Psychological Bulletin
2014, Vol. 140, No. 1, 308–338

0033-2909/14/$12.00 DOI: 10.1037/a0032899

The Flash-Lag Effect and Related Mislocalizations: Findings, Properties, and Theories

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If an observer sees a flashed (briefly presented) object that is aligned with a moving target, the perceived position of the flashed object usually lags the perceived position of the moving target. This has been referred to as the *flash-lag effect*, and the flash-lag effect has been suggested to reflect how an observer compensates for delays in perception that are due to neural processing times and is thus able to interact with dynamic stimuli in real time. Characteristics of the stimulus and of the observer that influence the flash-lag effect are reviewed, and the sensitivity or robustness of the flash-lag effect to numerous variables is discussed. Properties of the flash-lag effect and how the flash-lag effect might be related to several other perceptual and cognitive processes and phenomena are considered. Unresolved empirical issues are noted. Theories of the flash-lag effect are reviewed, and evidence inconsistent with each theory is noted. The flash-lag effect appears to involve low-level perceptual processes and high-level cognitive processes, reflects the operation of multiple mechanisms, occurs in numerous stimulus dimensions, and occurs within and across multiple modalities. It is suggested that the flash-lag effect derives from more basic mislocalizations of the moving target or flashed object and that understanding and analysis of the flash-lag effect should focus on these more basic mislocalizations rather than on the relationship between the moving target and the flashed object.

Keywords: flash-lag effect, representational momentum, Fröhlich effect, spatial representation, motion perception

When we perceive a visual stimulus, neural processes pass that information from the retina to and throughout the cortex. These processes are fast but not instantaneous, and there is a delay of at least 100 ms between when the retina is stimulated and when conscious perception of the stimulus occurs (De Valois & De Valois, 1991; Nijhawan, 2008). Real-time interaction with stimuli must involve some form of compensation for these neural delays, or else our responses to dynamic and changing (e.g., moving) stimuli would be too late (e.g., as noted in Nijhawan, 1994, neural delays would result in an object moving at 30 miles per hour appearing 4.4 feet behind its actual location). Several types of mislocalization potentially related to compensation for neural delays have been studied, and the type of mislocalization that has received the most attention is the *flash-lag effect*. In the flash-lag effect, a flashed (i.e., briefly presented) object that is aligned with a moving target is perceived to lag behind the position of that target. Previous reviews of the flash-lag effect focused on historical antecedents (Maus, Khurana, & Nijhawan, 2010) or specific potential theories (Krekelberg & Lappe, 2001; Nijhawan, 2002; Schlag & Schlag-Rey, 2002; Whitney, 2002). In addition to considering potential theories, this review presents the first catalog of variables that influence the flash-lag effect and examines potential connections between the flash-lag effect and other phenomena.

The most common types of stimuli used to investigate the flash-lag effect are illustrated in Figure 1. In Figure 1A, a rotating bar is shown, and two sets of dashed lines are briefly presented in alignment with the bar (e.g., Nijhawan, 1994). In Figure 1B, a revolving annulus is shown, and a disk is briefly presented inside the annulus (e.g., Khurana, Watanabe, & Nijhawan, 2000). In Figures 1C and 1D, a translating bar is shown, and a stationary bar is briefly presented away from the translating bar (e.g., Kanai, Seth, & Shimojo, 2004) or within a gap in the translating bar (e.g., Murakami, 2001b). There are two common ways to assess whether a flash-lag effect occurred. One way is to have participants judge whether the flashed object was presented before or after the moving target passed the position of the flashed object (e.g., was the flashed object to the left or right of a horizontally moving target? e.g., Whitney, Murakami, & Cavanagh, 2000) or whether the moving target was approaching or had passed the flashed object when the flashed object was presented (e.g., was the target ahead of or behind the flashed object? e.g., Moore & Enns, 2004). The actual position of the flashed object relative to the moving target varies across trials, and a point of subjective alignment or simultaneity can be estimated (e.g., López-Moliner & Linares, 2006). A second way is to use a nulling procedure (method of adjustment) in which participants adjust presentation of the flashed object relative to the moving target so that the two stimuli appear aligned or simultaneous (e.g., Lappe & Krekelberg, 1998).

The first account of a flash-lag type of effect was in Mach (1885/1897), who reported a flash (spark) presented during a saccadic eye movement appeared displaced. Metzger (1932) passed a vertical line behind an occluder containing a horizontal slit and a small hole above the midpoint of the slit. When the line

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This article was published Online First June 24, 2013.

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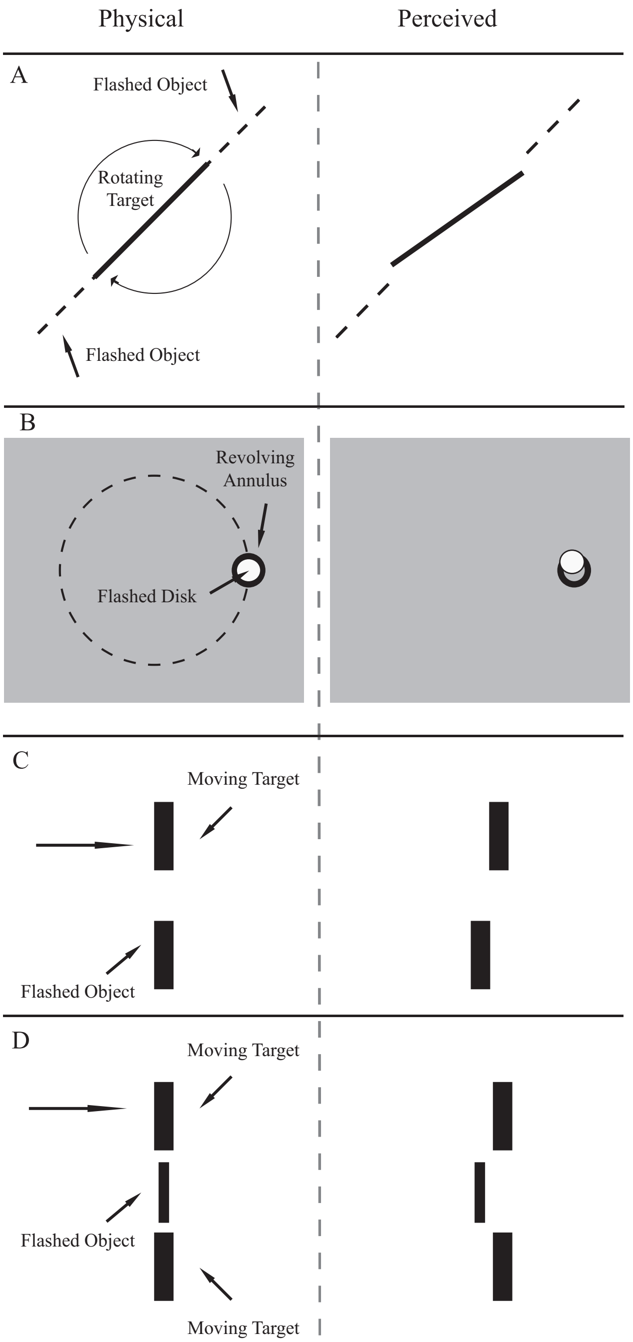

Figure 1. Illustrations of common stimulus displays in studies of the flash-lag effect. The actual physical stimulus is depicted on the left, and the typical perceived stimulus is depicted on the right; in each case, the position of the flashed object appears to lag behind the position of the moving target. (A) The target consists of a bar rotating clockwise, and the flashed object consists of two dashed line segments that are briefly flashed when they are in alignment with the bar (adapted from Nijhawan, 1994, p. 256). (B) The target consists of a black annulus moving clockwise on a circular path (indicated by the dashed line), and the flashed object consists of a white disk flashed within the annulus (adapted from Khurana et al., 2000, p. 679). (C) The target consists of a vertical bar moving from left to right in the upper part of the display, and the flashed object is a vertical bar in the lower part of the display that is briefly flashed when it is aligned with the moving target (adapted from Kanai et al., 2004, p. 2607). (D) The moving target consists of two vertically aligned vertical bars moving from left to right, and the flashed object consists of a vertical bar flashed in the gap within the target (adapted from Murakami, 2001a, p. 126).

passed behind the hole, it provided a flashed object aligned with the part of the line visible in the slit; however, the part of the line visible in the hole appeared to lag the part of the line visible in the slit. MacKay (1958) presented a self-luminous object and a nonluminous object in a stroboscopically lit visual field and passively moved the eye, and he reported a stroboscopically lit object subjectively lagged a self-luminous object. Mitrani and Dimitrov (1982) and Mateeff and Hohnsbein (1988) reported a similar effect in which the position of a flashed stimulus was displaced in the presence of a moving target. However, it was with Nijhawan's (1994) rediscovery of this effect that an explosion of interest in the flash-lag effect, and in the question of how sensory or motor systems compensate for delays in perception due to neural processing times, occurred. Part 1 reviews variables that influence the flash-lag effect. Part 2 considers general properties of the flash-lag effect and how the flash-lag effect is related to several other perceptual and cognitive phenomena. Part 3 reviews theories of the flash-lag effect, and Part 4 provides a summary and conclusions.

Part 1: Variables that Influence the Flash-Lag Effect

Variables that influence the flash-lag effect are classified as characteristics of the stimulus or characteristics of the observer. This distinction is helpful in organization but does not suggest these categories are exhaustive (i.e., other categories or variables might be documented by future research) or mutually exclusive (e.g., presentation of a cue, which is a characteristic of the stimulus, might influence allocation of attention, which is a characteristic of the observer).

Characteristics of the Stimulus

Characteristics of the stimulus considered here include (a) timing of the presentation of the flashed object, (b) continuity of target motion, (c) distance traveled by the target, (d) distance between the moving target and the flashed object, (e) eccentricity, (f) target velocity, (g) target direction, (h) binocular disparity, (i) color, (j) luminance, (k) contrast, (l) spatial frequency, (m) target identity, (n) pattern entropy, (o) duration of the flashed object, (p) motion of the flashed object, (q) presence of cues, (r) predictability of the flashed object, (s) uncertainty of target location, (t) number of targets, and (u) presence of unrelated stimuli. The effects of these variables are summarized in Table 1.

Timing of the presentation of the flashed object. Perhaps the most important stimulus variable in the flash-lag effect is the timing of the presentation of the flashed object relative to target motion. If the flashed object is presented at target motion onset (i.e., moving target and flashed object simultaneously appear), this is usually referred to as a *flash-initiated* display. If the flashed

Table 1
Effects of Stimulus Characteristics on the Flash-Lag Effect

Characteristic	Flash-lag effect	Primary sources
Timing of presentation of flashed object	Occurs with flash-initiated and flash-midpoint displays, but not with flash-terminated displays	Eagleman & Sejnowski (2000b); Khurana & Nijhawan (1995); Nijhawan et al. (2004); Watanabe (2004)
Continuity of target motion	Occurs with sampled, continuous, and random motion	Arrighi et al. (2005); Fukiage & Murakami (2010); Murakami (2001b); Rizk et al. (2009)
Distance traveled by moving target	Decreases if target travels further before the flashed object appears (and flashed object is more predictable)	Vreven & Verghese (2005)
Distance between moving target and flashed object	Increases if moving target and flashed object are farther apart	Baldo, Kihara, et al. (2002); Baldo & Klein (1995); Kanai et al. (2004)
Eccentricity of moving target or flashed object	Increases if flashed object is more eccentric than moving target	Baldo, Kihara, et al. (2002); Baldo & Klein (1995)
	Decreases if moving target is more eccentric than flashed object	Linares et al. (2007)
Target velocity	Increases with increases in target velocity	Krekelberg & Lappe (1999); Lee et al. (2008); Nijhawan (1994); Wojtach et al. (2008)
Target direction	Occurs if flashed object is presented immediately after target changes direction	Eagleman & Sejnowski (2000b); Whitney & Murakami (1998); Whitney, Murakami, & Cavanagh (2000)
	Is larger if target moves toward fixation than away from fixation	Brenner et al. (2006); Kanai et al. (2004); Mateeff et al. (1991); Shi & Nijhawan (2008)
	Is larger for approaching motion than receding motion, and with stereomotion than with looming	Harris et al. (2006); Ishii et al. (2004); Lee et al. (2008)
Binocular disparity	Is larger if moving target and flashed object are defined by disparity as well as by monocular cues	Harris et al. (2006); Lee et al. (2008); Nieman et al. (2006)
Color	Prevents additive color mixing if flashed object is superimposed on moving target	Nijhawan (1997); Nijhawan et al. (1998)
	Occurs for changes in saturation	Kreegipuu & Allik (2004); Sheth et al. (2000)
Luminance	Decreases if luminance of flashed object is increased	Öğmen et al. (2004); Purushothaman et al. (1998)
	Occurs for changes in luminance	Chappell & Mullen (2010); Ichikawa & Masakura (2006); Sheth et al. (2000)
Contrast	Increases with decreases in contrast of moving target and flashed object with background	Kanai et al. (2004)
	Increases with increases in contrast between the moving target and flashed object	Arnold et al. (2009)
Spatial frequency	Increases with decreases in spatial frequency	Cantor & Schor (2007); Fu et al. (2001)
	Occurs with changes in spatial frequency	Sheth et al. (2000)
Identity of moving target	Is disrupted by changes in moving target size	Moore & Enns (2004)
	Disrupts composite face effect	Khurana et al. (2006)
Pattern entropy	Occurs with changes in pattern entropy	Sheth et al. (2000)
Duration of flashed object	Occurs with stationary flashed object durations under 80 ms	Brenner & Smeets (2000); Eagleman & Sejnowski (2000b)
	Occurs with flashed object durations up to 500 ms	Krekelberg & Lappe (1999); Lappe & Krekelberg (1998)
Motion of flashed object	Decreases with increased motion of flashed object	Bachmann & Kalev (1997); Gauch & Kerzel (2008a); Krekelberg & Lappe (1999)
Presence of cues	No effect of cuing	Khurana et al. (2000)
	Decreases with (valid) cues	Brenner & Smeets (2000); Namba & Baldo (2004); Rotman et al. (2002); Shioiri et al. (2010)
Predictability of the flashed object	Increases with decreases in predictability of when the flashed object would appear	Baldo & Namba (2002); Vreven & Verghese (2005)
Uncertainty of target location	Increases with increases in uncertainty of moving target location	Fu et al. (2001); Kanai et al. (2004); Maus & Nijhawan (2006, 2009)
Number of moving targets	Increases with increases in the number of moving targets	Shioiri et al. (2010)
Presence of unrelated stimuli	Increases if another stimulus close to the moving target moves toward the target	Maiche et al. (2007)

object is presented at target motion offset (i.e., moving target and flashed object simultaneously vanish), this is usually referred to as a *flash-terminated* display. If the flashed object is presented after target motion onset but before target motion offset, this has been referred to as a *complete cycle* (e.g., Nijhawan, Watanabe, Khurana, & Shimojo, 2004), *full-view* (e.g., Watanabe, 2004), or *continuous motion* (e.g., Eagleman & Sejnowski, 2000b) display. However, the latter term is ambiguous (*continuous* describes motion of the target as well as timing of the presentation of the flashed object), and the two former terms are not sufficiently descriptive.

The term *flash-midpoint* is more consistent with *flash-initiated* and *flash-terminated*, and so *flash-midpoint* is adopted here. Unless noted otherwise, experiments discussed in this review presented a flash-midpoint display. Also, the moving (changing) stimulus is referred to as the *target*, and the flashed (unchanging or briefly presented) stimulus is referred to as the *object*.

Khurana and Nijhawan (1995) and Watanabe (2004) presented a flash-initiated display and reported a flash-lag effect occurred, and Nijhawan et al. (2004) replicated this finding and reported a flash-lag effect in flash-initiated displays increased with faster target velocities. Watanabe presented a flashed object before, at the moment of, or after motion onset. A stationary version of the moving target then appeared, and participants adjusted the location of a small disk to indicate the location of the flashed object relative to the moving target. A larger flash-lag effect occurred if the flashed object was presented near the leading edge than near the trailing edge of the moving target. Rizk, Chappell, and Hine (2009) reported a flash-initiated flash-lag effect was larger than a flash-midpoint flash-lag effect, and Öğmen, Patel, Bedell, and Camuz (2004) reported the flash-lag effect for a stationary target that changed in luminance was larger in flash-initiated displays than in flash-midpoint displays. Existence of a flash-lag effect in flash-initiated displays seems inconsistent with theories of the flash-lag effect involving differential latencies to perceive the moving target and flashed object, perceptual acceleration, or motion extrapolation (see Part 3), as onset times of the moving target and the flashed object would be the same.

Chappell and Hine (2004) presented a target that was stationary before the flashed object appeared, and when the flashed object appeared, target motion began. The flash-lag effect decreased if the target was stationary for 50 or 250, but not 750, ms prior to flash-initiated motion. Kreegipuu and Allik (2003) presented a target that was stationary before the flashed object appeared and a probe bar that was visible until the target vanished. Participants judged whether the probe bar appeared before or after the start of target motion (time judgment) or whether target motion began to the left or right of the probe bar (position judgment). If the target was stationary when the probe bar was presented, time judgments and localization judgments were accurate. If the target was moving when the probe bar was presented, then in order to achieve perceptual simultaneity, the probe bar had to be presented 40–70 ms before motion onset (i.e., a flash-lag effect occurred). Findings of Chappell and Hine and of Kreegipuu and Allik suggested claims of Brenner and Smeets (2000) and Eagleman and Sejnowski (2000b) that information presented prior to the flashed object does not influence the flash-lag effect were not entirely correct. Chappell and Hine suggested there is a moving temporal window of integration extending prior and subsequent to the flashed object (cf. Krekelberg & Lappe, 2000a, 2000b).

