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Edited by Romi Nijhawan, Beena Khurana

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Chapter

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History and theory of flash-lag: past, present, and future

GERRIT W. MAUS, BEENA KHURANA, AND ROMI NIJHAWAN

Summary

Some basic versions of the flash-lag effect have been known since the early decades of the twentieth century. Intriguingly, neural delays were as central in the early attempts at explaining the effect, as they are in the more recent investigations into its cause. For a changing visual stimulus a delayed registration of the stimulus by the central nervous system (CNS) constitutes an “error” between the instantaneously registered state of the stimulus on the one hand and its physical state on the other. Therefore, for animals to acquire food, mate, and avoid predators, compensation of sensory delays is essential. One may ask which component(s) of the CNS compensate for visual delays. Logically compensation could be carried out either by visual or motor mechanisms, or both. The motion extrapolation account of the flash-lag effect challenged the dominant view that only motor mechanisms compensate for visual delays, suggesting instead that visual mechanisms also contribute. Controversy fueled by empirical observations with unpredictable motion, in particular the flash-initiated and flash-terminated conditions of the flash-lag effect, soon followed; *prima facie* motion extrapolation could not accommodate these results. Armed with these challenging findings (primarily) several alternative accounts of flash-lag were proposed. In light of new developments, this chapter evaluates the motion extrapolation, motion sampling, motion integration, postdiction, differential latency, and attentional cuing accounts of flash-lag.

27.1 Introduction: time delays in the nervous system and need for compensation

One key function of neural systems is to detect change in external environments or internal states. A fundamental type of environmental change is movement of a stimulus across a receptor surface. Movement, for example on the skin of remote body parts or in the periphery of the retina, attracts attention such that organisms direct high-resolution sensory surfaces (e.g., fingertips or the fovea) to the locations of movement (James 1890/1952). Movement often stems from another organism, which could either be a conspecific, a potential mate or competitor, or another species, a potential prey or predator. Even inanimate moving objects are likely to be of importance, as they could present an obstacle or possible threat while the animal itself is in motion. In all cases, having information about the exact position of anything that moves is a prerequisite for successful interaction with the moving object, whether the goal be to avoid or intercept.

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There are several problems the nervous system has to solve before it can determine the position of a moving object. One general property of biological neural systems that compounds the localization of moving objects is that biological processes take time. Processes such as phototransduction in receptor cells, signal conductance along nerve fibers, and synaptic transmission all rely on electrochemical mechanisms that work on the order of several milliseconds. The contribution from each of these processes can add up to behaviorally significant time delays. Problematically, during the time delay the environment is dynamic; other organisms and objects move and change position. In principle, it is impossible for an organism to have absolute knowledge about the positions of all relevant objects. However, to be able to interact with moving objects in a dynamic environment, organisms have developed sophisticated mechanisms to overcome these processing delays.

Without any kind of compensation for delays in neural processing it would be impossible for an organism to successfully interact with moving objects, as the position represented at any stage in the central nervous system would always lag behind the physical position of the object in the environment. Hence action directed at this lagging position would fail to make contact with the object in question. Wild cats would jump short of fast-moving prey and forest-dwelling animals would run into trees. Modern high-speed ball games provide nice examples to evaluate the potential error of localizations without compensation. If we assume neural delays from the retina to some cortical processing stage of about 100 msec, a tennis ball flying at a speed of 100 km/hr (27.8 msec^{-1}) would be misrepresented by 2.78 m. Obviously, in many instances predators are able to catch fast-moving prey and players are able to hit tennis balls. Therefore, compensation of delays at some stage of the neural processing is mandatory.

Given the sluggishness of muscle responses and the inertia in the actual movement of limbs, compensation for delays in the motor system is well established in neuroscience (Ghez & Krakauer 2000). It is commonly accepted that delays in other (sensory) parts of the nervous system are also compensated for at the motor stage of neural processing (Jordan 1995). However, there is no a priori reason why all compensation should take place at one summative stage, as processing delays are prevalent in all parts of the nervous system. Visual effects involving moving objects have led to the proposal of predictive mechanisms that compensate for delays in sensory pathways, thereby facilitating the accurate perception of positions (Nijhawan 1994). This discussion of neural delays and compensatory mechanisms has been revitalized by the flash-lag effect (Nijhawan 1994) in which a brief flash, presented in spatial alignment with a moving object, appears to lag behind the moving object (Fig. 27.1).

27.2 History of flash-lag

Research in the last fifteen years, following the publication of Nijhawan's (1994) motion extrapolation proposal, has engendered considerable debate in the scientific community on the underlying mechanisms of the flash-lag effect. However, around the time of the birth of experimental psychology as an independent field, similar perceptual phenomena

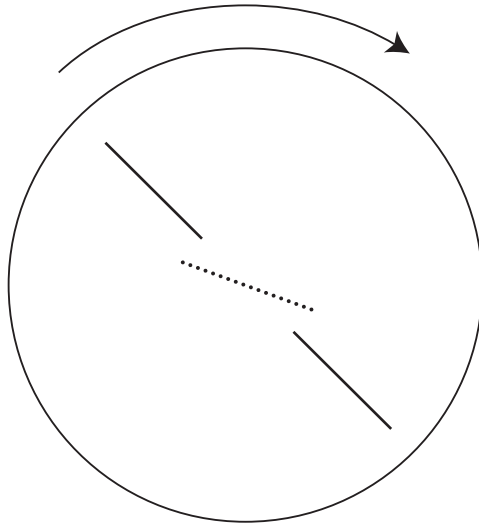


Fig. 27.1 In a dark room a single physical rod, made of three segments, rotates in the direction of the arrow. The two outer segments (solid lines) are illuminated with a continuous light source, whereas the central segment (dashed line) is illuminated with a briefly flashed light source. The figure shows the percept of the observers, with the central segment lagging behind (from Nijhawan 1992; see Appendix).

relating to the localization of moving objects had been studied. For example, in astronomical measurements, it was often necessary to record the accurate transit times of stars crossing the North-South meridian. To measure these time points astronomers had to record the moment when a star moved across a meridian wire in a telescopic view by estimating the perceived position of the star at certain clock beats (Mollon & Perkins 1996). This method relied on the perception of the instantaneous visual position of a moving object at the instant an auditory time marker sounded, thus potentially giving rise to a cross-modal flash-lag effect (Alais & Burr 2003). Observations of intersubjective differences in this method triggered the first experimental investigations of reaction times and temporal order judgments and laid the foundations of experimental psychology (Fröhlich 1929; Mollon & Perkins 1996).

27.2.1 Measurement of “sensation time”

In the 1920s and early 1930s several researchers, mainly in Germany, set out to measure the time it takes from a physical event to its perception. This time was referred to as *Wahrnehmungszeit* (“perception time,” Hazelhoff & Wiersma 1924) or *Empfindungszeit* (“sensation time,” Fröhlich 1923); today it would most likely be called the *perceptual latency* of an event.

