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Faster processing of moving compared to flashed bars in awake macaque V1 provides a neural correlate of the flash lag illusion

Abbreviated title: **Neural correlates of flash lag illusion**

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Abstract

Computing object motion is vital for the survival of animals. However, while the brain is processing moving objects, these have already moved to new locations. A well-known visual illusion – the flash lag effect – suggests that the brain has acquired mechanisms to compensate for motion processing delays, so we perceive moving objects closer to their veridical locations. Although many psychophysical models have been suggested to explain this phenomenon, their predictions have not been tested at the neural level, particularly in animals that are known to perceive the illusion. To address this, we recorded neural responses to flashed and moving bars from primary visual cortex (V1) of awake, fixating monkeys. We found that the response latency for moving bars was shorter than that of flashes, in a manner that is consistent with psychophysical results from humans and monkeys. At the level of V1, our results support the differential latency model of the flash lag effect and suggest that an active position judgment – as predicted by the postdiction/motion-biasing model – may not be necessary for observing a neural correlate of the illusion. Our results provide a neural correlate of the flash lag illusion and suggest that the nervous system may have evolved mechanisms to process moving stimuli faster and closer to real time compared with briefly appearing stationary stimuli.

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Significance Statement

Localizing moving objects in real time poses a fundamental problem for the brain because they move to new locations during the anatomical delays in processing retinal signals. A well-known illusion called the flash lag illusion, suggests that the brain may be using different mechanisms in locating moving compared to static objects. Many theories have been proposed to explain this phenomenon but their predictions have never been tested at the neural level in subjects that are known to perceive the illusion. Recording neural responses from macaque V1, we found that moving objects are processed faster compared to static ones and that the neural responses under different stimulus manipulations are consistent with the predictions of the differential latency model of the illusion.

Introduction

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Moving objects in nature typically follow smooth predictable trajectories. A well-known visual illusion – the flash lag effect – suggests that the brain has acquired mechanisms to compensate for motion processing delays to perceive moving objects closer to their veridical locations (Fig.1). In this illusion, observers report that a moving bar is located ahead of an aligned flash (Mackay, 1958; Nijhawan, 1994). While this phenomenon has been studied extensively at the behavioral level, its underlying neural mechanisms are poorly understood.

In an initial attempt to explain this illusion, it was posited that the brain extrapolates the position of moving stimuli to an extent that compensates its own processing delays (Nijhawan, 1994). Since then, many alternative models have been proposed. These diverse models have pointed towards equally diverse neural mechanisms which range from simple bottom up explanation such as latency difference to high level top-down mechanisms such as attention and feedback (Baldo and Klein, 1995; Purushothaman et al., 1998; Whitney and Murakami, 1998; Brenner and Smeets, 2000; Krekelberg and Lappe, 2000; Patel et al., 2000; Sheth et al., 2000; Bachmann and Poder, 2001; Öğmen et al., 2004; Eagleman and Sejnowski, 2007). For example, the differential latency model (Purushothaman et al., 1998; Whitney and Murakami, 1998) maintains that moving stimuli are processed faster compared to flashed ones, leading to the perception of flashes temporally coinciding with a moving bar further along its trajectory. Alternatively, the motion-biasing model (Eagleman and Sejnowski, 2007) argues that motion signals affect position judgments, such that observers report a misalignment between a flash and a moving stimulus.

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Figure 1. The flash lag illusion. When a flash (bottom) is presented aligned to a moving bar (top), observers perceive the moving bar to be located further along the motion trajectory at the moment when they perceive the flash. Left: veridical locations; right: perceived locations. Since the flash appears to spatially lag behind the moving bar, this phenomenon has been called the flash lag illusion.

Despite this wealth of psychophysical literature, only a few physiological studies have explored the neural mechanisms of the illusion and they found a shorter latency for motion signals compared to flashes in the rabbit and salamander retina (Berry et al., 1999), and the cat LGN (Orban et al., 1985) and V1 (Jancke et al., 2004), providing evidence for a bottom up latency difference between flashes and moving stimuli. Although these studies provide valuable hints at plausible neural mechanisms of the flash lag illusion, they were done either *in vitro* or in anesthetized animals and it is unknown if the animals used in these studies actually perceive the illusion.

We recently showed that, similar to humans, macaque monkeys perceive the flash lag illusion (Subramaniyan et al., 2013). Hence we performed the physiological experiments in awake macaque monkeys, which allowed us to measure neural response latencies and correlate them with the behavioral data from the same species. Specifically, we manipulated two independent stimulus parameters – speed and luminance - to test if the resulting changes in neural responses accounted for the corresponding changes in perception. Under both manipulations, neural response latency difference between flash and motion in V1 explained a large part of the perceptual changes. Thus, our results show that even at the

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very first cortical visual information processing stage a neural correlate of the illusion can be observed and provide mechanistic constraints for the psychophysical models of the flash lag illusion.

Results

We investigated if moving stimuli are processed faster than briefly flashed stimuli in primary visual cortex (V1) and whether this could account for the perceived spatial misalignment or spatial lag in the flash lag illusion. To this end, we recorded neural activity from V1 while the monkeys were shown either a flashed or a moving bar in a passive fixation task (Fig. 2A, see Methods). We performed two experiments: In the first, we manipulated the speed of the moving bar. In the second, we kept the speed constant and manipulated the luminance of the flash and the moving bar. In both cases, we measured the effect of the manipulation on the latency difference between the moving and the flashed bar and compared it to the psychophysical results from monkeys (Subramaniyan et al., 2013) and humans (Purushothaman et al., 1998; Whitney et al., 2000; Murakami, 2001; Wojtach et al., 2008; Subramaniyan et al., 2013).

For experiment 1, we recorded from 524 multiunits in three animals using chronically implanted tetrode arrays. For experiment 2, we collected responses of 256 multiunits in one animal, using a 96-channel Utah array. After an initial receptive field mapping session, the main task began. We presented bright bars on a gray (experiment 1) or dark (experiment 2) background. In a given trial either a flash or a moving bar was shown. Since we recorded from many neurons simultaneously, the flash locations were not optimized for any particular neuron. Instead, in each recording session, flashes were shown at five to seven fixed locations covering the receptive fields of all the recorded neurons (Fig. 2B). The moving bar swept across the receptive fields horizontally at a constant speed from left to right or from right to left with equal probability (Fig. 2C).