Eagleman and Sejnowski (2000b) reported a flash-lag effect occurred if target motion continued or reversed direction after the flashed object was presented but did not occur in a flash-terminated display. Moore and Enns (2004) presented a target moving along a circular path in a flash-terminated display or a flash-midpoint display, and the flashed object could be behind, aligned with, or ahead of the target. A flash-lag effect occurred with flash-midpoint displays but not flash-terminated displays. Watanabe (2004) reported a flash-lag effect did not occur with flash-terminated displays, and Kessler, Gordon, Cessford, and Lages (2010); Munger and Owens (2004); and Rizk et al. (2009) reported a flash-lag effect with flash-midpoint displays but not with flash-terminated displays. Only two studies reported a flash-lag effect with flash-terminated displays: Kanai et al. (2004) reported a flash-lag effect if the moving target and flashed object were far apart and in the periphery. Gauch and Kerzel (2008a) reported a flash-lag effect if the flashed object moved but not if the flashed object was stationary. In general, a flash-lag effect usually occurs with flash-initiated and flash-midpoint displays (and is sometimes larger with flash-initiated displays) but not with flash-terminated displays.

Continuity of target motion. Rizk et al. (2009) presented flash-lag stimuli in which target motion was intermittently sampled (referred to as moving "from station to station") rather than continuous; in other words, a static target was displayed at one position, and after a clear delay, another static depiction of the target was displayed at a different position. A flash-lag effect occurred for continuous motion and for sampled motion with flash-initiated displays and flash-midpoint displays, although the flash-lag effect decreased as continuity of motion decreased. Lappe and Krekelberg (1998) presented a flash-lag stimulus in which the moving target consisted of three circles along a single rotating line and the flashed object consisted of four circles (two each on opposite ends of the rotating line). After the stimulus was presented, participants indicated the perceived relative locations of the moving target and flashed object by pressing the left or right mouse button to adjust the offset angle between the moving target and the flashed object. Consistent with MacKay (1958), objects in stroboscopic motion (i.e., flashed) appeared to lag objects in continuous motion (but see Vreven & Verghese, 2005, for disruption of the flash-lag effect with extreme stroboscopic motion).

Murakami (2001b) presented a display in which the moving target jumped between random locations along the horizontal meridian of the display. A flashed object was presented within the gap in the target. Participants judged whether the flashed object was perceived to the left or right of the target, and a flash-lag effect occurred. Murakami argued that (a) because motion of the target was random, motion extrapolation theory could not account for the flash-lag effect, and (b) a differential latency theory in which latency fluctuated could account for the flash-lag effect. However, some direction of motion must be attributed to the target (if only from the last jump) to distinguish whether the flashed object lagged or led the moving target, and such an attribution might be sufficient for extrapolation (cf. Nijhawan's, 2008, suggestion that the 100 ms between presentation and perception of a moving target is enough for extrapolation). Vreven and Verghese (2005) presented a continuously moving target that unpredictably changed direction, and the flash-lag effect decreased from that found if the moving target maintained the same direction. Also, Bachmann and Põder (2001) reported a flash-lag effect occurred if the moving target was a sequence of discrete letters and the flashed object was a single letter.

Arrighi, Alais, and Burr (2005) presented stimuli in which the moving target was a visual Gaussian blob or auditory white noise, and the moving target jumped randomly between positions along the horizontal axis. The flashed object was a white disk or a 400-Hz pure tone. A weak flash-lag effect occurred with visual moving targets and visual flashed objects, and a stronger flash-lag effect occurred with visual moving targets and auditory flashed objects. Latencies for visual stimuli and for auditory stimuli were not consistent with differential latency theory. Fukiage and Murakami (2010) presented a moving target composed of a tilted grating that randomly jumped between orientations and a flashed object composed of a vertical grating. Presentation of the flashed object varied relative to the jump of the moving target, and the effect of timing suggested a flash-lag effect occurred. A tilt aftereffect occurred, and Fukiage and Murakami concluded the flash-lag effect had a negligible influence on, and was generated at a different processing stage than, the tilt aftereffect. In general, findings regarding a lack of continuity of target motion (i.e., unpredictable changes in direction of target motion, target motion involving spatially and temporally discrete positions) suggest continuity of target motion is not required for a flash-lag effect.

Distance traveled by the target. Vreven and Verghese (2005) reported increases in the distance traveled by the target prior to presentation of the flashed object decreased the flash-lag effect, and they referred to this as an *interval effect* (as they divided the target trajectory into intervals). Vreven and Verghese suggested the position of the flashed object becomes more predictable over time (i.e., if the flashed object did not appear in the first or second of three possible intervals, then it would appear in the third interval) and that this is not consistent with differential latency theory. However, it seems plausible that predictability could prime an expected appearance and thus influence processing latency. Linares, López-Moliner, and Johnston (2007) presented a flashed object at latencies between 0 and 3,000 ms after the moving target appeared. If the flashed object was close to the target, duration of preflash trajectory did not influence the flash-lag effect (see also Brenner & Smeets, 2000; Eagleman & Sejnowski, 2000b; Whitney, Murakami, & Cavanagh, 2000). If the flashed object was farther from the target, then the flash-lag effect increased with increases in duration of preflash trajectory. Linares et al. attributed this to duration of target motion, but an alternative hypothesis regarding distance traveled by the target cannot be ruled out. Maus and Nijhawan (2006) reported the threshold for a moving target was lower if the target traveled farther, and they suggested this involved larger forward displacement of the target.

Distance between moving target and flashed object. Increases in distance between the moving target and the flashed object increased the flash-lag effect in Baldo and Klein (1995); Baldo, Kihara, Namba, and Klein (2002); and Kanai et al. (2004). In these experiments, the moving target was located at different spatial coordinates than the flashed object. However, in other experiments, a single flashed object was centered at the same spatial coordinates as the moving target and enclosed within the moving target (e.g., a flashed disk within an annulus, Becker, Ansorge, & Turatto, 2009; Eagleman & Sejnowski, 2000b; Nijhawan, 2001), or the flashed object was interleaved with the moving target (e.g., Khurana & Nijhawan, 1995). These different types of displays appear to have been presumed to provide equally valid measures of the flash-lag effect, but there are differences between these types of displays that could potentially influence the flash-lag effect (e.g., it might be easier to attend to a flashed object closer to or contained within a moving target, and masking might be more likely to influence the flash-lag effect if the flashed object is contained or interleaved within the moving target). Also, many studies that manipulated distance between the moving target and the flashed object did not control for eccentricity of the moving target or flashed object.

Eccentricity. Baldo and Klein (1995) and Baldo, Kihara, et al. (2002) varied the distance of the flashed object from fixation (which was centered on a rotating target), and they reported the flash-lag effect increased with increases in distance of the flashed object from fixation (i.e., from the moving target). Kanai et al. (2004) reported a flash-lag effect was more likely to occur with flash-terminated displays as eccentricity of moving targets increased and as eccentricity of flashed objects decreased. Linares et al. (2007) reported the flash-lag effect decreased as eccentricity of the flashed object increased. Linares et al. presented flashed objects at a smaller eccentricity than moving targets, whereas Baldo and Klein presented flashed objects at a larger eccentricity than moving targets; in Linares et al. and in Baldo and Klein, though, increasing eccentricity led to a larger flash-lag effect. Linares et al. suggested their data, in conjunction with data of Baldo and Klein, demonstrated that distance between the moving target and the flashed object, rather than absolute eccentricity of the moving target or flashed object, influenced the flash-lag effect. Also, Lappe and Krekelberg (1998) suggested the effect of eccentricity in their stimuli was due to differences in tangential velocity rather than eccentricity per se.

Target velocity. Many researchers referred to the "speed" of target motion, although "velocity" is more correct (as target motion exhibited magnitude and direction), and so the latter term is used here. Several researchers reported the flash-lag effect increased linearly with increases in target velocity in the picture plane (e.g., Bachmann & Kalev, 1997; Brenner & Smeets, 2000; Krekelberg & Lappe, 1999, 2000a; López-Moliner & Linares, 2006; Murakami, 2001b; Nijhawan, 1994). Wojtach, Sung, Truong, and Purves (2008) presented a wider range of velocities than did previous studies (3°/s–50°/s); they reported the flash-lag effect was related to target velocity by a logarithmic function, and they suggested the effect of velocity appeared linear in earlier studies because those studies used smaller ranges of velocity. Lee, Khuu, Li, and Hayes (2008) reported increases in target velocity in depth increased the flash-lag effect in depth. Shioiri, Yamamoto, Oshida, Matsubara, and Yaguchi (2010) reported increases in the flash-lag effect with increases in target velocity were smaller in a multitarget display if the target by which the flashed object would appear was cued, and they suggested this reflected differences in attention allocated to a given target if tracking only that target relative to attention allocated to a given target if tracking multiple targets.

Whitney, Murakami, and Cavanagh (2000) presented displays in which the moving target unpredictably accelerated or decelerated, and they suggested the resultant increases and decreases in the flash-lag effect, respectively, were consistent with a temporal advantage in processing the moving target relative to the flashed object and were not consistent with motion extrapolation. However, whether the flashed object was presented prior to, concurrent with, or subsequent to a change in target velocity would presumably influence a flash-lag effect and potential extrapolation, but such analyses were not reported. Brenner and Smeets (2000) presented a flash-lag display in which target velocity doubled or halved when the flashed object was presented. The flash-lag effect was influenced by target velocity after the flashed object was presented, and Brenner and Smeets suggested this was evidence against motion extrapolation theory. Kessler et al. (2010) presented biological motion stimuli (and control stimuli consisting of geometric shapes with the same velocity profile as biological motion), and they reported a robust flash-lag effect. Blohm, Missal, and Lefèvre (2003) reported the effect of velocity on the flash-lag effect was larger if target motion was toward fixation than away from fixation.

There are a few exceptions to the typical finding that increases in target velocity increase the flash-lag effect. Cantor and Schor (2007) reported the flash-lag effect decreased with increases in velocities above 1°/s (0.5 Hz); they suggested this occurred because their stimuli were Gabor patches without sharp edges, whereas previous studies generally presented stimuli with sharp edges that produced relatively high spatial frequency energy (cf. Fu, Shen, & Dan, 2001). Kanai et al. (2004) found no effect of velocity on the flash-lag effect in flash-terminated displays if lag was considered in units of space, whereas the flash-lag effect decreased with increases in velocity if lag was considered in units of time. Kreegipuu and Allik (2004) reported velocity did not influence the flash-lag effect, but in their experiments, participants judged the spatial or temporal relationship between flashed objects and color changes in moving targets. Vreven and Verghese (2005) reported random changes in velocity decreased the flash-lag effect relative to the flash-lag effect that resulted from a consistent velocity. In general, faster target velocities are linked with a larger flash-lag effect, but exceptions occur, especially if uncertainty regarding target position is high and the flash-lag effect is considered in terms of spatial differences rather than temporal differences.

Target direction. There have been few studies that examined effects of absolute target direction on the flash-lag effect. Ichikawa and Masakura (2006, 2010) reported the flash-lag effect was not influenced by whether targets ascended or descended. More common are studies of the flash-lag effect in which target direction changes during a trial. Eagleman and Sejnowski (2000b) presented a moving target that reversed direction after presentation of the flashed object. As latency between the flashed object and reversal of target motion decreased from 80 ms to 26 ms, the flash-lag effect decreased, and mislocalization of the flashed object reversed direction with latencies less than 26 ms. Shen, Zhou, Gao, Liang, and Shui (2007) presented two targets that moved toward each other along different curved trajectories and reversed direction upon contact. A flashed object was presented at a random position along one of the trajectories. If judgments of alignment with the flash were used to determine perceived reversal position, targets appeared to reverse before contact (cf. Whitney, Murakami, & Cavanagh, 2000). If participants judged whether targets contacted, the difference between actual reversal position and perceived reversal position decreased. Shen et al. argued this was not consistent with a theory of the flash-lag effect based on position integration.

Whitney and Murakami (1998) presented a display involving a translating bar, and direction of target motion reversed at a random position. A flashed object was presented before or after reversal of target motion. Whitney and Murakami suggested if the flashed object was presented at the moment of reversal, then motion extrapolation theory predicted the moving target should be perceived to be beyond the reversal position, but this did not occur. Whitney, Cavanagh, and Murakami (2000) presented a target that moved upward and then turned to the left or right. A flash-lag effect occurred even if the flashed object was presented immediately after a change in direction. Because the change in target direction was unpredictable, and motion extrapolation theory is based on predictability of target motion, Whitney et al. argued a flash-lag effect immediately after a change in target direction could not result from motion extrapolation. Similarly, Whitney, Murakami, and Cavanagh (2000) had the moving target unpredictably reverse direction; judgments of alignment suggested the target was never perceived to be beyond the reversal point, and they argued this was evidence against motion extrapolation. Whitney and colleagues suggested their data were most consistent with differential latency theory.

Kanai et al. (2004) and Shi and Nijhawan (2008) reported the flash-lag effect was larger if targets moved toward rather than away from a fixated region (see also Mateeff & Hohnsbein, 1988; Mateeff et al., 1991; van Beers, Wolpert, & Haggard, 2001). Brenner, van Beers, Rotman, and Smeets (2006) explained the larger flash-lag effect with motion toward fixation as resulting from a combination of a bias toward the fovea and a delay in sampling position of the moving target. If a target moved toward the fixation point, foveal bias and delay in sampling operated in the same direction, and so they summed, and forward displacement of that target was relatively larger. If a target moved away from the fixation point, foveal bias and delay in sampling operated in opposite directions, and so they partially canceled, and forward displacement of that target was relatively smaller.[1] Kanai et al. reported the flash-lag effect was larger if motion was in the left than in the right visual field, and Shi and Nijhawan reported the flash-lag effect was more influenced by target direction if target motion was in the right than in the left visual field. However, Ichikawa and Masakura (2006, 2010) reported the flash-lag effect for vertically moving targets was not influenced by whether stimuli were in the left or right visual field.

Ishii, Seekkuarachchi, Tamura, and Tang (2004) presented a moving target composed of two vertical bars that appeared to move in depth. A stationary vertical bar was flashed. Participants verbally indicated which stimulus appeared closer or if the stimuli appeared at equal depths, and participants indicated perceived depth with a vernier caliper. A flash-lag effect in depth occurred, and Ishii et al. suggested the flash-lag effect occurred after images from the two eyes were fused. Harris, Duke, and Kopinska (2006) presented targets that appeared to move in depth. Some targets exhibited looming, disparity, and perspective cues, and other targets involved random dot stereograms in which depth was indicated only by disparity. The flash-lag effect was stronger with random dot stimuli and for approaching motion than for receding motion. Lee et al. (2008) presented stereo images of a square that appeared to approach or recede from the participant. A Gaussian blob appeared for 33 ms near the midpoint of the target trajectory.

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[1] Brenner et al.'s (2006) findings of a larger forward displacement if a target moved toward fixation paralleled findings of a larger representational momentum (see Part 2) if a target moved toward a landmark in Hubbard and Ruppel (1999). Furthermore, Brenner et al.'s account of their data paralleled Hubbard and Ruppel's account for representational momentum: If a target moved toward a landmark, representational momentum and the landmark attraction effect operated in the same direction, and so they summed, and forward displacement of that target was relatively larger. If a target moved away from a landmark, representational momentum and the landmark attraction effect operated in opposite directions, and so they partially canceled, and forward displacement of that target was relatively smaller.

After target motion, participants indicated perceived depth of the blob by pressing different keys to increase or decrease binocular disparity of a probe blob or by adjusting a probe blob to match the size of the blob flashed during target motion. Participants indicated a larger size for approaching motion and a smaller size for receding motion, and this effect was larger with stereomotion than with looming.

Binocular disparity. Nieman, Nijhawan, Khurana, and Shimojo (2006) presented moving targets and flashed objects within random dot stimuli, and stimuli were isoluminant and distinguished from the background and from each other by binocular disparity. A moving bar appeared in the lower part of the display, and a flashed bar of the same size appeared in the upper part of the display. A flash-lag effect occurred if participants viewed the display binocularly. If the moving target was monocularly detectable and the flashed object was disparity defined, a flash-lag effect occurred. If the moving target was disparity defined and the flashed object was monocularly detectable, a flash-lag effect occurred, but it was weaker than if the flashed object or both the moving target and the flashed object were disparity defined. Given that a flash-lag effect occurred if stimuli lacked luminance boundaries but were disparity defined, Nieman et al. suggested the flash-lag effect does not result from retinal mechanisms but instead results from cortical processes subsequent to spatial pooling of neurons in V1 (cf. Maus, Ward, Nijhawan, & Whitney, 2013). As noted earlier, Lee et al. (2008) obtained a flash-lag effect with stimuli that differed in binocular disparity, and Harris et al. (2006) obtained a flash-lag effect with random dot stimuli (in which the only depth cue was disparity).

Color. Nijhawan (1997) presented participants with a moving target consisting of a green bar, and the flashed object consisted of a red bar briefly superimposed on the moving target. If participants integrated the spatially overlapping red and green, then a single yellow bar should have been observed for the duration of the flash. However, participants reported perceiving a stationary red bar that lagged a moving green bar. Nijhawan, Khurana, Kamitani, Watanabe, and Shimojo (1998) had participants execute smooth pursuit eye movements past a continuously visible and stationary green bar (that appeared to move across the retina in the direction opposite to eye movement). A red bar was briefly superimposed on the green bar, and participants reported displacement of the red bar in the direction of pursuit. Sheth, Nijhawan, and Shimojo (2000) presented a stationary target that continuously changed in color, becoming more green or more red. Halfway though the change, another stationary object was briefly flashed nearby, and participants judged which of the two stimuli was greener. The flashed object was the same color as the concurrent color of the changing target, but participants judged the target to be more extreme (i.e., to have changed more). In other words, a flash-lag effect for perceived color change occurred.

