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Latency differences and the flash-lag effect

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Abstract

The tendency for briefly flashed stimuli to appear to lag behind the spatial position of physically aligned moving stimuli is known as the flash-lag effect. Possibly the simplest explanation for this phenomenon is that transient stimuli are processed more slowly than moving stimuli. We tested this proposal using a task based upon the simultaneous tilt illusion. When an oriented stimulus is surrounded by another oriented stimulus, the inner stimulus can appear to be rotated away from the orientation of the surround. By flashing central static sinewave gratings at specific phases of an annular gratings rotation cycle, we were able to determine the temporal dependence of the tilt illusion. Our results suggest a small, ~20 ms, processing advantage for the rotating stimulus relative to the flashed stimulus. Such a small advantage, if due to differential latencies, is insufficient to account for the flash-lag effect.

Keywords: Flash-lag effect; Differential latency; Orientation; Tilt illusion

1. Introduction

When stationary objects are presented transiently in physical alignment with a moving stimulus, they do not appear aligned. Instead, the moving stimulus appears to be spatially advanced relative to the apparent position of the transient stimulus (Mackay, 1958; Mateeff & Hohnsbein, 1988; Nijhawan, 1994). This flash-lag effect could be readily explained if moving objects were processed more rapidly than stationary objects, and if these differences in processing speeds had a consequence in terms of perceptual experience (Mateeff & Hohnsbein, 1988; Murakami, 2001; Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney & Murakami, 1998; Whitney, Murakami, & Cavanagh, 2000).

It has been argued, in light of some recent findings, that differential latency is untenable as an explanation for the flash-lag (Eagleman & Sejnowski, 2002). When observers are required to make judgments concerning the relative timing of the offset of motion and the presentation of a flashed object, there is no systematic temporal advantage for either stimulus (Eagleman & Sejnowski, 2000). If moving stimuli were processed more rapidly than stationary stimuli one might expect the offset of motion to be detected more rapidly, and therefore before, a coincident transient stimulus.

When stimuli that suddenly appear and then move are compared with stimuli that transiently appear but remain stationary, the spatial positions of the transient stimuli appear to lag behind those of the moving stimuli (Eagleman & Sejnowski, 2000). In this situation, neither moving nor stationary stimuli might be expected to have a temporal advantage because both stimuli are transient in that they appear simultaneously. However, it is unclear if the proposed latency difference is between moving and stationary stimuli, or between sustained and transient stimuli. If the former, we might expect a temporal advantage for stimuli that suddenly appear and move as opposed to stimuli that suddenly appear but remain stationary (Krekelberg & Lappe, 2002).

Although some psychophysical evidence appears to refute the differential latency hypothesis, it gains support from other findings. For instance, the spatial positions of bars that are randomly displaced horizontally have been compared with flashed bars. In this situation, the spatial position of the flashed stimulus appears to be

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judged relative to the physical position of the moving stimuli at a variable point in time after the flash. This is consistent with the flash-lag effect arising as a consequence of stationary (or transient) stimuli being processed more slowly than moving (or sustained) stimuli, but the extent of the processing advantage is highly variable (Murakami, 2001).

The physiological evidence concerning the differential latency hypothesis is less ambiguous. It has been demonstrated that neurons within MT respond more rapidly to transient, as opposed to moving, stimuli (Raiguel, Lagae, Gulyas, & Orban, 1989). This would appear to preclude activity within this cortical region from serving as the neural basis of the flash-lag. In contrast, a small temporal advantage for moving, as opposed to stationary (or transient), stimuli has been observed within the LGN (Orban, Hoffmann, & Duysens, 1985). However, the extent of the advantage is approximately 15 ms and is therefore too small to provide a credible explanation for the flash-lag effect, which has variously been estimated as being 45–80 ms (Eagleman & Sejnowski, 2000; Purushothaman et al., 1998; Whitney & Murakami, 1998). Therefore, if differential latency plays a causal role within the flash-lag effect, the latency difference might arise as early as the LGN and become exaggerated within visual cortex. For this reason, it would be interesting to examine the flash-lag in relation to a perceptual phenomenon that is known to be cortical in origin.