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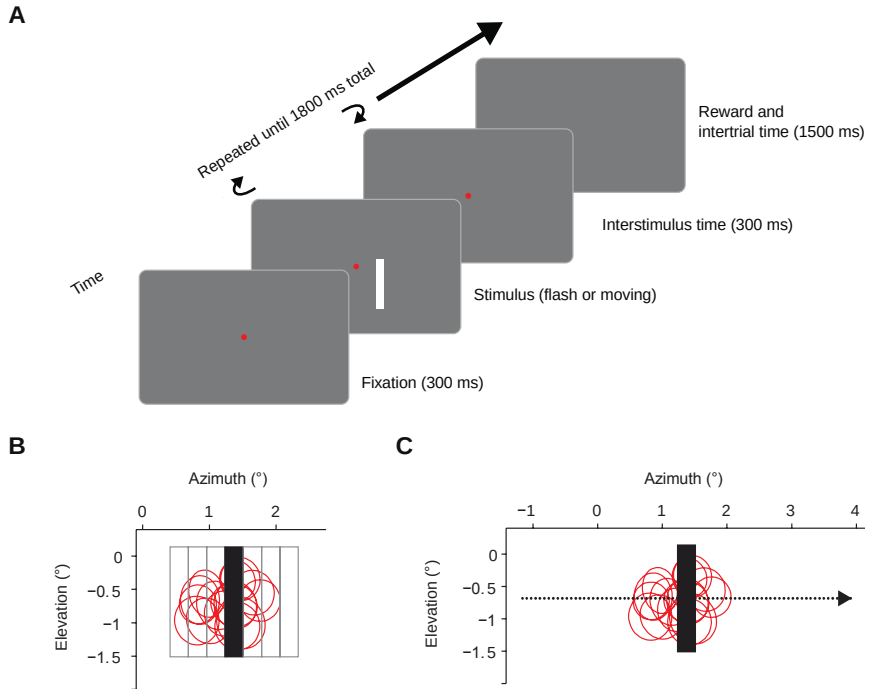

Figure 2. Fixation task and stimuli. ***A***, Monkeys fixated their gaze at a red circular dot at the center of the monitor within a fixation radius of 0.6°. After they maintained fixation for 300 ms, a single randomly chosen bright flash or moving stimulus was presented in a gray or dark background. The stimulus offset was followed by a 300 ms period in which no stimulus was presented except for the fixation spot. Then a randomly chosen flash or moving bar was presented again. With the monkeys maintaining fixation, this cycle continued until at most 1800 ms elapsed, after which they obtained a squirt of juice as reward. The next trial started after an inter-trial period of 1500 ms. ***B***, A flash (black bar) was presented at one of five to seven adjoining locations (gray rectangles) tiling the receptive fields (red circles) of all recorded neurons. ***C***, The moving bar (black bar) had the same size as the flash and moved from left to right or from right to left. The dots denote the positions of the bar center along the entire trajectory as the bar moved from left to right at a speed of 7 °/s. In ***B*** and ***C***, the coordinate (0°Azimuth, 0° Elevation) marks the center of fixation and the bars and receptive field outlines are drawn to scale. Note that the red circles show the outlines of only a subset of the recorded neurons.

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In the first experiment, we varied the speed of the moving bar (7, 14 or 29 °/s), while keeping the stimulus at a fixed luminance (23 or 36 cd/m^2). We found that moving bars are processed with lower latency than flashed bars and that this latency difference depends on speed (Fig. 3 and Fig. 4). To compute the processing delay of flashed bars, we measured the time it took for the neural response to reach its maximum after the flash hits the center of the receptive field of the neuron (Fig. 3A). Our example neuron fired most strongly around 60 ms after the flash onset (Fig. 3B). To compare this measurement with that of the motion response, we first centered the motion response times to the time when the instantaneous position of the moving bar matched the flash location (Fig. 3A). For the moving stimulus, the activity of the neuron was more spread out in time and the response onset was much earlier than that of flash (Fig. 3C and Fig. 3D). This is expected as the receptive fields extend over space and get stimulated as the moving bar smoothly enters and leaves the receptive field. However, the peak of the response to the moving bar also occurred much earlier (by ~30 ms) compared to that of the flashed bar (Fig. 3E). In addition to the peak, the entire motion response was shifted earlier in time compared to that of flash (Fig. 3E).

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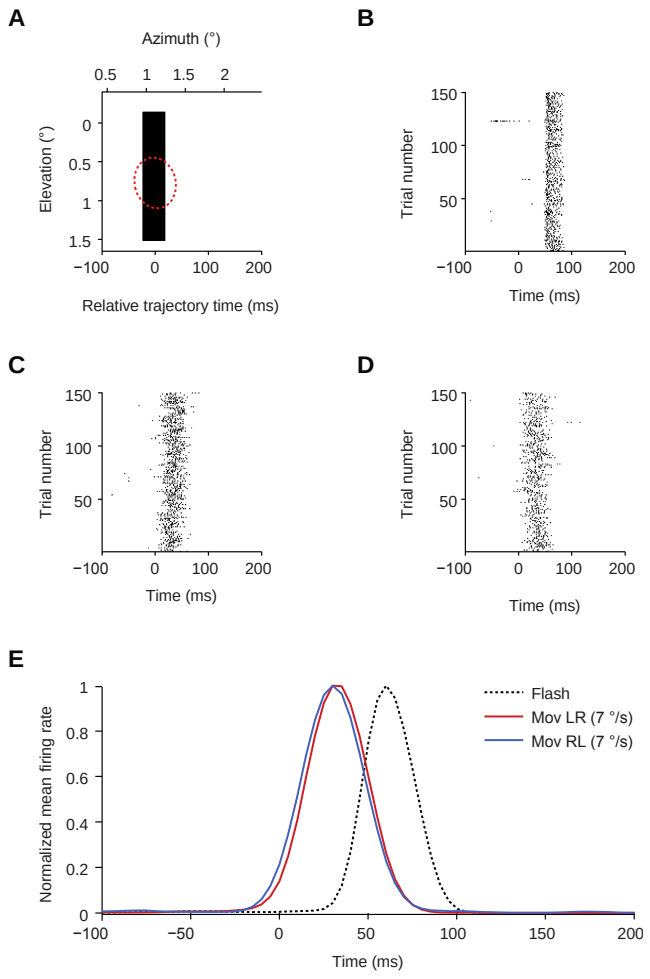

Figure 3. Single neuron responses to flash and a bar moving at 7 °/s. ***A***, Location of the flash (black bar) in the visual space relative to the receptive field (red outline). This location is also the instantaneous position of the moving bar as it reaches the center of the receptive field; the corresponding time is set to zero in the time axis at the bottom. ***B,*** Raster plot showing neural responses to the flash shown in ***A***, aligned to the onset of the flash. Each dot denotes a spike and each row is a trial***. C & D***, Raster plot of responses to the bar shown in ***A,*** moving from left to right (***C***) and right to left (***D***). ***E***, Normalized (to peak) mean firing rate response to flash (dotted trace) and bar moving from left to right (red trace) and from right to left (blue trace). Time axes for ***C***, ***D*** and ***E*** are as defined in ***A***.

