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Nijhawan, Romi (2001) The flash-lag phenomenon: Object motion and Eye movements. Perception, 30 (3). pp. 263-282. ISSN 0301-0066

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Perception, 2001, volume 30, pages 263 – 282

DOI:10.1068/p3172

The flash-lag phenomenon: object motion and eye movements

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Received 15 July 1999, in revised form 6 October 2000

Abstract. An object flashed briefly in a given location, the moment another moving object arrives in the same location, is perceived by observers as lagging behind the moving object (flash-lag effect). Does the flash-lag effect occur if the retinal image of the moving object is rendered stationary by smooth pursuit of the moving object? Does the flash-lag effect occur if the retinal image of a stationary object is caused to move by smooth-pursuit eye movements? A disk was briefly flashed in the center of a moving ring such that the ring center was completely 'filled' by the disk. In this display, observers perceived the flashed disk to lag such that it appeared only to partially 'fill' the ring center. The 'unfilled' portion (perceived void) of the moving ring was seen in the color of the background. With smooth pursuit of the ring, the flash-lag effect was eliminated, and observers saw the flashed disk centered on the moving ring. A strong flash-lag effect was observed when observers smoothly pursued a moving point target past a continuously visible stationary ring. Once again, the flashed disk appeared to only partially fill the center of the continuously visible stationary ring, yielding a vivid 'perceived void'. These results are discussed in terms of neural delays and their compensation.

1 Introduction

Delivering accurate information about position of objects in visual space is perhaps the most important requirement of the visual system. Consistent with this, but not immediately obvious from the structure of the peripheral visual system, is the finding that observers can precisely localize objects to within a fraction of a diameter of a single photoreceptor. What is truly remarkable is that this hi-fidelity response of the visual system in the spatial domain is not diminished even for objects shifting over the retina (Westheimer and McKee 1975).

Moving objects, however, pose another challenge for the visual system. There are nontrivial transmission delays of neural signals between the photoreceptors and the 'higher' cortical areas devoted to analyzing those signals. Even for conservative estimates of the delay, moving objects can travel a significant distance in this time. One immediate consequence of these delays is that moving objects should appear significantly behind in their motion trajectory. How would these delays impact an observer's performance on a moving vernier, say on judging the horizontal separation between two vertical lines moving laterally? If the two lines travel with the same velocity, then there should be equal visual lag for both lines, which should pose no special problem for the observer in the vernier task. Thus, perhaps not surprisingly, in evaluating the spatiotemporal response of the visual system to a moving vernier, the inherent time delays of the visual system are typically not considered (Burr 1979; Morgan and Watt 1983; Poggio and Fahle 1983).

Several researchers have considered the impact of neural transmission delays on visual delays (Anstis 1989; Ramachandran and Anstis 1990; De Valois and De Valois 1991). De Valois and De Valois presented observers with vernier targets consisting of a Gabor patch with a stationary envelope within which sinusoidal gratings moved either leftward or rightward. Three patches were presented in a vertical arrangement, with the top and bottom patch located on the same vertical line. The observers judged the horizontal position of the middle patch relative to the top and the bottom patch. A significant bias was observed, such that observers perceived the location of the middle Gabor to be shifted in the direction of the moving gratings. Thus, when the three patches were located on the same vertical line, and the gratings in the middle patch moved left, the middle patch appeared shifted to the left. Ramachandran and Anstis (1990) reported analogous findings with vernier patches that were equiluminous edges of rectangles within which dot elements moved either leftward or rightward. Once again, the moving dots caused the rectangles in which they were visible to appear shifted in the direction of motion.

De Valois and De Valois (1991) considered the implications of this so-called 'movement-based positional bias' from the point of view of successful interceptive actions commonly observed in nature and high-speed ball games. A successful catch, for example, is contingent on the compensation of the significant delays that exist in the visuomotor loop. Anatomically, the *visual* and the *motor* delays are due to information transmission along completely different neural pathways. It is usually believed that the compensation for visuomotor delays occurs at some relatively 'late' stage of motor planning. In interpreting the 'movement-based positional bias' of vernier targets, the above researchers raised the possibility that a mechanism within the visual system itself may partially compensate for the visuomotor delays, by causing the forward shift of the moving items.

Consider, however, two further observations related to this 'movement-based positional bias'. First, the effect increases rapidly with increasing eccentricity, being relatively weak or absent in the fovea (De Valois and De Valois 1991). Although this finding no doubt reflects greater acuity of the fovea, it casts a new light on the interpretation of the effect in terms of compensation of neural delays. A characteristic of interceptive (or avoidance) behavior, the success of which would be the ultimate goal of any compensatory mechanism, is that animals with a fovea usually attempt to foveate the moving targets of interest. Clearly, there are significant delays from the fovea to the cortex. A compensatory mechanism for the periphery but not the fovea does not seem very plausible. Second, the displacement effect occurs only if the targets are equiluminous with the background or, more generally, when clear information about the location of the borders of the stimuli is absent (Ramachandran and Anstis 1990; De Valois and De Valois 1991). These conditions are rarely, if ever, satisfied by moving objects in the natural environment, where any type of compensatory mechanism would have evolved. These considerations pose a difficulty for the interpretation of the 'movement-based positional bias' in terms of compensation of neural delays.

The present report explores the problem of transmission delays and their possible compensation using a rather different phenomenon which, furthermore, occurs unabated with high-contrast stimuli and foveal viewing. On a gray background, a black ring moved along a circular trajectory. At a given instant, the center of the moving ring was filled with a briefly flashed white disk. With stationary fixation, observers reported the position of the flashed disk relative to the moving ring. In addition to reporting the lag of the flashed disk, referred to as the flash-lag effect (Nijhawan 1994a), observers perceived the center of the moving ring to be only partially filled. The 'unfilled' portion of the center of the moving ring, which will be referred to as the 'perceived void' was seen in the color of the gray background (Nijhawan 1994b). In experiment 1 the perceived-void phenomenon was investigated by two different procedures. Experiment 2 addressed the following question: Could the flash-lag effect and the 'perceived-void' phenomena observed in experiment 1 be due to eye movements? Simultaneous presentation of two rings moving in opposite directions was employed to address this question.

Ernst Mach (1897) might have been the first to document a strange mislocalization effect involving a flash and an eye movement (page 61). An observer, who happened to be making a saccade while viewing a flash (spark) produced by a mechanical device, sometimes perceived the flash as displaced in the direction of the saccade relative to the device. Several researchers (Matin and Pearce 1965; MacKay 1970; Matin 1972; Mateeff 1978; O'Regan 1984; Honda 1989) have systematically investigated this effect. It is known that an analogous mislocalization effect is observed with other types of eye movements such as smooth pursuit (Ward 1976). The often-cited work of MacKay (1958) in connection with the flash-lag effect is, in fact, concerned with eye movements. In MacKay's experiment, the perceived position of flashes was mislocalized during eye movements resulting from externally applied force oscillating the eyeball.

