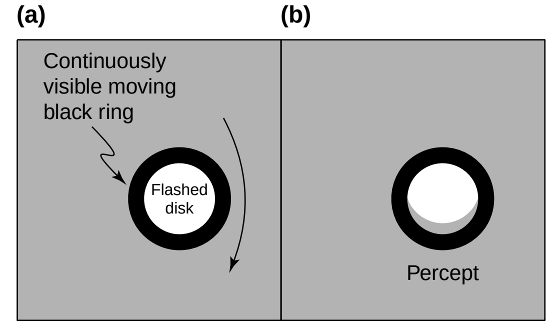
The half-cycle displays

The standard flash-lag display (Fig. 2a) can be divided into flash-terminated and flash-initiated cycles. In the flash-terminated cycle (Fig. 2b) the pre-flash trajectory of the moving object is indistinguishable from that of the standard display. However, simultaneous with the disappearance of the flash, the moving object also disappears. In the flash-initiated cycle, there is no motion stimulus until the flash; the moving object appears simultaneously with the flash (Fig. 2c). The basic findings using half-cycle displays are: (1) the flash-terminated cycle produces no flash-lag effect, (2) the flash-initiated cycle produces an effect that is comparable in magnitude to that in the standard display. Although these results have been known for a decade (R. Nijhawan, unpublished), recent investigations using these displays have provided a wealth of findings that have had an impact on explanations of the effect [4–12]. The reversed cycle can be considered as a special type of complete cycle in which motion direction in one-half-cycle is the opposite of that of the other half-cycle [5]. Other complete cycle displays can be obtained by using different velocity (speed and direction) parameters for the two-half cycles [8].

Neural delays and their consequences

Most of the recent articles on the topic consider neural delays to be central to the study of the flash-lag effect. Consider two visual areas, the retina and a retinotopic cortical area [13] denoted by x–y and x'–y' coordinate systems, respectively (Fig. 3a). Let a brief flash at time t_0 stimulate retinal position (x_3,y_3), and let the transmission delay be Δt. Cortical activity at (x'_3,y'_3) representing the flash will occur at $t_0+\Delta t$. Let a second moving object arrive at retinal position (x_3,y_2) at time t_0. Assuming the same delays, the peak of the cortical wave of neural activity generated by the moving object will arrive in (x'_3,y'_2) at $t_0+\Delta t$. At $t_0+\Delta t$, the object's retinal coordinates will be (x_4,y_2) (Fig. 3b). Thus, the observer should perceive the moving object as trailing its 'real' position.

Kuffler proposed that a fundamental goal of the visual cortex is to ascertain which part of the retina has been stimulated [14]. This localization function



TRENDS in Cognitive Sciences

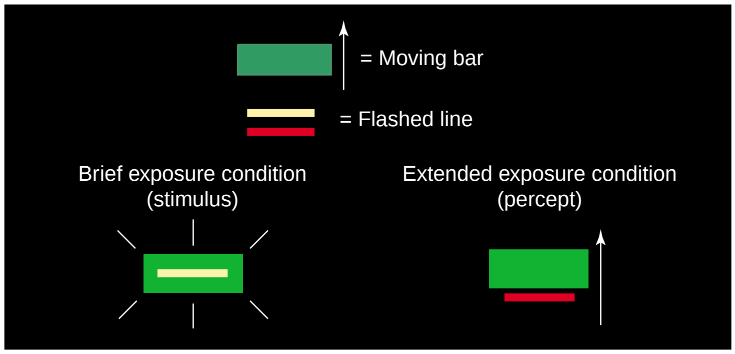
Fig. 1. A demonstration of the flash-lag effect. (a) Observers fixate a stationary point (not shown) centered on a flashed white disk. The flashed disk is presented in the center of a moving black ring. Thus at the instant of the flash, the centers of the flashed disk, the moving ring and the fixation point are co-localized. The flashed disk is perceived, however, in a lagging position relative to the moving ring [62]. One noteworthy feature of the resulting percept that is immediately apparent is its 'purity'; the percept contains no hint of contradiction, paradox or top-down contamination. In addition, a gray crescent-shaped 'perceived void' is seen inside the ring. This crescent shape is bounded by 'spurious edges' with white → gray transition at the top and gray → black transition at the bottom, which are not physically present. Between the 'spurious edges' the crescent is filled-in with gray. As reported by Watanabe *et al.*, observers' percept also consists of a distortion of the flashed disk into an elliptical shape (shown here) [63].

Romi Nijhawan
Cognitive and Computing Sciences, University of Sussex, Falmer, Brighton, East Sussex, UK BN1 9QH.
e-mail: romin@cogs.susx.ac.uk

http://tics.trends.com 1364-6613/02/$ – see front matter PII: S1364-6613(02)01963-0

Box 1. Visual decomposition of color

If red and green light stimuli in the right balance of intensities overlap, the overlapping region is perceived as yellow. Will two stimuli 'mix' to yield yellow in a flash-lag display in which a green moving stimulus is presented with an overlapping red flashed stimulus? In an experiment to test this, observers viewed a moving green bar with an overlapping flashed red line such that the mixture of the two produced a 'yellow' stimulus at the retina. Nonetheless, when the movement of the bar was visible, observers perceived the color of the flashed line, lagging behind the green bar, as red (Fig. I). This suggests that a mechanism for the flash-lag effect is present early enough in the visual pathway, such that 'unmixed' red and green color signals can still be retrieved [a].