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Across our sample of multiunits from all three monkeys, the peak response latencies for the motion condition at all three speeds were shorter compared to those for flashes (Fig. 4A and Fig. 4B; $p < 0.0005$, Bonferroni corrected, bootstrap test; see Methods). The mean latency for flashes was 57.4 ms (95% bootstrap confidence interval: 56.8–58.1 ms); for the motion conditions, it was 36.6, 47.1 and 51.1 ms for 7, 14 and 29 °/s respectively (all three 95% confidence intervals within 1 ms of the mean). As the speed increased, the latency of the motion response approached that of the flash (Fig. 4B). Therefore, the latency difference between flash and motion decreased as the speed increased (Fig. 4C; $p < 0.0005$, bootstrap test) but remained greater than zero ($p < 0.0005$, Bonferroni corrected; bootstrap test).

This effect is consistent with the speed dependence of the magnitude of the flash lag effect observed in the psychophysical data collected in macaques (Subramaniyan et al., 2013). In the psychophysical tests, we manipulated the speed of the bar and measured the perceived spatial misalignment between the flashed and moving bar. This misalignment is also referred to as spatial lag. However, in our electrophysiological experiments, we manipulated the speed and measured the latency difference, not spatial lag. Spatial lag cannot be computed directly from the neural responses since it is a subjectively perceived quantity. However, assuming that the latency difference between flash and moving bar measures the time difference (Δt) in their neural representations, we computed a neural equivalent of the spatial lag (Δx) by multiplying the speed (s) by the latency difference, i.e.,

$$\Delta x = s \times \Delta t. \tag{1}$$

Although the latency difference decreased with speed, the equivalent spatial lag increased with speed (Fig. 4D), as higher speeds overcompensated for lower latency differences. The increase of the equivalent spatial lag with speed is consistent with our psychophysical results (Subramaniyan et al., 2013) from two other monkeys of the same species (Fig. 4E) and with human psychophysical studies (see Discussion).

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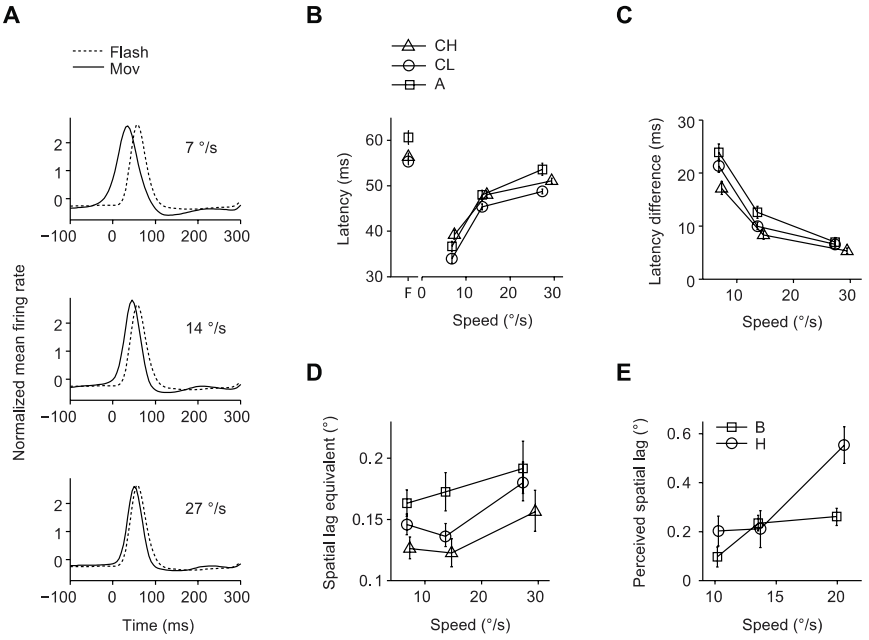

Figure 4. Population response and its correlation to flash lag psychophysics. ***A***, Normalized multiunit responses to flash (dotted trace) and motion (solid trace), averaged over all recorded multiunits from monkey A (n = 178). The speed of motion is indicated on the top right corner of each panel. ***B***, Mean response peak latency for flash and motion plotted as a function of speed, for the three monkeys (n = 178, 166 and 180 for A, CH and CL respectively). The latencies for flash are plotted at the abscissa location marked by 'F'. Error bars: 95% bootstrap percentile-based plug-in estimate of confidence intervals (note that most CIs are smaller than the markers). ***C***, Mean latency difference (flash latency minus motion latency) as a function of speed. Markers, sample size and error bars are as in ***B***. ***D***, Speed dependence of spatial lag equivalent computed from latency differences shown in ***C***. Markers and error bars are as in ***B***. ***E,*** Speed dependence of spatial lags measured from two separate monkeys (B and H), re-plotted here from Subramaniyan et al. (2013).

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The latency difference between moving and flashed bars also depends on bar luminance. In the second experiment, we fixed the speed of the moving bar at 18 °/s and presented flashes and moving bars with luminance values of 0.2, 0.8, 9 and 49 cd/m^2. We found that the motion response occurred earlier in time relative to the flash response (Fig. 5A). For all luminance values tested, the motion response peak latency was lower than that of the flash (Fig. 5B, $p < 0.0005$, bootstrap test). For both the flash and moving bar, the peak response latencies decreased as the luminance increased, although they decreased differently (Fig. 5B). Accordingly, the latency difference decreased as the luminance increased (Fig. 5C, $p < 0.0005$, bootstrap test).

To compare physiological and psychophysical data, we again converted the latency differences into equivalent spatial lags by multiplying the latency differences with speed (Eq. 1). The equivalent spatial lag decreased with luminance (Fig. 5C, $p < 0.0005$, bootstrap test). Although we currently do not have psychophysical data on the luminance dependence of the flash-lag effect in monkeys, we have previously shown that monkeys perceive the illusion similar to humans (Subramaniyan et al., 2013). We therefore measured perceived spatial lags from two human subjects using the same luminance and stimulus parameters used for the monkey physiology. Indeed, the spatial lag decreased with luminance in both observers (Fig. 5D and Fig. 5E; $F(1, 24) = 14.6$; $p = 0.001$; linear mixed model), in good agreement with the physiological results.