The tilt illusion occurs when an oriented stimulus is surrounded by another oriented stimulus. As seen in Fig. 1(a) and (c), the perceived orientation of the central stimulus is typically distorted away from that of the surrounding stimulus (Gibson & Radner, 1937). As the tilt illusion necessitates a neural correlate that is sensitive to orientation, it must be cortical in origin.

Several factors suggest that the tilt illusion may be a useful tool for the investigation of the flash-lag effect. First, the tilt illusion has been ascribed to activity within the primary visual cortex (Clifford, Wenderoth, & Spehar, 2000; Coltheart, 1971). Second, the tilt illusion is finely tuned to angular difference. The direction of the tilt illusion reverses depending upon whether the surrounding stimulus is tilted to the left or to the right of the inner one, making it a sensitive measure of relative position. Just as significantly, no tilt illusion occurs when the central and surrounding stimuli are of the same orientation. The magnitude of the illusion is also tuned to the angular difference between the outer and inner stimuli, increasing in magnitude until they differ by ~15°, and thereafter diminishing. Third, the tilt illusion is exaggerated when test stimuli are flashed (Wenderoth

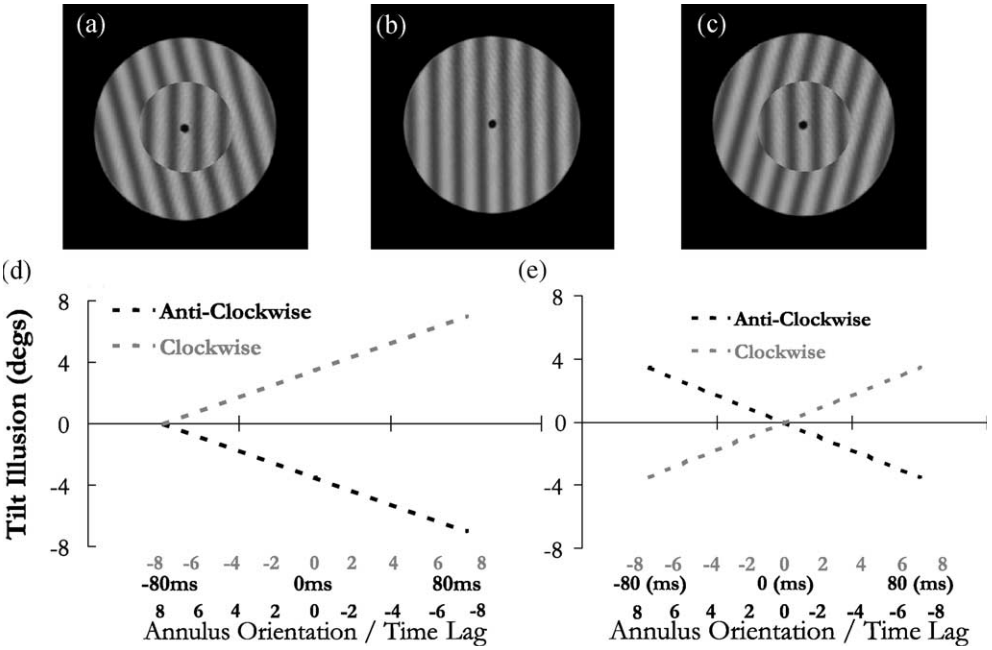

Fig. 1. (a–c) Examples of the tilt illusion. When the inner oriented stimulus is surrounded by an outer stimulus of a different orientation, it appears to be rotated away from the orientation of the outer stimulus. When the two stimuli are aligned, there is no distortion of perceived orientation. (d–e) Schematic simulations of the predicted consequences of flashing the inner stimulus at specific points of the rotation cycle of the outer stimulus, with (d) and without (e) a latency difference. If a 80 ms latency difference is assumed (d), no tilt illusion should be observed when the inner stimulus is flashed 80 ms before the outer stimulus becomes vertical. For c.w. rotation, this would mean that the inner stimulus should be flashed while the outer stimulus is slanted to the left (a). For c.c.w. rotation, the inner stimulus should be flashed when the outer stimulus is slanted to the right (c). If no latency difference exists (e), no tilt illusion should be expected if the inner stimulus is flashed in physical alignment with the outer stimulus (b) and tilt illusions, of opposite sign for c.w. and c.c.w. rotation, are expected if the inner stimulus is flashed 80 ms before the outer stimulus becomes vertical.