TRENDS in Cognitive Sciences

Fig I. Observers viewed a moving green bar. In the brief exposure condition, the moving green bar was visible only through a narrow slit in a surface that occluded the rest of the motion trajectory of the bar. A flashed red line was presented, overlapping the moving green bar, just as the bar passed behind the slit. The observer adjusted the intensity of the flashed line until the line appeared yellow. In the extended exposure condition the occluding surface was removed such that the motion of the green bar was now fully visible. The same flashed line that appeared yellow in the brief exposure condition now appeared red.

References

a Nijhawan, R. (1997) Visual decomposition of color through motion extrapolation. *Nature* 386, 66–69

of the cortex is crucial for behavior directed at moving objects. In visually guided behavior in primates, neural delays are present at the level of visual processing, coordinate transformation [15], planning, and execution of motor behavior [16,17]. Compensation for these delays certainly occurs at motor planning and execution stages, however, work on 'motion-based-position-bias' also invokes compensation within the visual system [18,19]. Visual compensation has also been invoked in explaining the flash-lag effect [20].

Motion extrapolation

This account suggests that retinal signals triggered by the flash arrive in the corresponding cortical area after some delay Δt, but the lack-of-correspondence between the retinally stimulated location and the cortically activated area representing the moving object, expected from similar delays, is compensated [20]. On this view if the moving object travels a distance Δs in time Δt, then the expected lag of Δs between the object's perceived position and its 'real' position is reduced by a compensation mechanism. A complete compensation would lead to a cortical representation for the moving object in the extrapolated position (x'_4,y'_2) in Fig. 3a, as opposed to the one shown in position (x'_3,y'_2), which is sans any compensation. On this view, a corrected cortical representation of the moving object (x'_4,y'_2) leads the cortical representation of the flashed object (x'_3,y'_3), causing the flash-lag effect.

This account, however, is incompatible with the lack of effect in the flash-terminated cycle. As motion-termination is registered after a delay, compensation should cause the moving object to perceptually overshoot the termination point. Both the flash-terminated and the reversed-cycle displays [5] fail to show this overshoot.

Differential latency

Stimuli with different attributes are processed with different delays; for example, a bright stimulus is processed faster than a dim stimulus [21–23]. Whitney and Murakami proposed that the flash-lag effect results from moving objects being processed with shorter latencies [5]. They presented a flashed object as the moving object revered direction, in spatial alignment with the reversal point. In this elegant experiment, the moving object did not appear to 'overshoot' the flashed object. The authors suggest that the visual system processes moving objects more efficiently than flashes, leading to a difference in latencies that corresponds to the flash-lag effect.

The differential latencies account [5,21,24], however, raises concerns similar to motion extrapolation. What is the latency for detecting unpredictable movement reversal? Is this latency comparable to that for smooth motion or that for the flash? Mechanisms responsible for latency reduction, such as path-dependent facilitation [25], would be ineffectual for abrupt reversals. Thus latency for abrupt reversals should exceed that for smooth motion, which in turn should produce an overshoot proportional to the latency difference. Furthermore, it is difficult to conceive that the moving object, when it first comes into view, could be processed faster than a flash. And yet the flash-initiated cycle produces an undiminished flash-lag effect.

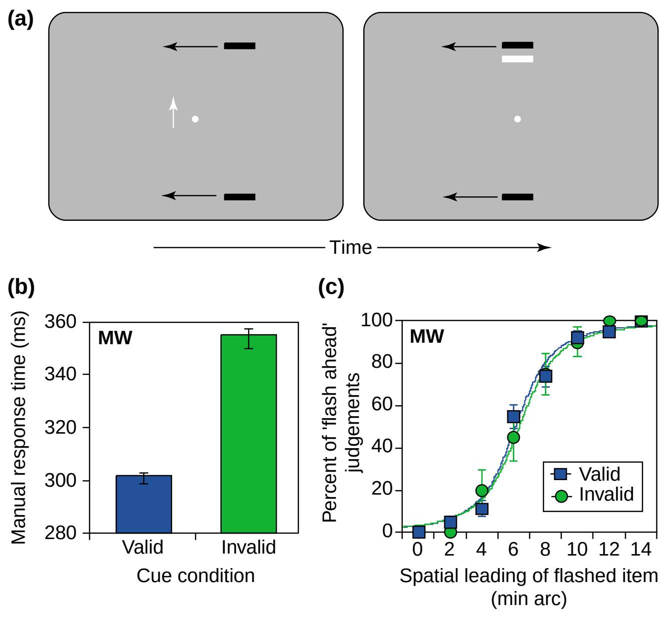
Attentional allocation

In their explanation of the flash-lag effect, Baldo, Klein and colleagues invoke reduced latency for moving objects due to attentional allocation, and the shift of attention caused by the flash [26,27].