To determine “sensation time” Fröhlich used a simple visual stimulus of an illuminated bar moving from behind an occluder. The basic finding was that the bar did not appear

to start moving right at the edge of the occluder, but at a position a short distance farther ahead in its trajectory (Fröhlich 1923). Many variants of this basic finding were reported in a monograph (Fröhlich 1929). Fröhlich's assumption was that the time it takes the bar to move from the edge of the occluder to the first perceived position corresponds to the "sensation time" of the bar. He argued that it takes time for the bar to be processed, such that by the time the sensation is formed, the bar has moved on and therefore is visible in the shifted position. Early on this argument was criticized (Rubin 1929; Metzger 1932) for not making evident why after the "sensation time" has passed the bar should be seen in a forward shifted position.

Hazelhoff and Wiersma (1924), using a different methodology to determine the time of perception, had their observers track a moving fixation mark with ocular movements. A briefly flashed target was presented at the position of the moving mark when it had traversed half of the visual display. The position of this flash was misperceived as shifted in the direction of the eye movement. In this case, they argued that the position of the eye moves before the flash is processed and perceived, and the flash is perceived at the position the eyes point to after this "perception time" has passed.

Metzger (1932) accounted for the above findings as a special variant of the Hess phenomenon (1904). Stimuli of different contrasts have different "perception times" and are therefore perceived to move at different speeds. He explained the basic findings of Fröhlich with the assumption that, initially, a newly appearing object has a longer "perception time" than during later stages in its trajectory. In another experiment, Metzger tested the prediction that a bar already in motion would perceptually lead a bar starting from behind an occluder. This prediction was experimentally confirmed. Following from this Metzger studied an additional stimulus, which seems to be the earliest example of what would be considered a typical flash-lag display, although the term was coined much later by Nijhawan (1994). A single vertical slit is moved behind a cardboard occluder with two cutouts, one large horizontal cutout, where the moving slit is seen as a moving bar, and a small one above the large cutout, with the same width as the moving slit. Here the illuminated slit was seen as a flash (Fig. 27.2). Observers perceived the flash in the small cutout when the moving slit in the large cutout was already in a position further along the trajectory of movement. Metzger held that this phenomenon was in fact identical with Hazelhoff and Wiersma's earlier findings. Although Metzger's experiment did not involve any eye movements, the retinal stimulation was actually very similar to their earlier setup. In Hazelhoff and Wiersma's experiment, the moving object was stabilized on the retina by smooth pursuit eye movements, the flash was briefly presented next to the fixation position, and the background was moving continuously on the retina due to smooth pursuit eye movements.

Metzger concluded that both Hazelhoff and Wiersma (1924) and Fröhlich (1929) had measured the relative difference in the sensation time of a moving object and an abrupt onset. He deemed it impossible to measure absolute sensation time. His explanation of the flash-lag phenomenon is therefore in principle identical with later proposals of differential latencies for moving objects and flashes (Purushothaman et al. 1998; Whitney & Murakami 1998).

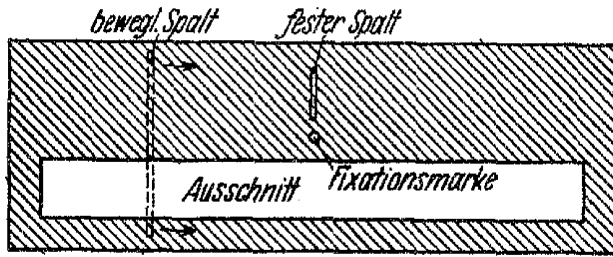


Fig. 27.2 To the best of our knowledge the first “flash-lag” stimulus display. A movable slit (*bewegl. Spalt*) is presented behind a cardboard occluder with two cutouts: a large horizontal cutout (*Ausschnitt*), where the slit is seen as a continuously moving object, and a small stationary slit (*fester Spalt*) above the fixation point (*Fixationsmarke*), where the moving slit appears as a brief flash. Metzger reported that observers saw the flash only when the continuously visible part of the slit was further ahead in the direction of motion. Source: Figure 3 from Metzger (1932).

27.2.2 Stroboscopically lit visual field

Unrelated to the reports of the flash-lag phenomenon from Germany in the early literature on perceptual latencies, another similar finding was published from England. MacKay (1958) observed that when the eyes are moved involuntarily, for example, by applying light pressure with the finger to the side of the eyeball, continuously lit objects in the visual field are perceived to move, whereas a stroboscopically lit background (at 5–6 Hz) does not. Instead it seems to “move sluggishly to ‘catch up’ with the self-luminous objects” (MacKay 1958). It was suggested that change and movement in the visual world have special significance and therefore are salient percepts, whereas the comparative amount of information in the stroboscopically lit field is not actually changing as much from one flash to the next.

Much later Mateeff and Hohnsbein (1988) replicated Metzger’s first flash-lag finding and found differentially larger effects for motion toward the fovea compared to motion away from the fovea. These findings were also interpreted in terms of differential latencies.

27.2.3 The flash-lag effect in other features and modalities

The flash-lag effect has been measured using other visual features than motion, and cross-modally. Sheth et al. (2000) showed that other continuously changing features of an object are similarly “extrapolated” as position in the more standard motion flash-lag effect. When a visual stimulus patch continuously changes color, luminance, spatial frequency, or pattern entropy, and a second test patch with an identical feature value as in the changing patch is briefly flashed, observers perceive the continuously changing stimulus as further ahead in the dimension of change (Sheth et al. 2000). Although the degree of misalignment was highly variable depending on the feature in question, all features tested showed the forward shift.

Alais and Burr (2003) extended the flash-lag effect into the auditory domain. They found misalignments for both auditory frequency changes compared to a short burst of a

single frequency, and auditory stereo position changes compared to a short tone from a static stereo position. Furthermore, when observers compared the position of an auditory stimulus moving in space to a visual flash, or a visual moving stimulus to an auditory burst, typical flash-lag results were obtained, with the moving stimulus cross-modally leading the “flashed” static stimulus (Alais & Burr 2003). These cross-modal flash-lag effects were found to be larger than unimodal effects within vision or audition. In other stimulus configurations, however, an additional auditory tone at the time of the flash can decrease the flash-lag effect, which might be the result of cross-modal temporal binding (Vroomen & de Gelder 2004).

Other cross-modal flash-lag effects have also been reported. When observers move their arm in the dark and compare the felt arm position to a visual flash (“motor flash-lag,” Nijhawan & Kirschfeld 2003), or when observers compare the position of a moving tactile object on their forearm to a visual flash (Rojas-Anaya et al. 2005).