In experiments 3 and 4 the flash-lag effect was measured while observers executed smooth-pursuit eye movements. Experiment 3 addressed the following question which has not been systematically investigated before: Does the flash-lag effect occur if the moving item is smoothly pursued by the observer? If retinal image motion is necessary for the flash-lag effect, then smooth pursuit of the ring should eliminate the effect. In experiment 4, the perceived position of the flashed disk was determined by the observer smoothly pursuing a point target moving past a continuously visible stationary ring. In this case, the retinal image of the stationary ring moved owing to smooth-pursuit eye movements. If retinal image motion is sufficient, then this experiment should produce a version of the flash-lag effect, despite the stationarity of the continuously visible ring.

2 Experiment 1: The ring – disk display

The experimental display consisted of a moving black ring translating on a circular path on a gray background, and a flashed white disk (figure 1). The position of the flashed disk was fixed, but the instant of the flash could be adjusted (by the experimenter or the observer) to coincide with any position of the moving ring in its path. This display was motivated by questions like: When the disk is flashed in the center of the moving ring, where does it appear relative to the ring? Does the lag of the flashed disk cause sections of its boundary to appear against the gray background inside the moving ring, such that the observers perceive spurious white – gray (disk – background) luminance boundary, despite the retinal image consisting of gray – black (background – ring) and black – white (ring – disk) boundaries? Do observers see a 'perceived void' inside the moving ring in the color of the background?

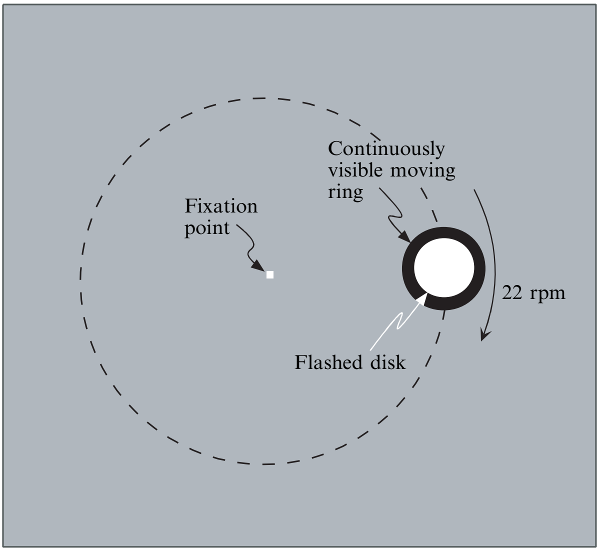

Figure 1. The basic display shown at the instant of the flash of the disk (duration 1.5 μs), with the centers of the ring and the disk aligned. The ring moved clockwise at 22 rpm. The disk flashed once every revolution of the ring.

2.1 *Observers*

Six observers participated in two different procedures to investigate the flash-lag phenomenon using the ring–disk display. All six observers (four naïve to the hypothesis) participated in procedure I. Four of these observers (two naïve to the hypothesis) also participated in procedure II.

2.2 *Apparatus*

The movement of the ring was analog produced with a DC motor connected to a speed controller. The ring was mounted on a rotary-motion table, positioned in the observer's frontal plane, connected directly to the motor shaft. A magnetic trigger attached to the motor shaft closed the circuit through a magnetic reed switch, which in turn triggered a variable time delay. Thus, the circuit was closed once every rotation of the motor shaft. The time delay could be adjusted with a resolution of 0.1 ms by the rotation of a dial. At the termination of the time delay a flash (duration 1.5 μs) was produced by a General Radio stroboscope. Mirror-type beam splitters were used to present the flashed disk and a fixation point in the optical plane of the moving ring. The observer's head was positioned on a chin-and-forehead rest with the eyes at a viewing distance of 150 cm from the display. The precise alignment of the annulus and the flashed disk required not only precise timing, but also precise positioning of these items in the laboratory coordinates. Gross position adjustments were made with lab jacks and fine adjustments with two- and three-axis translation stages with 65 or 80 TPI screw adjustment.

2.3 *Stimuli*

The intensity of various stimuli was controlled either with pairs of cross-polarized filters or with neutral-density filters. Diffusing material was used to provide uniform illumination for the stimuli. The luminance of the gray background was 6.4 cd m^{-2}. The black ring (luminance 0.0 cd m^{-2}; inner diameter = 0.82 deg, outer diameter = 1.20 deg) revolved clockwise on a circular path at 22 revolutions min^{-1} (rpm) (instantaneous speed 7.25 deg s^{-1}, path diameter 6.3 deg). The diameter of the flashed disk was 0.82 deg, same as the inside diameter of the moving ring. The flashed disk was presented at the 3 o'clock position at 0.37 Hz (one flash per rotation of the ring). The intensity of the flashed disk was fixed at 200 times detection threshold. For procedure I, the fixation point was located at the center of rotation of the ring, while for procedure II the fixation point was located at the 3 o'clock position, centered on the flashed disk.

2.4 *Procedure*

Initially, the time delay was adjusted such that the flash of the disk occurred physically in the center of the moving ring. The physical centering of the flashed disk relative to the moving ring was achieved as follows: A second stroboscope (Strobotac$^{\mathrm{TM}}$), synchronized to flash simultaneously with the first stroboscope, illuminated the otherwise invisible moving ring for 1.5 μs. The moving ring and the flashed disk were deemed physically aligned when they appeared visually aligned to the experimenter and another observer who did not participate in the experiment. This method of aligning moving and flashed elements is extremely precise as confirmed by a photograph of the display. The reading for the specific time delay (T_{A}) which produced this alignment was then recorded from a scale on the time-delay unit. Rotation of a dial in either the clockwise or the counterclockwise direction changed the value of the delay, which in turn changed the position of the moving ring relative to the flashed disk. The rotation of the dial was controlled either by the observer or the experimenter. The experiment was performed in a dimly illuminated laboratory. The observers viewed the display binocularly through natural pupils.

2.4.1 *Procedure I.* For the first procedure six observers fixated the center of rotation of the ring (see figure 1). Their task was to rotate the dial, which changed the time delay, till the flashed disk appeared centered on the moving ring. The observers could view the display for as many cycles as necessary. After the observer's setting, the value of the time delay (T_S) was recorded from the scale (invisible to observer). The initial time delays were set to a value that caused the flashed disk to appear in either a significantly leading or lagging position. These time delays corresponded to $T_A \pm 100$ ms. Each observer ran in ten interleaved trials, five ascending and five descending.

2.4.2 *Procedure II.* In the second procedure, the observers performed a rather different task. The fixation point was now located at the 3 o'clock position, centered on the flashed disk. In this procedure, the time delay was fixed at T_A (flashed disk physically centered on moving ring). This procedure was geared to find out if a 'perceived void', which corresponds to the 'unfilled' portion of the center of the moving ring, is perceived by observers against which the 'spurious edge', that is portion of the boundary of the flashed disk, is perceived. Foveal viewing was used to improve acuity for these perceptual phenomena. The observer's task was to view a comparison stimulus consisting of a ring and a disk (both of which were static and continuously visible), and change the position of the comparison disk relative to the comparison ring till the comparison stimulus matched their percept. Each observer participated in 10 trials.