In the above analysis, we computed latency difference data between flash and moving bar with identical luminance and showed that they correlate well with human psychophysical data. Given that we presented each luminance condition in isolation, it is possible to compute the latency difference between a flash and a moving bar having different luminance values. In human psychophysics, when the flash luminance is fixed at a very low detectability level, the perceived spatial lag increases with the moving bar luminance (Purushothaman et al., 1998; Öğmen et al., 2004). To see if this is also evident in our neural data, we used the latency of the flash condition with the lowest luminance to compute latency difference at all moving bar luminance conditions. Interestingly, qualitatively similar to the human psychophysical results, we

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found that the spatial lag equivalent increased ($p < 0.0005$, bootstrap test) with the moving bar luminance (Fig 5F). An even more interesting psychophysical result is obtained when the moving bar luminance is fixed at a very low detectability level and the flash luminance in varied. For a sufficiently high flash luminance, the flash-lag effect is reversed where humans perceive the flash to be in front of the moving bar (flash-lead effect) (Purushothaman et al., 1998; Öğmen et al., 2004). We again found a qualitatively similar result in our neural data (Fig. 5G) where the spatial lag equivalent decreased ($p < 0.0005$, bootstrap test) changing from being positive (flash-lag) to negative (flash-lead) as the flash luminance level was increased, correlating well with the human psychophysical results.

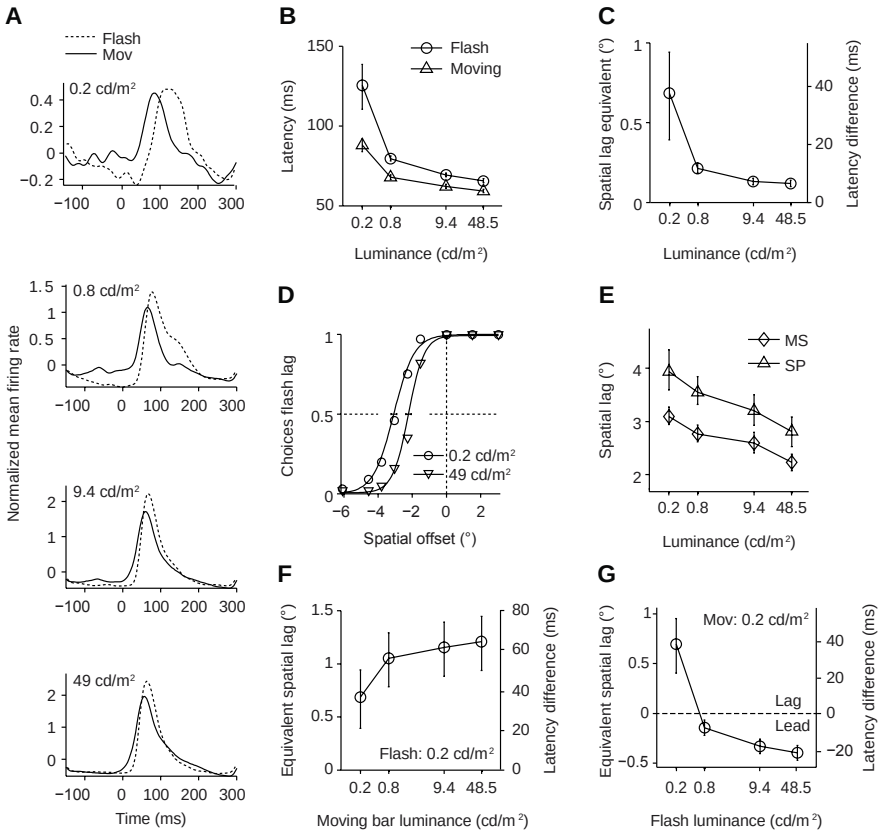

Figure 5. Luminance dependence of population response to flash and motion and its correlation to flash lag psychophysics. ***A***, Normalized firing rate responses to flash (dotted trace) and moving bar (solid trace) averaged across multiunits (n = 256) from all sessions (n = 7) from monkey L. In each subpanel the flash and moving bar had

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the same luminance (indicated on the top left corner). ***B***, Response peak latencies as a function of luminance, for flash and motion obtained from the data shown in ***A***. Error bars: 95% bootstrap percentile-based plug-in estimate of confidence intervals. ***C***, Luminance dependence of latency difference (flash latency minus motion latency, right vertical axis) computed from data shown in ***B***. Left vertical axis shows equivalent spatial lag computed by multiplying the latency difference by speed (18 °/s). Error bars as in ***B***. ***D***, Psychometric functions from human subject MS (for each data point, n = 100 trials, pooled from 5 sessions; for subject SP, n = 40 trials (2 sessions) per data point). The probability of the subject reporting that the flash is spatially lagging behind the moving bar is plotted against the veridical spatial offsets between the flash and moving bar at two luminance values (indicated at the bottom right corner). Error bars as in ***B***. ***E***, Luminance dependence of perceived spatial lags for human subjects (MS and SP). The spatial lags were computed from the psychometric functions using the method of compensation. Error bars as in ***B***. ***F*** and ***G***, Latency difference and spatial lag equivalent as a function of moving bar luminance (***F***) for a constant flash luminance (0.2 cd/m^2) or as a function of flash luminance (***G***) for a constant moving bar luminance (0.2 cd/m^2). The dotted line in ***G*** separates the luminance conditions that gave rise to equivalent spatial lags corresponding to psychophysically measured flash-lag ('Lag') and flash-lead ('Lead') conditions. Error bars as in ***B***.

In summary, our physiological data from speed and luminance manipulation are in good agreement with psychophysical results. One potential caveat is that in our physiology experiments we presented the flashes and moving bars in isolation. However, to generate the flash lag illusion, the flashed and the moving bar are presented simultaneously with perfect alignment. It is thus conceivable that if we had presented the flash and the moving bar together, the results might have been different. To rule out this possibility, we conducted a control experiment in which we presented the flash and moving bar at three different spatial offsets, including a zero offset condition, where the flashed and the moving bar were in alignment. This allowed us to determine whether there is a change in latency as a function of spatial offset for simultaneously displayed stimuli.