27.3 Flash-lag: theory and recent debates

27.3.1 *The standard view and the ds-error postulate*

Discussion of visual neural delays, the logically derived *ds-error* postulate (the assertion that there is a spatial lag in the perceived position of moving objects), and the flash-lag effect have appeared together time and again in recent articles (e.g., see Nijhawan 1994; Cavanagh 1997; Berry et al. 1999; Gegenfurtner 1999; Fu et al. 2001; Krekelberg & Lappe 2001). Fu et al. (2001) state: “Processing delay in the neural pathway on the order of tens of milliseconds should cause a significant offset between the perceived and the actual positions of a moving object. An appealing hypothesis is that the visual system can compensate for the neural delay and reduce the perceptual misalignment by extrapolating the trajectory of the moving object. . . . Evidence for motion extrapolation originally came from the flash-lag illusion. . . .” In order to outline a coherent theoretical framework for the flash-lag effect, neural delays, and the broader topic of “neural representation of space and time,” we present the following analysis and then go on to evaluate accounts of the flash-lag effect.

A human observer should perceive a flash after a significant delay relative to the actual time of the flash. It is unlikely that the nervous system can overcome this delay (van de Grind 2002). Likewise, one may reason that a moving object should be visible in a position it occupied in the recent past (*ds-error* postulate). Figure 27.3 presents this *standard view* graphically.

In 1994, Nijhawan suggested that the *ds-error* postulate was untenable. Other research on the flash-lag effect has also supported a revision of the *standard view*. The differential latency (Metzger 1932; Baldo & Klein 1995; also see Purushothaman et al. 1998; Whitney & Murakami 1998) and the spatial extrapolation (Nijhawan 1994) accounts of the flash-lag effect posit that the moving object is not perceived behind its actual position, but rather the percept of the moving object follows the physical object more closely than neural delays measured by discrete stimulation (e.g., by flashes) might suggest (Fig. 27.4).

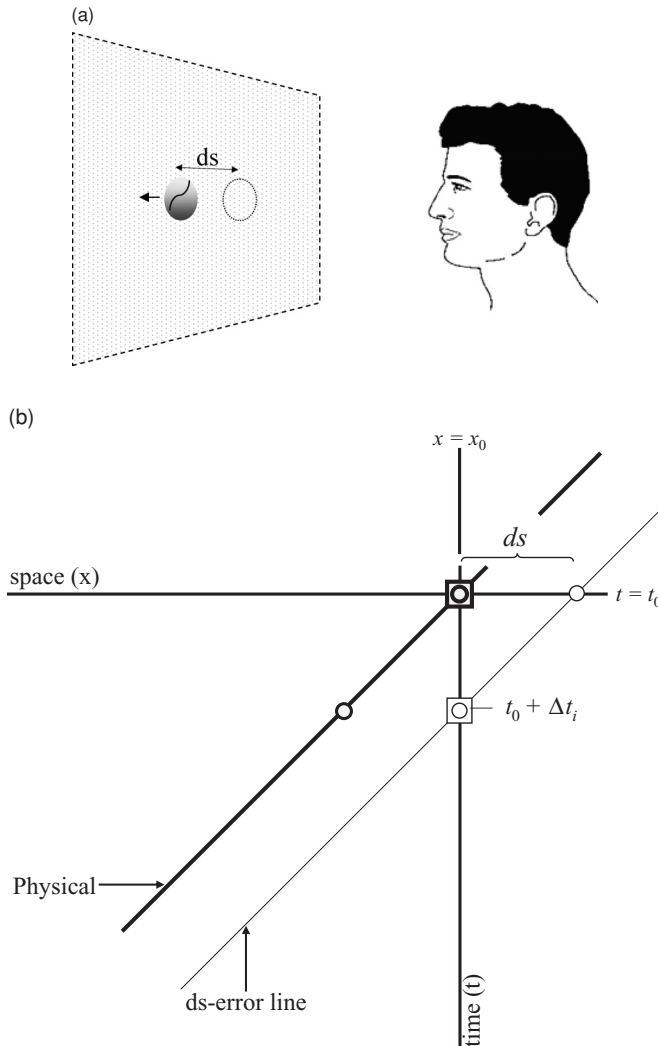


Fig. 27.3 (a) The standard view. The “average” observer views a ball moving leftward at constant velocity. At the instant depicted the physical position of the ball is shown by a distance ds ahead of the ball’s perceived position (broken circle). This picture is a result of the ds -error postulate, which states that due to input delays in the visual pathways, the moving object should be visible where it was in the recent past. (b) The representation of the “standard” view with space–time plots of an object moving at constant velocity v (thick line) and how a neuron “sees” the object with some delay (thin line). A brief flash (square, thick outline) presented in position x_0 at time t_0 is seen (square, thin outline) by the same neuron in position x_0 at time $t_0 + \Delta t_i$, where Δt_i is input delay. Two events, the arrival of the moving object in position x_0 as seen by the neuron (thin outline circle on the $x = x_0$ line), and the physical arrival of the object in position x_0 (thick outline circle on $x = x_0$ line), occur at different times due to neural latency. At a given time (say t_0) there is spatial lag between the physical position of the moving object (thick outline circle on $t = t_0$ line) and the position in which the neuron “sees” the object (thin outline circle on $t = t_0$ line). The spatial lag between the physical position and the neurally represented position will be referred to as ds -error. The standard view asserts that the above is an accurate picture of neural delays and their impact on perception.

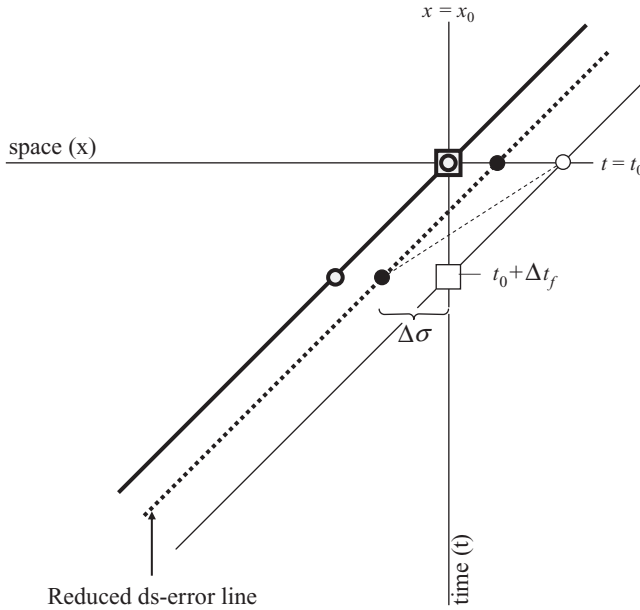


Fig. 27.4 A revision of the standard view is required by the flash-lag effect. The differential latency and spatial extrapolation accounts suggest that the percept of the moving object (filled black circle) is closer to the object's physical position than expected from measurements of neural delays with discrete stimuli-like flashes. So the thick broken ("reduced *ds-error*") line more accurately represents the perceived trajectory of the moving object. The *reduced ds-error* line is derived from the *ds-error* line by a shift corresponding to $\Delta\sigma = \text{flash-lag effect}$. On the standard view a flash-lag effect could not occur unless the object appeared to speed up to cover the additional distance $\Delta\sigma$ (represented by thin broken line segment of different slope).