2.5 *Results and discussion*

When procedure I was used, the average difference between the time delay set by the observer to achieve the perceived alignment of the flashed disk with the moving ring, and that at which the disk was physically aligned with the ring, gave the magnitude and direction of the effect. A T_S (time delay for perceived alignment) smaller than T_A (time delay for physical alignment) implies that the flash must occur earlier. In other words, the flash of the disk presented at the 3 o'clock position must occur before the moving ring arrives in the 3 o'clock position for the flashed disk to appear centered on the moving ring. All $T_S - T_A$ values for all observers were negative. Figure 2 gives the means and the standard errors for six observers. On average, the flash had to occur 44 ms earlier for it to appear centered on the moving ring.

In the matching task (procedure II), observers positioned the comparison disk in a trailing position relative to the comparison ring. Thus, although in the retinal image the flashed disk was centered on the moving ring, the flashed disk appeared to overlap the trailing contours of the moving ring, and a gap was perceived between the leading

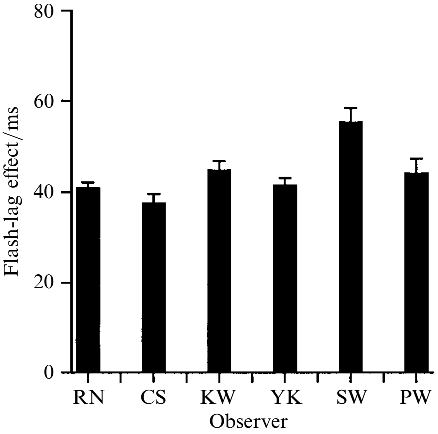

Figure 2. Bar graph showing data for six observers (four naïve to the hypothesis) who participated in procedure I of experiment 1. The ordinate shows the values $T_S - T_A$ (see text). T_S = time delay at which the flashed disk appears to the observer to be aligned with the ring; T_A = time delay at which the flashed disk is physically aligned with the ring. $T_S - T_A$ is equivalent to the flash-lag effect. Error bars represent standard error.

contour of the ring and the boundary of the disk (figure 3). The crescent-shaped 'unfilled' portion of the moving ring (perceived void) appeared the same color as the background. Verbal reports of observers also point to a vivid percept of a 'spurious edge', such that some of the boundary of the white flashed disk is seen against a gray 'perceived void'. Figure 4 shows the data for four observers (two naïve to the hypothesis) in procedure II. Note that the perceived spatial misalignment between the moving ring and the flashed disk has been converted into a time measure (ratio of spatial misalignment to ring velocity).

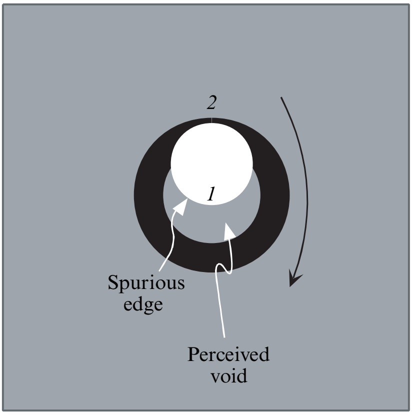

Figure 3. A schematic depiction of the observer's percept in the matching task of experiment 1. Illusory regions, marked spurious edge and perceived void, are vividly seen by observers. The boundary of the white flashed disk closest to the leading and trailing contours of the ring are labeled *1* and *2*, respectively (see discussion experiment 1).

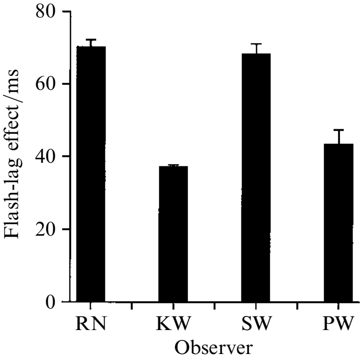

Figure 4. Bar graph showing data for four observers, in the matching task (experiment 1, procedure II). The ordinate shows values which were obtained by dividing the observed spatial misalignment between the comparison ring and the comparison disk by the velocity of the ring.

It is worth reporting that an analogous flash-lag effect occurs if the background is kept the same but the contrast polarity of the moving ring and the flashed disk is reversed—a black flashed disk presented in the center of a white moving ring. Formal data (obtained with procedure II above) with these stimuli were collected on four observers (three naïve to the hypothesis). All observers reported that the black flashed disk appeared to lag the white moving ring, and also reported the accompanying 'perceived void' against which the edge of the black disk was seen. Furthermore, the magnitude of the flash-lag effect was comparable to that observed with the black moving ring and white flashed disk. This suggests that the flash-lag effect observed here cannot be explained simply by assuming different latencies for the ON and OFF visual channels.

Since the first observations made with the ring–disk display in July 1990 at Berkeley, over two hundred observers have informally seen this display. All observers have reported the visual lag of the flashed disk relative to the moving ring and have reported, without any prompting, the presence of the spurious gray–white edge seen in figure 3. Thus, like the Kanizsa triangle and other illusory contours, the present display produces vivid contours that are not present in the retinal image.

Two further findings deserve comment. First, there are significant individual differences in the magnitude of the flash-lag effect obtained with procedure II (see figure 4). In this situation, since the observers' fixation was directed at the 3 o'clock position, a likely explanation of these differences is that observers differ in the ability to hold their eyes stationary while viewing an object moving across their fovea. Even small tracking eye movements can lead to a significant change in the magnitude of the flash-lag effect (see experiment 3). Second, with the ring – disk display a further striking effect was noted. Close to the trailing contours of the moving black ring, observers reported a curious masking of the flashed disk if the luminance contrast of the disk was reduced to below 20 times detection threshold. For a reduced-contrast flashed disk the boundary of the disk closest to the leading contours of the moving ring (labelled *1* in figure 3) did appear distinct and in a lagging position; however, the boundary of the disk closest to the trailing contours of the moving ring (labeled *2* in figure 3) that should, as a consequence, have appeared outside the moving ring was not seen. Thus, the shape of the flashed disk appeared elliptical as if it was compressed in the direction of motion of the ring. Observers report a similar 'compression' of the flashed disk when the ring – disk pair with a higher-contrast flashed disk is viewed in the far periphery. This compression effect is formally explored elsewhere (Watanabe et al, in press), but it is likely to be a consequence of the 'capture' effect which also increases with lowered contrast and peripheral viewing of the stimulus (Ramachandran 1987).

3 Experiment 2: Role of eye movements in the flash-lag effect

What causes the displaced appearance of the flashed disk relative to the moving ring in experiment 1? Could this effect be due to eye movements? To rule out the possible involvement of eye movements, two moving rings that were positioned diametrically opposite each other were used (figure 5). Observers fixated the center around which the rings rotated while two disks, one at the 3 o'clock and the other at the 9 o'clock position, were flashed simultaneously. As described in experiment 1, procedure I, rotation of the time delay dial changed the position of the moving rings with respect to the flashed disks. The observer's task was to adjust the delay till both flashed disks appeared centered in their respective rings.