It is known that attended objects are processed with smaller delays [28,29], flashed objects 'capture' attention [30], and shifting of attention from one location to another takes time [31,32]. Kirschfeld and Kammer [33], drawing parallels between the flash-lag and Fröhlich effect [34], invoked attention as a causal mechanism in both effects. They suggest that greater attention to moving objects leads to their faster processing than flashes. Baldo and Klein suggest, in addition, that initially the smoothly moving object sustains the observer's attention, while a flash 'captures' and draws the observer's attention away

Box 2. Visual attention and the flash-lag effect

Posner used a cost–benefit cuing paradigm in which observers pressed one of two keys in response to one of two possible stimuli that followed a valid or invalid pre-cue [a]. Observers were faster to respond on valid pre-cue trials. Is the speeding-up of responses due to facilitation of the visual pathways devoted to action [b], or to speeding-up of visual perception *per se*? In a recent experiment, Khurana *et al.* combined the flash-lag and attention-cuing paradigms [c]. Observers viewed two horizontally moving lines (Fig. Ia). An arrow pre-cue, which pointed towards one of the moving lines and was valid on 80% of trials, was presented 500 ms before a third line was flashed either in the cued or in the opposite position. The observers performed two tasks: (1) a speeded task in which they pressed one of two keys to indicate the flashed line position; (2) judgement of whether the flashed line appeared to lag or lead the moving line next to it. Consistent with Posner's result, observers' response times were significantly shorter on the valid-cue trials (Fig. Ib). However, the magnitude of the flash-lag effect remained unchanged in the two types of trials (Fig. Ic). This suggests that the speeding-up of responses in the Posner task is more likely to be due to facilitation of action pathways [b].



TRENDS in Cognitive Sciences

Fig. I. The effect of attention. (a) The stimulus for the combined attention-cuing and flash-lag experiment. Observers viewed two leftward moving black lines, while holding their eyes fixed on the central white dot. An arrow cue, presented 500 ms before the flash, indicated with 80% validity the flash of a white line next to one of the moving black lines. In the trial shown the arrow cue is valid. (b) Average response times for one naïve observer (MW) to the flash on valid and invalid cue trials. (c) Psychometric functions for observer MW measuring the flash-lag effect in the valid and the invalid cue trials. Despite the large difference in response times, the magnitude of the flash-lag effect was the same (Ref. [c]).

Brenner and Smeets recently showed that observers' expectation of the time of the flash significantly changes the magnitude of the flash-lag [d]. From the start of each trial they presented a continuously visible but faint bar that was later flashed, as the moving object passed the bar. In this condition, the flash-lag effect was significantly reduced.

In addition, Eagleman and Sejnowski [e] and Baldo *et al.* [f] showed an increment in the flash-lag effect based on the unpredictability of the flash.

References

a Posner, M.I. (1980) Orienting of attention. *Q. J. Exp. Psychol.* 32, 3–25
b Goodale, M.A. and Milner, A.D. (1992) Separate visual pathways for perception and action. *Trends Neurosci.* 15, 20–25
c Khurana, B. *et al.* (2000) The role of attention in motion extrapolation: are moving objects 'corrected' or flashed objects attentionally delayed? *Perception* 29, 675–692
d Brenner, E. and Smeets, J.B.J. (2000) Motion extrapolation is not responsible for the flash-lag effect. *Vision Res.* 40, 1645–1648
e Eagleman, D.M. and Sejnowski, T.J. (2000) The position of moving objects. *Science* 289, 1107a
f Baldo, M.V. *et al.* (2002) Evidence for an attentional component of the perceptual misalignment between moving and flashing stimuli. *Perception* 31, 17–30

from the moving object. During the time it takes for the observer's attention to shift back to the moving object, the moving object has shifted in position.

The attentional account cannot explain the results of the flash-initiated display in which the moving and the flashed objects have an equally abrupt onset, and neither object can be said to selectively capture the observer's attention. Thus, the flash-lag effect should be reduced or eliminated, which is not the case. Furthermore, several recent experiments [35] that explicitly manipulate attention through cuing have found evidence contradicting the attentional account (see Box 2).

Temporal averaging

Mach [36] attributed mislocalization of flashes to persistence [37], by likening the persistence of a flash to a permanent after image. This is reminiscent of the recently proposed concept of position persistence that lasts beyond visible persistence [10,11]. Krekelberg and Lappe suggest that the flash-lag effect is due to slow temporal averaging of position signals of the moving object over a time window of 500 ms [11]. On this view, the flash-lag effect is seen because the moving object's position is compared with the last seen position of the persisting flash [38].

There are two weaknesses in this account. First, the time window of 500 ms is unrealistically long. It is known that motion integration is more or less complete within 100 ms [39,40]. Second, this account assumes an equal neural delay, Δt, in the processing of moving and flashed objects implying that a moving object's perceived position lags behind its actual instantaneous position by a distance $\Delta s = v\Delta t$ (where v = object velocity). As we know, however, at the moment the flash is perceived the moving object is seen ahead of the flash (flash-lag effect). Thus, the moving object must move from a position lagging the flash to a position leading the flash in Δt. This predicts a speed-change of the moving object that has not been observed (see below).

Postdiction

Eagleman and Sejnowski suggest that in estimating position of moving objects the visual system collects position signals not only from the past but also from

Box 3. Flash-lag effect with retinally stationary stimuli

Eye-movements

A flash presented around the time of a saccade [a–d], or during smooth pursuit [e–h], appears displaced in the direction of the eye-movement. Schlag *et al.* recently reported a flash-lag effect with the observer's head in motion (relative to the body), the eyes stationary relative to the head, and the continuous stimulus stationary relative to the retina (and the head) [i]. Thus, it can be concluded that proprioceptive information alone is sufficient to produce a flash-lag effect.

Non-motion feature spaces

Recently, Sheth *et al.* investigated the flash-lag effect with changing but non-moving stimuli [j]. In one experiment, the luminance of one of two stimuli was continuously varied while the other stimulus was briefly flashed at a fixed luminance. The observers' task was to judge the luminance of the flashed stimulus relative to the continuously changing stimulus. Other experiments manipulated spatial frequency, color or entropy (departure from regularity) [j]. A form of flash-lag occurred for all these feature dimensions. Thus, a stimulus becoming continuously coarser was perceived to be more coarse than a flashed stimulus of the same instantaneous coarseness. Bachmann and Põder noted, however, that a change along some dimension is not essential to produce the flash-lag effect [k].