Arnold, Ong, and Roseboom (2009) presented participants with stimuli consisting of an annulus containing a grating that changed in orientation and an inner disk containing a stationary grating. The stimuli could change in color, and participants judged whether color changes in the moving parts and static parts of the stimulus were synchronous or whether the moving parts and static parts of the stimulus were aligned at the time of color change. For judgments of synchronicity, color change of the annulus occurred slightly before, at the same time as, or slightly after color change of the inner disk. For judgments of alignment, color change of the moving annulus occurred slightly before, at the same time as, or slightly after the grating in the moving annulus was aligned with the stationary grating in the inner disk. A temporal advantage for alignment judgments (i.e., a flash-lag effect) occurred, but no temporal advantage for color judgments occurred. Kreegipuu and Allik (2004) reported a flash-lag effect if the moving target changed in color, and Cai and Schlag (2001) reported perceived color change lagged perceived position change. Gauch and Kerzel (2008b) reported perceived color change lagged perceived position change in flash-midpoint displays but not in flash-initiated displays.

Luminance. Purushothaman, Patel, Bedell, and Öğmen (1998) and Öğmen et al. (2004) reported the flash-lag effect decreased if luminance of the flashed object increased. With high luminance of the flashed object and low luminance of the moving target, the flash-lag effect reversed and the flashed object led the moving target (i.e., a flash-lead effect). Sheth et al. (2000) and Ichikawa and Masakura (2006) reported a flash-lag effect for changes in luminance, and in Ichikawa and Masakura, the flash-lag effect decreased if participants controlled changes in target luminance. Nieman et al. (2006) suggested a motion detector activated only by luminance differences would not detect motion for stimuli whose average luminance matched the luminance of the background (e.g., random dot stimuli). Thus, if retinal mechanisms were responsible for the flash-lag effect, no effect should occur with random dot stimuli. However, and as noted earlier, Nieman et al. obtained flash-lag effects with random dot stimuli. Kerzel (2003) presented a moving target that changed in luminance without warning, and participants indicated where the luminance change occurred. The perceived location of luminance change was displaced in the direction of motion, and Kerzel claimed time-to-consciousness was longer for luminance than for motion and that this was consistent with the flash-lag effect.

Chappell and Mullen (2010) presented stimuli in which the flashed object or the moving target was luminance modulated, equiluminant, or equiluminant in luminance noise. The flashed object was an inverted isosceles triangle (pointing downward) in the upper half of the display, and the moving target was an upright isosceles triangle (pointing upward) in the bottom half of the display. Participants judged whether the vertex of the flashed object was to the left or right of the vertex of the moving target. A flash-lag effect occurred in all conditions except those containing a luminance-modulated flashed object and an equiluminant or equiluminant-in-luminance-noise moving target. Adding luminance noise to an equiluminant moving target, but not to an equiluminant flashed object, decreased the flash-lag effect. Chappell and Mullen suggested the magnocellular pathway contributes to the flash-lag effect. This might confer a temporal advantage for the moving target (e.g., Purushothaman et al., 1998), but even so, magnocellular pathway processing was not limited to the moving target, as the flash-lag effect was influenced by luminance of the flashed object or the moving target. Overall, luminance influences a flash-lag effect involving relative spatial position of a moving target and a flashed object, and a flash-lag effect occurs for changes in luminance.

Contrast. Kanai et al. (2004) varied contrast of a moving target and a flashed object to the background. The lowest contrast resulted in the largest flash-lag effect, and Kanai et al. suggested mislocalization arose from positional uncertainty (cf. blurriness in Fu et al., 2001). Arnold et al. (2009) varied contrast between two rotating gratings, one of which surrounded the other. The inner grating was vertically oriented and static, and the outer grating was rotating; contrast of the inner grating was constant, and contrast of the outer grating was higher or lower than contrast of the inner grating. In the higher contrast condition, a flash-lag effect occurred, whereas in the lower contrast condition, a flash-lead effect occurred (i.e., the flashed object was perceived in front of the moving target). Arnold et al. suggested their data were inconsistent with differential latencies, causing participants to perceive moving stimuli before they perceived stationary stimuli, and that latency differences modulate, but do not cause, the flash-lag effect. Maus and Nijhawan (2009) reported larger forward displacement of the moving target if contrast between the target and background gradually decreased than if the target abruptly vanished, and this is consistent with the larger flash-lag effect with decreases in contrast in Kanai et al.

Spatial frequency. Cantor and Schor (2007) presented participants with pairs of Gabor patches that were vertically separated; one patch was presented for a brief duration, and another patch was presented for a longer duration. The patches were stationary, but within the longer duration patch the grating appeared to drift. Participants judged whether the top grating was offset to the left or right of the bottom grating. The flash-lag effect decreased as spatial frequency increased from .25 to 1 cycles per degree, and the decrease with higher spatial frequencies is consistent with involvement of the magnocellular pathway (cf. Chappell & Mullen, 2010). Cantor and Schor suggested variations in the flash-lag effect reflect interactions of velocity, temporal frequency, and spatial frequency. Sheth et al. (2000) presented a stationary square wave grating that increased or decreased in spatial frequency, and a stationary square wave grating of a single spatial frequency was flashed nearby. Participants judged which grating had higher spatial frequency, and judgments were consistent with a flash-lag effect. Fu et al. (2001) suggested forward displacement of a moving target is more likely if the target is blurry (i.e., if high spatial frequencies have been removed). Spatial frequencies influence the flash-lag effect for spatial position, and a flash-lag effect occurs for changes in spatial frequency.

Target identity. Moore and Enns (2004) varied size of the moving target during presentation of the flashed object. A change in target size nearly eliminated the flash-lag effect, and Moore and Enns suggested large and transient changes to the moving target resulted in perception of two separate targets rather than perception of change in a single target. A decrease in the flash-lag effect with perception of an apparent additional target is consistent with previous suggestions that perceptual organization influences the flash-lag effect (cf. Watanabe, Nijhawan, Khurana, & Shimojo, 2001). Furthermore, Moore and Enns suggested a flash-lag effect occurs in flash-midpoint displays but not in flash-terminated displays because object updating occurs with flash-midpoint displays but not with flash-terminated displays. Khurana, Carter, Watanabe, and Nijhawan (2006) presented stimuli consisting of the top half of a face that was flashed and the bottom half of a face that was moving or stationary (cf. composite face effect; recognition of either half of a face composed of two halves from different individuals is impaired when the halves are aligned; Young, Hellawell, & Hay, 1987). Participants identified the individual in the top half. Faces in which the bottom half was initially in motion were recognized better than stationary faces, and this was attributed to a lack of perceptual alignment due to a flash-lag effect.

Bachmann and Põder (2001; Bachmann, Luiga, Põder, & Kalev, 2003) considered the moving target and flashed object as occupying different perceptual streams. In the motion stream, a sequence of repetitions of the letter *I* was presented, and within this sequence a single letter *Z* was presented. In the flashed stream, a single letter *Z* was presented. Bachmann and Põder reported the *Z* in the motion stream appeared to occur before a simultaneous *Z* in the flashed stream, and they suggested this reflected a flash-lag effect. Bachmann and Põder argued the flash-lag effect did not depend upon motion (see also Sheth et al., 2000) or changes in features. However, the letter *Z* involves different features than the letter *I*, and so their argument about features seems overstated unless features are limited to those aspects of a stimulus that undergo continuous change. Also, given that the letter *Z* is a different stimulus than the letter *I*, findings of Bachmann and colleagues suggest maintenance of a single continuous target identity is not essential for the flash-lag effect if the task of the participants involves comparing identities (shapes) of stimuli in the moving and flashed streams rather than comparing spatial positions (cf. Linares & López-Moliner, 2007).

Many researchers presented a flashed disk within a moving annulus (e.g., Becker et al., 2009; Eagleman & Sejnowski, 2000b; Khurana et al., 2000; Nijhawan, 2001), but Kanai and Verstraten (2006) reversed this and presented a moving disk and a flashed surrounding annulus (see also Rotman, Brenner, & Smeets, 2002). Most theories of the flash-lag effect suggest a flash-lag effect should occur under these conditions, but Kanai and Verstraten reported that in addition to a portion of the disk being perceived as ahead of the annulus (as in a typical flash-lag effect), the entirety of the interior of the annulus was filled by the color of the moving disk. If the moving target was a vertically oriented bar that moved to the right, the part of the bar inside a flashed annulus was correctly perceived, but the parts of the bar extending above and below the annulus were perceived to be ahead of the bar. Kanai and Verstraten suggested the veridical position of the flashed object can be made visible if the moving target is enclosed by a transient (flashed) stimulus, and that this involves a filling-in process that propagates from the interior edges of the transient stimulus. Thus, whether the target encloses, is enclosed by, or is spatially separated from the flashed object, and whether a single target identity is maintained, can influence the flash-lag effect.

Pattern entropy. Sheth et al. (2000) presented a stationary target square that changed in pattern entropy. The target contained a fixed number of dots, and the dots were initially aligned to a grid pattern (0% entropy) or randomly distributed (100% entropy). Successive presentations of the target varied the number of dots that deviated from their position on the grid and exhibited increasing (from 0% to 100%) or decreasing (from 100% to 0%) pattern entropy. Midway through the target presentation, another stationary square briefly flashed, and participants judged which of the two squares appeared more disordered. The flashed square exhibited the same entropy as the target square at the moment the flashed square was presented, but participants judged the flashed square to be more disordered if entropy of the target was decreasing and less disordered if entropy of the target was increasing (i.e., a flash-lag effect for pattern entropy occurred). Sheth et al. noted there are no known neural structures in visual cortex dedicated to processing information regarding pattern entropy, and they suggested a flash-lag effect for a stimulus changing in pattern entropy demonstrates the flash-lag effect reflects processes widespread throughout the brain.

Duration of the flashed object. Some researchers did not report the duration of the flashed object in their stimuli (e.g., Chappell & Hine, 2004; Ichikawa & Masakura, 2006; Namba & Baldo, 2004). Among researchers who did report the duration of the flashed object, durations of 5 (e.g., Shi & Nijhawan, 2008), 9 (e.g., Rotman et al., 2002), 10 (e.g., Becker et al., 2009; Linares et al., 2007), 13 (e.g., Durant & Johnston, 2004; Kanai et al., 2004; Vreven & Verghese, 2005), 15 (e.g., Whitney, Murakami, & Cavanagh, 2000), 30 (e.g., Harris et al., 2006), 33 (e.g., Bachmann et al., 2003), 60 (e.g., Whitney & Cavanagh, 2000), and 70 (e.g., Moore & Enns, 2004) ms have been reported. Some researchers used a range of flashed object durations (e.g., 1, 43, 93, and 193 ms in Rotman, Brenner, & Smeets, 2005; 24, 40, 80, 120, 160, and 200 ms in Cantor & Schor, 2007). Brenner and Smeets (2000) and Eagleman and Sejnowski (2000b) suggested a flashed object can be presented for up to 80 ms and produce a flash-lag effect, and Cantor and Schor (2007) suggested the flash-lag effect plateaued with flash durations longer than 80 ms. Eagleman and Sejnowski (2000c) reported a flash-lag effect did not occur with flash durations of 200 ms, but Lappe and Krekelberg (1998) reported a flash-lag effect with durations of up to 500 ms (see also Krekelberg & Lappe, 1999).

Baldo, Kihara, et al. (2002) reported a flash-lag effect if a flashed object appeared at the beginning of a trial and vanished in midtrajectory or appeared at midtrajectory and vanished at the end of a trial. In this case, the "flash" involved an abrupt change in a continuously visible stimulus and not a briefly presented stimulus. Kreegipuu and Allik (2004) reported a flash-lag effect if the reference object was a stationary (and continuously) visible target that abruptly changed color. Kreegipuu and Allik suggested a flashed object was not necessary in order for a flash-lag effect to occur; even so, it could be argued that an abrupt color change is functionally equivalent to a flash. Given the results of Kreegipuu and Allik (and comparisons of position change with color change in Gauch & Kerzel, 2008b, and with luminance change in Kerzel, 2003), a single onset or offset during target motion might be all that is necessary in order to induce a flash-lag effect (cf. "offset-lag" in Maus & Nijhawan, 2009). Duration of the flashed object is less critical. Rather than reflecting characteristics of the flashed object or the relationship of the flashed object and moving target, onset or offset of the flashed object might simply be a marker indicating when the position of the target is to be sampled (cf. Brenner & Smeets, 2000), similar to using actual target onset or offset location as a marker in the Fröhlich effect or in representational momentum, respectively (see Part 2).

Motion of the flashed object. In most studies of the flash-lag effect, the flashed object was stationary. Indeed, Eagleman and Sejnowski (2007, p. 4) claim "flash-lag is turned into flash-drag when motion is attributed to the flash." However, such a claim is too broad, as several studies reported a flash-lag effect occurred if the flashed object was in motion (i.e., if motion was attributed to the flashed object). In MacKay's (1958) report, motion information was available continuously for self-luminous objects but available only intermittently for stroboscopically illuminated (flashed) objects, and stroboscopically illuminated objects appeared to lag self-luminous objects. Krekelberg and Lappe (1999) presented a rotating target and a flashed object that rotated in alignment with the target for varying durations. A flash-lag effect occurred, and the flash-lag effect decreased with increasing rotation (duration) of the flashed object and was not eliminated until duration of the moving flashed object reached 500 ms (cf. flashed object duration in Eagleman & Sejnowski, 2000b). Curiously, Lappe and Krekelberg (1998; also Cantor & Schor, 2007) reported the flash-lag effect increased if duration of an intermittently visible target increased, and so increasing duration of the flashed object appears to produce an effect opposite to increasing duration of the moving target.

Bachmann and Kalev (1997) presented a pair of vertically separated vertical lines that moved horizontally in the same direction and at the same velocity. The bottom line was visible for a relatively long spatial extent, and the top line was only visible within a narrow window centered on the midtrajectory of the bottom line. The bottom line started its motion first, and the top line appeared when the bottom line reached alignment with the initial edge of the window. A flash-lag effect occurred and decreased with increases in the length of the flashed object's trajectory. Bachmann et al. (2003) suggested the decrease in the flash-lag effect reflects acceleration of perceptual processing over time; however, it could be argued this result reflects misperception of velocity (see Palmer & Kellman, 2002, 2003) or extrapolation/facilitation due to preceding motion of the flashed object. The larger flash-lag effect at the beginning of the flashed object's motion parallels Watanabe et al.'s (2001) finding that the flash-lag effect was larger if the flashed object was presented at the leading edge of the moving target. In Cantor and Schor (2007), a briefly presented moving target in one condition was the same as a moving flashed object in another condition, and a flash-lag effect occurred in both conditions.

Gauch and Kerzel (2008a) presented a moving target and a flashed object in the upper and lower portions, respectively, of the visual field, and flash-initiated, flash-midpoint, and flash-terminated displays were shown. The flashed object was stationary or moving. For flash-initiated displays, a flash-lag effect occurred with stationary flashed objects and moving flashed objects, and the flash-lag effect was larger with moving flashed objects. For flash-midpoint displays, a flash-lag effect occurred with stationary flashed objects and moving flashed objects, and the magnitudes did not differ. For flash-terminated displays, a flash-lag effect did not occur with stationary flashed objects, but a flash-lag effect did occur with moving flashed objects. Gauch and Kerzel suggested motion extrapolation, postdiction, and differential latency theories cannot account for differences in the flash-lag effect across conditions. In general, a flash-lag effect can occur regardless of whether the flashed object is stationary or moving. However, moving flashed objects are typically visible for longer durations than stationary flashed objects. Given that duration of the flashed object might influence the flash-lag effect (e.g., Eagleman & Sejnowski, 2000c; Lappe & Krekelberg, 1998), future studies should explicitly separate duration and motion of the flashed object.

Cues. Khurana et al. (2000) presented cues instructing participants to expect the flashed object to appear on the left or right side of the display. Cues were presented 100 ms prior to presentation of the flashed object, and cues were valid on 70% of the trials and invalid on 30% of the trials. Cue validity did not influence the flash-lag effect. Khurana et al. then presented cues 500 ms prior to presentation of the flashed object, and cues were valid on 80% of the trials and invalid on 20% of the trials. Valid cues led to faster responses regarding whether the flashed object was above or below the fixation point, but cue validity did not influence the flash-lag effect. Khurana et al. also reported that cuing which target in a multitarget display would be closest to the flashed object did not influence the flash-lag effect. Namba and Baldo (2004) presented cues instructing participants to expect the flashed object on the left or right of the target. Cues were presented between 3,000 and 5,000 ms prior to presentation of the flashed object, and cues were valid on 80% of the trials and invalid on 20% of the trials. A flash-lag effect occurred regardless of cue validity, and the flash-lag effect was smaller with valid cues than with invalid cues. Namba and Baldo suggested their findings differed from those of Khurana et al. because of differences in latency between presentation of cues and presentation of flashed objects.

Brenner and Smeets (2000) presented a rotating stimulus, and a stationary bar was flashed. If a cue consisting of a faint outline of the bar was visible from the beginning of a trial until the bar appeared, then the flash-lag effect was decreased. Rotman et al. (2002) reported that the perceived location of a flashed object was mislocalized in the direction in which participants' eyes were moving as they tracked a moving target (see also Rotman, Brenner, & Smeets, 2004; Rotman et al., 2005).[2] Cues in the form of warning beeps or warning flashes that predicted when a flashed object would appear did not influence mislocalization, but if the stimulus was shown twice and participants responded after the second showing, mislocalization decreased. Rotman et al. reported that informing participants the flash was about to appear did not influence mislocalization, but informing participants where the flashed object would appear decreased mislocalization, and they suggested the type of cue rather than the presence of a cue determined whether a cue influenced mislocalization. Rotman et al. suggested it was not predictability per se that influenced mislocalization, but rather whether the target appeared at a spatially cued position. Consistent with this notion, Shioiri et al. (2010) reported that cuing which target in a multitarget display would be nearest the flashed object decreased the flash-lag effect.