& van der Zwan, 1989). Therefore, far from being diminished, we could reasonably expect the tilt illusion to be exaggerated by the type of experimental procedure that is used to determine flash-lag effects.

If the tilt illusion is to be used to investigate the flash-lag effect some methodological difficulties must be considered. If we wish to examine the temporal and spatial tuning of the tilt illusion, we must first consider the fact that rotation alone can induce a perception of tilt (Hughes, Brecher, & Fishkin, 1972). As a consequence, we cannot simply compare the perceived orientation of a grating when it is flashed at a specific point in time (while surrounded by a rotating grating) with the perceived orientation of the same grating in the absence of rotation. Instead, we must compare the influence of rotation per se with the effects of flashing the inner annulus at specific spatial and temporal offsets.

Consideration of these points suggests a clear and testable prediction based upon the differential latency hypothesis. If, while viewing a rotating annulus grating, a central near vertical test grating is flashed approximately 80 ms before the annulus becomes vertical, no tilt illusion should occur because the test stimulus will not be processed until the rotating stimulus becomes vertical. In contrast, if there is no significant latency difference between flashed (stationary) and moving stimuli, no tilt illusion should occur when the test stimulus is flashed at the point in time when the rotating grating is physically vertical (refer to Fig. 1).

2. Methods

Sinusoidal gratings in a centre-surround configuration (refer to Fig. 1(a)–(c)) were displayed on a 19″ Sony Trinitron Multiscan 400 PS monitor, with a refresh rate of 100 Hz, driven by a VSG 2/5 (Cambridge Research Systems). Stimuli were viewed binocularly in darkened conditions from 57 cm with the head placed in a headrest. Twelve observers participated in the study, including the authors and nine observers who were naïve as to the purpose of the study. All observers had normal, or corrected to normal, visual acuity.

The sinusoidal gratings shown to observers had a spatial frequency of 2 cpd and were presented at 100% contrast. The annular grating rotated either clockwise (c.w.) or counter-clockwise (c.c.w.) at 0.5 Hz and had a diameter of 5°. In all trials, the test stimulus was shown once every 2 s for a period of 10 ms. As a consequence, during each trial the rotating annulus was at the same orientation on each occasion that the test stimulus was presented. A mean grey circle, of the same luminance as the background (39.6 cd/m^2), filled the central region whenever the test stimulus was not present. A central dark fixation point, with a diameter of 0.2°, was constantly displayed. On each individual trial, the observer indicated if the flashed test stimulus was slanted toward the left or right by pressing one of two response levers. The stimulus was displayed until a response was made.

The orientation of the flashed stimulus was manipulated according to the method of constant stimuli. During a run of trials, four functions were determined. Two of these were experimental functions determined with c.w. and c.c.w. rotations while the other two were baseline functions, again determined with both c.w. and c.c.w. rotations. Each of the four functions were determined by sampling 12 test stimulus orientations (ranging ±5.5° from vertical) on four occasions. The data for the experimental functions were determined from trials in which the test stimulus was flashed at a specific point of the outer stimulus' rotation cycle, and therefore from trials in which there was a specific difference between the orientations of the inner and outer annuli.

To determine the general influence of rotation, baseline functions were determined from trials in which the test stimulus was flashed at a random point within the rotation cycle of the outer stimulus. As the point within the rotation cycle at which the test stimulus appeared was randomized from trial to trial, the relative difference between the orientations of the inner and outer annuli differed in a random fashion from trial to trial. Two of these functions were determined to reflect the influences of c.w. and c.c.w. rotations per se. During a run of trials, the baseline and experimental trials were randomly interleaved.