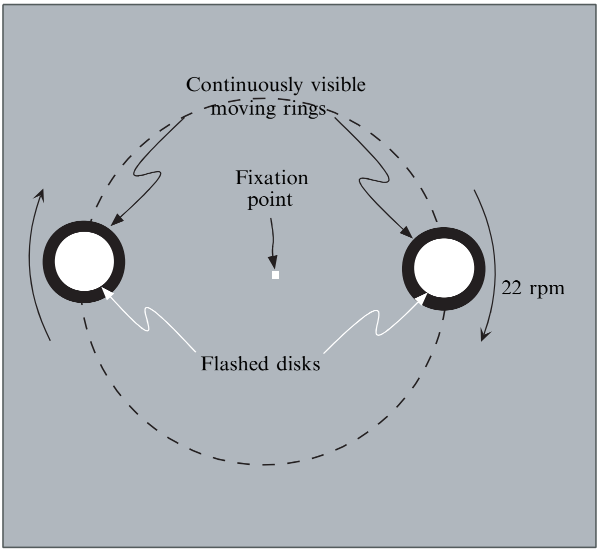

Figure 5. The two-ring – two-disk display with the flashed disks shown at the 3 o'clock and 9 o'clock positions. The flashed disks are shown as centered on the two moving rings.

3.1 *Observers*

Three observers (two naïve to the hypothesis), who also participated in experiment 1, participated in the two-ring – two-disk experiment.

3.2 *Apparatus*

The apparatus was identical to that used in experiment 1.

3.3 *Stimuli*

The essential difference was that the rotary-motion table consisted of two black moving rings in place of one, and two white disks were flashed, one at the 3 o'clock and the other at the 9 o'clock positions. The luminance contrast of the disks was 200 times detection threshold. The moving rings were positioned diametrically opposite each other, and so were the disks. The fixation point was located at the center of rotation of the rings.

3.4 *Procedure*

The procedure was essentially the same as in experiment 1, procedure I. The disks were flashed at 0.37 Hz. First, the centers of the two flashed disks were physically aligned with the centers of the moving rings by the method described in experiment 1. The time delay that produced this alignment, T_A, was noted from the time-delay unit. The observers' task was to adjust the time delay till the two flashed disks appeared centered on the moving rings. Observers made ten settings starting with a time delay of $T_A \pm 100$ ms. They could view as many cycles of the display as they wished to make their adjustments comfortably.

3.5 *Results and discussion*

This display yielded a flash-lag effect in which both flashed disks appeared to lag relative to their respective rings. Figure 6 shows the average magnitudes and standard errors of the flash-lag effect for the three observers. The observers were asked to report whether both flashed disks appeared equally aligned/misaligned relative to the moving rings. All three observers reported that the ring/disk relationship for the two pairs was symmetrical—if one flashed disk appeared misaligned by a certain amount, so did the other by the same amount (figure 7). Since the rings moved in opposite directions, eye movements cannot be held responsible for producing the apparent lag of the flashed disk relative to the moving ring in experiment 1. Interestingly, the magnitude of the effect observed with two flashed disks was essentially the same as that observed with only one flashed disk. The purpose of the next two experiments was to explore the relationship between smooth-pursuit eye movements and the flash-lag effect.

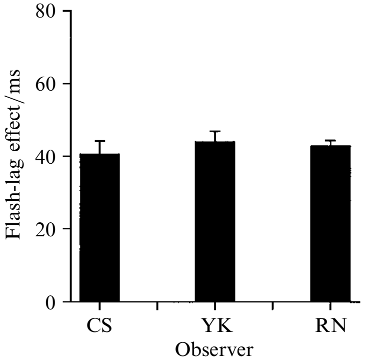

Figure 6. Bar graph showing data for three observers in the two-ring – two-disk display. Error bars represent standard error.

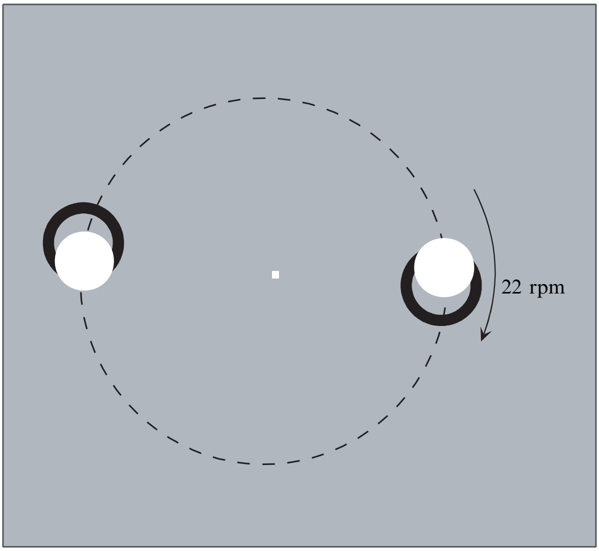

Figure 7. Schematic depiction of the observer's percept when both flashed disks of the two-ring–two-disk display are physically centered on the respective moving rings. All observers reported the perceived symmetry of the flash-lag effect between the two ring–disk pairs.

4 Experiment 3: Smooth pursuit of the moving ring and the flash-lag effect

In a preliminary experiment, it was observed that the flash-lag effect, when measured relative to the moving object, is greatly diminished or eliminated with smooth pursuit of that object. In other words, when the flasked disk was physically aligned with the center of the moving ring, it also appeared so to an observer smoothly pursuing the ring. The impact of smooth pursuit on the flash-lag effect has not been systematically investigated before. In this experiment observers were given explicit instructions to smoothly pursue the moving black ring by keeping their eyes fixated in the ring's center, and judging the position of the flash relative to the ring.

4.1 *Observers*

Three observers (two naïve to the hypothesis) participated in this experiment.

4.2 *Apparatus*

The apparatus was identical to that used in experiment 1.

4.3 *Stimuli*

A single ring–disk pair (black moving ring/white flashed disk) was used with the disk flashed (for 1.5 μs) in the 3 o'clock position. No fixation point was used.

4.4 *Procedure*

As in experiment 1, the time delay was first adjusted such that the flash of the disk occurred physically in the center of the moving ring (see experiment 1). The reading for the specific time delay, T_{A}, which produced the alignment of the flashed disk with the moving ring, was recorded. The observer's task was to align the flashed disk with the center of the moving ring while smoothly pursuing the ring. Initially the time delay was set at values which caused the flashed disk to appear either in a significantly leading or lagging position relative to the smoothly pursued moving ring. The initial time delays were $T_{\mathrm{A}} \pm 100$ ms for the ascending and descending trials. Each observer made 10 settings by rotating a dial which adjusted the time delay. The time delay readings at which the flashed disk was perceptually aligned with the moving ring were recorded.

4.5 *Results and discussion*

This display led to a dramatically reduced flash-lag effect in which the average difference between the times for perceived and physical alignment of the flashed disk with the moving ring ($T_S - T_A$) was -2.63 ms. Figure 8 shows the average magnitudes and standard errors of the flash-lag effect for the three observers. Interestingly, however, all the $T_S - T_A$ values of individual trials, as well as the averages, for the two naïve observers were negative. This means that the flashed disk was seen in a slightly lagging position even during pursuit. However, it is likely that this small effect is due to the tendency of the observers to briefly stop pursuit of the moving ring in the spatiotemporal vicinity of the flash. It is not too surprising that observers are unable to completely suppress the tendency to stop pursuit close to the position of the flashed disk, whose position relative to the moving ring they have been asked to judge. Observers who have an extended experience with similar psychophysical displays do not show any consistent effect.