In the past decade and a half, the flash-lag effect has invited several accounts (Nijhawan 1994; Baldo & Klein 1995; Purushothaman et al. 1998; Whitney & Murakami 1998; Brenner & Smeets 2000; Eagleman & Sejnowski 2000; Krekelberg & Lappe 2000; Bachmann et al. 2003; Wojtach et al. 2008), and since the original publications (Nijhawan 1994, 1997; Baldo & Klein 1995; Khurana & Nijhawan 1995; Purushothaman et al. 1998; Whitney & Murakami 1998; Berry et al. 1999; Kirschfeld & Kammer 1999; Brenner & Smeets 2000; Eagleman & Sejnowski 2000; Krekelberg & Lappe 2000; Schlag et al. 2000; Sheth et al. 2000) these accounts have undergone various revisions and generalizations. Here for purposes of analysis we partition the accounts under three headings: Visual Prediction; Spatiotemporal Integration, Sampling, & Postdiction; Differential Latency & Attention.

Based on various assumptions and theoretical constructs used, the accounts may be separated into three different categories: (1) accounts that place the perceived object on the **thick** broken (*reduced ds-error*) line, throughout some extended motion trajectory (namely, differential latency and visual prediction), (2) accounts that place the perceived object on the **thick** broken line for a short period of the motion trajectory (namely, postdiction account,

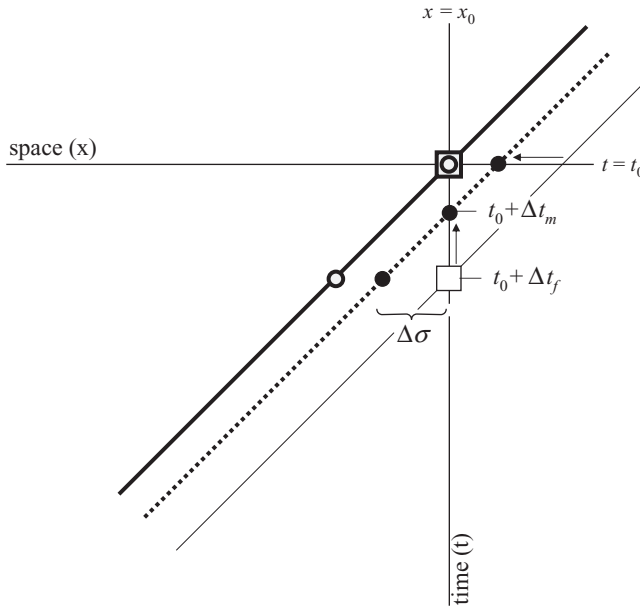


Fig. 27.5 The differential latency account places the moving object on the thick broken line as it assumes that moving objects are processed with a shorter latency (Δt_m) in relation to the latency (Δt_f) with which flashes are processed. This reduced latency, depicted by the upward pointing vertical arrow leading to the filled black circle, places the moving object on the *reduced ds-error* line (the thick broken line). Latency reduction occurs for any extended motion trajectory. As this account is strictly temporal the shift in coordinate must be parallel to the vertical (time) axis. The spatial extrapolation account assumes a spatial displacement that places the perceived object on the *reduced ds-error* line, depicted by the leftward pointing horizontal arrow leading to the filled black circle. Like differential latency spatial extrapolation occurs for any extended motion trajectory. Adapted from Krekelberg and Lappe (2001).

see the following), and (3) accounts that place the perceived object on the **thin** continuous (*ds-error*) line throughout (namely, position-averaging and motion-sampling accounts; see the following). Although the visual prediction and differential latency accounts both place the moving object on the *reduced ds-error* line throughout, the reasons they do so are different (see Fig. 27.5 and text following).

27.3.2 Visual prediction

Visual prediction holds that motion is of fundamental importance to the animal. The visual system is designed to exploit the occurrence of motion at constant speeds in fixed directions over short periods of time to predict a moving object's position. This prediction is not of future position, but of the present position (Cavanagh 1997), which achieves the compensation of visual processing delays. The moving object is therefore not seen in a position lagging behind the physical position, in contrast to the *standard view*, but closer to

its real position at any point along its trajectory. Because the flash is a sudden unpredictable event, neural delays in its registration cannot be compensated for in the same way. In the time it takes the visual system to process the flash, the moving object has moved on, which gives rise to the flash-lag effect (Nijhawan 1994).

27.3.2.1 *Laying-to-rest the ghosts of flash-lag past and flash-lag future*

For a number of years, the results of the following two experimental conditions seriously undermined the viability of the visual prediction account of the flash-lag effect: (1) The flash-terminated condition (originally called the “past-interval,” see Nijhawan 1992 in appendix) consists of events only up to and inclusive of the flash. In this condition the flash is aligned with a moving object’s last seen position. In other words, the moving object disappears from view simultaneous with flash offset. (2) In the flash-initiated condition (originally called the “future-interval,” see Nijhawan 1992 in appendix), the flash is aligned with the first position of a moving object. The moving object appears simultaneous with flash onset. The counterintuitive findings are as follows: the flash-terminated condition produces no flash-lag effect, whereas the flash-initiated condition produces an effect equal in magnitude to that observed with the standard full motion display (see Nijhawan 1992, in Appendix; Khurana & Nijhawan 1995).

Although intuitively these results are inconsistent with, and would even seem to rule out the visual prediction account, intuitions can be overturned in the presence of new experimental investigations. Recent analyses and experimental findings related to the flash-terminated and flash-initiated conditions (Maus & Nijhawan 2006, 2008, in press; Nijhawan 2008a) have not only made visual prediction compatible with these results but actually even more viable (also see Nijhawan 2002). Briefly, the transient signals produced by the abrupt disappearance of the moving object in the flash-terminated condition eliminate the flash-lag effect. These signals, which are present for any significant velocity changes (not just disappearances), suppress the perception of the forward shift. Indeed elimination of transients brings back the forward shift (Maus & Nijhawan 2006, 2008; also see Section 27.3.3.1 “Empirical challenges for the integration and sampling accounts” following).

In the flash-initiated condition, the intuition that extrapolation should take a significant time to be initiated after motion onset is wrong by about two orders of magnitude! Even by conservative estimates, the time taken for an extrapolated percept to be produced can be less than 2% of the 100 msec baseline delay typically thought to exist between stimulation of the retina and perception (De Valois & De Valois 1991; Nijhawan 2008a). Given that the required time for spatial extrapolation is so small, motion extrapolation is an extremely efficient mechanism that could start and finish virtually anytime during the required baseline (100 msec) delay after motion onset (Khurana & Nijhawan 1995). For a thorough analysis of time requirements of spatial extrapolation see Nijhawan (2008a, Section 5.2.1, page 185).