Obtaining the four functions described above allowed us to differentiate the effects of a specific spatial and temporal offset (the experimental functions) from the average effects of rotation (the baseline functions). Psychometric functions were fitted to each of the four functions determined during each trial run, and the 50% points were taken as estimates of subjective vertical.

Six naïve observers each completed three runs of trials so that we could determine tilt illusions, for both c.w. and c.c.w. rotations, over three spatial and temporal offsets. During one of the runs of trials, the experimental functions were determined by flashing the test stimulus when the rotating grating was vertical. During the other two, the experimental functions were determined by flashing the test stimulus 80 ms before and after the rotating stimulus became vertical. At these points, the rotating grating was slanted ±7.2° from vertical, depending upon the direction of rotation. All possible orders of presentation were sampled to control for the possible influence of the order of presentation.

For two of the authors, the spatial and temporal tuning of the tilt illusion was also determined for a broad range of spatial and temporal offsets, from −80 ms (or ±7.2°) to +1000 ms (or ±90°). These tilt illusions were determined using the same methodology that was used with the naïve observers, with the exception that the authors completed four trial runs for each of the spatial and temporal offsets.

To demonstrate that a flash-lag effect could be observed under similar experimental conditions, estimates of the flash-lag were obtained for the authors and three naïve observers. During the trial runs used to obtain these estimates, test stimuli were flashed at one of 10 offsets. These ranged from 230 ms prior to until 130 ms after the point at which the rotating and flashed stimuli were aligned. Each offset was sampled 10 times for both c.w. and c.c.w. rotation. Observers were required to indicate if the rotating stimulus was tilted to the left or the right relative to the orientation of the flashed test stimulus. The orientation of the flashed stimulus was randomized within ±10° from vertical, so that the relative spatial offset was not signaled by the perceived orientation of the test stimulus. Psychometric functions were fitted to the two functions obtained and the 50% points were taken as estimates of the flash-lag. Analysis of these data was based upon the average value of the flash-lag effects obtained by each observer.

3. Results

Tilt illusions were calculated, for both c.w. and c.c.w. rotation, by subtracting the points of subjective vertical determined by the experimental trials within a run of trials from the points of subjective vertical determined by the corresponding baseline trials. Each run of trials therefore provided two estimates of the tilt illusion, one for c.w. rotation and one for c.c.w. As the six naïve observers each completed three runs of trials testing different spatial and temporal offsets, we were able to determine six estimates of the tilt illusion, for both c.w. and c.c.w. rotation, for each of the three spatial and