Hommuk, Bachmann, and Oja (2008) presented a moving target in the form of a sequence of discrete presentations of the letter *I*, and at one position within this motion stream, the letter *Z* was superimposed and was the stimulus to be detected. In a separate perceptual stream on the other side of fixation, a single flashed letter *Z* was presented. Presentation of the *Z* in the flashed stream appeared to lag a simultaneously presented *Z* in the motion stream, and this is consistent with a flash-lag effect (see also Bachmann & Põder, 2001). However, if the *Z* in the flashed stream was precued, a flash-lead effect occurred if that *Z* appeared within the first 250 ms, and a flash-lag effect did not occur unless that *Z* did not appear for at least 400 ms. Such a finding seems inconsistent with a flash-lag effect in flash-initiated displays, but the precue might have provided additional facilitation (cf. Maiche, Budelli, & Gómez-Sena, 2007) not evoked by flash-initiated displays and that potentially decreased processing latency. In Hommuk et al., the precue potentially primed recognition of the *Z* in both streams, and intervening objects interfered with this priming in the motion stream but not in the flashed stream.

Predictability of the flashed object. Vreven and Verghese (2005) noted the position of the flashed object in studies of the flash-lag effect was usually quite predictable. They presented a moving target consisting of a line of three dots that pivoted around one of the end dots. The flashed object was a dot outside the circle defined by rotation of the line and presented at one of three locations; in the absence of other information, participants had no way to predict in which location the flashed object would be presented. In a spatial cue condition, a dot indicated where the flashed object would be presented. In a temporal cue condition, there was a series of beeps, and one of the beeps occurred at the same time that the flashed object was presented. In a both-cues condition, both a spatial cue and a temporal cue were presented. There was also a no-cue condition in which neither a spatial cue nor a temporal cue was presented. The flash-lag effect was largest in the no-cue condition, followed by temporal, spatial, and both-cues conditions; thus, the flash-lag effect was largest when unpredictability of the flashed object was highest (cf. Rotman et al., 2002). Consistent with this, the spatial cue unequivocally indicated where the flashed object would be presented, whereas the temporal cue was not unequivocal, as only one of the beeps coincided with presentation of the flashed object.

Baldo and Namba (2002; Namba & Baldo, 2004) presented a flashed object in one of two positions relative to a rotating target. The position of the flashed object was fixed at a single position, alternated between positions, or varied randomly. The flash-lag effect was larger if position of the flashed object varied randomly (i.e., was not predictable) than if position was fixed. Baldo, Kihara, et al. (2002) presented the flashed object at a blocked and highly predictable eccentricity or allowed eccentricity of the flashed object to vary randomly. The flash-lag effect increased with increases in eccentricity of the flashed object, and if predictability was low, the increase was larger. López-Moliner and Linares (2006) presented an auditory tone 300 ms prior to the flashed object, and this did not decrease the flash-lag effect as much as if participants triggered occurrence of the flashed object by a keypress. However, there was no effect of a slight delay between the keypress and presentation of the flashed object, and López-Moliner and Linares concluded the keypress was not a temporal marker for the flashed object. In general, increased predictability of the flashed object (based on cues or other expectations) might decrease processing latency of that stimulus, and this would diminish the time required for perception of the flashed object (and diminish the difference in processing latencies between the moving target and the flashed object), and thus diminish the flash-lag effect.

Uncertainty of target location. Fu et al. (2001) presented two horizontally moving targets that were vertically offset and moved toward each other; if targets were vertically aligned when motion

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[2] It should be noted that participants in Rotman et al. (2002) visually tracked the moving target and that visual tracking of a moving target has been linked to decreases in the flash-lag effect (e.g., Nijhawan, 2001). Indeed, displacement of the flashed object in the direction of target motion that Rotman et al. obtained was more similar to a flash-drag or flash-lead effect. Also, in Rotman et al. the target would have been stationary on the retina, and so mislocalization was not due to target motion across the retina (cf. Blohm et al., 2003; Nijhawan, 2001; van Beers et al., 2001).

stopped, then there was perceived misalignment (forward displacement of targets) if target edges were blurry (i.e., more positional uncertainty), but there was no perceived misalignment if target edges were sharply defined. Kanai et al. (2004) reported the flash-lag effect increased with decreases in contrast of the moving target with the background, and they suggested this reflected an increase in positional uncertainty. Maus and Nijhawan (2006, 2009) reported forward displacement of a moving target increased if contrast of the target and the background decreased. The findings of Fu et al., Kanai et al., and Maus and Nijhawan suggest increases in uncertainty regarding target location increase the flash-lag effect. Brenner et al. (2006) found judgments of synchronization of stimuli in flash-lag effect displays were more variable than judgments of localization, and they suggested a limiting factor in determining a moving target's location was temporal resolution of underlying signals. Such a suggestion is consistent with low temporal precision in judgments of location found by Linares, Holcombe, and White (2009).

Number of moving targets. In many studies of the flash-lag effect, a moving target was composed of separate stimuli grouped as a single target (e.g., three circles along an imaginary line, Baldo & Klein, 1995; two vertically aligned rectangles, Murakami, 2001b; pairs of lines grouped by color, Watanabe et al., 2001). In other studies of the flash-lag effect, separate stimuli were not grouped as a single moving target, but were considered as multiple targets. Shioiri et al. (2010) presented one, two, or six targets that revolved along the same circular path. The flashed object consisted of two black dots adjacent to (and on either side of) a single target. The flash-lag effect increased with increases in the number of targets, and the increase was smaller if the moving target that would be closest to the flashed object was cued in advance (i.e., if participants could track a single target rather than divide attention over multiple targets). Khurana et al. (2000; but see Baldo, Kihara, et al., 2002) presented five equally spaced targets moving along a circular path but reported no difference in the flash-lag effect as a function of whether the target closest to where the flashed object would be presented was cued in advance. Relatedly, Krekelberg and Lappe (1999) reported the flash-lag effect decreased as the number of flashed objects increased (to a temporal horizon of approximately 500 ms).

Presence of unrelated stimuli. Maiche et al. (2007) examined whether the presence of a stimulus unrelated to the moving target or flashed object could influence the flash-lag effect. They presented an annulus moving from left to right in the upper visual field, and a thin vertical bar flashed over the target (cf. Kanai & Verstraten, 2006, who presented a moving vertical bar and a flashed annulus). Additionally, a disk-shaped stimulus moved vertically in the lower visual field (to the right of where the flashed object was presented). If the disk moved toward the position where the flashed object appeared, then the flash-lag effect was larger than if the moving disk was not presented, and the increase was larger if contrast between the moving disk and the background was increased. However, if the disk moved away from the position of the flashed object or if the disk's path of motion was farther from the flashed object, then the moving disk did not influence the flash-lag effect. Maiche et al. suggested there was a general facilitation of processing along the path of motion by a nearby stimulus. Such facilitation is consistent with differential latency theory and appears to exhibit a gradient based on proximity to the location of the flashed object.

Characteristics of the Observer

There has been relatively little research regarding how characteristics of the observer influence the flash-lag effect. Characteristics of the observer considered here include (a) allocation of attention, (b) eye movements and fixation, (c) body movement, (d) control of the moving target or flashed object, (e) perceptual set, (f) perceptual organization, and (g) conceptual knowledge. The effects of these variables are summarized in Table 2.

Allocation of attention. Baldo and Klein (1995) reported the flash-lag effect increased as distance of the flashed object from the moving target increased, and they attributed this to the time required to shift attention from the moving target to the flashed object. Khurana and Nijhawan (1995) responded to Baldo and Klein by presenting participants with a display in which a rotating target consisted of a line of equally spaced rectangles, and the flashed object consisted of circles within the gaps between the rectangles. A flash-lag effect occurred, and Khurana and Nijhawan suggested the flash-lag effect was not due to a shifting of attention, because interleaving the flashed object and moving target removed the need for a (spatial) shift of attention. As noted earlier, Khurana et al. (2000) presented multiple moving targets (annuli) and a flashed object that filled the inner area of one of the targets. A flash-lag effect occurred and was not influenced by whether the target or flash position had been cued or by cue validity, and Khurana et al. concluded the flash-lag effect is not influenced by the distribution or allocation of attention (but see Shioiri et al., 2010). However, confidence in this conclusion is weakened by potential methodological issues (e.g., inappropriate analyses, insufficient stimulus onset asynchronies; see Baldo, Kihara, et al., 2002).

Baldo, Kihara, et al. (2002) presented a rotating target and a flashed object consisting of an extension of the diameter of the target. The flashed object was visible (a) during a single frame near the midpoint of target motion (onset–offset condition), (b) from the midpoint of target motion until the target vanished (onset condition), (c) from the appearance of the target until the midpoint of target motion (offset condition), or (d) from the appearance of the target until the target vanished (moving offset condition). A flash-lag effect occurred in the onset–offset, onset, and offset conditions, and a flash-lead effect occurred in the moving offset condition. The data suggest the flash-lag effect depends upon abrupt onset or offset of the flashed object during target motion, and this would involve a shift of attention during target motion (rather than at target onset or offset). The large flash-lag effect with random dot stereograms in Nieman et al. (2006) is also consistent with a role of attention: Tracking the moving target demanded a high level of attention, leaving less attention available for detecting the flashed object. Thus, the flashed object would take even longer to enter perceptual awareness, resulting in a larger flash-lag effect. Such a notion is consistent with findings of a larger flash-lag effect if participants engaged in a concurrent task (e.g., Sarich, Chappell, & Burgess, 2007; Scocchia, Actis-Grosso, de'Sperati, Stucchi, & Baud-Bovy, 2009).

Chappell, Hine, Acworth, and Hardwick (2006) suggested a flashed object automatically captures attention (see also Kirschfeld

Table 2
Effects of Observer Characteristics on the Flash-Lag Effect

Characteristic	Flash-lag effect	Primary sources
Allocation of attention	Increases with shifts of attention across a larger distance	Baldo & Klein (1995); Shioiri et al. (2010)
	Increases if participants attend to multiple targets or multiple tasks	Sarich et al. (2007); Shioiri et al. (2010)
Eye movements and fixation	Is eliminated if participants track a smoothly moving target	Nijhawan (2001)
	Occurs if flashed object is presented during an eye movement	Blohm et al. (2003); Nijhawan (2001); van Beers et al. (2001)
	Might reflect allocentric encoding of the target	Becker et al. (2009); Blohm et al. (2003)
Body movement	Reflects active or passive body movement	Cai et al. (2000); Nijhawan & Kirschfeld (2003); Schlag et al. (2000)
	Occurs for biological motion stimuli and nonbiological motion stimuli	Kessler et al. (2010)
Control	Decreases if participants control presentation of the flashed object	López-Moliner & Linares (2006)
	Decreases if participants control movement of target using a mouse but not keypad or trackball	Ichikawa & Masakura (2006, 2010)
	Increases if participants control movement of target with a robotic arm	Scocchia et al. (2009)
Perceptual set	Decreases if participants have perceptual set to attend the flashed object	Gauch & Kerzel (2009)
Perceptual organization	Increases at leading edge and decreases at trailing edge of a target (or set of stimuli perceptually grouped as a single target)	Watanabe (2004); Watanabe et al. (2001)
	Decreases if participants judge shape rather than judge location	Linares & López-Moliner (2007)
Conceptual knowledge	Decreases if stimuli are semantically meaningful	Noguchi & Kakigi (2008)
	Is influenced by whether target moves in the "typical" direction	Nagai et al. (2010)

& Kammer, 1999). They presented a target that moved in a single direction or reversed direction, and a flashed object was presented at motion onset, offset, or reversal. In a landmark condition, participants compared the perceived position of the moving target with the perceived position of a stationary landmark (fixation crosshairs), and in a flash-irrelevant condition, participants made the same judgments in the presence of an irrelevant flash. A significant Fröhlich effect occurred, and an irrelevant flash increased the Fröhlich effect in onset or reversal conditions. Participants also judged relative positions of the moving target and the flashed object. A flash-lag effect occurred; there was no difference between reversal and midtrajectory conditions, and both were smaller than the flash-lag effect in the motion-onset condition. Interestingly, the flash-lag effect was larger than the Fröhlich effect. Müsseler, Stork, and Kerzel (2002) reported displacement of the moving target decreased if an irrelevant flash was presented at motion onset or offset, but they did not assess whether a flash-lag effect occurred. It is possible that different tasks (i.e., judging relative location in Chappell et al., 2006; judging absolute location in Müsseler et al., 2002) resulted in different effects of the irrelevant flash.

Shioiri et al. (2010) manipulated allocation of attention to the flashed object by varying the number of targets and by cuing or not cuing the target by which the flashed object would be presented. Increasing the number of targets and not cuing the flashed object both increased the flash-lag effect, and they suggested decreases in attention increase the flash-lag effect. Shioiri et al. presented flashed objects near the cued target and also near other targets, and the flash-lag effect increased as distance of the flashed objects from the cued target increased. Shioiri et al. admitted their results seem inconsistent with Khurana et al.'s (2000) lack of an effect of cuing, but they suggested a small effect of cuing is apparent in Khurana et al.'s data. Sarich et al. (2007) had participants identify a briefly presented numeral while simultaneously judging position of the flashed object, and they reported the flash-lag effect increased if attention was divided. Scocchia et al. (2009) manipulated allocation of attention to the moving target by having participants in some conditions also indicate when the moving target changed shape. The flash-lag effect in the shape-change condition did not differ from that in a control condition. Differences in findings of Sarich et al. and Scocchia et al. might result from whether the secondary task involved the attended flash-lag stimulus (Scocchia et al., 2009) or a different stimulus (Sarich et al., 2007).

Eye movements and fixation. Nijhawan (2001) presented a flashed disk within an annulus revolving along a circular path. If participants fixated the center of the circular path or fixated the location where the flashed object would be presented, a flash-lag effect occurred. However, if participants tracked the annulus, the flash-lag effect was eliminated (see also Nijhawan, 1997).[3] If participants tracked a smoothly moving object past a stationary annulus and a disk flashed inside the annulus, a flash-lag effect involving the stationary annulus and the flashed object occurred. Nijhawan argued this latter finding demonstrated an eye move-

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[3] An anonymous reviewer pointed out that differences between fixation and pursuit conditions cannot be used in evaluating theories of the flash-lag effect such as motion extrapolation and differential latency, because localization errors during smooth pursuit movements result from errors in

ment based flash-lag effect. Similarly, Blohm et al. (2003) reported a flash-lag effect occurred if a flashed object was presented during a smooth anticipatory eye movement. Van Beers et al. (2001) presented a display in which participants fixated a stationary point or pursued a moving target, and then judged whether a flashed object was aligned with two stationary reference points. Judgments were consistent with a flash-lag effect. Although Blohm et al. and van Beers et al. discussed their results as reflecting mislocalization of the flashed object during eye movements, in their studies the flashed object was not compared to a tracked target, and so their findings do not conflict with findings of Nijhawan (2001) or Rotman et al. (2002).

Findings of Blohm et al. (2003) and van Beers et al. (2001) suggested participants' frame of reference influenced the flash-lag effect. Blohm et al. reported early localization of the flashed object did not suggest a flash-lag effect, but after the position of the flashed object was translated from egocentric coordinates into allocentric coordinates, gaze direction suggested a flash-lag effect. Blohm et al. speculated the influence on the flash-lag effect of target motion immediately after the flashed object was presented (e.g., Eagleman & Sejnowski, 2000b; Krekelberg & Lappe, 2000a) might reflect the time required to translate from initial egocentric coordinates to allocentric coordinates (cf. Becker et al., 2009). Interestingly, a flash-lag effect occurred even though participants were not aware of their eye movements and reported no sense of motion. Van Beers et al. reported a flash-lag effect occurred in a two-dimensional pursuit condition (in which a single flashed object was presented above or below the horizontal trajectory of the pursuit target). In addition to mislocalization along the (horizontal) axis of motion, there was a smaller mislocalization away from the trajectory of the pursued target (along the vertical axis), and this mislocalization was relatively larger if the flashed object was below the trajectory than if the flashed object was above the trajectory.[4]

The potential importance of the frame of reference for the flash-lag effect was examined by Becker et al. (2009), who presented a flashed object that filled or was slightly in front of or behind an annulus revolving along a circular path. Participants judged whether the flashed object lagged, was at the same position as, or led the moving target. After the stimuli vanished, participants saccaded from the fixation point to the position where the flashed object appeared or to the position of the moving target at the time of the flash. Saccades to the position of the flashed object were not displaced from the actual flash position, but saccades to the position of the moving target at the time of the flash were displaced in the direction of target motion. In a subsequent experiment, the flash involved an object at a specific spatial position or a change in the entire background. After the stimuli vanished, participants saccaded to the position of the moving target at the time of the flash. If the flash involved a specific spatial position, saccades were displaced in the direction of target motion, but if the flash involved the entire background, saccades were not displaced from the actual target position. Becker et al. suggested the flash-lag effect did not show dissociation between perceptual and motor systems typical of other visual illusions (e.g., Aglioti, DeSouza, & Goodale, 1995) and that a frame-of-reference theory could account for the flash-lag effect.