27.3.2.2 *Neurophysiological support for visual prediction*

The earliest stage of visual processing is in the retina itself. Interestingly, prediction can already be found in retinal ganglion cells, which form the output layer of the retina. In

response to a moving stimulus, the peak-firing rate in the ganglion cell population is found to be at or even ahead of the leading edge of the stimulus (Berry et al. 1999). There is no anatomical input from higher areas in the visual pathway back to the retina, so this predictive forward shift of the neural representation must come about due to local interactions in the retina.

Neural activity in lateral geniculate nucleus (LGN) is highly shaped by cortical feedback. In fact, although only ~10% of synaptic input into LGN cells stems from the retina, far more – about 30% – stems from cells in layer 6 of V1, which in turn receive fast feedback from motion area MT/V5 (Sillito et al. 2006). Anatomically, the feedback from V1 to the LGN, though local, spreads to nearby retinotopic locations along the orientation of the receptive field and in the direction of motion selectivity of the V1 cell. The spread of feedback to other retinotopic locations in the LGN could cause a shift in the retinotopic position of activity toward future stimulus positions. In experiments manipulating the responsiveness of MT/V5 by local drug application in macaque cortex, significant changes in the response properties of cells in V1 and the LGN have been shown (Sillito & Jones 2002). This feedback loop from MT/V5 via V1 to the LGN has been interpreted to “enable predictive modulation of circuitry at earlier levels, *even before* (italics added) the input arrives” (Sillito et al. 2006, p. 307).

Directionally selective neurons exist in primate V1 and other visual cortical areas. Studies have shown position shifts in the neural activity in retinotopic maps that could underlie predictive mislocalization phenomena. Sundberg et al. (2006) convincingly showed a distortion of retinotopy in macaque area V4 for stimuli that involved a color singleton in an apparent motion sequence (Cai & Schlag 2001). Neurons responded to an odd-colored “flash” even before it entered the neuron’s receptive field. This shift of the receptive field also occurred when the odd-colored flash was the final presentation of the bar in apparent motion, in contrast to human observers not showing a perceptual shift of the perceived position (Sundberg et al. 2006). This finding is consistent with the idea of neurons predictively coding positions in the visual field.

27.3.3 Spatiotemporal integration, sampling, and postdiction

Motion averaging (Krekelberg & Lappe 2000), motion sampling (Brenner & Smeets 2000), and postdiction (Eagleman & Sejnowski 2000) accounts all begin with the premise that the percept of a moving object lags behind the object’s physical instantaneous position. In other words, these accounts do not subscribe to the above-proposed revision of the *standard view* (see Fig. 27.4). On the spatial-averaging account, the visual system averages the position of the moving object over some temporal window. Thus the precise position of the moving object becomes available some time after the perception of the flash (Fig. 27.6). The motion-sampling account offers a similar explanation. Another variant of temporal integration has been advanced in which averaging is weighted toward the most recently sampled positions (Roulston et al. 2006). This is offered as an explanation for a

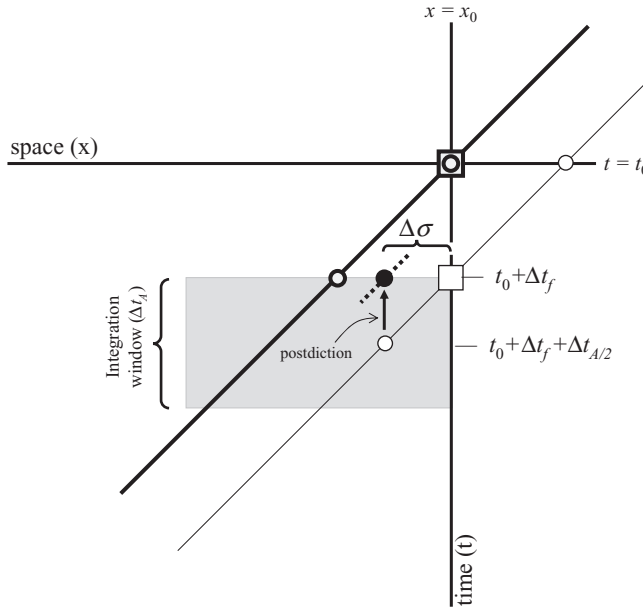


Fig. 27.6 Accounts that do not subscribe to a revision of the standard view claim that the thick broken (*reduced ds-error*) line in Figure 27.4 does *not* describe the correct trajectory of the perceived moving object. These accounts either place the object on the thin continuous (*ds-error*) line throughout (spatial-averaging and motion-sampling accounts) or on the thick broken line briefly (postdiction account). On the spatial-averaging account the moving object's perceived position is based on an average of the moving object's position in a certain time window (filled light gray rectangle of height Δt_A). Thus the precise position of the moving object (thin outline circle) becomes available after some time ($\Delta t_{A/2}$) of the perception of the flash. The "integration and postdiction" account assumes further that the output of integration (similar to averaging) is "postdicted" to the time the flash is registered (vertical arrow leading to filled black circle shown on short segment of thick broken line).

small undershoot of the final perceived position of a moving object (Baldo et al. 2002; Roulston et al. 2006), as well as the Fröhlich and standard flash-lag effects.

Both motion averaging and motion sampling accounts assume that the temporal mismatch ($= \frac{1}{2}$ the temporal window) between the perception of the flash and output of the averaging processes is not so relevant, as small temporal asynchronies are not detected by the visual system. The postdiction account (Eagleman & Sejnowski 2000) suggests that the output of the motion integration process (similar to averaging) is "postdicted to the time of the flash" (p. 2038), depicted by the upward pointing vertical arrow leading to the filled black circle (Fig. 27.6).

Motion averaging and integration in the visual system is not only well supported by various psychophysical observations, but also by commonly seen behavior of neurons. In response to change in stimulation, neurons do not increase or decrease their activity level instantaneously. For example, retinal ganglion cells continue to be active for a significant duration after cessation of stimulation (Kratz & May 1990). If persisting neural output were

“directly” used by the visual system in determining a moving object’s instantaneous position, then this representation would be a “fuzzy” indicator of the object’s physical position. So, position averaging is necessary for accurate localization. Thus position averaging is not just a likely neural mechanism for more precise visual localization of moving objects (Burr & Morgan 1997) but also necessary for visually guided behavior, such as catching moving objects for which accurate localization is essential. Given such a strong basis for position averaging, it should take place whenever the animal encounters motion in the world.