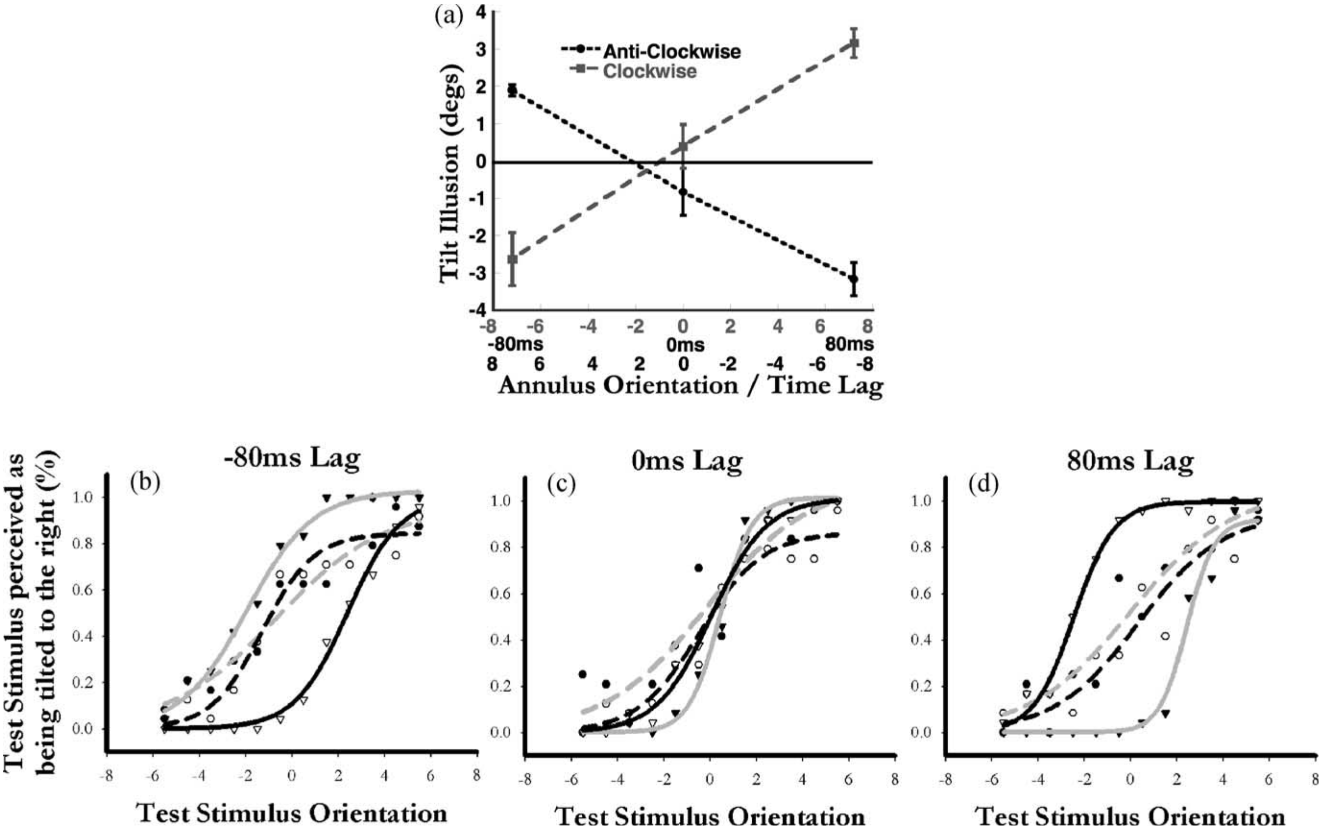

Fig. 2. Tilt illusions for six naïve observers as a function of the spatial and temporal offset between the centre and surround stimuli. Throughout the figure, data points and functions that were determined from trials with c.w. rotation are depicted in grey, c.c.w. in black. (a) The average size and direction of the tilt illusions observed, for both c.w. and c.c.w. rotations, at three different spatial and temporal offsets. Error bars depict ±1 standard error from the mean illusion observed in each condition. Significant tilt illusions are evident when the inner stimulus is flashed either 80 ms before or after the outer stimulus becomes vertical. The directions of the illusions in these conditions are reversed, suggesting that the point where no tilt illusion occurs rests between these two points. There is some evidence for tilt illusions when the inner stimulus is flashed in physical alignment with the outer stimulus. The small temporal advantage, if due to a latency difference, is not sufficient to explain the flash-lag effect. (b–d) XY scatter plots showing the percentage of times that all the naïve observers indicated that the test stimulus was tilted to the right for each of the test orientations. Triangular symbols depict data points determined during experimental trials, whereas the circular symbols depict data points determined during baseline trials. For illustrative purposes, psychometric functions have been fitted. Dotted functions depict baseline functions and solid lines depict experimental functions. The extent of the tilt illusions reported differs slightly from those suggested by these functions as the data was analysed on an individual basis, and not collectively.