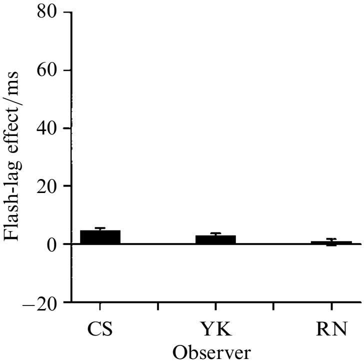

Figure 8. Bar graph showing data for three observers (two naïve to the hypothesis), where the observers smoothly pursued the moving ring. The observers nulled the perceived misalignment of the white flashed disk relative to the moving (and pursued) black ring. Error bars represent standard error.

The results of the present experiment suggest that retinal image motion is necessary for the flash-lag effect to occur (however, see Schlag et al 2000). The following conclusion emerges from this experiment: If the observer smoothly pursues the moving item relative to which the position of the flashed item is to be judged, then the flash-lag effect is eliminated.

5 Experiment 4: Eye-movement-based flash-lag effect

Thus far, in all the experiments, observers have judged the position of the flashed disk relative to the moving ring either during stationary fixation or during smooth pursuit. In this experiment observers smoothly pursued a moving point target past a continuously visible stationary ring and judged the position of the flashed disk relative to the ring. During pursuit, will observers perceive the position of the disk flashed in the center of the continuously visible stationary ring to be displaced relative to the center of the ring? Is there a version of the flash-lag effect that occurs for smooth pursuit?

The elimination of the flash-lag effect in experiment 3 predicts a smooth-pursuit version of the flash-lag effect. Consider the following: There are few exceptions to the widely held assumption that a flashed object is perceived after a significant delay of the actual flash (however, see Libet 1991). In the present context, the delay is significant as the moving (and pursued) ring can travel a significant distance during this time. Assume the flashed disk to be physically centered on the pursued moving ring. Let the time of the physical onset of the flashed disk and the time of the perceptual registration of its onset be $T_{\mathrm{F,phys}}$ and $T_{\mathrm{F,perc}}$, respectively. During the interval $T_{\mathrm{F,perc}} - T_{\mathrm{F,phys}}$ the moving ring will occupy a sequence of positions along its trajectory. In particular, for a clockwise moving ring, its position at $T_{\mathrm{F,perc}}$ will be further clockwise (closer to the 4 o'clock position) relative to its position at $T_{\mathrm{F,phys}}$. In experiment 3, the flashed disk was presented at the 3 o'clock position at $T_{\mathrm{F,phys}}$ when the moving ring was also at the

3 o'clock position. Since at the time of the perceived onset of the flashed disk (ie at $T_{\mathrm{F,\,perc}}$) the position of the moving ring is shifted past the 3 o'clock position, and furthermore, since the flashed disk appeared centered on the moving ring (no flash-lag), it follows that the perceived position of the flashed disk should also be shifted past the 3 o'clock position. This prediction was tested by the present experiment.

Two essential changes were made to the display. The observers now judged the position of the flashed white disk relative to a continuously visible stationary white ring presented at the 3 o'clock position, while smoothly pursuing a moving point target. The purpose of the moving point was only to yield smooth pursuit. The continuously visible stationary ring was now white against a black background. This change was introduced to eliminate the retinal image motion of the contours of the gray background used in the previous experiments, and to ensure that retinal image motion occurs only for the continuously visible stationary ring during smooth pursuit.

5.1 *Observers*

Four observers (three naïve to the hypothesis) participated in this experiment.

5.2 *Apparatus*

The apparatus was identical to that used in experiment 1. The DC motor produced the movement of the pursuit point target.

5.3 *Stimuli*

The dimensions of the ring and the disk were identical to those in experiment 1. The flashed disk (flash duration 1.5 μs) was white and the continuously visible stationary ring was also white (10.0 cd m^{-2}), visible against a black background (0.0 cd m^{-2}). The continuous white ring was stationary at the 3 o'clock position. The white disk (200 times detection threshold), located at the 3 o'clock position, was flashed in the center of the stationary ring. In addition, this display consisted of the moving pursuit point (0.15 deg) that moved in the clockwise direction at the speed that matched the ring speed in experiment 1. The flash occurred when the pursuit point target coincided with the center of the ring (figure 9).

5.4 *Procedure*

Observers were given explicit instructions to smoothly pursue the moving point target. Following the flash of the disk in the center of the continuously visible stationary ring, the observer's task was to estimate the perceived position of the disk relative to the ring. The observers could view as many revolutions of the pursuit point as they deemed necessary to perform the task. At the observer's "ready" signal the pursuit point stopped which, in turn, stopped any further presentations of the flashed disk. The observer then adjusted the comparison ring – disk stimulus, and performed the task of matching the relative position of the comparison ring and the comparison disk to their percept. Ten trials were run for each observer. The flashed disk was always centered on the continuously visible stationary ring.

5.5 *Results and discussion*

Observers showed a significant bias in which the position of the flashed disk selected by them to match their percept was advanced well past the 3 o'clock position, in the direction of pursuit. Figure 10 shows data for the four observers. Furthermore, a perceived void corresponding to a crescent-shaped 'unfilled' portion of the center of the ring was seen against which the 'spurious' contour of the flashed disk was perceived (figure 9, percept). As expected on the basis of the results of experiment 3, observers showed a significant pursuit version of the flash-lag effect with respect to the continuously visible stationary ring.