References

a Matin, L. and Pearce, D.G. (1965) Visual perception of direction for stimuli flashed during voluntary saccadic eye movements. *Science* 148, 1485–1488

b Honda, H. (1989) Perceptual localization of visual stimuli flashed during saccades. *Percept. Psychophys.* 45, 162–174

c Cai, R.H. *et al.* (1997) Perceived geometrical relationships affected by eye-movement signals. *Nature* 386, 601–604

d Schlag, J. and Schlag-Rey, M. (1995) Illusory localization of stimuli flashed in the dark before saccades. *Vision Res.* 35, 2347–2357

e Mateeff, S. *et al.* (1981) Localization of brief stimuli during pursuit eye-movements. *Acta Psychol.* 48, 133–140

f van Beers, R.J. *et al.* (2001) Sensorimotor integration compensates for visual localization errors during smooth pursuit eye movements. *J. Neurophysiol.* 85, 1914–1922

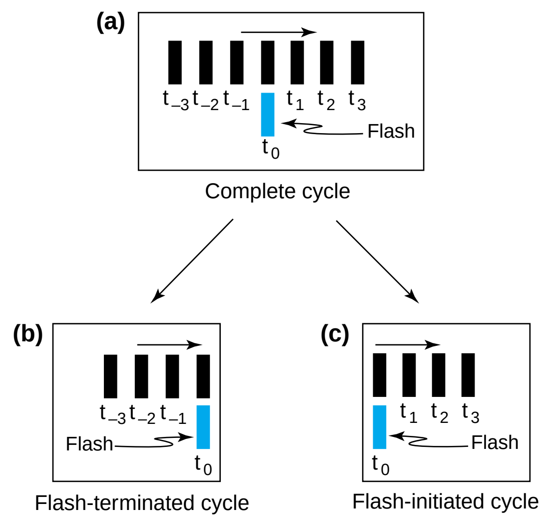
g Brenner, E. *et al.* (2001) Smooth eye movements and spatial localization. *Vision Res.* 41, 2253–2259

h Nijhawan, R. (2001) The flash-lag phenomenon: object-motion and eye-movements. *Perception* 30, 263–282

i Schlag, J. *et al.* (2000) Extrapolating movement without retinal motion. *Nature* 403, 38–39

j Sheth, B. *et al.* (2000) Changing objects lead briefly flashed ones. *Nat. Neurosci.* 3, 489–495

k Bachmann, T. and Põder, E. (2001) Change in feature space is not necessary for the flash-lag effect. *Vision Res.* 40, 1645–1648



TRENDS in Cognitive Sciences

Fig. 2. Half-cycle displays. (a) The standard (complete cycle) display with a moving bar (top) and a flashed bar (bottom) that had been used in flash-lag studies until the early 1990s. This display can be divided into two half cycles. (b) In the flash-terminated half cycle, motion offset occurs simultaneously with the flash. Observers perceived the moving object to stop in alignment with the flash (as it actually does). Thus, no flash-lag is observed. (c) In the flash-initiated half cycle, motion onset occurs simultaneously with the flash. In this case the flash-lag is perceived, and the effect is comparable to the complete cycle display [4]. In general, different complete cycle displays (displays in which a moving stimulus is present both before and after the flash) can be obtained by varying the velocity (speed and direction) parameters for the two half-cycles [8].

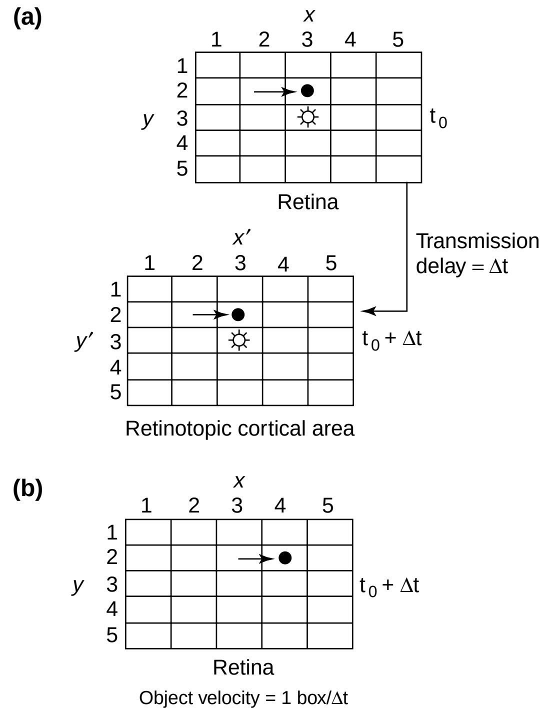
the future [7,41]. The postdiction model assumes that the flash 'resets' motion integration [7]. Thus, the flash affects other processes in the neighborhood, such as motion processing, analogous to capture of attention by the flash in Baldo and Klein's attention model. Flash-reset causes the visual system to integrate position signals from the post-flash positions of the moving object, causing it to perceptually lead the flash [7].