So the first challenge for the position averaging account is: Why does the averaging start after $t_0 + \Delta t_f$, that is, after the registration of the flash (Fig. 27.6)? In other words, why is the lower bound of the integration window aligned with $t_0 + \Delta t_f$ in Fig. 27.6 (and in Figure 2D of Krekelberg & Lappe 2001)? According to the logic outlined above, a moving integration window, whose output is also moving, better captures the integration process. If position averaging took place for moving objects throughout their trajectory, then the output of averaging should be available not just at $t_0 + \Delta t_f + \Delta t_{A/2}$ (as required to explain flash-lag) but also at the earlier time when the flash is first registered at $t_0 + \Delta t_f$. (This output would be based on motion input, which was presumably there prior to the flash). A moving output of the integration process, carried out over a fixed window height, should be aligned with the flash. Thus, the perceived position (given by the average) of the moving object at the time the flash is first perceived should be aligned with the flash, thus rendering a lack of a flash-lag effect. In that first instant, there shouldn’t be a lag, but rather it should “develop” in the time immediately following $t_0 + \Delta t_f$ (during the time the flash visibly persists). This is contrary not just to the phenomenological observations of the flash-lag effect (Nijhawan 1994), where observers claim that the flash lags the moving object when first seen, but would render certain flash-lag results impossible. For example, the color decomposition result (Nijhawan 1997), in which a red flashed line superimposed on a moving green bar appears to lag behind the bar and appears red (as opposed to yellow), critically depends on the flashed line appearing in a lagging position when first seen. Indeed, inconsistencies are seen in Krekelberg and Lappe’s (2001) Figure 2D (and its adaptation, our Fig. 27.6). These figures show a continuous delayed line, which by definition depicts the moving object’s registered positions between times $t_0 + \Delta t_f$ and $t_0 + \Delta t_f + \Delta t_{A/2}$ (and earlier), and yet the account works only if the *instant* corresponding to $t_0 + \Delta t_f + \Delta t_{A/2}$ is selected. The figure, in fact, shows that there should be no effect at $t_0 + \Delta t_f$, which counters the very definition of flash-lag.

Further challenges arise for the postdiction account due to the notions of “flash reset” and “postdiction to the time of the flash.” On the postdiction view (Eagleman & Sejnowski 2000), the flash “resets” motion integration (p. 2037), and the output of motion integration (similar to averaging) is “postdicted to the time of the flash” (p. 2038). Clearly, for this account flashes are critical. However, there are numerous forward-shift motion phenomena that do not involve flashes, so for such phenomena the concepts of “flash-reset” and “postdiction to the time of the flash” do not logically arise.

More problematic, however, is the notion that the visual system “postdicts” the output of motion integration to the time of the flash registration. In other words, the “postdicted”

object (based on motion integration) should lie on the horizontal line passing through $t_0 + \Delta t_f$. But this point is on the *reduced ds-error* line (see thick broken line segment in Fig. 27.6). The question then is what happens to this postdicted object when motion continues after the flash. Does the object now continue its trajectory as given by the thick broken (*reduced ds-error*) line, or does the object trajectory return to the delayed thin continuous (*ds-error*) line? (The postdiction account assumes that prior to the flash, and sometime after it, the *ds-error* line accurately reflects the perceived positions of the moving object.) According to the postdiction account, the object trajectory cannot continue to be the thick broken line as then, after the flash (for example, if a second flash is presented in alignment with the moving object), this account will become indistinguishable from the differential latency and spatial extrapolation accounts. On the other hand, if the object trajectory returned to the thin continuous (*ds-error*) line, then the object would need to slow down (converse of the process depicted by the thin broken line segment in Fig. 27.4). Because this predicted slowdown would be easy to note, and has never been noted, this account clearly cannot be an explanation of the flash-lag effect.

27.3.3.1 Empirical challenges for the integration and sampling accounts

The postdiction account claims that future events (after the flash) impact the position of the moving object. Likewise, the sampling account claims the flash-lag effect is based on the speed of motion after the flash (Brenner & Smeets 2000). In addition to the above-mentioned logical challenges faced by these accounts, two recent studies provide evidence against the claim that the forward shift of a moving object is influenced by information from the future trajectory of the moving object. The first study consisted of two experimental conditions (Maus & Nijhawan 2006). In the first condition, a stationary white dot was presented in a series of positions $P_1, P_2, P_3, \dots, P_{N-1}, P_N$ (on an imaginary circle), such that the dot intensity at $P_1 >$ dot intensity at $P_2 >$ dot intensity at $P_3 >$ dot intensity at P_4 , and so on. At P_N the dot was invisible. Between positions P_1 and P_N a position was determined, for each observer, where the dot's intensity was at the observer's absolute detection threshold (defined as 50% detectability). This position was called the "edge of visibility," P_{Tstat} (detection threshold position for the stationary dot). Note: In positions just beyond (after) P_{Tstat} the dot did not provide sufficient input to lead to the observer seeing the dot reliably.

In the second condition, a smoothly moving dot underwent exactly the same intensity decrement as the dot in the first condition; the intensity-position relationship was identical to the first condition. Is the "edge of visibility" in the motion condition (P_{Tmov}) the same as P_{Tstat} , or is it shifted forward? In other words, does the smoothly moving dot perceptually disappear for the observer at P_{Tstat} , or is the disappearance position shifted forward? We found that P_{Tmov} was shifted by 175 msec relative to P_{Tstat} , in the direction of motion. Thus the dot in the motion condition was visible in positions where the stationary dot could not be seen because the latter's intensity was below detection threshold in those positions. This shift cannot be caused by input from the dot in positions beyond P_{Tstat} , as this position was

(by definition) the point beyond which input was insufficient to yield visibility of the dot. So, this forward shift can only have occurred due to the input from the past positions of the moving dot before it reached P_{Tstat} .

In a second study, a smoothly moving line segment moved from the signaling part of the retina toward the retinal blind spot and then crossed into the blind spot (Maus & Nijhawan 2008). Where do observers perceive the line to disappear in the visual field? In this case, again, it was found that the line segment was visible in positions past the boundary of the blind spot in regions well into the blind spot. Once again, in this case the forward shift was seen, but the stimulus input from the future (later) positions was missing. Clearly, there is no input from the blind spot. So any visibility of the moving line in the blind spot region could only be based on earlier input from the moving object, before it reached the blind spot boundary.

It is clear from both these studies that the forward shift in the position of moving objects, at least in the stimuli studied, could not be due to later motion signals being integrated with earlier motion signals. Earlier motion signals impacting the position of the moving object parsimoniously explains not just the results of the above-mentioned studies but also flash-lag results, including flash-initiated and flash-terminated results (as discussed in the section on visual prediction, see previous).