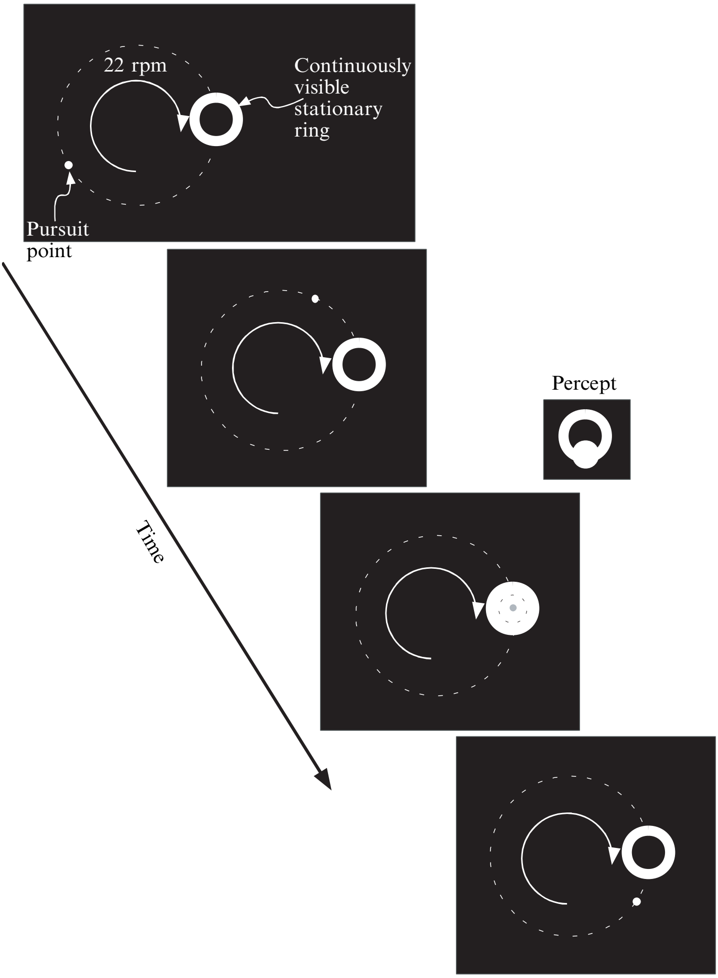

Figure 9. Schematic depiction of the display used in experiment 4. The white ring was stationary at the 3 o'clock position while the observer pursued the point target moving along the dashed circle. At the instant the point target arrived in the ring's center, the white disk was flashed in the ring's center (small dashed circle). The observers reported the position of the flashed disk relative to the ring. The disk was perceived as displaced in the direction of pursuit relative to the ring, and observers saw a vivid crescent-shaped 'perceived void' (percept).

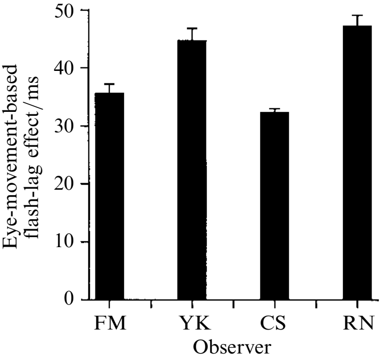

Figure 10. Eye-movement version of the flash-lag effect. Bar graph showing data for four observers (three naïve to the hypothesis). The observers perceived the flashed disk to be located past the 3 o'clock position, shifted in the direction of pursuit. The data are reported in terms of time taken by the pursuit point to cover the distance of the perceived lag of the flashed disk relative to the continuously visible stationary ring.

Mislocalization of flashes caused by various types of eye movements has been investigated before (Mach 1897; MacKay 1958; Matin and Pearce 1965; MacKay 1970; Matin 1972; Ward 1976; Mateeff 1978; O'Regan 1984; Honda 1989). MacKay (1970) was the first to raise the possibility that saccadic mislocalization of test flashes was not due to saccadic eye movements per se. He observed that a similar flash-mislocalization effect results when the retinal image is displaced by external means in a 'saccadic' fashion while the eyes are held stationary. Thus, retinal image motion produced either by external movement of an object or by saccadic eye movements was sufficient to cause the flash-mislocalization effect. The present experiment shows that when the retinal image of an object moves smoothly over the retina, owing to smooth pursuit past a stationary object, the result is the flash-mislocalization effect. Is this a flash-lag effect? At the outset, the difference between flash mislocalization and flash lag is that the former is nondirectional, while the latter ascribes a trailing position to the flash relative to the moving object. Consider the retinal image motion of the ring in the present experiment. At the time of the flash, the retinal image of the ring was moving downward

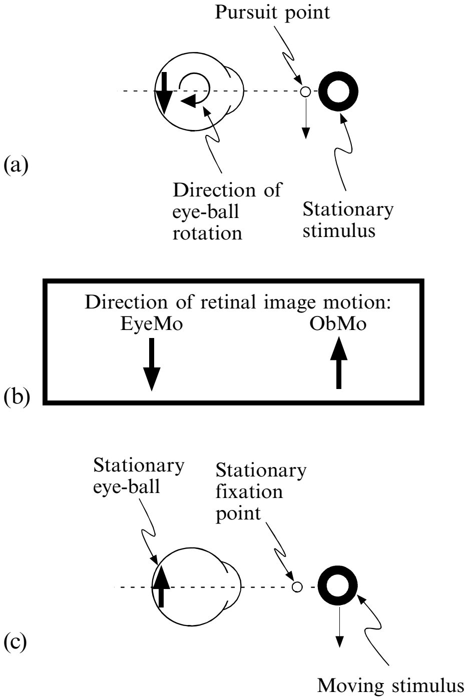

Figure 11. Depiction of retinal image motion of the ring for the smooth-pursuit (a) and object-motion (c) cases. (a) In experiment 4, at the instant of the flash the pursuit point is moving down (thin straight arrow pointing down). The bold arrow at the back of the eye shows the direction in which the retinal image of the stationary ring moves during the smooth-pursuit eye movements. (b) The direction of the retinal image motion for the object-motion case and the eye-movements case is summarized. The straight downward-pointing bold arrow depicts retinal image motion in the eye-movement case (EyeMo), and the straight upward-pointing bold arrow depicts retinal image motion in the object-motion case (ObMo). The tail of each bold arrow represents the position of retinal stimulation that occurred in the recent past, while the head represents the position of retinal stimulation that will occur in the near future. A lagging perceived position of a moving item (due to neural delays) means that the percept corresponds to retinal stimulation closer to the tail of the arrow. A compensation of neural delays would cause the perceived position of the moving item to correspond with retinal stimulation closer to the arrowhead. (c) At the instant of the flash the ring in experiment 1 is moving downward (thin straight arrow pointing down). The bold arrow at the back of the eye shows the direction of retinal image motion in the object-motion case.

(for downward pursuit) (see figure 11a). Now consider the retinal image motion for the object-motion case in experiment 1. For a downward moving ring, the retinal image of the ring at the time of the flash was moving upward (see figure 11c). In both cases the flashed disk appeared shifted towards the tail of the arrows depicting retinal image motion in figure 11b. Note that, for the eye-movement (EyeMo) case, a shift toward the tail of the arrow means that the flashed disk should appear lower than the continuously visible stationary ring. Similarly, for the object motion (ObMo) case, a shift toward the tail of the arrow means that the flashed disk should appear higher than the moving ring. Both these outcomes are in agreement with the actual results. Thus, in terms of retinal motion, the present effect certainly qualifies as a flash-lag effect.

6 General discussion

Visual processing of any event is susceptible to neural transmission delays. Consider, in turn each of the four stimulus events employed in the present experiments: (i) retinal image motion resulting from object motion with eyes stationary, (ii) retinal image motion resulting from smooth-pursuit eye movements with object stationary, (iii) change in gaze direction relative to head during smooth pursuit, and (iv) the flashed item. The first three types of events gradually unfold over time. If it is assumed that a given event of this type has a smooth trajectory over time, the future state of an item (ie object position or eye position) can, in principle, be computed from its past state (extrapolation). Extrapolation for object motion with eyes stationary [case (i)] has been suggested before (Nijhawan 1994a, 1997). Is the visual system also able to extrapolate the position of items in cases (ii) and (iii)? In the case of the flash, there is virtually no disagreement that such events are perceived after a non-trivial delay, and that no correction for these delays may be possible. What then causes the displacement of the flashed item in the direction of pursuit? To simplify the analysis, let us redefine the problem of neural delays in terms of retinotopic coordinates located on the neural tissue surface.