Body movement. Schlag, Cai, Dorfman, Mohempour, and Schlag-Rey (2000) noted previous studies of the flash-lag effect relied on retinal motion, and they demonstrated that a flash-lag effect could result from stimulus motion that was inferred on the basis of extraretinal signals resulting from active body motion. In a darkened environment, participants focused on a stationary bar and horizontally rotated their heads back and forth. Approximately halfway through the head movements, a flashed object consisting of a bar aligned with the stationary bar was presented. Participants reported the flashed object appeared to lag the stationary bar. Cai, Jacobson, Baloh, Schlag-Rey, and Schlag (2000) placed participants in a rotating chair in a darkened environment. A vertical line was continuously lit and rotated with the chair, and below this a set of five smaller vertical bars was flashed. The continuously lit bar was aligned with the middle of the flashed object, but at the beginning of rotation, participants reported the continuously lit bar appeared to be ahead of the middle of the flashed object. Also, Nijhawan and Kirschfeld (2003) reported a cross-modal flash-lag effect occurred if participants in a darkened environment moved their (nonvisible) hand and a visual flash was presented. Thus, a flash-lag effect can result from active or passive body movement.

In Schlag et al. (2000), Cai et al. (2000), and Nijhawan and Kirschfeld (2003), motion involved the participant's own body. Kessler et al. (2010) presented flash-lag stimuli in which the moving target was another person's body. In a biological motion condition, participants were shown an overhead view of a table, and a person was seated at one side of the table and a mug was placed near the opposite side. The person reached toward the mug, and a white rectangle (approximately the size of the person's hand) was briefly flashed near the center of the table, and the flashed object was presented slightly before, at the same time as, or slightly after it would have been aligned with the reaching hand. A control condition in which the reaching hand and the mug were replaced by a moving rectangle (the size of the hand and lower arm) and a circle, respectively, was also presented (and the moving rectangle exhibited the same velocity profile as the biological motion stimulus). A robust flash-lag effect occurred in both biological motion and control conditions. The flash-lag effect in the

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sensorimotor integration and thus involve different mechanisms than would localization errors during fixation. Additionally, it is not clear how oculomotor behavior would (a) be involved in a flash-lag effect with changes in visual stimuli that did not involve changes in location (e.g., color; Sheth et al., 2000), (b) be involved in a flash-lag effect with nonvisual stimuli (e.g., auditory stimuli; Alais & Burr, 2003), or (c) account for effects of higher level processes on the flash-lag effect (e.g., conceptual knowledge; Nagai et al., 2010; Noguchi & Kakigi, 2008).

[4] The larger displacement away from the horizontal trajectory of the target for flashed objects below the trajectory in van Beers et al. (2001) is consistent with displacement in the direction of implied gravitational attraction that has been referred to as *representational gravity* in studies of visual (Hubbard, 1997) and auditory (Hubbard & Ruppel, 2013) localization. If the flashed object was below the horizontal trajectory, then representational gravity and bias away from the trajectory operated in the same direction, and so they summed, and displacement away from the trajectory was relatively larger. If the flashed object was above the horizontal trajectory, then representational gravity and bias away from the trajectory operated in opposite directions, and so they partially canceled, and displacement away from the trajectory was relatively smaller. Thus, the frame of reference used by participants in van Beers et al. appeared to include an external axis aligned with the direction of implied gravitational attraction, and although not noted as such by van Beers et al., their findings provide the first evidence that representational gravity can influence the flash-lag effect.

biological motion condition, but not in the control condition, was influenced by whether a first-person (aligned with participants' perspective) or third-person (opposite to participants' perspective) perspective was shown, and this suggests a possible role of perceived agency.

Control. Ichikawa and Masakura (2006) had participants control with a computer mouse a moving target that ascended or descended. Hand motion believed by participants to control target motion decreased the flash-lag effect, and Ichikawa and Masakura suggested active control of a target in a specific visual field facilitated processing for that visual field. Ichikawa and Masakura (2010) found that if participants controlled the target by moving a computer mouse, the flash-lag effect decreased if the mapping between movements of the mouse and movements of the target was typical of computer operating systems with which participants were familiar (i.e., motion of the mouse away from or toward the participant produced upward or downward motion, respectively, of the target) but not if the mapping was unfamiliar. The decrease with a familiar mapping occurred regardless of whether participants could view their hand, suggesting proprioceptive information rather than visual information regarding their hand influenced the flash-lag effect. Training with an unfamiliar mapping had minimal effect. If participants controlled the target with a sustained keypress or manipulation of a trackball, a decrease in the flash-lag effect did not occur. The latter types of hand movements might not have mapped as clearly onto target motion.

Participants in Ichikawa and Masakura (2006, 2010) controlled motion of the target, but participants in López-Moliner and Linares (2006) controlled presentation of the flashed object. Participants in López-Moliner and Linares viewed a bar that pivoted around an end point, and the bar contained a small gap. A small rectangle was briefly presented in or near the gap. In one condition, participants triggered presentation of the flashed object by pressing the space bar, and in other conditions, participants had no control over when the flashed object was presented. The flash-lag effect decreased if participants triggered presentation of the flashed object. López-Moliner and Linares attributed the decrease to control rather than to predictability, as a similar decrease was not observed if the flashed object was cued by a sound 300 ms prior to presentation of the flashed object. The greater importance of control rather than predictability is consistent with Ichikawa and Masakura's (2006, 2010) finding that participants' beliefs regarding control of target motion, rather than actual control of target motion, was related to the flash-lag effect. These findings are consistent with the notion the flash-lag effect is not a low-level phenomenon but depends on high-level attributions regarding the source of target motion.

Scocchia et al. (2009) presented a moving circular target, and a flashed object was displayed at unpredictable times. The flash-lag effect was larger if participants controlled the target (via a robotic arm) than if participants did not control the target. Scocchia et al. suggested motor information provided by control of the target reduced processing latency of the target. Findings of Scocchia et al. seem inconsistent with findings of Ichikawa and Masakura (2006, 2010), but as noted by Scocchia et al., there were numerous methodological differences between their experiments and those of Ichikawa and Masakura. Scocchia et al. also noted presentation of the flashed object in Ichikawa and Masakura was triggered when the moving target passed a predetermined location, thus participants (indirectly) controlled timing of the flashed object (but whether participants were aware of this is not clear), which López-Moliner and Linares (2006) demonstrated decreased the flash-lag effect. Active control of the target would require more attention, and so effects of control are consistent with proposals that attention modulates the flash-lag effect (e.g., Baldo, Kihara, et al., 2002; Sarich et al., 2007; Shioiri et al., 2010). Overall, participant control of the moving target or flashed object can influence the flash-lag effect, but the type of control determines whether the flash-lag effect is increased or decreased.

Perceptual set. Gauch and Kerzel (2009) suggested participants respond differently if they are certain a flashed object will be presented than if they are uncertain whether a flashed object will be presented. Gauch and Kerzel presented a moving target accompanied by a flashed object or by a stationary object that was visible until the end of target motion. In a pure condition, only flashed object trials were presented. In a mixed condition, flashed object trials and stationary object trials were presented in a random order. A flash-lag effect occurred in the pure condition but not in the mixed condition with both flash-initiated displays and flash-midpoint displays. Gauch and Kerzel suggested mixed trials induced a perceptual set to attend the onset position because participants did not know how long the stimulus would remain visible. However, given the brief presentation in flashed object trials, it might be argued that pure trials should also induce a perceptual set to attend onset position. A role of perceptual set in the flash-lag effect distinguishes the flash-lag effect from illusions that are not influenced by knowledge and expectation (e.g., subjective contours) but not from mislocalizations that can be influenced by knowledge and expectation (e.g., representational momentum).

Perceptual organization. Watanabe et al. (2001) investigated how perceptual organization of the moving target influenced the flash-lag effect. Moving targets consisted in part of (a) a square, (b) two parallel vertical bars, (c) four parallel vertical bars, (d) two squares created by connecting the first and second vertical bars and by connecting the third and fourth vertical bars, or (e) four parallel vertical bars in which the first and second bars were one color and the third and fourth bars were a different color. Manipulation of color and of whether bars or squares were presented was designed to influence whether or which stimuli were perceptually grouped with other stimuli. A flashed object near the leading edge of a moving target (e.g., first of four bars, leading edge of a square) resulted in a larger flash-lag effect than a flashed object near the trailing edge of a moving target (e.g., fourth of four bars, trailing edge of a square). Watanabe et al. suggested differences in the flash-lag effect were related to perceptual grouping. Watanabe (2004) found differences in the flash-lag effect as a function of perceptual grouping in Watanabe et al. (2001) occurred with flash-initiated and flash-midpoint displays but not with flash-terminated displays. Watanabe suggested relative positions between moving targets and flashed objects are computed after motion grouping.

Linares and López-Moliner (2007) presented Glass patterns (pairs of dots in which members of each pair are separated by rotating the radius connecting one dot to the center of the pattern by a fixed amount). One member of each pair was the moving target, and the other member of that pair was the flashed object. If a flash-lag effect occurred, then the best recognition of the global shape of the Glass pattern should have occurred if the flashed object was presented prior to when the moving target arrived at the position that would have resulted in a Glass pattern. However, the best recognition of the Glass pattern occurred if the flashed object was presented at the time the moving target occupied the position that resulted in a Glass pattern. Linares and López-Moliner suggested a flash-lag effect did not occur; more specifically, they suggested that local spatial relationships between moving targets and flashed objects were preserved if those differences are used to detect global shape.[5] The lack of a flash-lag effect if participants did not engage in judgment of position is consistent with the view that high-level processes contribute to the flash-lag effect; if the flash-lag effect resulted solely from low-level processes, it would have occurred regardless of participant intent (cf. Gauch & Kerzel, 2009).

Conceptual knowledge. Noguchi and Kakigi (2008) presented native Japanese speakers and non-Japanese English speakers with moving targets and flashed objects that were segments of Kanji (ideographic) letters, and performance with Kanji segments was compared to performance if moving targets and flashed objects were composed of bars, grids, gratings, or pseudo-Kanji shapes. The flash-lag effect decreased with Kanji segments for Japanese speakers knowledgeable of Kanji but not for non-Japanese English speakers not knowledgeable of Kanji. The flash-lag effect was influenced by conceptual knowledge of Kanji letters. Also, differences in visual evoked fields in participants knowledgeable of Kanji occurred as early as 160 ms after presentation of the flashed object, and this suggested a substantial effect of top-down knowledge on the flash-lag effect. Nagai et al. (2010) presented a flash-lag display in which the moving target was a picture of an automobile that moved forward or backward, and the flashed object was a white dot above the roof of the automobile. The flash-lag effect was larger for backward motion than for forward motion,[6] and the flash-lag effect was larger for backward or forward motion than if the automobile was stationary. The flash-lag effect was influenced by conceptual knowledge of the typical direction of motion of an automobile.

Part 2: Properties and Related Phenomena

In addition to questions regarding effects of specific variables on the flash-lag effect that were addressed in Part 1, there are questions regarding more general properties of the flash-lag effect and the relationship of the flash-lag effect to other perceptual and cognitive phenomena that can be addressed. These include whether the flash-lag effect (a) is temporal or spatial, (b) results from mislocalization of the moving target or the flashed object, (c) is limited to visual stimuli, (d) reflects low-level or high-level processes, (e) is related to flash-drag and flash-lead effects, (f) is related to temporal order judgments, (g) is related to the Fröhlich effect, (h) is related to representational momentum, (i) is related to backward referral, (j) is related to anisotropic distortion, and (k) is related to flag errors in football.

Temporal or Spatial?

There has been debate regarding whether the flash-lag effect is a spatial or temporal phenomenon (e.g., Eagleman & Sejnowski, 2002; Krekelberg & Lappe, 2002). Theories based on motion extrapolation (e.g., Nijhawan, 1994, 2008) suggest the flash-lag effect is a spatial phenomenon. Theories based on latency differences (e.g., Whitney & Cavanagh, 2000; Whitney & Murakami, 1998) suggest the flash-lag effect is a temporal phenomenon. Theories based on postdiction suggest the flash-lag effect is a spatial phenomenon (e.g., Eagleman & Sejnowski, 2002) or a temporal phenomenon (e.g., Whitney, 2002). Ichikawa and Masakura (2006) defined the flash-lag effect as a temporal lag between the moving target and the flashed object, and Shen et al. (2007) suggested the flash-lag illusion is a temporal phenomenon. Murakami (2001a) suggested the flash-lag effect is a "spatiotemporal correlation structure" in which the spatial position of a flashed object in the past is compared to the spatial position of a moving target in the present. As space cannot be crossed without passing through time (and for a moving target, elapsed time relates to crossed space), Murakami's suggestion that the flash-lag effect involves spatial and temporal components seems appropriate. Indeed, there is precedent for interaction of spatial information and temporal information in perception (e.g., tau and kappa effects; Collyer, 1977; Jones & Huang, 1982).

Kreegipuu and Allik (2004) noted the flash-lag effect is usually measured in terms of spatial offset (between the moving target and the flashed object), and they attempted to separate spatial offset and temporal offset. The moving target was a bar that changed color. Participants judged whether the color change occurred after (a) the reference object flashed (time judgment) or (b) the target passed a reference object that flashed (position judgment). In time judgment, there was no systematic bias, but in position judgment, responses were displaced further along the path of motion. If the flashed reference object was replaced with a stationary bar that changed color, the results were similar: no bias for time judgment, and displacement further along the path of motion for position judgment. A similar dissociation between perceived color and perceived position was reported by Gauch and Kerzel (2008b), and Kerzel (2003) reported a similar dissociation between perceived luminance and perceived position. Kreegipuu and Allik (2003)

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[5] Linares and López-Moliner (2007) also suggested judgment of position is necessary in order for a flash-lag effect to occur. However, this suggestion seems overly broad given that a flash-lag effect can be found with changes in color or in luminance (e.g., Sheth et al., 2000), as those dimensions do not involve changes in (spatial) position per se. It might be that a flash-lag effect occurs if the changing quality of the target can be described in terms of a position along a continuous dimension (e.g., smaller to larger, dimmer to brighter, left to right) in some (potentially abstract) feature space rather than as an entry in a discontinuous list of discrete categories (e.g., shapes). However, occurrence of a flash-lag effect if stimuli are composed of discrete letters (Bachmann et al., 2003; Bachmann & Põder, 2001; Hommuk et al., 2008) suggests continuity of change in some feature space is not necessary for a flash-lag effect.

[6] Nagai et al. (2010) referred to this result as "surprising" (p. 370) because it differed from previous findings of a larger representational momentum for forward motion than for backward motion. One possible explanation for the pattern in Nagai et al. is that forward displacement of the moving target in the flash-lag effect display decreased with backward motion (consistent with previous studies of representational momentum), but that forward displacement of the flashed object decreased even more with backward motion (e.g., perhaps the relative lack of experience with backward motion resulted in a relatively smaller [percentage of] spreading activation from the representation of the position of the target to the representation of the position of the flashed object); therefore, relative differences between the target and the dot looked larger for backward motion than for forward motion, and so the flash-lag effect appeared larger for backward motion.

noted performance in timing judgments and performance in localization judgments were not equivalent. Consistent with this, Kanai et al. (2004) noted a dissociation between the flash-lag effect measured in units of space and measured in units of time. The flash-lag effect involves temporal information and spatial information, but the relationship between these types of information is not clear.

Moving Target or Flashed Object?

The flash-lag effect reflects bias in the relative positions of the moving target and the flashed object, but as traditionally described and measured, it is not clear whether this bias in relative position results from bias in perception of the absolute position of the flashed object or from bias in perception of the absolute position of the moving target. Hazelhoff and Wiersma (1924) reported observers misperceived the position of a flashed object as further in the direction of an eye movement, and van Beers et al. (2001) reported a flashed object was displaced forward. Whitney and Cavanagh (2000) reported displacement in the direction of motion for horizontal lines flashed on either side of a rotating grating or pairs of vertically moving gratings. Durant and Johnston (2004) reported displacement in the direction of motion for stationary bars flashed on either side of a rotating bar. Rotman et al. (2002, 2004, 2005) reported a flashed object was displaced in the direction of motion or in the direction of gaze. Hubbard (2008) reported a briefly presented stationary object near the end of a moving target's trajectory was displaced in the direction of motion. Brenner et al. (2006) and Maus and Nijhawan (2006, 2008, 2009) reported a moving target could be displaced in the direction of motion. Also, large literatures on the Fröhlich effect and on representational momentum provide ample evidence that the represented position of a moving target is displaced in the direction of motion.

Many researchers reported displacement for the flashed object or for the moving target, but these two types of displacement have rarely been directly compared. A notable exception is Shi and de'Sperati (2008), who presented a moving target in the form of an arc that traveled a circular path and a flashed object in the form of a dot along the circular path in front of or behind the leading edge of the moving target. Participants indicated (a) the position of the moving target at the time the flashed object was presented or the position of the flashed object or (b) whether the flashed object was ahead of or behind the leading edge of the moving target. A flash-lag effect occurred. Judgment of position was displaced in the direction of motion for moving targets and for flashed objects, and displacement was larger for moving targets than for flashed objects (cf. displacements in Hubbard, 2008; saccades in Becker et al., 2009). One possible explanation is that the flash-lag effect results from mislocalization of the absolute positions of the moving target and of the flashed object, with larger mislocalization for the moving target resulting in an apparent lagging of the flashed object. Given this, the flash-lag effect would be a derived or second-order illusion that emerges from more basic illusions involving perceived absolute positions of the moving target and/or the flashed object.

Limited to Vision?