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We presented the flashes and moving bars simultaneously ('combined' condition) in two different arrangements. In the first, we presented flashes at the receptive fields and the moving bar (speed: 14 °/s) outside the receptive fields (Fig. 6A, left panel) and vice versa (Fig 6A, right panel) in the second, at three spatial offsets in a gray background. We then computed the flash response peak latencies from the first arrangement and the motion response peak latencies from the second. The latency difference was not significantly different among the three spatial offsets ($p > 0.76$, bootstrap test). In the same recording sessions, we also presented flashes and moving bars in isolation inside the receptive fields. To test whether in the combined condition, a second stimulus affected response latencies, we pooled the latency difference data across monkeys and spatial offsets in the combined condition and compared it to those obtained where stimuli were presented in isolation ('single' condition; 's' in Fig. 6B and C). We found no significant difference between the combined and the single condition ($p > 0.99$, bootstrap test). These results suggest that in awake fixating macaques, the latencies of the flash or moving bar representation in V1 are not influenced by the presence of a second bar stimulus outside the classical receptive field.

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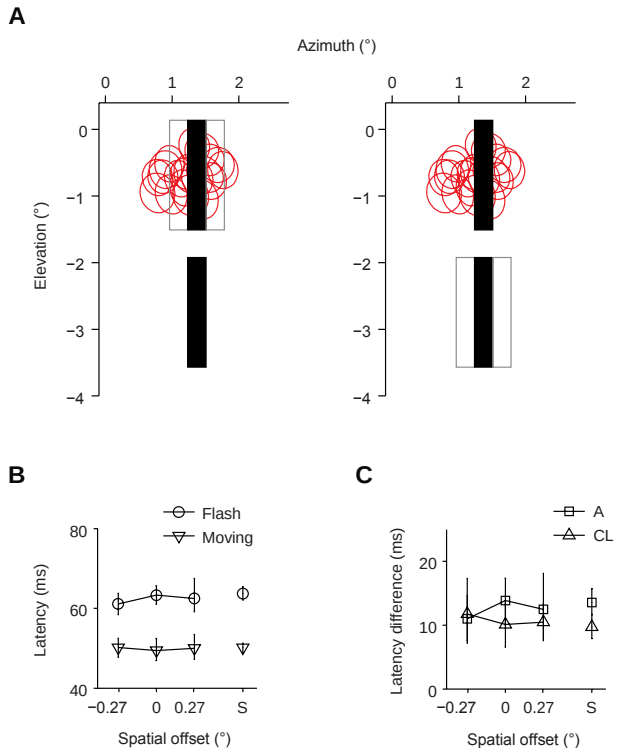

Figure 6. Control experiment**.** ***A***, Stimulus configurations. The red circles show the outline of receptive fields of a subset of the multiunits used in the analysis. Left panel: The filled rectangles show an example stimulus configuration. The two outlined rectangles show the other locations where we presented the flashes. Right panel: Same as the left panel except that the flash is now presented outside the receptive fields. ***B****,* Response peak latencies of flash and moving bar conditions from monkey CL (n = 25 ±7 multiunits per condition; mean ±1 S.D; for monkey A, n = 14 ±3 per condition), plotted as a function of the horizontal spatial separation between the flash and the instantaneous position of the moving bar (spatial offset). Data points from either flash or motion condition presented without an accompanying stimulus, are plotted at the abscissa location marked by 'S' (n = 76 multiunits; for monkey A, n = 59). Error bars: 95% bootstrap percentile-based plug-in estimate of confidence intervals. ***C****,* Latency difference between flash and moving bar conditions from monkey A and CL, plotted as a function of spatial offset. Error bars as in ***B***.

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Discussion

Our results show that moving stimuli are processed faster than flashed stimuli in awake macaque V1. In particular, the latency difference between the neural representations of the two stimuli depends on luminance and speed in a way that resembles the perceptual effects of these manipulations in both monkeys (Subramaniyan et al., 2013) and humans (Nijhawan, 1994; Purushothaman et al., 1998; Krekelberg and Lappe, 1999; Patel et al., 2000; Murakami, 2001; Ogmen et al., 2004; Subramaniyan et al., 2013).

Both pre-cortical and cortical mechanisms likely contribute to the observed faster motion processing. These mechanisms potentially include motion induced dynamic shift in the receptive field location and faster conduction/processing of motion signals. Our data cannot distinguish between these two possibilities since both will give rise to a shift in motion response relative to flash response. Motion-induced receptive field shift has not been reported in the pre-cortical stages in macaques. However, there is some evidence for faster conduction of motion signals. For example, signals in the magnocellular pathway arrive earlier in cortex than those from the parvocellular pathway (Nowak et al., 1995; Maunsell et al., 1999). Since the moving bar likely activates the magnocellular pathway more than the flash, the neural signals of motion may arrive at the cortex earlier than those of flashes. This possibility needs to be tested to precisely locate the mechanisms underlying the flash lag effect (FLE), e.g. recording from LGN with the same stimuli and manipulations we used here. Previous studies comparing signal arrival times of the magnocellular and parvocellular pathways at the cortex used flashed stimuli only (Nowak et al., 1995; Maunsell et al., 1999) and the dependence of the latency difference between the two pathways on factors such as luminance or speed remains largely unexplored. Cortical processing such as gain control and motion-related feedback signals may contribute to dynamic shift in the receptive field location towards the motion direction. For example a recent study (Ni et al., 2014) found that V1 receptive fields in fixating macaques shifted by about 10 % (0.1°) on average in the direction that accounted for the size-

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distance illusion. Such receptive field shifts if induced by motion can readily explain part of the faster motion processing.

We found that the moving bar response peak latency increased with speed. Consistent with our results, conversion of the direction-averaged spatial lag data reported by Jancke et al. (2004) (Fig. 6 in their study) into latency also revealed a similar trend in the speed dependency of motion peak latency. Our data show that latency difference between flash and motion condition decreased with speed. This is in sharp contrast to the constant latency difference that the majority of psychophysical studies assume when interpreting the effect of speed in perceived lag (Nijhawan, 1994; Krekelberg and Lappe, 1999; Whitney et al., 2000; Murakami, 2001). Equivalent latency difference computed from the spatial lags from a recent psychophysical study (Wojtach et al., 2008) however clearly decreases with speed (Fig. 7) similar to our findings. The discrepancy among the psychophysical studies can be reconciled by noting that Wojtach et al. (2008) used a wide range of speeds whereas the previous ones used a narrow speed range, which missed the full trend of the speed effect.