Consider an observer fixating a stationary point while viewing a moving object (figure 11c). Light from the object first photoisomerizes pigment molecules by successively stimulating new photoreceptors along the motion trajectory. The resulting neural signals then arrive in some given retinotopic cortical map after a delay. Assume this delay to be 100 ms. If the object is traveling at 7.25 deg s^{-1}, then the positions of the object at the beginning and end of any given 100 ms period will subtend 0.725 deg. Consider a set of motion-sensitive cortical neurons representing a given 0.725 deg span of visual space. Before a moving object enters the corresponding visual space and stimulates the neurons, the set of neurons will display some baseline neural activity. Next consider what happens when a moving object stimulates these neurons. By definition of delays, the trailing edge of this set of cortical neurons (ie neurons at the edge that represents the part of the retina that was stimulated approximately 100 ms in the past) will show strong activity. The leading edge, however, will manifest only weak activity, as majority of the signals resulting from the currently stimulated retinal location would not have yet made it up to the cortical region under consideration. In this sense, it may be said that at any given instant the maximally active *cortical* site representing the object lags the maximally active *retinal* site representing the object.

Were vision to be based on a delayed neural representation in the 'higher' cortical areas, then moving objects should be seen as lagging their actual instantaneous location (ie they should appear displaced toward the tail of the bold ObMo arrow in figure 11b). On the other hand, a successful action is based on the animal keeping track of the actual position of the moving object. Does the animal use a delayed visual position of the object to 'infer' the object's actual current position, or does the visual system provide the animal 'directly' the corrected visual position of the moving object?

The present experiments and others (Nijhawan 1994a, 1997) suggest that the output of the visual system is 'corrected' such that visual position of a moving object matches the object's actual position (Nijhawan and Khurana 2000). This point of view implies that the visual position of moving objects, which is the final output of the visual system, is already veridical, so no further compensation, such as to explain the 'movement-induced positional bias' (see eg De Valois and De Valois 1991), need be postulated. On this 'extrapolation and delay' hypothesis, the perceived position of the moving item is veridical (as opposed to lagging) while the flash is seen after a delay, leading to the flash-lag effect.

Consider now the analogous problem of delays when retinal image motion results from the observer smoothly pursuing a moving point past a continuously visible stationary object (figure 11a). The neurons in the primate striate cortex cannot establish whether retinal image motion is produced by object motion or by eye movements (Wurtz 1969). Thus, a mechanism for the flash-lag effect located in the visual pathway before the striate cortex would produce the same effect, whether object motion or eye movements are employed. One recent study has reported evidence for a retinal contribution to the flash-lag effect (Berry et al 1999). These experiments were carried out on the retinae of the rabbit and the salamander, which contain directionally selective neurons. Since the primate retina does not manifest direction selectivity, these authors were careful to point out that the neurons that contribute to the flash-lag effect in the retinae of the 'lower' species are not directionally selective. This raises the possibility that retinal mechanisms in humans may also contribute to the flash-lag effect (Gegenfurtner 1999). If this were the case then an eye-movement version of the flash-lag effect is precisely what human observers should report.

How might the eye-movement version of the flash-lag effect (experiment 4) be explained? The perceived position of an item in visual space relative to the head (say) is determined through a process that integrates the retinal image position of the stimulus with the position of the eyes relative to the head (Helmholtz 1867/1962). This statement, however, holds true only in static conditions with no eye movements. Consider the problem of determining the perceived position of a continuously visible stationary item being viewed during smooth pursuit. Scientists have wondered at length how the visual system achieves the stability of the static visual world during eye movements (see eg Wallach 1985); however, the implicit problem of neural delays that accompanies eye movements seems to have been overlooked. Consider again the observer making a downward pursuit movement across a continuously visible stationary stimulus (figure 11a). Because of the delays, the cortical representation of the object should lag its retinal representation (see above). If the perceived position of such an object were based on a delayed cortical representation, then its perceived position would lag its actual position. A lag in this case means that the continuously visible stationary stimulus should appear to be shifted in the direction of pursuit. Note that this shift is equivalent to a shift toward the tail of the EyeMo arrow (depicting retinal image motion) in figure 11b. We conducted an additional experiment to address this question. During smooth pursuit, do observers make an error of localizing a continuously visible stationary object too far in the direction of pursuit? A continuously visible stationary item appeared and remained visible while observers pursued a point moving horizontally. The stationary item was presented after the pursuit had already begun, and it disappeared just before the end of the pursuit. After a 2-s interval of the item's disappearance and the termination of pursuit, a second stationary item appeared. Observers' task was to report whether the second item was to the left or right of the first item. The shift in the item's perceived position in the pursuit direction, expected on the basis of neural delays, was not found. While this *lack of effect* explains why this particular consequence of neural delays may have been overlooked, it suggests that there must be a compensatory mechanism analogous to the case for object motion (Nijhawan 1994a), which corrects for transmission delays in the localization of continuously visible stationary stimuli during smooth pursuit. Thus, during pursuit, the perceived position of a stationary item relative to the head is based on eye position relative to the head (see below), and the object's cortical representation that may be corrected for neural delays by a mechanism similar to that for the object motion case (Nijhawan 1994a; Berry et al 1999).

Now consider the central representation of eye position relative to the head during pursuit. Is this representation delayed? In other words, for a rightward pursuit (say) is there a moment when the eyes are pointing straight ahead relative to the head while the centrally represented eye position is to the left of straight ahead? Despite controversy over how the eye position in head-centered coordinates is monitored (Steinbach 1987), there is general agreement that an internal reference signal, such as a copy of the central command (efferent copy), plays an important role (Helmholtz 1867/1962; Sperry 1950). There is also evidence that efferent signals are important in the monitoring of eye position during pursuit (Steinbach and Held 1968). The problem of neural delays in the central registration of peripheral information, such as resulting from proprioceptive signals from muscles controlling eye movements, is well-defined (Bridgeman and Stark 1991). However, consider the analogous problem when the eye position is determined by a central command. Since the commands themselves are generated centrally, the question of a delay in the central representation of successive eye positions during the actual eye movements does not arise (Miller and Bockisch 1997). This implies that, during smooth pursuit, the 'current' (as opposed to delayed) eye-position information is available to the visual system. This suggestion is consistent with previous suggestions that in the central representation eye-position information is accurate (Skavenski 1976). Thus, in the process of determining the position of a continuously visible stationary item during pursuit, the visual system combines 'current' eye-position information with a 'corrected' cortical representation of that item.