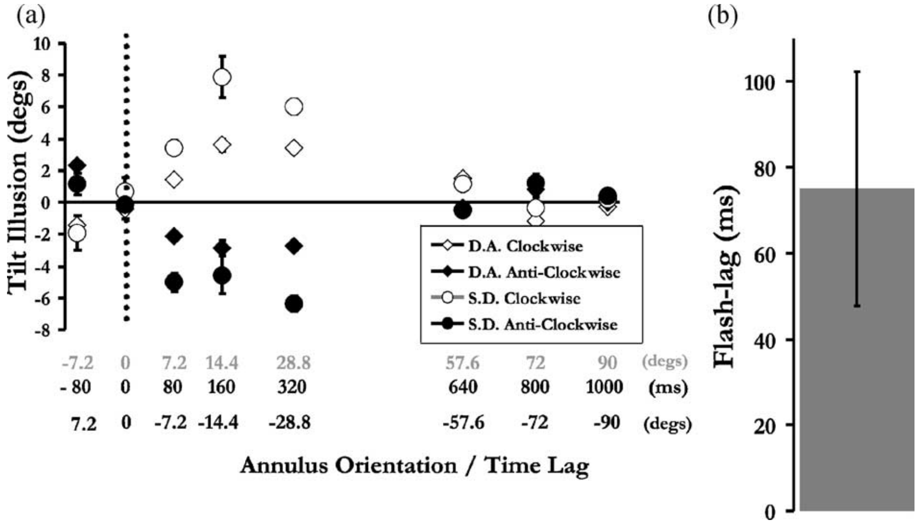

Fig. 3. (a) Perceptual consequences of flashing an inner oriented stimulus at specific points within the rotation cycle of an outer oriented stimulus for the authors D.A. (◇) and S.D. (○) under the same conditions used to determine the tilt illusions with the naïve observers. Each point on these functions reflects the average difference between eight estimates of subjective vertical determined during four runs of trials with either experimental or baseline trials. The average estimates are depicted by white (for test stimuli surrounded by c.c.w. rotation) and black (for c.w.) symbols. The error bars are calculated on the basis of the standard error between each group of four estimates, and represent ±1 standard error from the mean. (b) Estimate of the flash-lag effect obtained by requiring observers to indicate, when the inner stimulus was flashed, if the outer stimulus was slanted to the left or right relative to the orientation of the inner stimulus. In order for the two stimuli to look aligned, on average the inner stimulus had to be flashed ~75 ms before it became physically aligned with the rotating stimulus.

temporal offsets. The average of these values, and the standard error between them, are plotted in Fig. 2.

While there was some evidence for tilt illusions within each of the experimental conditions, the illusions were only statistically significant when the test stimuli were flashed 80 ms before or after the rotating stimulus became vertical. We determined the statistical significance of the illusions by calculating the difference between the tilt illusions obtained with c.w. and c.c.w. rotations for each of the naïve observers at each of the three spatial and temporal offsets. Doing so provided six difference scores, one for each observer, for each of the three spatial and temporal offsets. When the experimental test stimuli were flashed 80 ms before the rotating stimulus became vertical, the mean difference was 4.53° ($t_5 = 5.5$; $p = 0.003$). When the experimental test stimuli that were flashed when the rotating stimulus was vertical, the mean difference was −1.22° ($t_5 = -2.16$; $p = 0.083$). When the experimental test stimuli were flashed 80 ms after the rotating stimulus was vertical, the mean difference was −6.32° ($t_5 = 9.07$; $p < 0.001$).

To provide a more comprehensive description of the temporal tuning of the tilt illusion, tilt illusions were measured over a broad range of spatial and temporal offsets by two of the authors. As seen in Fig. 3(a), the direction of the illusion reverses sharply when the relative difference between the orientations of the inner and outer stimuli is reversed (±80 ms or 7.2°). No illusion is evident when the inner stimulus is presented while the rotating stimulus is vertical, and the illusion is greatest when the relative difference in orientation between the two stimuli is approximately 15° (+160 ms or 14.4°). Thereafter the extent of the illusion diminishes. However, a small reversal of the illusion is also apparent when there is a substantial difference in orientation (+800 ms or 72°). All of these characteristics are observed when static gratings are used to determine tilt illusion functions (Gibson & Radner, 1937; Westheimer, 1990).

For six observers, we also estimated the spatial and temporal offset at which the flashed test and rotating outer stimuli appeared aligned. As shown in Fig. 3(b), the test and rotating stimuli appeared to be aligned when the test stimulus was presented ~75 ms before the stimuli became physically aligned ($t_5 = 2.74$; $p = 0.041$).