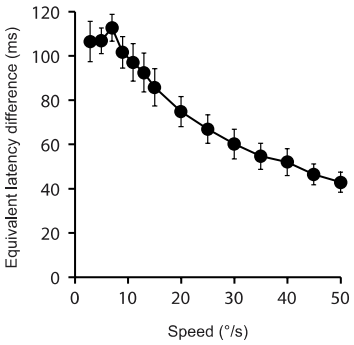

Figure 7. Equivalent latency difference as a function of the speed of the moving object in humans. The equivalent latency difference (flash temporally lagging the moving object) data points in the plot were computed by dividing the perceived spatial lag by speed reported in Figure 4 of Wojtach et al. (2008). Error bars are ±1 SEM.

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Although we found that the equivalent spatial lag increased with speed (Fig. 4D) similar to the psychophysical results (Fig. 4E), its magnitude appears to be lower than the behaviorally measured values (Fig. 4E). However, this is not surprising given that 1) we measured neural responses from the very first cortical processing stage and the effect may get larger as the information is processed further in the higher cortical areas, 2) the smaller receptive field sizes in V1 may potentially limit the extent to which receptive field shifts can occur in order to reduce motion stimulus representation delays and 3) the monkeys we recorded from did not perform the task as making position judgment actively may lead to a larger effect. The magnitude of the equivalent spatial lag in the luminance modulation experiment (Fig. 5C) is also smaller compared to the human psychophysical data (Fig. 5E). However this is expected given that the flash lag effect is generally smaller in monkeys compared to humans (Subramaniyan et al., 2013).

Our data provide two independent lines of evidence supporting the differential latency (DL) model (Purushothaman et al., 1998; Whitney and Murakami, 1998; Patel et al., 2000; Öğmen et al., 2004), which predicts shorter time needed for representing moving stimuli. First, as predicted, the spatial lag equivalent computed directly from the latency difference, increased with the speed of the moving bar. Second, the luminance dependence of the flash and motion representation delays (Fig. 5B) are also consistent with the key predictions of DL (Purushothaman et al., 1998; Whitney and Murakami, 1998; Patel et al., 2000; Öğmen et al., 2004) namely, for a fixed low flash luminance, the spatial lag should increase with moving bar luminance and for a fixed low moving stimulus luminance, progressively increasing the flash luminance should change the flash-lag to flash-lead effect. Our neural data support both of these predictions (Fig. 5 F & G). In addition, latency differences (Fig. 5C) also explained the trend in the luminance modulation of perceived spatial lag using identical luminance for flash and moving bar which we showed in humans (Fig. 5E) for the first time.

According to the motion-biasing model (Eagleman and Sejnowski, 2007), the illusion arises because "when the brain is triggered to make an instantaneous position judgment, motion signals that stream in over ~80 ms after the triggering event (e.g., a flash) will bias the localization". This would predict that a

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neural correlate of the illusion would be observed only when the subjects are asked to make an explicit position judgment. However, the animals used in our study were neither trained to make any position judgment nor were trained in any other task similar to the current task and we still found a neural correlate of the FLE in V1. First, these results suggest that reporting position judgment is not necessary for observing a neural correlate of the flash lag illusion in visual area V1. Second, they argue against pure version of the motion-biasing model involving higher cognitive functions (Eagleman and Sejnowski, 2007) and suggest that low level mechanisms underlying the observed latency differences need to be taken into account.

In summary, our data suggest that moving objects are processed faster in a speed and luminance dependent way compared to suddenly appearing static stimuli in the primary visual cortex and provide a neural correlate of the flash lag illusion.

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Materials and Methods

Subjects. Four male macaque (*Macaca mulatta*) monkeys (A, CH, CL and L) weighing 8, 9, 12 and 9.5 kg respectively and aged 10, 8, 8 and 8 years respectively, were used in the physiological experiments. Cranial head post and scleral search coil were implanted in each monkey using standard aseptic surgical procedures. All animal procedures were approved by the Institutional Animal Care and Use Committee of Baylor College of Medicine and followed NIH regulations. Two of the authors (MS and SP) participated in psychophysical experiments following procedures approved by the Institutional Review Board of Baylor College of Medicine.

Electrophysiological recording and data processing. We used chronically implanted tetrode arrays for recording neural activity from monkeys A, CL and CH as described previously (Tolias et al., 2007; Ecker et al., 2010). Briefly, in each monkey, we implanted chronically, arrays of 24 tetrodes on the left hemisphere over the operculum in area V1. The tetrodes were custom built from Nichrome or Platinum/Iridium wires. We implanted a 96-electrode microelectrode array ('Utah' array, Blackrock Microsystems, Salt Lake City, UT, USA) over area V1 on the right hemisphere in monkey L. For both tetrode arrays and Utah array, the neural signals were pre-amplified at the head-stage by unity gain preamplifiers (HS-27, Neuralynx, Bozeman MT, USA). These signals were then digitized at 24-bit analog data acquisition cards with 30 dB onboard gain (PXI-4498, National Instruments, Austin, TX) and sampled at 32 kHz. Broadband signals (0.5 Hz – 16 kHz) were continuously recorded using custom-built LabVIEW software for the duration of the experiment. For tetrode array data, the spike detection and spike sorting methods have been described previously (Tolias et al., 2007; Ecker et al., 2014). For the Utah array, spikes were detected from individual electrodes following the same procedure. In this study, the term 'multiunit' refers to the set of all the spikes detected from a single tetrode or a single electrode (Utah array).

Behavioral task. Visual stimuli were presented in a dark room using dedicated graphics workstations

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using Psychophysics Toolbox 3 (Brainard, 1997; Pelli, 1997; Kleiner, 2007). For all experiments with monkeys A, CH and CL we presented stimuli on CRT monitors (model: Sgi C220 Flat Diamondtron; display size: 22 × 16° from a distance of 100 cm; resolution: 1600 × 1200 pixels; refresh rate: 100 Hz). For monkey L, we presented stimuli on an LCD monitor (Samsung – model S23A950D; refresh rate of 120 Hz; monitor resolution: 1920 × 1080 pixels, subtending visual angles of 29 × 16° from a viewing distance of 100 cm). We gamma-corrected the monitors to achieve a linear luminance response profile. The monitor background luminance was 6.1 cd/m^2 (monkeys CL & A), 9.5 cd/m^2 (monkey CH) or 0.04 cd/m^2 (monkey L). The monkeys sat in a custom primate chair at a distance of 100 or 107 cm from the stimulus display monitor. Eye positions were continuously monitored online with scleral search coil for monkeys A, CH and CL and using a custom-built video tracker (frame rate: 250Hz) for monkey L. Eye position signals were also saved for offline analysis. Each trial began with a brief sound that instructed the monkeys to start fixating at a red dot (0.12– 0.14°) within a circular window of radius of 0.5–0.6° of visual angle. After the monkeys fixated for 300 ms, we presented different visual stimuli. The monkeys fixated for an additional 300 ms after the stimulus offset. For successfully completing the trials, the monkeys received juice or water reward. The next trial began after an inter-trial time of 1500 ms.