The postdiction account successfully explains the lack of flash-lag effect in the flash-terminated cycle; since the moving object's position doesn't change after the flash this account predicts no flash-lag. However, this model has difficulty explaining the standard flash-lag effect. Suppose a flash presented at t_0 is subject to neural delay of Δt. The postdiction model assumes that neural delay for flash equals Δt, which equals neural delay for motion. The postdiction model further assumes that the flash 'resets' motion integration. Thus, on the postdiction view the perceived position of the moving object changes from a distance Δs ($=v\Delta t$) behind the flash at t_0 to a distance $\Delta\sigma$ ahead of the flash at $t_0+\Delta t$ ($v=$ object velocity; $\Delta\sigma=$ flash-lag effect). Thus, the moving object's speed must increase from $v=\Delta s/\Delta t$ to $v_n=(\Delta s+\Delta\sigma)/\Delta t$, in the spatiotemporal vicinity of the flash. The temporal averaging model makes a similar prediction.

Until now this most direct prediction of the postdiction account has not been tested. Humans can detect speed increments of as little as 2.5% [42]. Thus, the fact that investigators have failed to notice any speed-change concomitant with the flash in numerous flash-lag experiments suggests a negative result. Our recent experiments instructing observers to note $v\rightarrow v_n$ speed-change in flash-lag displays have confirmed our expectation. Observers showed near perfect performance on speed-change detection, and correct identification of trials with no speed-change, both in displays with and without flashes (R. Nijhawan *et al.*, unpublished).

Comparing the accounts

In summary, different accounts of the flash-lag effect fall into two categories on the basis of their assumptions. Accounts in one category invoke previously un-established neural processes underlying motion. Both latency-correction (extrapolation) and latency-reduction (differential latency) models invoke the biological significance of detecting a moving object quickly and its position accurately, and the ensuing



TRENDS in Cognitive Sciences

Fig. 3. The *x*–*y* and *x′*–*y′* coordinate systems. (For simplicity, the fact that the retina is mapped onto a log–polar map in the striate cortex is not incorporated in the figure [64]). (a) Two events, a flash (sunburst) in retinal position (x_3, y_3) and the arrival of a moving object (solid black dot) in retinal position (x_3, y_2) occur simultaneously at time t_0. Both events are registered in a retinotopic cortical area after a delay Δt at time $t_0 + \Delta t$: the flash at (x'_3, y'_3) and the moving object at (x'_3, y'_2). (b) However, at time $t_0 + \Delta t$, the retinal position of the moving object (velocity = 1 box/Δt) is (x_4, y_2), in 'disagreement' with the object's cortical coordinates (x'_3, y'_2) at that instant. In other words, because of the transmission delay, the cortical position (x'_4, y'_2) does not show significant neural activity at $t_0 + \Delta t$, as depicted by the *absence* of the solid black dot in position (x'_4, y'_2) in (a). Thus, at time $t_0 + \Delta t$ the observer can be said to be visually 'unaware' of an object in position (x_4, y_2), the moving object's 'real' instantaneous position.

increased likelihood of successful interceptive behavior. The flash, on this view, is simply a spatiotemporal marker with no special properties other than those already known (neural delay and visual persistence). Accounts in the second category invoke previously un-established neural processes underlying flashes. The postdiction model assumes that the flash interacts with ongoing motion processing. The temporal averaging model assumes a neural representation triggered by the flash lasting beyond visual persistence. The attention model assumes both a quicker processing of motion, and an interaction of the flash with motion processing [26,27,33]. These assumptions will be the focus of discussion below.

Visually guided action

Successful interceptive behavior is not only vital for survival of many species, but also requires compensation of delays in the visuomotor pathways. Cortical processes underlying planning and execution of motor behavior in primates could potentially compensate for all the visuomotor delays [15,43], so a mechanism specifically compensating for visual processing delays may not be necessary for successful interceptive behavior. This 'late' compensation view is reinforced by adaptation experiments that show that primates can quickly learn to compensate for visual displacements caused by prisms and achieve normalcy in overt localization behaviors [44,45]. Thus if successful interceptive behavior is the criterion, then 'early' compensation for delays in the visual position of moving objects seems unnecessary.

Consider though the visual systems of lower species; chickens and frogs show no compensation for visual displacements [46,47]. Under displaced vision conditions these animals would starve to death even though food was nearby. This suggests that although the high degree of cortical plasticity in primates [48] might allow for compensation for visual displacements (due to neural delays) through adjustments in motor plans, lower species might not similarly compensate. Thus visual compensation probably contributes to accuracy in the tongue-snap response in the frog [49]. As older mechanisms are adapted rather than replaced, it is likely that 'early' compensation for neural delays in the visual system of lower species continues to be present in primates. On this view, the flash-lag and other effects [18,19] reveal a compensation mechanism in primates. Physiological studies by Barlow in the frog retina [49] and by Berry *et al.* in the rabbit and salamander retinas [50], have uncovered potential mechanisms for visual compensation.