Research on the flash-lag effect generally used visual stimuli, and given the effects of oculomotor behavior on the flash-lag effect discussed earlier, an appropriate question is whether the flash-lag effect requires or is based on visual or visuospatial processes or representations. If the flash-lag effect is limited to vision, that might suggest the flash-lag effect results from isolated low-level perceptual processes or representations rather than from high-level cognitive processes or representations. Nijhawan and Kirschfeld (2003) had participants move their (nonvisible) hand within a darkened environment and judge the felt position of their hand relative to the position of a visual flash. If the flash was aligned with their hand, participants perceived the flash as lagging their hand (cf. body motion and visual flash-lag in Cai et al., 2000; Schlag et al., 2000). Nijhawan and Kirschfeld referred to this as a *motor flash-lag*, but it is more appropriately described as a cross-modal flash-lag, as the moving target and the flashed object were in different modalities (cf. cross-modal flash-lag in Alais & Burr, 2003; Arrighi et al., 2005); a true motor flash-lag would require that both the moving target and the flashed object involved motor activity. Nijhawan and Kirschfeld suggested visual flash-lag and motor flash-lag resulted from a common mechanism involving forward models in the motor system that compensated for neural processing delays.

Alais and Burr (2003) presented a moving target consisting of an auditory frequency sweep and a flashed object consisting of a brief tone, and a flash-lag effect occurred. This finding is consistent with previous findings of forward displacement of the initial (Hubbard & Ruppel, 2013) or final (Johnston & Jones, 2006) pitch of an auditory target changing in frequency. Alais and Burr also presented a constant frequency translating across space and a brief static sound, and a flash-lag effect occurred. This finding is consistent with previous findings of forward displacement of a moving sound source in spatial hearing (Getzmann, 2005). Alais and Burr then combined an auditory translating stimulus with a flashed visual stimulus or a visual translating stimulus with a flashed auditory stimulus. Participants judged whether the spatial position of the flashed stimulus was ahead of or behind the spatially translating stimulus. Flash-lag effects resulting from cross-modal stimuli were smaller than if the moving target and the flashed object were both auditory, but larger than if the moving target and the flashed object were both visual. Alais and Burr argued cross-modal flash-lag effects were inconsistent with differential latency theory; latencies for auditory stimuli are shorter than latencies for visual stimuli, and so differential latency theory predicts a flash-lead effect in the auditory-flash/visual-motion condition (see also Arrighi et al., 2005; Krekelberg, 2003).

Vroomen and de Gelder (2004) presented a visual moving target and a visual flashed object. Presentation of the flashed object on some trials was accompanied by an auditory tone synchronized with the flashed object. A flash-lag effect occurred regardless of whether a tone was presented, but if a tone was presented, magnitude and variability of the flash-lag effect decreased. Vroomen and de Gelder suggested presentation of the tone facilitated processing of the flashed object, and this reduced the difference between processing latencies for the moving target and the flashed object. Vroomen and de Gelder then presented the tone slightly before, at the same time as, or slightly after the flashed object was presented. If the tone was presented before or after the flashed object, the flash-lag effect decreased or increased, respectively. Stekelenburg and Vroomen (2005) presented similar stimuli and recorded event-related potentials. A sound presented before or after the flashed object decreased or increased, respectively, the flash-lag effect and amplitude of the N1 component of the event-related potential. Timing of the sound relative to the flashed object did not influence latency of the N1. Overall, the flash-lag effect is not limited to visual or visuospatial processes or representations, but occurs in multiple modalities, cross-modally, and is modulated by cross-modal information.

Low Level or High Level?

The flash-lag effect does not occur before perceptual grouping (Watanabe, 2004; Watanabe et al., 2001) or pattern recognition (Linares & López-Moliner, 2007), and this suggests the flash-lag effect results from relatively high-level processes. Influences of conceptual knowledge (Nagai et al., 2010; Noguchi & Kakigi, 2008), beliefs regarding control of the target (Ichikawa & Masakura, 2006, 2010), predictability of the flashed object (Baldo & Namba, 2002; Vreven & Verghese, 2005), and perceptual set (Gauch & Kerzel, 2009) also suggest high-level processes contribute to the flash-lag effect. Nieman et al. (2006) reported a flash-lag effect in the absence of luminance boundaries (with random dot stereograms), and this would require cortical processes sensitive to binocular disparities and be consistent with high-level processes. Neurons in cat V1 (Jancke, Erlhagen, Schöner, & Dinse, 2004) and in monkey V4 (Sundberg, Fallah, & Reynolds, 2006) respond more quickly to moving targets than to flashed objects, and transcranial magnetic stimulation of human MT+, but not V1/V2, reduces the flash-lag effect (Maus et al., 2013). A temporal advantage for moving stimuli relative to stationary stimuli occurs in cat LGN (Orban, Hoffman, & Duysens, 1985), but this advantage is only 15 ms, and so is smaller than the 45- to 80-ms difference in a typical visual flash-lag effect.

Arnold, Durant, and Johnston (2003) examined the flash-lag effect relative to a perceptual phenomenon known to be cortical in origin: the tilt illusion (a vertical grating is perceived to tilt in the direction opposite to the tilt of a surrounding grating; e.g., Schwartz, Sejnowski, & Dayan, 2009). Participants viewed a circular stimulus divided into an annulus and an inner disk. The annulus consisted of a grating that rotated clockwise or counterclockwise; during most of the trial, the inner disk consisted of a solid gray stimulus, but a test stimulus consisting of a stationary vertical grating was briefly flashed during each trial. The test grating could be flashed before the rotating grating reached alignment, at the moment of alignment, or after the rotating grating passed alignment. If a flash-lag effect occurred, then a tilt illusion should not have occurred if the test grating was presented before the rotating annulus reached alignment; however, a robust tilt illusion occurred. Indeed, the strength of the tilt illusion at different latencies of test presentation did not differ from previous reports of the tilt illusion with static targets. Arnold et al. suggested it is unlikely the flash-lag effect arises before the tilt illusion, and this suggestion is consistent with the notion that the flash-lag effect does not result from low-level processes (cf. Fukiage & Murakami, 2010).

A visual flash-lag effect can be modified by presentation of an auditory tone (Vroomen & de Gelder, 2004), a flash-lag effect occurs if the moving target is visual and the flashed object is auditory (Alais & Burr, 2003; Arrighi et al., 2005), and a flash-lag effect occurs if the moving target is a participant's (nonvisible) hand and the flashed object is visual (Nijhawan & Kirschfeld, 2003). Findings of such cross-modal contributions to the flash-lag effect are not consistent with the hypothesis that the flash-lag effect results from low-level mechanisms, as the flash-lag effect in such cases involves cross-modal or multisensory processes that presumably occur at a higher level. Whitney and Cavanagh (2000) reported a flash-lag effect occurred with dichoptic displays in which moving targets were presented to one eye and flashed objects were presented to the other eye, and coupled with findings of a flash-lag effect with random dot stereograms (Harris et al., 2006; Nieman et al., 2006), this suggests the flash-lag effect involves processing at or beyond the level of binocularly sensitive neurons. Krekelberg and Lappe (2001) suggested the flash-lag effect is unlikely to be understood in terms of low-level processing and that the origin of the flash-lag effect is likely to be beyond the point of integration of retinal and extraretinal signals (cf. Cai et al., 2000; Schlag et al., 2000).

Although findings from most studies suggest the flash-lag effect involves high-level processes, a few exceptions have been reported. Activation patterns of retinal ganglion cells can appear to extrapolate a moving target's trajectory (for review, see Gollisch & Meister, 2010), although whether this extrapolation matches the magnitude of the flash-lag effect is not clear. Neurons in monkey V5/MT respond more rapidly to transient (flashed) stimuli than to moving stimuli (Raiguel, Lagae, Gulyàs, & Orban, 1989). Anstis (2007, 2010) presented participants with a "chopsticks illusion" in which a horizontal bar and an intersecting vertical bar moved in different circular motions. Participants adjusted the perceived position of a flashed dot to coincide with the moving intersection of the two bars. A flash-lag effect occurred. Anstis (2010) presented a reversed phi stimulus consisting of radii that rotated around a common center and alternated between black and white. A flashed object consisting of arrows at the 12 and 6 o'clock positions was presented, and participants judged whether the arrows aligned with a radius. A flash-lag effect occurred. Anstis argued responses to a flashed object with chopsticks illusion stimuli or reversed phi stimuli were driven by the physical, rather than the perceived, direction of motion. Overall, it appears that high-level processes and low-level processes both contribute to the flash-lag effect (cf. Erlhagen, 2003; Jancke & Erlhagen, 2010).

Flash-Drag and Flash-Lead?

Investigation of the flash-lag effect revealed other types of flash mislocalization, but it is not clear why these rather than a flash-lag effect sometimes occur. One such type of flash mislocalization is the flash-drag effect, in which perceived position of a briefly flashed stimulus is shifted in the direction of nearby motion (cf. Hubbard, 2008; Shi & de'Sperati, 2008). Hine, White, and Chappell (2003) had participants judge the location of a moving visual stimulus relative to a stationary visual stimulus when a click ("auditory flash") occurred, and they reported a flash-drag effect. Fukiage, Whitney, and Murakami (2011) presented a phase-shifted grating at a different random location every 125 ms, and they reported a larger flash-drag effect if the flashed object was presented 50 to 150 ms before the grating changed location; however, Murakami (2001b) previously reported a robust flash-lag effect with a randomly moving stimulus and a flashed object, and the reason for the discrepancy between Fukiage et al. and Murakami's earlier article is not clear. Murai and Murakami (2012) reported the flash-drag effect started to increase about 100 ms prior to onset of target motion and decreased 100 ms prior to disappearance of a moving target. Eagleman and Sejnowski (2007) suggested the flash-lag effect and the flash-drag effect worked in opposite directions and that an increased flash-drag effect diluted the flash-lag effect.

A second such type of flash mislocalization is the flash-lead effect, in which a flashed object leads rather than lags a moving target. Purushothaman et al. (1998) and Öğmen et al. (2004) reported that increasing luminance of a flashed object resulted in a flash-lead effect. Hommuk et al. (2008) reported that precuing a flashed object resulted in a flash-lead effect if the flashed object was presented within the first 250 ms of the moving target, and Baldo, Kihara, et al. (2002) reported a flash-lead effect if the flashed object was visible during target motion and vanished at target offset. Arnold et al. (2009) reported a flash-lead effect if contrast between stimuli decreased. Whitney and Cavanagh (2000) presented flashed objects on either side of a rotating target, and participants judged whether the flashes were aligned. Judgments were displaced in the direction of target motion but were not influenced by eccentricity. Durant and Johnston (2004) presented two gratings, one of which drifted upward and one of which drifted downward. Two flashes, one on either side of the gratings, were presented. Participants judged alignment of the flashes. Judgments were displaced in the direction of motion of the nearest grating, and perceived misalignment decreased with increases in eccentricity. However, in both the flash-drag and flash-lead effects, the flashed object is shifted in the direction of target motion, and so whether these are actually different effects is not clear.

Temporal Order Judgment?

The relationship between the flash-lag effect and temporal order judgment of the moving target and flashed object is critical for theories of the flash-lag effect involving differential latencies for moving targets and flashed objects. Nijhawan et al. (2004) presented a flash-initiated display and varied whether the flashed object appeared slightly before, at the same time as, or slightly after the moving target appeared. Participants judged which stimulus appeared first. Nijhawan et al. suggested latency for perceiving a flashed object was shorter than latency for perceiving a moving target (cf. Raiguel et al., 1989), and although data figures were presented, statistical tests supporting this claim were not reported. Chappell et al. (2006) had participants judge whether a flashed object was presented before or after target motion onset, reversal of target direction, or target motion offset. A point of subjective simultaneity for each condition was calculated, but none of these differed from zero. Cravo and Baldo (2008) presented moving targets and flashed objects in opposite hemifields, and temporal onset asynchrony of moving targets and flashed objects varied. The mean point of subjective simultaneity did not differ from zero. All these findings challenge the claim of differential latency theory that the flash-lag effect results from shorter latencies in processing moving targets than in processing flashed objects.

Fröhlich Effect?

The perceived initial (onset) position of a moving target is displaced forward from the actual initial position of that target, and this is referred to as the *Fröhlich effect* (Fröhlich, 1923; for review, see Kerzel, 2010). Forward displacement of the moving target in the Fröhlich effect appears similar to forward displacement of the moving target in a flash-initiated display; indeed, if the flashed object is not considered, then displacement of initial target position in a flash-initiated display would seem to be nothing more than a Fröhlich effect. Given this, a flash-lag effect in a flash-initiated display might be a Fröhlich effect in which perceived initial target position is measured relative to an external stimulus (the flashed object) rather than relative to the actual initial target position. Several variables have similar influences on the flash-lag effect and Fröhlich effect (see also Kreegipuu & Allik, 2003). The flash-lag effect (Wojtach et al., 2008) and Fröhlich effect (Müsseler & Aschersleben, 1998) increase with increases in target velocity. The flash-lag effect (Öğmen et al., 2004) and Fröhlich effect (Carbone & Ansorge, 2008) are influenced by luminosity. The flash-lag effect (Namba & Baldo, 2004) and Fröhlich effect (Müsseler & Aschersleben, 1998) are decreased by a valid cue prior to stimulus presentation. However, the flash-lag effect (Baldo, Kihara, et al., 2002; Lappe & Krekelberg, 1998) but not Fröhlich effect (Müsseler & Aschersleben, 1998) increases with increases in eccentricity.

Some mechanisms proposed for the flash-lag effect are similar to mechanisms proposed for the Fröhlich effect (e.g., the time required to shift attention to the onset position of the flashed object, Baldo & Klein, 1995, or moving target, Müsseler & Aschersleben, 1998). Kirschfeld and Kammer (1999) and Eagleman and Sejnowski (2007) suggested the same mechanisms underlie the flash-lag effect and the Fröhlich effect. However, Kreegipuu and Allik (2003) reported dissociation between the flash-lag effect and Fröhlich effect if a flashed object was presented near the time a previously stationary target began moving and participants estimated whether the flashed object appeared (a) before or after motion began or (b) to the left or right of where motion began. It is not clear, though, whether this reflected dissociation of (a) spatial and temporal components of the flash-lag effect or (b) the flash-lag effect and Fröhlich effect. Whitney and Cavanagh (2000) reported presentation of a cue decreased the Fröhlich effect but not the flash-lag effect; however, Brenner and Smeets (2000), Namba and Baldo (2004), and Vreven and Verghese (2005) reported presentation of a cue decreased the flash-lag effect. Chappell et al. (2006) reported the flash-lag effect was larger than the Fröhlich effect; they suggested temporal integration might underlie the flash-lag effect and the Fröhlich effect but that the window of integration began later in the flash-lag effect than in the Fröhlich effect.

Representational Momentum?

The perceived final (offset) position of a moving target is displaced forward from the actual final position of that target, and this is referred to as *representational momentum* (Freyd & Finke, 1984; for review, see Hubbard, 2005). Many studies in the flash-lag effect literature suggest perceived position of the moving target is displaced forward, and this seems equivalent to representational momentum. However, literature on the flash-lag effect usually does not consider representational momentum or else dismisses representational momentum based on incomplete or incorrect information.[7] In a notable exception, Munger and Owens (2004) presented participants with a rotating bar and a flashed square, and they found (a) a flash-lag effect occurred with flash-midpoint but not flash-terminated displays and (b) robust representational momentum in a flash-terminated display (cf. Müsseler et al., 2002) or if a flashed object was not presented. Thus, for the same moving target, typical representational momentum findings and typical flash-lag effect findings were obtained (see also Shi & de'Sperati, 2008). Munger and Owens suggested robust representational momentum in a flash-terminated display might reflect a contribution of a flash-lag effect: If a flashed object aligned with the target is perceived to be behind the target, participants might be even more likely to accept a probe in front of the target's actual location as reflecting the target's actual location.

Table 3 lists similarities of representational momentum and the flash-lag effect. The number of similarities suggests there might be a common mechanism underlying representational momentum and the flash-lag effect, or more radically, that the flash-lag effect is an example of representational momentum in which represented target location is measured relative to an external stimulus (the flashed object) rather than relative to actual target location. However, lack of a flash-lag effect in flash-terminated displays initially appears inconsistent with representational momentum. Hubbard (2008) reported displacement in the direction of target motion for a stationary object briefly presented near the end of target motion, and this displacement was not significantly different from displacement of the target; thus, it could be speculated that relative locations of a briefly presented object and a moving target were veridical (i.e., a flash-lag effect did not occur) even though absolute locations of that briefly presented object and moving target were displaced forward (i.e., representational momentum occurred). Also, effects of oculomotor behavior on representational momentum and on the flash-lag effect for continuous motion differ (e.g., pursuit eye movements increase representational momentum, Kerzel, 2000, but decrease the flash-lag effect, Nijhawan, 2001), but such differences do not rule out a common higher level mechanism (cf. differences in oculomotor behavior on representational momentum with continuous or implied motion; Hubbard, 2005, 2006b, 2010).

The flash-lag effect and representational momentum both involve forward displacement of a moving target, and the role, if any, the flashed object plays in displacement of the moving target in the flash-lag effect is not clear. As forward displacement in representational momentum occurs without reference to an external stimulus, representational momentum offers a more parsimonious explanation for many findings in flash-lag effect literature. In arguing for motion extrapolation and against differential latencies, Nijhawan et al. (2004, p. 278) stated, "A newer interpretation of a given phenomenon can be accepted over and above an existing one only if the newer interpretation is conceptually simpler (requires fewer assumptions) and/or is capable of explaining a wider class of empirical findings." Representational momentum is conceptually simpler (involving one stimulus rather than the relationship between two stimuli) and accounts for a wider class of empirical findings (displacement of moving targets when a flashed object is presented and when a flashed object is not presented). Many cases of what has been identified as a flash-lag effect might result from a combination of representational momentum of the moving target and less (no) displacement of the flashed object (cf. Shi & de'Sperati, 2008); assessment of displacement of the moving target by reference to an external (flashed) object rather than to the actual target location might just be a different way to measure representational momentum.