4. Discussion

If the flash-lag occurs because moving (or sustained) objects are processed ~80 ms more rapidly than stationary (or transient) objects, we would not expect to observe a tilt illusion when the central test grating is flashed 80 ms before a rotating annulus becomes vertical. Our results demonstrated that this situation does elicit a robust tilt illusion. Furthermore, the tilt illusions observed in these circumstances were of opposite sign to those observed when the test stimuli were flashed 80 ms after the rotating stimulus became vertical. In fact, the tuning of the tilt illusion over a broad range of spatial and temporal offsets is not substantially different to previous findings determined with static patterns (Gibson & Radner, 1937; Westheimer, 1990).

These observations are incompatible with a latency difference of ∼80 ms, or greater, arising at or before the point within the visual hierarchy that gives rise to the tilt illusion. Given that electrophysiological recordings suggest that visually evoked response latencies typically vary by no more than 20 ms across macaque monkey cortical visual areas (Schmolesky et al., 1998) it seems improbable that a differential latency of sufficient magnitude, to provide a satisfactory explanation for the flash-lag effect, could develop within extrastriate cortex.

If the small temporal advantage observed here is the consequence of differential latencies, they are not of sufficient magnitude to provide a credible explanation for the flash-lag. Inducing stimuli that rotated c.w. and c.c.w. elicited oppositely signed tilt illusions when the test stimuli were aligned with the surrounding annulus, although in this case they were not significantly different. However, it is important to note that the tilt illusions observed in such circumstances are in the same direction as those that are observed if the test stimulus is flashed 80 ms later within the rotation cycle. If we were to assume a linear increase of the illusion the data would indicate a processing advantage of ∼20 ms, but the tilt illusion does not increase in a linear fashion and so the extent of any processing advantage might be less than 20 ms.

It is important to demonstrate that the flash-lag could be elicited under similar experimental conditions (refer Fig. 3 (b)). Using a standard flash-lag methodology, we observed an apparent temporal advantage for moving, relative to flashed, gratings that was in close agreement with previous estimates of the flash-lag (Eagleman & Sejnowski, 2000; Nijhawan, 1994; Whitney & Murakami, 1998; Whitney et al., 2000).

As the flash-lag effect is unlikely to be generated at, or before, the point where the tilt illusion arises, it is probable that the flash-lag is primarily the consequence of a process that occurs at a higher level of the visual hierarchy. This is a suggestion that is broadly consistent with alternative theoretical accounts of the flash-lag. For instance, according to the positional sampling model, flash-lag effects arise because information about the precise location of a moving object is not available instantaneously. According to this theory, when a flash is used to indicate the point in time at which relative alignment should be determined, a process of spatial localization is initiated and the size of the flash-lag effect is determined by the time taken to complete the process (Brenner & Smeets, 2000). A perceptual strategy of this kind is consistent with the suggestion that the extent of flash-lag effects may be variable, depending upon how long it takes to determine the current state of a given attribute.

While the flash-lag has predominantly been determined by requiring observers to judge relative position, qualitatively different tasks have also been used. For instance, large apparent flash-lags have been observed within the contexts of colour change (∼400 ms, Sheth, Nijhawan, & Shimojo, 2000), and auditory localization (∼200 ms, Alais & Burr, 2003). It seems improbable that such large effects could credibly be ascribed to either differential latencies (Mateeff & Hohnsbein, 1988; Murakami, 2001; Patel, Ogmen, Bedell, & Sampath, 2000; Purushothaman et al., 1998; Whitney & Murakami, 1998; Whitney et al., 2000) or to processes that are designed to correct for their consequences (Eagleman & Sejnowski, 2000; Nijhawan, 1994; Rao, Eagleman, & Sejnowski, 2001). However, it seems reasonable to propose that it may take longer to determine the precise state of some stimulus dimensions relative to others. The determination of relative position is certainly less accurate when it is determined by auditory (Carlile, Leong, & Hyams, 1997) as opposed to visual cues (Levi, McGraw, & Klein, 2000). The former determination may require more time and, because of an extended process of positional sampling, therefore prompt larger apparent flash-lags (Brenner & Smeets, 2000).

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