Does the 'perceived' position of a moving object lag its 'real' position? Not only does this persistent question [5,7,8,21,26,38,41,51,52] appear perfectly sensible, but investigators also feel compelled to give an answer in the affirmative. What might be the analogous question for a lower species, such as a frog? It is suggested that the question is rife with the same philosophical problems when raised for the visual system of a lower species as for the human visual system. A more productive question for all species may be: does visual position of the moving object lag relative to the position information supplied by an older sensory system that was the basis of evolution of the earlier motor system? Evidence suggests that early motor systems evolved to serve the older touch system [53]. Primitive phototropic responses to light were generated by the already evolved touch-based motor system [53,54]. In older systems (such as earthworms) the skin itself is sensitive to light. However, the older nervous systems needed reorganization as light-based information departed from the touch-based information in the image forming eyes; e.g. the retinal image is inverted and varies in size with distance. Richard Gregory has argued that size-constancy reflects such a reorganization that functions to compensate for variations in image size [55]. It is suggested that motion extrapolation reflects another reorganization of the nervous system due to added delays in visual

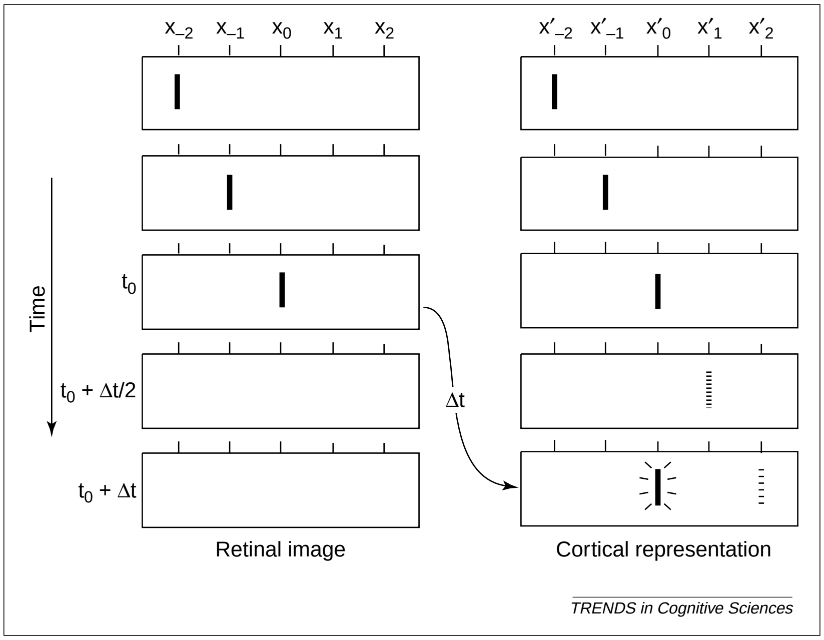


Fig. 4. Representation of motion termination. When a target is briefly presented and followed by a spatially neighboring stimulus, the target can be rendered invisible [65,33]. A similar process might underlie the suppression of visibility of the moving stimulus beyond its point of termination, and the 'lack of effect' in the flash-terminated cycle. The left panels show retinal image positions (x_m) and the right panels the positions of the corresponding cortical representations (x'_m). A rightward moving bar terminates in retinal image position x_0 at time t_0. The signals generated by motion-termination (e.g. by 'off' cells if the bar is extinguished) will be registered after a delay Δt in position x'_0 of the corresponding cortical area. The presence or absence of bars in the 'retinal image' and the 'cortical representation' panels depict presence or absence of the stimulus and the cortical activity generated by the stimulus, respectively. If neural delays are compensated, then the cortical representation should 'overshoot' the cortical position x'_0, and the observer should see the object in positions x'_1 and x'_2. However, the decaying cortical activity (owing to cessation of retinal input) in positions x'_1 and x'_2 is masked by the delayed arrival of motion-termination signals in cortical position x'_0, as depicted by the sunburst.

processing [56] relative to touch-based information. This suggests that motion extrapolation occurs when a sensory system with greater delays employs a motor system that evolved to serve a sensory system with smaller delays.

Backward masking at motion-termination

Particularly challenging to the compensation accounts is the lack of effect in the flash-terminated display. However, recent experiments by Fu *et al.* have cast new light on this; if blurred objects moving in opposite directions abruptly stop then they do appear to overshoot their termination positions [57]. This, and other recent studies [58] have addressed the problem of delays with moving objects without use of flashes. Most importantly, Berry *et al.* found a 'flash-lag effect' by comparing neuron responses to moving stimuli presented alone with neuron responses to flashed stimuli presented alone [50]. Thus accounts that rely on flashes 'resetting' motion processing (Postdiction) or persisting for an extended duration (Temporal averaging) cannot be correct. One important message of the above studies [50,57,58] is that the problem of delays with moving objects is ubiquitous, and flashes are not require to addressed it. The question to address is: given the transmission delays, why do ordinary moving objects not appear to overshoot fixed points in space at which they stop, disappear or reverse direction?

On the compensation view, a 'lack-of-effect' at motion-termination requires explanation. On the assumption that a compensation mechanism is present within the visual system, it is suggested that a second mechanism delivers accurate position information at motion-termination. Visual movement generally encountered by animals has an onset and an offset. However, motion onsets and offsets are clearly different in their biological significance. Mislocalization at motion onset (as reflected by the flash-initiated cycle) has little cost; simple reaction time of more than 100 ms in humans [59] precludes any coordinated action during the object's initial trajectory. However, accurate representation of position at motion-termination would be advantageous to animals. For example, with accurate motion offset position a predator can direct attention to the correct position and search efficiently, thus increasing chances of nourishment. The significance of motion offset is seen in adaptations, both in the predator and prey, corresponding to the 'freezing' response in many species [53]. Furthermore, keeping track of motion-offset position has been noted not only at the level of intact animals, but also at the level of single cells [60]. What might be the mechanism responsible specifically for removing errors at motion offset? Consider two facts: (1) Moving object's do not appear to overshoot the termination position; (2) A moment after motion offset, cortical area(s) representing the moving object will receive new retinal signals contradicting existing cortical signals. Both these facts suggest the involvement of backward masking, which in view of compensation may allow for correct motion-termination position (Fig. 4).