Finally, consider the perceived position of the flashed item during pursuit. A very brief flash has three significant properties: (i) the retinal image motion of such a flash is negligible; (ii) transmission delays inherent in the pathways that bring the flash from the retina to its 'higher'-level representation are significant and may, furthermore, be impossible to overcome; (iii) the neural activity triggered by the flash persists for more than 100 ms beyond the physical flash (Newton 1730/1952). Assume both the transmission delays and the duration of visible persistence are each equal to 100 ms. If a 1.5 μs flash strikes the retina at t_0 (say) then the final decay of its visibility will occur at $t_0 + 200$ ms. Let us refer to the period t_0—($t_0 + 100$ ms) as the 'pre-visibility' phase of the flash (ie the flash is in transit within the visual system but is still invisible), and the period ($t_0 + 100$ ms)—($t_0 + 200$ ms) as the 'visibility' phase of the flash. The perceived onset of the flash and the final decay of its visibility 100 ms later straddle the 'visibility' phase. Mach (1897) first suggested that the eye-movement-based mislocalization of a flash was due to its visible persistence. Clearly, if 'visible persistence' lasted for several seconds then a 'persisting flash' would be seen as following the eye movements just like the afterimage (Coltheart 1980). Mach suggested that the persisting flash does follow eye movements just as the afterimage does, but for a short duration. Mach's explanation, however, is only partially correct, as he failed to consider the transmission delays. A parsimonious account based on the present results is that the neural representation of the flash shifts with the eyes (ie it is retinocentric), whether a given flash representation within the visual system (feed-forward signals only) is in the 'pre-visibility' or the 'visibility' phase. Thus, the smooth-pursuit version of the flash-lag effect (experiment 4) is explained as follows: During pursuit the instantaneous visual position of the continuously visible stationary ring is determined by a 'corrected' cortical representation of the ring, and the 'current' eye-position information. This eye-position information is also available for localizing the flashed disk in visual space, which is thus determined through the integration of the 'current' eye position and the retinal coordinates of the flashed disk. The flash is seen after a delay, while the centrally represented position of the eyes changes continuously before the flash, during the time the flash is in transit within the visual system, and during the persisting 'visibility' period of the flash. Thus the flash appears displaced in the direction of pursuit. It is specifically because of the neural delays that, when the flash first appears (at the end of the 'pre-visibility' phase), it is already in a displaced position (Nijhawan 1994a) relative to the continuously visible stationary object. On the other hand, visible persistence of the flash is responsible for its later apparent displacement during the 'visibility' phase, which is completely analogous to the movement of the afterimage during pursuit. A similar account may be given for other eye-movement-based flash mislocalization effects (Mach 1897; MacKay 1958, 1970; Matin and Pearce 1965; Matin 1972; Mateeff 1978; O'Regan 1984; Honda 1989).

An observation further strengthens the analogy between the smooth-pursuit and object-motion versions of the flash-lag effect. In a previous experiment (Nijhawan 1997) observers, while holding their eyes stationary, viewed a moving green bar. A flashed red line was optically added to the green bar to produce a stimulus which should yield a yellow (red + green) perceived color of the flashed line. The questions raised were whether the flashed line appears to lag the moving green bar, and whether it appears red or yellow in color. The observers saw the flashed line as lagging the moving green bar and its color as red and not yellow. Is there an eye-movement version of this 'color decomposition' effect? In a recent experiment (Nijhawan et al 1998), observers executed smooth pursuit past a continuously visible stationary green bar. A flashed red bar was superimposed on the green bar. Consistent with the previous (Ward 1976) and the present findings, observers reported the apparent displacement of the flashed bar in the direction of pursuit relative to the stationary green bar. Furthermore, they reported the color of the flashed bar as red, despite the stimulus being 'yellow'. Thus, the eye-movements and the object-motion versions of the flash-lag effect produce analogous results.

The notion of motion extrapolation has as yet left some questions unanswered. The fact that prediction plays a crucial role in successful action is well recognized, and so is the fact that compensation for transmission delays could be accomplished anywhere within the visuomotor loop. From this point of view the introduction of a new concept of a 'visual compensation' for transmission delays seems unnecessary. However, consider two further issues: First, it is clear that a 'visual compensation' could be accomplished easily by mechanisms found commonly in the visual system of primates and other 'lower' species. Two visual systems, one that compensates for transmission delays versus one that does not, will be vastly different, both anatomically and physiologically. So investigation of the problem is important. Second, a visual compensation simply implies a unification of two pieces of information (the lagging perceived position of the moving item and the magnitude of the lag) combined into a single percept that represents the veridical position of the moving item. There are numerous examples in the study of visual perception where two separate pieces of information are combined into a unitary percept that is veridical (see Rock and Nijhawan 1989). For example consider size constancy, where the perceived size of the item is the unified percept that results from combining the perceived distance of the object and the object's retinal image size. It may be argued that size constancy aids efficient catching action (say), such that the observer in planning the action is able to adjust his/her grasp appropriately for object size. A similar argument may be made for motion extrapolation. Motion extrapolation aids the grasping action by guiding the hand movement along the trajectory appropriate for object position. What then is the role of prediction in action?

The present view ascribes to predictive action the role of compensating for motor delays per se, that is the delays incurred during the travel of outgoing signals along the motor pathways and those incurred owing to inertia of bodily movement.

It has been asked if the 'flash-lag' effect is an appropriate term for the phenomenon under investigation here. Might not an expression such as the 'motion-lead' effect be more accurate (Andrew Derrington, personal communication)? It may be argued that a flash is an 'elementary' stimulus that should form the basis of comparison of more complex stimuli, such as moving items, and not the other way around. Indeed it is the moving item that appears shifted forward not the flashed item shifted back. Thus, might not a term such as 'motion-onset-lead' effect be more appropriate (Christopher Tyler; personal communication)? Choosing a term for a phenomenon is always tricky because of the possibility that, in view of newer findings, the term might become inappropriate at some future point in time. Indeed, treating the flash as the frame of reference relative to which the moving item leads during stationary fixation (experiment 1, procedure II) is justifiable, as the position of a foveally viewed flashed item is perceived correctly (Mateeff and Gourevich 1983). However, keeping in view the results of experiment 4, it may be argued that it is the flash that appears displaced relative to a continuously visible stationary object, which certainly qualifies as a frame of reference. Furthermore, in this case a 'motion-lead' terminology would be most inappropriate, as the item that must then be considered as 'leading' would in fact be stationary. Motion-lead terminology is inappropriate for yet another reason. It was recently shown that the phenomenon under discussion here also occurs for non-motion features such as luminance, color, and spatial frequency (Sheth et al 2000). The term flash-lag effect may be used without alteration to describe these non-motion-based effects.

Finally, it is clear that the phenomena of 'spurious edges' and 'perceived voids' examined here are a result of computations occurring within the visual system either before or after the physical flash, as at the instant of the flash the center of the ring is completely filled with the disk. In the case of the gray background, the inside of the ring is gray both before and after the flash, so the perceived gray color of the crescent-shaped region inside the ring could be due to computations occurring either before or after the flash. This question may be resolved by asking: What would be the color of the perceived void if the color of the background were changed at the instant of the flash, say from green to red? That is, prior to the flash, a black ring (say) moves on a green background, then simultaneously with the presentation of a white flash filling the ring the background is changed from green to red. Will the perceived void be seen as green or red? Our preliminary observations indicate that it is the color of the background presented after the flash that marks the perceived void color. Thus, the perceived void color is red (Nijhawan et al 2000). Thus, consistent with previous findings (Khurana and Nijhawan 1995), the events (movement of the ring) between the physical flash and its perception, that is the period during which the flash is in transit within the nervous system, determines many of the outcomes concerning the flash-lag effect.

Acknowledgments. This work was supported by the Sloan foundation, and NSF grant SBR9710116 to RN, principal investigator.

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