Receptive field mapping. We mapped the spatiotemporal receptive fields using a white noise random dot stimulus. On a gray background, we presented black and white squares (0.11–0.14° side) on a rectangular grid covering the receptive field of all recorded neurons. The squares were presented one at a time for three video frames (25–30 ms) in a pseudorandom sequence for 1200–2000 ms. The sequence consisted of many iterations, in each of which every grid location was visited exactly once in a random order, thus balancing the number of times each location was visited over the course of the experiment. The monkeys performed 242 ± 56 trials (mean ± S.D.) in a session that lasted for around 20 min. Since primate V1 contains many complex cells and we were interested primarily in the location of the receptive fields, we performed reverse correlation ignoring the sign of the stimulus (i.e. both black and white were treated as positive). We assessed the quality of the receptive field estimation by the following heuristic method. We

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first averaged the receptive field maps obtained at lags ranging from 40 to 100 ms, resulting in a single spatial kernel for each multiunit. We fitted the spatial kernel with a two dimensional Gaussian and computed the percentage of variance explained (across pixels) by the model. For all analyses in this study, we included multiunits for which the model explained more than 75% of the variance. From the model fitting, we also extracted receptive field centers and outlines. We obtained receptive field outlines for illustration purposes by computing the elliptical contour at two standard deviations from the center.

Speed manipulation experiment. Monkeys A, CH and CL were used in this experiment. Moving and flashed vertical bars of identical luminance and size (0.28 × 1.7°) were used as visual stimuli. The bar luminance was either 23 cd/m^2 (monkeys A & CL) or 37 cd/m^2 (monkeys CH). We defined a stimulus center for each monkey as the average of the receptive field centers of the neurons we recorded from; the eccentricity of this location was 1.5 ± 0.11° (azimuth: 0.87 ± 0.3° and elevation: 1.2 ± 0.3°; mean ± S.D.). In each stimulus period, only a flash or a moving bar was presented. We presented flashes for one video frame (10 ms). Since we recorded from many neurons simultaneously, to stimulate all the recorded neurons, we presented flashes at 5–7 locations around the stimulus center (Fig. 2B). These locations were abutting each other without any overlap. The trajectory length of the moving bar was 4.6 or 5.4°. The midpoint of the moving bar's trajectory was at the stimulus center. The moving bar translated horizontally from left to right or from right to left at one of three speeds: 7, 14 or 29°/s (range: 6.9-7.4, 13.8-14.7 and 27.5-29.5 °/s respectively). All stimulus conditions were presented with equal probability. In a given trial, we chose more than one stimulus condition randomly (two flashes and one moving stimulus for example) and presented them one after the other with an inter-stimulus period of 300 ms; this allowed us to use the monkeys' fixating period efficiently and present multiple stimulus conditions within every trial. During the stimulus period of ≤ 1800 ms, we presented 4 ± 1 (mean ± S.D.) stimuli. In a session, we repeated each stimulus condition for 426 ± 216 (mean ± S.D.) times. The monkeys performed 1597 ± 718 (mean ± S.D.) trials per session. Each session lasted for 3 ± 1 (mean ± S.D.) hours.

Luminance manipulation experiment. Monkey L was used in this experiment. The stimulus presentation

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followed the same overall design as the speed manipulation experiment (see above) with the following exceptions. The size of the bar was 0.15 × 1.8°. Moving and flashed bars with luminance values of 0.24, 0.82, 9.4, 48.5 cd/m^2 were presented in each session. Flashes were presented at one of nine abutting locations with the stimulus center at an eccentricity of 0.92 ± 0.07° (azimuth –0.46 ± 0° and elevation 0.79 ± 0.08°; mean ± S.D.). The trajectory length of the moving bar was 8.7°. The moving bar translated horizontally from left to right or from right to left at 18°/s. In the stimulus period of each trial, we presented 5 ± 1 (mean ± S.D.) stimuli. Each stimulus condition was repeated for 120 ± 46 (mean ± S.D.) times. The monkey performed 1128 ± 432 (mean ± S.D.) trials per session with each session lasting 2 ± 1 (mean ± S.D.) hours.

Control experiment. Monkeys A and CL were used in this experiment. Stimuli were presented as outlined in the speed manipulation experiment. However, in addition to presenting flashed and moving bars separately as above, we also interleaved additional stimulus conditions where we presented the flash and moving bar together in two arrangements A1 and A2 (Fig. 6A). In A1, we presented a flash inside the receptive fields and the moving bar below the flash but outside the receptive fields. To mimic the psychophysical experiment of the flash lag illusion, in arrangement A1, when the instantaneous position of the moving bar hit the azimuth of the stimulus center, a flash was presented at one of 5–7 horizontal spatial offsets (0°, ±0.27°, ±0.55°, ±0.82°). We assigned a negative sign to the offsets if the flash appeared ahead of the moving bar along the motion direction and a positive sign if the flash appeared behind the moving bar. In arrangement A2, the positions of the flash and moving bar in arrangement A1 were interchanged. The moving bar translated at a speed of 14°/s. The vertical center-to-center distance between the flash and the moving bar was 2.1°. With the bar height being 1.7°, the edge-to-edge separation between the flash and the moving bar was 0.4°. In each trial, we presented 3±1 (mean ± S.D.) stimulus conditions. Each stimulus condition was repeated 159±81 (mean ± S.D.) times. The monkeys completed 1930± 742 (mean ± S.D.) trials per session with each session lasting 3±1 (mean ± S.D.) hours.

Electrophysiological dataset. For the entire study, we recorded neural data from a total of 1457 multiunits

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(monkey A: 191, CH: 199, CL: 216 and L: 672) over 62 sessions (monkey A: 12, CH: 23, CL: 20 and L: 7) in an average period of six weeks from each monkey (A: 4, CH: 12, CL: 6 and L: 2). The majority (71%) of the multiunits showed significantly enhanced responses to the flash relative to baseline over a window of 30–130 ms after the flash onset. A minority (3%) of the multiunits showed flash-evoked suppressed responses. Multiunits with enhanced flash-evoked responses and with receptive fields for which the two-dimensional Gaussian model explained more than 75% of the variance, were included in the analyses. This resulted in a subset of 915 (63% of total) multiunits.