27.3.4 Differential latency and attention

27.3.4.1 Movement of attention

Soon after the original announcement of the flash-lag effect (Nijhawan 1994), an alternative to motion extrapolation was proposed by Baldo and Klein (1995). They showed that the illusory forward displacement of rotating moving dots relative to the perceived positions of flashed dots depends on the eccentricity of the flashes, with larger eccentricity leading to larger forward displacements. It was proposed that the time for the flashes to be perceived depends on their eccentricity, as it takes time to reallocate attentional resources to the more peripheral positions of the flashes. The flash-lag effect is thus a consequence of the time cost in shifting attention from the moving object to the flash and back. “Cue-induced visual focal attention” has been suggested as a mechanism to accelerate perceptual processing of a moving object along its trajectory (Kirschfeld & Kammer 1999), and thus to cause the flash-lag effect.

In reply to Baldo and Klein (1995), Khurana and Nijhawan (1995) created a similar stimulus in which flashing and moving objects were not presented in distinct spatial locations. In a rotating line of dashes, additional dots were flashed in positions interjected between the moving dashes, and the flash-lag effect was still perceived. Furthermore, when the flash was presented at the time the moving object was set into motion (the flash-initiated condition), an unabated flash-lag effect was perceived (Khurana & Nijhawan 1995). In this flash-initiated condition, attention is equally oriented to both of the two objects (moving or

flashed), so there is no attentional disadvantage for one or the other. These findings argue against an explanation of the flash-lag effect solely in terms of the delays associated with attention shifts.

In the above studies, (Baldo & Klein 1995; Khurana & Nijhawan 1995) allocation of attention was inferred. A later study explicitly manipulated and measured attention in the flash-lag paradigm by directing attention either toward or away from the positions of flashes (Khurana et al. 2000). Although simple reaction times to flashes at cued locations were quicker than for uncued locations, there was no difference in the magnitude of the flash-lag effect as a function of attentional modulation. These findings further argue against an explanation of the flash-lag effect based on delays in the redistribution of attentional resources from moving to flashed stimuli. In other studies, it has been shown that the effect size can be modulated by voluntary attention (Baldo et al. 2002; Namba & Baldo 2004). It is likely that attention here influenced perceptual latencies, but although attention is not the underlying cause of the flash-lag effect, it may be an additional influence (Namba & Baldo 2004).

27.3.4.2 Differential latency

Perhaps the simplest account of the flash-lag effect is the differential latency account (Metzger 1932; Purushothaman et al. 1998; Whitney & Murakami 1998). This view suggests that the percept of the moving object lags the object's physical position by a distance $v\Delta t_m$, which is less than $v\Delta t_f$; here Δt_m and Δt_f are the latencies for the moving and the flashed object, respectively. The flash-lag effect reflects the relationship $v(\Delta t_f - \Delta t_m) = \Delta\sigma$, where $\Delta\sigma$ is the flash-lag effect. This account has great intuitive appeal, as it is well known that different stimuli are processed with different delays.

The main weakness of the differential latency account is that $\Delta t_f - \Delta t_m$ must equal about 80 msec, the typically cited value of $\Delta\sigma/v$ (e.g., see Eagleman & Sejnowski 2000). This is a large latency difference that is a priori unlikely as flashes are extremely effective at stimulating the visual system. Furthermore, such a large difference should have been revealed and well established owing to the innumerable neurophysiological studies over the last century that have employed both static flashes and moving objects to stimulate the visual system. Failures to find differences usually go unreported; however, some articles have suggested that, if anything, neural response to flashes occurs slightly faster than to motion (Raiguel et al. 1989; however, see Jancke et al. 2004). Furthermore, the "differential latency" account is ruled out as a complete explanation of the flash-lag effect by the fact that the flash-initiated condition (Khurana & Nijhawan 1995), in which the moving object comes on simultaneously with the flash, produces an undiminished flash-lag effect. How can a moving object that suddenly appears on the screen be perceived more quickly than a flash, and that too by 80 msec? If this were the case, the automobile industry would have come up with a brake design, which would turn on a moving stimulus instead of turning on a stationary light! We note, again, that the spatial extrapolation account does not face this speed-of-processing challenge posed by the flash-initiated condition, as a spatial shift in coordinates of neural activity representing the moving object incurs a trivial added delay relative to baseline delay (see Nijhawan 2008a, Section 5.2.1, p. 185).

Not surprisingly several psychophysical studies have failed to find any reliable latency difference between moving objects and flashes (Eagleman & Sejnowski 2000; Alais & Burr 2003; Nijhawan et al. 2004; Ichikawa & Masakura 2006). At this juncture, the only safe conclusion can be that if there is a latency advantage to the processing of moving objects, in relation to flashes, then this advantage is probably small in comparison to $\Delta\sigma/v$ (=80 msec).

27.3.5 *Comparison of spatial and temporal accounts*

There is no doubt that the variables of differential latency and attention do play a role in the flash-lag effect. But their contributions are unlikely to be sufficient to explain the entire effect. A spatial account such as motion extrapolation fares better. An additional advantage of the motion extrapolation account is that it potentially explains not just the flash-lag effect but also numerous other forward-shift phenomena related to motion per se. There is also neurophysiological support for this account (discussed previously). But perhaps the greatest appeal of the motion extrapolation account is that it presents some remarkably simple modifications of existing facts and ideas to yield new insights into the connections between neurophysiology and perception. We consider two such insights here. One concerns a modification of the notion of a motion sensor to incorporate spatial extrapolation while adhering to the notion of retinotopic representation of visual space. The second introduces the notion of a “diagonal neural pathway.”

Among the modeling achievements concerning visual neural processes, the concept of a directional motion sensor stands out for its simplicity and elegance. A motion sensor, connected to two input lines with a delay in one of the lines, produces a response to motion in one direction (rightward in Fig. 27.7(a)) but not to motion in the opposite direction. Of all neural–perceptual isomorphisms, the concept of topographic retinal maps and their contribution to perception of visual space has been most fundamental to neurophysiology since retinotopic maps were first discovered. A neurally simple modification of the concept of the directional motion sensor is suggested by motion extrapolation that allows for compensation of neural delays while keeping the spatial isomorphism unaffected. Figure 27.7(b) shows a modified motion sensor that is not just a motion sensor but also provides location information of the moving object. This motion sensor is shifted in the direction for which it is tuned. The shift compensates for the transmission delay.

One interesting further possibility is revealed by this modified scheme. Two oppositely tuned directional motion/position sensors together could serve to localize stationary objects (Fig. 27.7(c)). This suggests that motion may be the medium that sets up retinotopic maps initially during development, for which there is evidence (Meister et al. 1991). These very maps are later used by the mature system for localizing both moving and stationary objects (Nijhawan 2008b).