Backward Referral?

Libet (1985; Libet, Gleason, Wright, & Pearl, 1983; Libet, Wright, & Gleason, 1982) asked participants to move a finger at a time of their choosing, and participants viewed a clock face in which a rotating hand was displayed. When participants made a

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[7] For example, Kanai and Verstraten (2006, p. 453) stated, "When a flash physically coincides with a continually moving object, the position of that moving object is perceived to be ahead of the flash. This visual phenomenon is called the flash-lag effect," and representational momentum was not identified by name, nor were any articles on representational momentum cited. Maus and Nijhawan (2009, p. 611) stated, "One hypothesis, termed *motion extrapolation*, states that moving objects are spatially shifted forward to counteract the influence of neural delays in the visual pathways on the perceived position of moving objects." Nijhawan et al. (2004, p. 296) stated, "The flash-lag phenomenon is: the position in which a moving item (visual object or limb) is sensed is not where the item was in the recent past, but closer to where the item probably is." These statements are quite similar to statements characterizing representational momentum and the purpose of representational momentum. For example, Finke et al. (1986, p. 176; see also Freyd, 1987) stated that representational momentum is useful for "anticipating the future positions of objects . . . [and] contributes to regulation and control of bodily movements," and Hubbard (2005, p. 847) suggested representational momentum and related types of displacement "adjusts the representation of a target to reflect where that target would (most likely) be at the moment an immediate motor response from the observer would reach the target" (see also Hubbard, 1995, 2006a, 2006b, and the discussion "Toward a Computational Theory of Displacement" in Hubbard, 2005). Although Maus and Nijhawan (2006, p. 4375) admitted "in representational momentum observers perceive the final position of a moving object as shifted in the direction of motion," their investigation of forward displacement of a moving target made no other reference to or contact with the representational momentum literature, even though they investigated effects (e.g., velocity) well investigated within the representational momentum literature. Finally, Maus and Nijhawan (2009, p. 612) stated, "Although representational momentum . . . states that moving objects are remembered to disappear beyond their final position, these findings can be explained by cognitive processes or eye movements and visual persistence," but this is not entirely correct. Although Maus and Nijhawan's statement might have been aimed at representational momentum that arises from smooth target motion, representational momentum also arises from implied motion and with single frozen-action photographs, and so cannot be explained by eye movements or visual persistence (for discussion, see Hubbard, 2005, 2006b, 2010). Furthermore, it is unclear why contributions of cognitive processes to representational momentum are problematic, as ample evidence suggests high-level (cognitive) processes contribute to the flash-lag effect (e.g., voluntary attention, Namba & Baldo, 2004; Shioiri et al., 2010; perceptual organization, Watanabe et al., 2001; conceptual knowledge, Nagai et al., 2010; Noguchi & Kakigi, 2008).

Table 3
Similarities Between Representational Momentum and the Flash-Lag Effect

Characteristic	Representational momentum	Flash-lag effect
Increases with increases in target velocity	Hubbard & Bharucha (1988); Hubbard (1990)	Krekelberg & Lappe (1999); Nijhawan (1994); Wojtach et al. (2008)
Increases when attention is divided	Hayes & Freyd (2002)	Sarich et al. (2007); Shioiri et al. (2010)
Is disrupted if continuity of identity of moving target is disrupted	Kelly & Freyd (1987)	Moore & Enns (2004)
Larger effects in the left visual field	Halpern & Kelly (1993); White et al. (1993)	Kanai et al. (2004)
Participation of cortical area MT/MST	Kourtzi & Kanwisher (2000); Senior et al. (2000, 2002)	Maus et al. (2013)
Decreases if preceded by a valid cue[a]	Hubbard et al. (2009)	Namba & Baldo (2004); Shioiri et al. (2010); Vreven & Verghese (2005)
Is influenced by conceptual knowledge of the target	Reed & Vinson (1996); Vinson & Reed (2002)	Nagai et al. (2010); Noguchi & Kakigi (2008)
Decreases if observers have control over the stimulus[b]	Jordan & Knoblich (2004)	López-Moliner & Linares (2006)
Is influenced by attributions regarding source of target motion	Hubbard (2013); Hubbard et al. (2001)	Ichikawa & Masakura (2006, 2010)
Increases with motion toward landmark/fixation	Hubbard & Ruppel (1999)	Brenner et al. (2006); Kanai et al. (2004); Shi & Nijhawan (2008)

[a] The data on effects of cuing are mixed. Brenner and Smeets (2000), Hommuk et al. (2008), Namba and Baldo (2004), Shioiri et al. (2010), and Vreven and Verghese (2005) all found an effect of cuing on the flash-lag effect, but Khurana et al. (2000) did not find an effect of cuing on the flash-lag effect. On balance, the evidence suggests there is an effect of cuing. [b] If the position of the flash is used as the marker in judging location of the target, then the decline in the flash-lag effect when participants control the flashed object is similar to the decline in representational momentum if participants control the moving target. However, control of the moving target has been shown to result in a larger (Scocchia et al., 2009) and smaller (Ichikawa & Masakura, 2006) flash-lag effect, and the relationship between control of the target and the size of the flash-lag effect is not clear.

decision to move a finger, they noted the time on the clock face. Libet also collected simultaneous electroencephalograms and examined the readiness potential. The average reported time of the decision to move was 200 ms prior to movement, but the readiness potential appeared up to 500 ms prior to movement. In one interpretation, a decision to move was made up to 300 ms before participants had a conscious experience of making a decision to move, and the time of the subsequent conscious intent was then "adjusted" backward in time to reflect the time of the unconscious decision (cf. postdiction). Libet referred to this as *backward referral*. Van de Grind (2002) and Klein (2002) suggested apparent backward referral reflected a flash-lag effect: Participants reported the position of a rapidly rotating hand on a clock face (the moving target) at the moment of a brief and transient event (the decision to move). Similarly, Joordens, Spalek, Razmy, and van Duijn (2004) suggested apparent backward referral reflected representational momentum for the clock hand. In explanations of backward referral based on the flash-lag effect or representational momentum, the perceived position of the hand on the clock face is displaced forward, and so the decision to move appeared to occur at a later time than it actually did.

Anisotropic Distortion?

Watanabe and Yokoi (2006, 2007) suggested the flash-lag effect reflected anisotropic distortion of two-dimensional spatial representation; specifically, the perceived position of the flashed object was displaced toward a point of convergence that followed the moving target at a fixed distance. Anisotropic representation of space is consistent with differences in the flash-lag effect as a function of perceptual grouping in Watanabe et al. (2001; Watanabe, 2004), a larger flash-lag effect if targets moved toward than away from fixation (Shi & Nijhawan, 2008), and a larger flash-lag effect at the onset than at the offset of a moving flashed object (Bachmann & Kalev, 1997). Kanai et al. (2004) reported a larger flash-lag effect for targets in the left than in the right visual field and for targets in the upper than in the lower visual field, and Shi and Nijhawan (2008) reported a larger effect of direction (toward or away from fixation) if motion was in the right than in the left visual field. It is not clear if anisotropy of visual space is consistent with a flash-lag effect involving nonspatial visual (e.g., Sheth et al., 2000), auditory (Alais & Burr, 2003), or motor (Nijhawan & Kirschfeld, 2003) stimuli, unless similar anisotropies occur in representation of nonspatial or nonvisual stimuli. Whether the flash-lag effect causes or results from these anisotropic distortions is not clear.

Flag Errors in Football?

Baldo, Ranvaud, and Morya (2002) suggested the flash-lag effect might contribute to a bias toward an offsides flag (i.e., an offsides penalty) in football (referred to as *soccer* in North America). In an offside situation, the attacker receiving the ball is running toward the opponent's goal and is equivalent to the moving target in a flash-lag effect. The passing of the ball is a transient event equivalent to the flashed object in a flash-lag effect. The attacker is therefore perceived to be ahead of his actual position when the ball is passed, and so an offsides flag is more likely. Gilis, Helsen, Catteeuw, and Wagemans (2008) found Fédération Internationale de Football Association and Belgium Association assistant referees were more likely to raise an offsides flag in ambiguous situations, and they suggested this bias was due to a flash-lag effect. Gilis et al. also pointed out that forward displacement of the attacker is consistent with representational momentum and that it is not clear whether bias toward an offsides flag is due to a flash-lag effect or to representational momentum. However, given that position of the attacker is judged relative to an external transient stimulus (the passed ball), an explanation based on the flash-lag effect might be more appropriate, although it is possible there is (also) representational momentum for the position of the attacker.

Catteeuw, Helsen, Gilis, van Roie, and Wagemans (2009) suggested experienced assistant referees partially compensated for the flash-lag effect. Catteeuw, Gilis, Wagemans, and Helsen (2010) reported a bias toward an offsides flag consistent with the flash-lag effect in less successful assistant referees, and they reported training and feedback improved accuracy in play calling but not accuracy in memory for player positions. The improved accuracy in play calling suggests the flash-lag effect might be influenced by experience or expertise. Catteeuw, Gilis, Jaspers, Wagemans, and Helsen (2010) reported simulations and computer animations were equally effective in training to compensate for the flash-lag effect. In such training studies, it would have been useful to examine whether the flash-lag effect (and perhaps representational momentum) also decreased on more traditional measures or whether learning was more stimulus specific, but such comparisons await future studies. Experimental design and analysis in Catteeuw, Gilis, Jaspers, et al. were actually more consistent with measures of representational momentum (cf. Thornton & Hayes, 2004) than with measures of the flash-lag effect, and it is possible displacement in Catteeuw, Gilis, Jaspers, et al. was due to representational momentum rather than to a flash-lag effect (cf. Gilis et al., 2008).

Part 3: Theories of the Flash-Lag Effect

Despite many years of study and debate, there is little consensus regarding potential mechanisms of the flash-lag effect. Theories considered here include (a) motion extrapolation, (b) attention shift, (c) visible persistence, (d) attention and metacontrast, (e) differential latency, (f) temporal integration, (g) postdiction, (h) temporal sampling, (i) perceptual acceleration, (j) frame of reference, and (k) misbinding. The major theories and evidence inconsistent with each of the major theories are summarized in Table 4.

Motion Extrapolation

Nijhawan (1994) suggested the flash-lag effect occurs because the visual system extrapolates the trajectory of a moving object to compensate for delays in perception due to neural processing times (cf. representational momentum occurs because of “a natural tendency to mentally extrapolate implied motion into the future”; Finke, Freyd, & Shyi, 1986, p. 176). Without such compensation, perceived position of a target would lag actual position. This extrapolation is based on previous motion of the target and biases perceived position forward to correspond to the target’s position in real time. The flashed object has no such history, and so it is not extrapolated. As a result, the neural delay in processing the flashed object results in the flashed object appearing to lag the forward-extrapolated moving target. Effects of target velocity (Nijhawan, 1994) and spatial facilitation by a nearby stimulus (Maiche et al.,

Table 4
Major Theories of the Flash-Lag Effect

Theory	Explanation of flash-lag effect	Inconsistent evidence
Motion extrapolation	Trajectory of a moving target is extrapolated forward.	Flash-lag effect occurs with random motion or unpredictable changes in direction or velocity, presence of flash-lag effect in flash-initiated displays, lack of flash-lag effect in flash-terminated displays
Attention shift	Shift of attention to the flashed object takes time, during which target continues to move.	Occurrence of flash-lag effect if moving target and flashed objects are interleaved, occurrence of flash-lag in effect in flash-initiated displays
Visual persistence	Visual persistence of a moving target is decreased because of processes that deblur that image.	Masking of flashed object does not influence flash-lag effect, effects of conceptual knowledge or perceptual grouping, auditory and cross-modal flash-lag effects, effects of control
Attention and metacontrast	Increased activation near leading edge of target and metacontrast masking of previous locations shifts the representation of the target forward.	Existence of flash-lag effect in flash-initiated displays, effects of conceptual knowledge or perceptual grouping, effects of control
Differential latency	Processing time for moving targets is less than for flashed objects, and by the time a flashed object enters awareness, the target is perceived as further along its trajectory.	Response times to moving targets or flashed objects do not differ, temporal order judgments suggest flashed objects might be processed faster than moving targets, effects of knowledge or perceptual grouping, auditory and cross-modal flash-lag effects, occurrence of flash-lag effect in flash-initiated displays, flash-lag effect with moving flashed objects
Postdiction	Appearance of the flashed object resets temporal integration, and representation of moving target position reflects an integration of target locations after the flashed object was presented.	Effect of preflash target behavior, effect of preflash cues, flash-lag effect with moving flashed objects
Perceptual acceleration	The initial stimuli in a perceptual stream are processed more slowly than subsequent stimuli. Moving target is presented later in its respective stream, and so it is processed more quickly.	Flash-lag effect in flash-initiated displays, lack of a flash-lag effect in flash-terminated displays

Note. Recent theories that have not been addressed or evaluated by researchers or laboratories other than those that initially proposed those theories (frame of reference, misbinding) are not included, as there is insufficient evidence to evaluate those theories.

2007) seem consistent with motion extrapolation theory. Nijhawan and colleagues have held to motion extrapolation theory (e.g., Maus & Nijhawan, 2008; Nijhawan, 2008; Nijhawan et al., 2004) despite numerous findings that appear inconsistent with this theory (e.g., Brenner & Smeets, 2000; Eagleman & Sejnowski, 2000b; Murakami, 2001b; Whitney, Murakami, & Cavanagh, 2000). Nijhawan (2008) now refers to motion extrapolation as *visual prediction*, which is curious in light of previous findings of a flash-lag effect with auditory stimuli and with motor stimuli.

Occurrence of a flash-lag effect with random motion (Murakami, 2001b), or with unpredictable changes in direction (Eagleman & Sejnowski, 2000b; Whitney, Cavanagh, & Murakami, 2000; Whitney & Murakami, 1998; Whitney, Murakami, & Cavanagh, 2000) or velocity (Brenner & Smeets, 2000), is inconsistent with motion extrapolation; motion of a target that moved randomly or unpredictability would not (by definition) be predictable and thus could not be extrapolated. Occurrence of a flash-lag effect in flash-initiated displays, and lack of a flash-lag effect in flash-terminated displays, are also problematic (e.g., Eagleman & Sejnowski, 2000b). Nijhawan et al. (2004; Nijhawan, 2008) suggested motion extrapolation in flash-initiated displays is based on motion of the target during the interval between presentation and perception of the flash: Because visual awareness of a flashed object does not occur for at least 100 ms after the flashed object is presented, the observer has at least 100 ms worth of trajectory to use in extrapolation. Nijhawan (2008; Maus & Nijhawan, 2006) suggested the lack of a flash-lag effect in flash-terminated displays reflects a correction-for-extrapolation based on offset transients. Lankheet and van de Grind (2010) suggested lack of a flash-lag effect in flash-terminated displays is not evidence against motion extrapolation in other types of displays; rather, motion just is not extrapolated if the target stops. However, this suggestion does not appear consistent with the large literature on representational momentum.

Attention Shift

Attention shift theory suggests the flash-lag effect occurs because attention is initially focused on the moving target, and when the flashed object is presented, attention is shifted to the flashed object. This shift takes time, and during this time, the target continues to move. By the time the flashed object is perceived, the target has already moved some distance, and so the flashed object is perceived as lagging the moving target. Effects of cuing (Namba & Baldo, 2004), target velocity (Nijhawan, 1994), and predictability of the flashed object (Baldo & Namba, 2002; Vreven & Verghese, 2005) are consistent with attention shift theory. Baldo and Klein (1995) suggested differences in allocation of attention caused the flash-lag effect, but Baldo and colleagues (Baldo, Kihara, et al., 2002; Baldo & Klein, 2010; Namba & Baldo, 2004) have subsequently taken a more conservative view that distribution and allocation of attention modulate, but probably do not cause, the flash-lag effect. The existence of a flash-lag effect if flashed objects and moving targets are interleaved (Khurana & Nijhawan, 1995), and the lack of an effect of spatial cuing and cue validity in Khurana et al. (2000; but see Baldo, Kihara, et al., 2002), are not consistent with attention shift theory. The existence of a flash-lag effect in flash-initiated displays (Nijhawan et al., 2004; Rizk et al., 2009; Sheth et al., 2000) is not consistent with attention shift theory, as there should be no difference between onset of the moving target and onset of the flashed object.

Visual Persistence

Visual persistence of a moving target might be decreased because of processes that deblur a changing image (Burr, 1980), whereas visual persistence of a flashed object would not be similarly decreased. Thus, visual persistence of a flashed object would last longer than visual persistence of a moving target (Efron, 1970; Hogben & Di Lollo, 1974), and this could result in a flashed object appearing to lag a moving target (Walker & Irion, 1982). Gauch and Kerzel (2009) suggested visual persistence, in conjunction with perceptual set, could account for most instances of the flash-lag effect. Whitney, Murakami, and Cavanagh (2000) presented a mask at the position of the flashed object immediately after the flashed object was presented. If visual persistence contributed to the flash-lag effect, then the mask should have influenced the flash-lag effect; however, the mask did not influence the flash-lag effect. Watanabe et al. (2001; Watanabe, 2004) suggested effects of perceptual grouping are not consistent with visual persistence. Visible persistence does not appear consistent with effects of conceptual knowledge on the flash-lag effect (Nagai et al., 2010; Noguchi & Kakigi, 2008) or with flash-lag effects involving auditory (Alais & Burr, 2003) or motor (Nijhawan & Kirschfeld, 2003) stimuli.