In conclusion, it is still unclear if any one mechanism can explain all the known flash-lag findings (for review, see Ref. [61]). It is also unknown if two seemingly different mechanisms are operationally different. For example if latency-correction and latency-reduction take the same amount of time to get established after motion onset [38], then perhaps these accounts are not as distinct as initially presumed.

Finally, it has been argued that as vision senses the distant environment more time is available before a motor response is required; thus a longer delay in the registration of visual stimuli, as compared with touch, is not disadvantageous to the animal [54]. However, from the evolutionary point of view a primary function of nervous systems is to detect movement [53]. Thus, longer delays in the visual system would constitute a significant disadvantage if these delays translated into visual position errors for moving objects. The function of compensation may then be to remove this deleterious byproduct of heightened sensitivity, and the consequent slowness, of the 'early' visual system.

Acknowledgement
I thank Beena Khurana for her helpful comments on the manuscript.

References

1 Hazelhoff, F. and Wiersma, H. (1924) Die Wahrnehmungszeit. *Zeitschrift für Psychologie* 96, 171–188
2 MacKay, D.M. (1961) Interactive processes in visual perception. In *Sensory Communication* (Rosenblith, W.A., ed.), pp. 339–355, MIT Press
3 Mateeff, S. *et al.* (1981) Localization of brief stimuli during pursuit eye movements. *Acta Psychol. (Amst.)* 48, 133–140
4 Khurana, B. and Nijhawan, R. (1995) Extrapolation or attention shift? *Nature* 378, 565–566
5 Whitney, D. and Murakami, I. (1998) Latency difference, not spatial extrapolation. *Nat. Neurosci.* 1, 656–657
6 Sheth, B. *et al.* (2000) Changing objects lead briefly flashed ones. *Nat. Neurosci.* 3, 489–495
7 Eagleman, D. and Sejnowski, T.J. (2000) Motion integration and postdiction in visual awareness. *Science* 287, 2036–2038
8 Brenner, E. and Smeets, J.B.J. (2000) Motion extrapolation is not responsible for the flash-lag effect. *Vision Res.* 40, 1645–1648
9 Whitney, D. *et al.* (2000) Temporal facilitation for moving stimuli is independent of changes in direction. *Vision Res.* 40, 3829–3839
10 Krekelberg, B. (2001) The persistence of position. *Vision Res.* 41, 529–539
11 Krekelberg, B. and Lappe, M. (2000) A model of the perceived relative positions of moving objects based upon a slow averaging process. *Vision Res.* 40, 201–215
12 Murakami, I. (2001) A flash-lag effect in random motion. *Vision Res.* 41, 3101–3119
13 Van Essen, D.C. *et al.* (1984) The visual field representation in striate cortex of the macaque monkey: asymmetries, anisotropies, and individual variability. *Vision Res.* 24, 429–448
14 Kuffler, S.W. (1952) Neurons in the retina: organization, inhibition and excitation. *Cold Spring Harb. Symp. Quant. Biol.* 17, 281–292
15 Andersen, R. (1987) Inferior parietal lobule function in spatial perception and visuomotor integration. In *Handbook of Physiology* (Plum, F. and Mountcastle, V.B., eds), American Physiological Society
16 Gnadt, J.W. and Andersen, R.A. (1988) Memory related motor planning activity in posterior parietal cortex of macaque. *Exp. Brain Res.* 70, 216–220
17 Bizzi, E. (1988) Arm trajectory planning and execution: the problem of coordinate transformation. In *Neurobiology of Neocortex* (Rakic, P. and Singer, W., eds), pp. 373–383, John Wiley & Sons
18 Ramachandran, V.S. and Anstis, S.M. (1990) Illusory displacement of equiluminous kinetic edges. *Perception* 19, 611–616
19 De Valois, R.L. and De Valois, K.K. (1991) Vernier acuity with stationary moving gabors. *Vision Res.* 31, 1619–1626
20 Nijhawan, R. (1994) Motion extrapolation in catching. *Nature* 370, 256–257
21 Purushothaman, G. *et al.* (1998) Moving ahead through differential visual latency. *Nature* 396, 424
22 Williams, J.M. and Lit, A. (1983) Luminance-dependent visual latency for the Hess effect, the Pulfrich effect and simple reaction time. *Vision Res.* 23, 171–179
23 Zanker, J.M. *et al.* (2001) Perceptual deformation induced by visual motion. *Naturwissenschaften* 88, 129–132
24 Whitney, D. *et al.* (2000) Illusory spatial offset of a flash relative to a moving stimulus is caused by differential latencies for moving and flashed stimuli. *Vision Res.* 40, 137–149
25 Whitney, D. *et al.* (2000) Temporal facilitation for moving stimuli is independent of changes in direction. *Vision Res.* 40, 3829–3839
26 Baldo, M.V. and Klein, S.A. (1995) Extrapolation or attention shift? *Nature* 378, 565–566
27 Baldo, M.V. *et al.* (2002) Evidence for an attentional component of the perceptual misalignment between moving and flashing stimuli. *Perception* 31, 17–30