The notions of horizontal and vertical pathways are well established in neurophysiology. Motion extrapolation leads naturally to considering a “diagonal pathway.” Consider a simple two-layered network in which an input layer of neurons is connected to an output

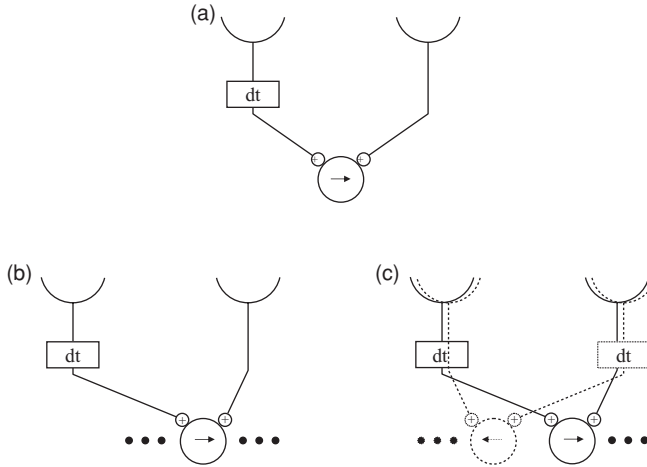
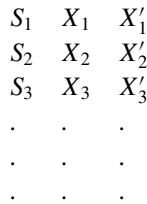


Fig. 27.7 (a) Shows the standard Reichardt-type directional motion sensor. (b) A modified sensor that also senses object position. When this sensor is active it gives a forward-shifted position (relative to that in (a)) to compensate for neural delays. (c) A pair of modified motion sensors that are oppositely tuned for motion direction. The output of this pair would signal position of stationary objects, which are caused to shift over the retina by small (oscillatory) eye movements.

(perceptual) layer. The input layer has two opposing requirements. One is to transmit information about significant world events onto the output layer as quickly as possible, whereas the second is to process the input so that it is usable by later neurons, so the animal is able to produce appropriate response. This processing is what slows down transmission (Nijhawan & Wu 2009). (As a contrast one could imagine transmission of raw data to spring-loaded effectors that reacted as quickly as possible.) In the case of moving objects, the visual system solves the problem of neural delays by sending information along diagonal pathways, which are made up of horizontal and vertical neural segments (e.g., in the retina the horizontal cells constitutes the horizontal segment, and the bipolar cells constitute the vertical segment; the two together make up the “diagonal” pathway). Consider a two-layered network with sensory neurons X_1, X_2, \dots connected to perceptual neurons X'_1, X'_2, \dots . Neuron X_1 is connected to neuron X'_1 , neuron X_2 is connected to neuron X'_2 , and so on. S_1, S_2 , and so on specify successive locations of a moving stimulus.



In order to compensate for the transmission delay, such a network has to be tuned to the delay such that when the stimulus arrives at S_2 (stimulating X_2), X_2 sends input “diagonally”

to X'_3 (not to X'_2) so that information gets to X'_3 simultaneously with the stimulus getting to S_3 (Nijhawan & Wu 2009).

27.4 Conclusion

Over the past decade the notion of visual prediction has led to a lively debate. The appeal of visual prediction is that on this view visual mechanisms are assigned the task of estimating *and* compensating for visual delays. Visual prediction opposes the *standard view* (the *ds-error* postulate; the notion that neural delays should cause a lag in the moving object's perceptual position relative to its physical position). New analyses (Nijhawan 2008a) and data (Maus & Nijhawan 2006, 2008) suggest that empirical results with unpredictable motion, in particular the flash-terminated and flash-initiated conditions, are compatible with visual prediction (also see Nijhawan 2002). In fact, the times involved by the putative extrapolation mechanism are so short that *ds-error* could be reduced to zero (or even have a negative value due to "overextrapolation," see Nijhawan 2008a).

On a final philosophical note, both the notions of differential latency and spatial extrapolation attempt to reduce the discrepancy between the "real" world and the "experienced" world, but there is a deep conceptual difference between the two accounts. Differential latency starts by assuming a "real" world and a delayed representation of it by the brain. Most of the thinking in psychophysics and neuroscience represents this view. Differential latency proposes that when possible the "reconstructed world" follows the "real" world closely. Visual prediction starts with a fundamentally different assumption. It assumes that neural representations (and not the "real" world) exist first. The notion of the "real" world emerges from these representations. This proposal is concordant with that of Ernst Mach (see Ratliff 1965, for a discussion of Mach's position). The use of the term "real" world, on this view, is justified only for everyday practical affairs. A most illuminating statement reflecting this challenge is by the Gestalt psychologist Wolfgang Köhler (1947): "If a wound is not the gun which emitted the projectile, then the thing which I have before me, which I see and feel, cannot be identical with the corresponding physical object."

In Mach's terminology, the complex of neural representations leads to the concept of the "real" world. By reversing this argument Mach produced a most informed critique of Kant's "thing in itself." Mach wrote: "The vague image that we have of a given permanent complex, being an image that does not perceptibly change when one or another of the component parts is taken away, gradually establishes itself as something that exists by itself. Inasmuch as it is possible to take away singly every constituent part without destroying the capacity of the image to stand for the totality and of being recognized again, it is imagined that it is possible to subtract all parts and to have something still remaining. Thus arises the monstrous notion of a thing in itself, unknowable and different from its 'phenomenal' existence" (Mach 1885/1897, pp. 5–6). Likewise, the impetus for the motion extrapolation view comes from a desire to remove the "vague image," a ghost that is unknowable (because all neural processes leading to knowledge are subject to delays) but that, nonetheless, trails behind the phenomenal object in motion.

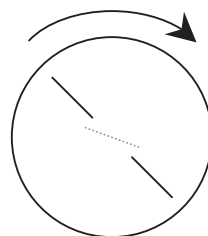
Appendix

1415 – 7:15

MISALIGNMENT OF CONTOURS THROUGH THE INTERACTION OF APPARENT AND REAL MOTION SYSTEMS.

Romi Nijhawan, Psychology Department, University of California Berkeley, CA

Observers viewed a rotating diameter of a physical disc whose central third segment flashed (for 5 msec) at predetermined times while the two, outer third segments, were illuminated continuously. Thus, the latter segments underwent real motion while the former flashed at rates which did or did not produce apparent motion. The outcome was quite unusual. The flashed segment appeared rotated by up to 10 degrees (for angular velocity of diameter = 38 rev/min) in the direction opposite to the rotation of the continuous segment (see Fig). The effect was directly related to the angular velocity of the diameter. When the flashing rate was adjusted so that the central segment underwent apparent rotation, the effect was reduced and was inversely related to the rate of flashing. Three possible explanations were considered: 1) Delayed processing of the flashed stimulus, 2) movement-induced positional bias, and 3) visible persistence in the flashed segment and the lack thereof in the continuously moving segments. To decide between these possibilities the display (for a flash rate = 1 flash/rev) was separated into two temporal intervals. One interval consisted only of events before the flash (past-interval) and the other interval only of events after the flash (future-interval). The observers reported no misalignment effect in the past-interval but did so in the future-interval. The magnitude of the effect for the future-interval was as strong as that for the past+future interval. This result supports the third account above indicating that motion perception is necessary to erase motion smear and that motion is computed prior to form.



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