Estimation of flash response peak latency. In each session, multiple flashes were presented covering the receptive field of a given multiunit. We sought to find the mean firing rate response profile to a flash that was horizontally aligned with the center of the receptive field. However, there might not be any flash that was presented perfectly over the receptive field center since we did not optimize the flash locations for any particular neuron. In such cases, the mean firing rate profile in response to a flash at the receptive field center was obtained by linearly interpolating the temporal response profiles of the two flash locations left and right of the receptive field center. The resulting response profile was z-scored to have zero mean and unit variance. After z-scoring, the responses of all multiunits under a given condition were averaged and smoothed using a Gaussian kernel with a standard deviation of 10 ms. Peak responses latencies were then computed from these averages. The responses of individual single and multiunits to flashed and moving bars were sometimes multimodal. Since we had a much larger multiunit dataset compared to single units, we chose to extract the latencies from responses averaged across multiunits. This procedure turned out to be more robust than extracting a latency for each unit (for a description of how we estimated confidence intervals on the latencies, see section *Statistical Analysis* below).

Estimation of motion response peak latency. We aligned the motion responses to the time the moving bar's instantaneous position matched the receptive field center. Since the moving bar occupied discrete positions along the trajectory that did not necessarily coincide with the receptive field center, we linearly interpolated the trajectory time points to obtain the time at which the trajectory crossed the receptive field

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center. Next we extracted the average responses from 150 ms before to 300 ms after the zero time point, z-scored and averaged across multiunits. After this step, we followed the same procedure as for the flash responses described above and computed response peak latencies for each stimulus condition. The latencies were then averaged across the two motion directions.

Latency estimation in control experiment. In the control experiment, we computed response peak latencies for flashes from arrangement A1 and for moving bars from arrangement A2 (see section *Control Experiment* above). To compute flash response latency for a given spatial offset, we first selected multiunits whose receptive field centers were within the spatial extent of the presented flash. Response peak latency was then extracted from this set of multiunits as described under the section *Estimation of flash response peak latency*. To compute the motion response latency for any spatial offset, we first selected multiunits whose receptive field centers were within the spatial extent of the moving bar when it hit the stimulus center. Since the flashes were presented at different horizontal locations when the moving bar hit the stimulus center, the same set of multiunits were used for extracting latencies under different spatial offsets. Motion response peak latencies were then computed as described under the section *Estimation of motion response peak latency*. Note that we chose to include a spatial offset for analysis only if there were more than ten multiunits for that condition. With this criterion, only the three spatial offsets around the stimulus center qualified.

Statistical analysis. All the statistical analyses on the neural data were done by bootstrapping (Efron and Tibshirani, 1994). From the absolute response peak latencies of flash and moving bar under various conditions, we computed the following test statistics: latency difference between flash and moving bar (Fig. 4B); slope of the trend in the latencies (Fig. 4B); latency differences and spatial lag equivalents when changing speed (Fig. 4C) and luminance (Fig. 5B); and for the control experiments: latency differences across multiple spatial offsets (Fig. 6B); latency differences for stimuli presented in isolation versus flash and moving bar presented together (Fig. 6C). To obtain significance levels and confidence intervals on these test statistics, we repeated 2000 times the entire procedure that generated a test statistic,

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each time with a different random set of multiunits obtained by resampling with replacement. From this bootstrap distribution we computed the 95% percentile confidence intervals, which are reported as error bars. We defined the significance level (p-value) as $p = 2\min(q, 1-q)$, where q is the percentile of the zero under the bootstrap distribution (this analysis assumes that the bootstrap distribution is an appropriate measure of the variability under the null hypothesis).

Human psychophysics: task. Two human subjects (authors MS and SP) performed the standard flash lag psychophysical experiment described previously (Subramanian et al. 2013). The subjects sat in a dark room with their heads stabilized by a chin-rest. After the subjects dark-adapted their eyes for five minutes, the stimulus presentation began. The subjects were simply instructed to stay fixated at the fixation spot during stimulus presentation; their eye movements were not tracked. In any given trial, we presented a flash below another bar that moved from left to right; the gap between the bottom edge of the moving bar and top edge of the flashed bar was 0.3° and both bars had identical luminance. We used seven different horizontal offsets between the flash and moving bar centers. The offset values ranged from around –6.3° to 2.4° in steps of around 1.5°. We used a constant flash location and created the spatial offsets by choosing the time of flash relative to the instantaneous position of the moving bar. To be comparable to the physiological experiments with monkey L, we made sure that at zero spatial offset, the average position of the flash and moving bar centers matched the stimulus center used for monkey L. In a given session, we randomly interleaved four bar luminance values. These luminance values, bar dimensions, monitor background luminance and speed of the moving bar were identical to those used in the luminance modulation experiment with monkey L, although here a longer motion trajectory of 18° was used. Using a keyboard, the subjects reported if the leading edge of the moving bar was on the right or left side of the flash at the moment the flash appeared. The subjects completed a total of seven sessions (MS: 5, SP: 2). In most sessions, we presented a total of 28 stimulus conditions (7 offsets × 4 luminance values × 1 motion direction × 1 speed). Each condition was repeated 20 times giving about 560 trials per session. Each session lasted for an average 23 min.

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Estimation of perceived spatial lag: To quantify the perceived spatial lag, we first converted the subjects' responses into a probability of reporting that the moving bar was ahead of the flash. Then we fitted a logistic function to these probabilities as a function of spatial offsets, using psignifit3.0 toolbox (Wichmann and Hill, 2001a, b; Frund et al., 2011). In the toolbox, we chose the constrained maximum likelihood method for parameter estimation and parametric bootstrapping for estimation of confidence intervals for parameters. We constrained the upper and lower asymptotes of the psychometric function to be equal with the prior distribution being a uniform distribution on the interval [0 0.1]. We defined the perceived spatial lag as the point of subjective equality, that is the veridical spatial offset at which subjects reported that the moving bar was ahead or behind the flashed bar with equal probability. To examine how the spatial lag changed with luminance, we pooled the responses across sessions for each bar luminance before fitting the psychometric function. To perform statistical tests however, we fitted psychometric function for each session separately and computed spatial lags.

Statistical analysis of human psychophysics. The slope of the trend of the spatial lag as a function of bar luminance was tested for significance by constructing linear mixed models in the statistical software PASW-18 with the following settings: subjects and temporal order of the sessions were treated as random effects, spatial lag as dependent variable and bar luminance as a covariate.

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