Attention and Metacontrast

Kirschfeld and Kammer (1999) suggested a moving target acts as a cue to its next position and metacontrast masking suppresses activation for previous positions of the moving target (cf. Erlhagen, 2003). Increased activation toward the leading edge of the target, coupled with suppression of activation for previous positions, could result in forward displacement of the moving target (see also Baldo & Caticha, 2005; Erlhagen & Jancke, 2004; Hubbard, 1995, 2005, 2006a, 2008; Jancke & Erlhagen, 2010; Müsseler et al., 2002). Although attention and metacontrast theory focused on the Fröhlich effect, Kirschfeld and Kammer discussed how such a framework could account for findings of Nijhawan (1994), and Kirschfeld (2006) discussed how such a framework could account for findings of Kanai et al. (2004). It is not initially clear how such a framework could account for the lack of a flash-lag effect in flash-terminated displays (as increased activation of the leading edge and suppression of previous positions should result in forward displacement of the target), but Kirschfeld suggested signals involving attention and metacontrast do not induce perception per se and so are not detected unless another stimulus is presented. It is not clear how such a framework could account for the flash-lag effect in flash-initiated displays (as there would not yet be increased activation of the leading edge or suppression of previous positions of the target).

Differential Latency

Metzger (1932) was among the first to suggest a flashed object aligned with a moving target appears to lag the moving target because the flashed object takes longer to be perceived. Differential latency theory suggests a moving target is processed more quickly than a stationary flashed object, and so the moving target reaches perceptual awareness more quickly. Thus, if a moving target and a flashed object were aligned, information regarding the moving target would reach perceptual awareness more quickly than information regarding the flashed object; as a result, when the flashed object entered awareness, the moving target would already be perceived as further along its trajectory (Öğmen et al., 2004; Purushothaman et al., 1998; Whitney & Murakami, 1998; Whitney, Murakami, & Cavanagh, 2000). A more developed form of differential latency theory is due to Öğmen et al. (2004; see also Kafaligönül, Patel, Öğmen, Bedell, & Purushothaman, 2010) and referred to as a *multichannel differential latency model*. This model suggests the (a) flashed object and moving target are processed by different but interacting neural systems (i.e., channels), (b) latency of each neural system depends upon intrinsic dynamic properties of that system and on attributes of the stimulus, and (c) computation of stimulus position and visibility are different processes with different dynamics (cf. Maus & Nijhawan, 2006, 2009).

Findings that response time to presentation of a flashed object does not differ from response time to presentation of a moving target (Chappell et al., 2006; Cravo & Baldo, 2008; Fouriezos et al., 2007), that a flashed object is processed more quickly than a moving target (Nijhawan et al., 2004; Raiguel et al., 1989), and that perceptual grouping (Watanabe, 2004; Watanabe et al., 2001) and semantic meaningfulness (Nagai et al., 2010; Noguchi & Kakigi, 2008) influence the flash-lag effect are not consistent with differential latency theory. Finding a flash-lag effect with sequences of letters (Bachmann et al., 2003) appears inconsistent with differential latency theory, as no perceived motion per se occurred. A flash-lag effect at the end of motion of a moving flashed object (e.g., Bachmann & Kalev, 1997) appears inconsistent with differential latency theory, because processing of the moving target and flashed object should both be facilitated. Becker et al. (2009) suggested use of a black annulus as a moving target and a white disk as a flashed object by many researchers is not consistent with differential latency theory, as the flashed object would exhibit greater luminance than the moving target and result in a flash-lead effect if mislocalization was due to differences in processing latencies. Differences in latencies cannot account for a flash-lag effect with visual–auditory cross-modal flash-lag stimuli (Alais & Burr, 2003; Arrighi et al., 2005).

Temporal Integration

Temporal integration theories, also referred to as *position integration* theories, of the flash-lag effect suggest that perceived position of a stimulus is based on an integration of the positions that stimulus occupies over some period of time. If positions of a moving target and a flashed object are compared, their relative positions are estimated by temporal averaging across persisting position signals for each stimulus (Krekelberg, 2001; Krekelberg & Lappe, 1999, 2000a, 2000b, 2001). For the flashed object, the averaged position is the same as its actual position. However, for the moving target, the averaged position is ahead of where the target was when the flashed object appeared, because the average includes not only the position of the target when the flashed object appeared but also subsequent positions of the target. Chappell et al. (2006) suggested temporal integration is consistent with the flash-lag effect and the Fröhlich effect. Rizk et al. (2009) suggested a flash-lag effect with sampled motion involves temporal integration (across "stations"). Shen et al. (2007) pointed out position integration theory predicts participants should not accurately perceive the reversal location of a moving target, and they found perceived reversal location occurred before actual reversal location (cf. Whitney, Murakami, & Cavanagh, 2000). Shen et al. suggested information regarding actual reversal location was potentially available but not integrated, and they rejected position integration theory.[8]

Postdiction

Postdiction theory of Eagleman and Sejnowski (2000b; Rao, Eagleman, & Sejnowski, 2001) is a special case of temporal integration. Eagleman and Sejnowski presented a moving target that after presentation of the flashed object continued in the same direction of motion, stopped, or reversed. A flash-lag effect occurred if the target continued in the same direction, but not if the target stopped, and if the target reversed, mislocalization was in the opposite direction (i.e., a flash-lead effect occurred). Preflash target behavior was the same across conditions, and Eagleman and Sejnowski argued the flash-lag effect depended on events following presentation of the flashed object and that the flash "reset" integration regarding target position. Use of information (i.e., target positions) presented after the flashed object to "adjust" perception of the target at the time the flashed object was presented was referred to as *postdiction* (cf. backward referral). Eagleman and Sejnowski suggested abrupt onset of a moving target acted like a flashed object, and so postdiction could also account for the Fröhlich effect. Eagleman and Sejnowski (2007) updated this approach to include other types of flash mislocalization, and this updated approach was referred to as a *motion-biasing model*. Brenner and Smeets (2000) and Rotman et al. (2005) similarly suggested target localization depended upon information available after presentation of the flashed object.

Krekelberg and Lappe (2000b) suggested temporal integration of motion signals from the target over a range of 500 ms can account for the observed data without a need to reset integration of motion signals and that without a reset, there is no need for postdiction. Whitney and Cavanagh (2000) suggested if a flashed object resets motion signals, then a moving target accompanied by a flashed object presented every 80 ms should be invisible along its entire trajectory, but such a result has not been reported. Postdic-

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[8] Roulston, Self, and Zeki (2006) also discussed a position integration theory of localization. In their experiments, they reported a moving target was displaced behind a stationary flashed object (a flash-lead effect) and that two moving targets that approached each other were displaced backward (which they referred to as *reverse-repmo*). These displacements are in the direction opposite to displacements typically obtained in studies on the flash-lag effect and in studies on representational momentum, and the reasons for these differences are not clear. One possible explanation involves the time course of displacement. Freyd and Johnson (1987) reported forward displacement peaked after a few hundred milliseconds and then decreased, and they attributed this pattern to two distinct processes: an initial forward extrapolation process that displaced represented location in the direction of target motion (representational momentum) and a subsequent memory averaging process that displaced represented location toward an average of the stimulus locations. Depending upon the latency of judgment in Roulston et al. (which was not reported), the apparent reverse-repmo might reflect this subsequent memory averaging. This remains an issue for further research.

tion theory suggests cues provided prior to presentation of the flashed object should not influence mislocalization, but effects of preflash cuing (e.g., Baldo, Kihara, et al., 2002; Namba & Baldo, 2004; Vreven & Verghese, 2005; but see Khurana et al., 2000; Whitney & Cavanagh, 2000) and other preflash information or experience (e.g., Chappell & Hine, 2004) have been reported. Patel, Öğmen, Bedell, and Sampath (2000) pointed out postdiction cannot account for a flash-lead effect. Eagleman and Sejnowski (2000a, 2000c) responded to these types of criticisms by suggesting reset did not necessarily disregard all preflash information; rather, the extent to which reset occurred was related to the amount of "surprise" in the stimulus, with greater surprise resulting in greater reset and less use of preflash information.

Temporal Sampling

Brenner and Smeets (2000) suggested the visual system has to select a moment at which to "sample" the moving target's position, and Brenner et al. (2006) suggested a moving target's position would be judged only if a specific moment of interest is specified. In the case of the flash-lag effect, this moment is specified by presentation of the flashed object, and the time required to initiate this sampling results in the actual sampled position corresponding to a later moment in time than when the flashed object was presented. Effects of cuing (e.g., Brenner & Smeets, 2000; Namba & Baldo, 2004; but see Khurana et al., 2000) are consistent with temporal sampling, as cuing would decrease the time required to initiate sampling and so decrease the flash-lag effect. The temporal sampling theory is similar to theories of Krekelberg and Lappe (2000a, 2000b) and Eagleman and Sejnowski (2000b), but sampling in Brenner and Smeets involves a single time or position, whereas sampling in Krekelberg and Lappe or in Eagleman and Sejnowski involves integrating multiple times or positions. Perhaps not surprisingly, many objections that apply to Krekelberg and Lappe's theory and to Eagleman and Sejnowski's theory also apply to temporal sampling theory (e.g., it is not clear how information presented prior to the flashed object could influence a sample of target motion from after the flashed object; e.g., Chappell & Hine, 2004).

Perceptual Acceleration

Bachmann et al. (2003) suggested a moving target and a flashed object in a flash-lag effect are in different perceptual streams. When a perceptual stream first appears, latency to explicit (conscious) perception of the initial stimuli in that stream is relatively long, but this latency decreases for subsequent stimuli. In other words, when the moving target stream first appears, the first few stimuli are processed relatively slowly, and subsequent stimuli are processed more quickly. This is referred to as *perceptual acceleration*. If a flashed object is presented in a second stream that begins after the onset of the moving target stream, that flashed object would be processed more slowly than a simultaneous stimulus in the moving target stream, and so a flash-lag effect occurs. This appears similar to differential latency theory, but differential latency theory specifies processing time as a function of stimulus type and not as a function of the amount of preceding stimuli. It is not clear whether perceptual acceleration might account for a flash-lag effect if the moving target and flashed object spatially overlapped (e.g., a flashed disk in a moving annulus). Perceptual acceleration theory does not seem consistent with a flash-initiated flash-lag effect (as processing speed is presumably the same for onset of the motion stream and for onset of the flashed stream; but see Bachmann, 2007, 2010, on perceptual "retouch") or consistent with the lack of a flash-lag effect in flash-terminated displays.

Frame of Reference

Becker et al. (2009) suggested the flash-lag effect arises because a saccade to the flashed object is programmed with egocentric encoding, whereas a saccade to the moving target is programmed relative to the location of the flashed object and with allocentric encoding. That is, the visual system first computes the location of the flashed object and, using that information as a reference or anchor, then computes the location of the moving target (cf. van de Grind, 2008; a moving target is a reference for a stationary object). By the time the visual system computes the location of the moving target, that target has moved beyond its location at the time the flashed object was presented. If the flashed object is not spatially localized (i.e., if the entire background flashed), then it is not used as a reference or anchor, and no flash-lag effect occurs. Thus, differences in encoding related to the frame of reference might account for mislocalization of the moving target. However, it seems possible that the sequence, rather than the encoding format, is more critical (i.e., in Becker et al., 2009, the flashed object is always encoded before the moving target is encoded).[9] Also, it is not clear whether differences between allocentric encoding and egocentric encoding could account for a flash-lag effect in nonspatial visual stimuli (e.g., Sheth et al., 2000) or nonvisual stimuli (e.g., Alais & Burr, 2003).

Misbinding

Gauch and Kerzel (2008a) reported a larger flash-lag effect occurred with a moving flashed object than with a stationary flashed object in flash-initiated or flash-terminated displays, but no differences in the flash-lag effect occurred as a function of whether the flashed object was moving or stationary in flash-midpoint displays. Thus, moving flashed objects produced a larger flash-lag effect if there was an abrupt change (e.g., onset, offset) in the target than if there was a continuous change in the target. This difference might involve differences between transient and sustained channels (cf. Maus & Nijhawan, 2006, 2009) that underlie processing of abrupt and continuous changes, respectively. Gauch and Kerzel suggested an abrupt change is (mis)bound to a continuous change that follows abrupt change, that onset of a moving target presents an abrupt change akin to a flash, and that asynchronous binding of abrupt and continuous changes produces a flash-lag effect. Alternatively, Sheth et al. (2000) suggested abrupt and continuous changes differ because of masking or priming from previous target presentations and because of attention shifts to the

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[9] An interesting test of this hypothesis would be to vary instructions regarding whether the position of the moving target should be compared to the position of the flashed object or the position of the flashed object should be compared to the position of the moving target, and to examine whether there is an effect of instruction on the flash-lag effect or eye movement patterns.

flashed object. A potential temporal misbinding was also addressed by van de Grind (2002), who suggested differences in latencies are experienced as differences in space rather than as differences in time.

Part 4: Summary and Conclusions

The flash-lag effect is robust and occurs with many variations in variables and stimuli. A flash-lag effect occurs with linear or curvilinear motion and if the flashed object spatially overlaps or is spatially separated from the moving target. A flash-lag effect occurs with flash-initiated or flash-midpoint displays, but does not usually occur with flash-terminated displays. A flash-lag effect occurs with continuous, sampled, or random motion, and the flashed object can be stationary or moving. The flash-lag effect occurs with changes in (a) spatial location, (b) luminance, (c) color, (d) spatial frequency, (e) pattern entropy, (f) binocular disparity, (g) auditory frequency, and (h) body position. The flash-lag effect occurs (a) with visual movement in the picture plane or in depth, (b) with auditory movement in frequency or in space, and (c) cross-modally with visual, auditory, and motor stimuli. The flash-lag effect is larger if (a) distance between the moving target and the flashed object is larger, (b) eccentricity of the moving target or flashed object is larger, (c) target motion is toward fixation, (d) target velocity is faster, (e) presentation of the flashed object is less predictable, (f) target position is less certain, (g) participants divide attention over multiple targets or tasks, (h) a nearby stimulus facilitates processing along the path of motion, (i) participants do not control presentation of the flashed object, (j) the flashed object is aligned with the leading edge of the moving target, (k) measured at the onset of flashed object motion, and (l) target size remains constant.

Several unresolved empirical issues remain. There are inconsistent findings regarding effects on the flash-lag effect of (a) preflash target behavior, (b) whether target motion is in the left or right visual field, (c) duration or distance of target motion, and (d) participant control of target motion. Dissociation of spatial aspects and temporal aspects of the flash-lag effect, and potential differences between types of stimulus displays (e.g., ease in distributing attention, susceptibility to masking), are not clear. Although most studies reported data consistent with or requiring high-level processes in the flash-lag effect, data from a few studies are consistent with operation of only low-level processes in the flash-lag effect. It is possible a flash-lag effect might be created in low-level structures by top-down processes based on previous experience or might arise in low-level structures and be modified by top-down connections if relevant information is available. The relationship of the flash-lag effect to representational momentum and to the Fröhlich effect is not clear, and it is possible that many examples of what has been considered a flash-lag effect are examples of representational momentum or a Fröhlich effect in which the represented position of a moving target is measured relative to the perceived position of an external stimulus (the flashed object) rather than relative to the actual final or initial position of that moving target, respectively. Also, principles specifying whether mislocalization related to a flashed object involves a perceived lag, lead, or drag are not clear.

Several theories of the flash-lag effect have been proposed, and many appear to suggest that the flash-lag effect results from a single mechanism. This has led to polarization among some researchers and to overly strong claims; indeed, titles of many articles bluntly state some single mechanism is or is not responsible for the flash-lag effect (e.g., Arrighi et al., 2005; Becker et al., 2009; Brenner & Smeets, 2000; Shen et al., 2007; Whitney, Murakami, & Cavanagh, 2000). There is significant disconfirming evidence for each of the major and well-known theories, and more recent theories have not yet been thoroughly tested. Some theories of the flash-lag effect seem to assume the correct level of explanation involves the relationship between the moving target and the flashed object, but as noted earlier, the flash-lag effect appears to arise from or be dependent upon more basic mislocalizations of the moving target and/or flashed object. An explanation that focuses on these more basic mislocalizations might be more appropriate. Also, it would not be surprising if multiple mechanisms contributed to the flash-lag effect (e.g., neither attention shifts nor differential latencies solely account for the flash-lag effect, but each appears capable of modulating the flash-lag effect). There is no reason why the proposed mechanisms must be mutually exclusive; rather, different mechanisms might contribute in different ways to different examples of the flash-lag effect.

In the flash-lag effect, a briefly presented object spatially aligned with a moving target is perceived to lag that target. This observation has attracted the attention and efforts of numerous researchers and laboratories, and research on the flash-lag effect has highlighted a fundamental question regarding perceptual, cognitive, and motor functioning: How do we compensate for neural processing times so that we can successfully interact with dynamic objects in real time? The answer to this question has significant theoretical and empirical implications, not just for understanding the flash-lag effect, but for understanding related phenomena such as the Fröhlich effect, representational momentum, backward referral, and anisotropic distortions in spatial representation. Moving stimuli are often more salient than stationary stimuli, and a representational system might be more useful if it was preferentially tuned to anticipate (and thus more accurately represent and respond to) behaviors of moving stimuli (cf. van de Grind, 2008; discussion of computational theory in Hubbard, 2005). The flash-lag effect and related mislocalizations might be one consequence of this tuning, and given that a moving stimulus is probably more likely to impact an observer than is a stationary stimulus, such a tuning would presumably be adaptive. Despite its apparent simplicity, the flash-lag effect reveals important properties of our representational system and provides insight into how our representational system is adapted to allow accurate perception of and interaction with stimuli in the environment.

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Received August 24, 2012
Revision received March 17, 2013
Accepted March 20, 2013 ■