28 Titchener, E.B. (1908) (reprinted 1973) *Lectures on the Elementary Psychology of Feeling and Attention*, Arno Press, New York
29 Hikosaka, O. *et al.* (1993) Focal visual attention produces illusory temporal order and motion sensation. *Vision Res.* 33, 1219–1240
30 Yantis, S. and Hillstrom, A.P. (1994) Stimulus-driven attentional capture: evidence from equiluminant visual objects. *J. Exp. Psychol. Hum. Percept. Perform.* 20, 95–107
31 Tsal, Y. (1983) Movement of attention across the visual field. *J. Exp. Psychol. Hum. Percept. Perform.* 9, 523–530
32 Weichselgartner, E. and Sperling, G. (1987) Dynamics of automatic and controlled visual attention. *Science* 238, 778–780
33 Kirschfeld, K. and Kammer, T. (1999) The Fröhlich effect: a consequence of the interaction of visual focal attention and metacontrast. *Vision Res.* 39, 3702–3709
34 Fröhlich, F.W. (1923) Über die Messung der Empfindungszeit. *Zeitschrift für Sinnesphysiologie* 54, 58–78
35 Khurana, B. *et al.* (2000) The role of attention in motion extrapolation: Are moving objects ‘corrected’ or flashed objects attentionally delayed? *Perception* 29, 675–692
36 Mach, E. (1897) *Contributions to the Analysis of the Sensations*, Open Court, Illinois
37 Hogben, J.H. and Di Lollo, V. (1974) Perceptual integration and perceptual segregation of brief visual stimuli. *Vision Res.* 14, 1059–1069
38 Krekelberg, B. and Lappe, M. (2001) Neuronal latencies and the position of moving objects. *Trends Neurosci.* 24, 335–339
39 Burr, D. (1980) Motion smear. *Nature* 284, 164–165
40 Burr, D. and Morgan, M.J. (1997) Motion deblurring in human vision. *Proc. R. Soc. Lond. B Biol. Sci.* 264, 431–436
41 Rao, R.P.N. *et al.* (2001) Optimal smoothing in visual motion perception. *Neural Comput.* 13, 1243–1253
42 Hick, W.E. (1950) The threshold for sudden changes in the velocity of a seen object. *Q. J. Exp. Psychol.* 2, 33–41
43 Fuster, J.M. (1989) *The Prefrontal Cortex* (2nd edn), Raven Press
44 Foley, J.P. (1940) An experimental investigation of the effect of prolonged inversion of the visual field in the Rhesus monkey. *J. Genet. Psychol.* 56, 21–51
45 Stratton, G.M. (1897) Vision without inversion of the retinal image. *Psychol. Rev.* 4, 463–481
46 Hess, E.H. (1956) Space perception in the chick. *Sci. Am.* 195, 71–80
47 Sperry, R.W. (1943) Effect of 180 degree rotation of the retinal field on visuomotor coordination. *J. Exp. Zool.* 92, 263–279
48 Merzenich *et al.* (1988) Cortical representational plasticity. In *Neurobiology of Neocortex* (Rakic, P. and Singer, W., eds), pp. 41–67, John Wiley & Sons
49 Barlow, H.B. (1953) Summation and inhibition in the frog’s retina. *J. Physiol.* 119, 69–88
50 Berry, M.J. *et al.* (1999) Anticipation of moving stimuli by the retina. *Nature* 398, 334–338
51 Cavanagh, P. (1997) Predicting the present. *Nature* 386, 19–21
52 Gegenfurtner, K. (1999) The eyes have it! *Nature* 398, 291–292
53 Walls, G.L. (1942) *The Vertebrate Eye and its Adaptive Radiation*, Cranbrook Press, Bloomfield Hills, Michigan
54 Sarnat, H.B. and Netsky, M.G. (1981) *Evolution of the Nervous System* (2nd edn), Oxford University Press
55 Gregory, R.L. (1967) Origin of eyes and brains. *Nature* 213, 369–372
56 Kandel, E.R. (1985) Processing of form and movement in the visual system. In *Principles of Neural Science* (Kandel, E.R. and Schwartz, J.H., eds), pp. 366–383, Elsevier
57 Fu, Y. *et al.* (2001) Motion-induced perceptual extrapolation of blurred visual targets. *J. Neurosci.* 21, RC172
58 Kerzel, D. (2000) Eye movements and visible persistence explain the mislocalization of the final position of a moving target. *Vision Res.* 40, 3703–3715
59 Cattell, J.M. (1986) The influence of the intensity of the stimulus on the length of the reaction time. *Brain* 9, 512–514
60 Lettvin, J.Y. *et al.* (1961) Two remarks on the visual system of the frog. In *Sensory Communication* (Rosenblith, W.A., ed.), pp. 757–776, MIT Press
61 Schlag, J. and Schlag-Rey, M. (2002) Through the eye slowly: delays and localization errors in the visual system. *Nat. Rev. Neurosci.* 3, 191–200
62 Nijhawan, R. and Khurana, B. (2000) Conscious registration of continuous and discrete visual events. In *Neural Correlates of Consciousness: Empirical and Conceptual Problems* (Metzinger, T., ed.), pp. 203–219, MIT Press
63 Watanabe, K. *et al.* (2001) Perceptual organization of moving stimuli modulates the flash-lag effect. *J. Exp. Psychol. Hum. Percept. Perform.* 27, 879–894
64 Schwartz, E.L. (1977) Spatial mapping in the primate sensory projection: analytic structure and relevance to perception. *Biol. Cybern.* 25, 539–560
65 Enns, J.T. and Di Lollo, V. (2000) What’s new in visual masking? *Trends Cogn. Sci.* 4, 345–352