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A Motion-Dependent Distortion of Retinotopy in Area V4

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Summary

When one element in an apparent motion sequence differs in color from the others, it is perceived as shifted along the motion trajectory. We examined whether V4 neurons encode the physical or perceived location of this "flashed" element by recording neuronal responses while monkeys viewed these stimuli. The retinotopic locus of V4 activity evoked by the flashed element shifted along the motion trajectory. The magnitude of the shift is consistent with the perceptual shift in humans viewing identical stimuli. This retinotopic distortion depended on the presence of a flashed element but was observed for both color-selective and non-color-selective neurons. The distortion was undiminished when the flashed element terminated the sequence, a condition that reduced the perceptual shift in humans. These findings are consistent with a Bayesian model of localization in which perceived location is derived from position signals optimally integrated across visual areas.

Introduction

A basic function of the visual system is to localize stimuli within the environment. Localization of moving stimuli is complicated by the fact that time is required to process visual information, and so a moving stimulus will change its location by the time it is perceived. Psychophysical studies have found that when asked to report the position of a moving stimulus relative to a briefly appearing stationary stimulus, subjects report that the moving stimulus appears to be shifted along its motion trajectory. This phenomenon, termed the flash-lag effect, has led to the development of several different models of motion-dependent mislocalization (Nijhawan, 1994; Baldo and Klein, 1995; Whitney and Murakami, 1998; Purushothaman et al., 1998; Eagleman and Sejnowski, 2000; Krekelberg and Lappe, 2000; Vreven and Verghese, 2005). In addition to the flash-lag effect, other psychophysical studies have documented related motion-dependent mislocalization errors (for example: Whitney and Cavanagh, 2000; Cai et al., 2000; Fu et al., 2001; De Valois and De Valois, 1991; Matin and Pearce, 1965; Brenner et al., 2001; Shim and Cavanagh, 2005). Relatively little, however, is known about how neuronal signals change under conditions that give rise to these mislocalization errors (Berry et al., 1999; Jancke et al., 1999; Fu et al., 2004; Whitney et al., 2003; Tolias et al., 2001), and virtually nothing is known about how responses in extrastriate visual cortex change under these conditions.

Cai and Schlag (2001) introduced a mislocalization illusion that is well suited for neurophysiological investigation. In their paradigm, one element of an apparent motion sequence differed in color from the other elements and was perceived to be shifted along the motion trajectory, relative to its veridical location. Because the different colored flashed element is perceived to be further along the motion trajectory, we refer to this illusion as the flash-jump illusion. We replicated their finding in human observers and then sought to find a neural correlate of this motion-dependent localization error. We hypothesized that the shift might manifest itself as a spatial distortion of one or more retinotopic visual maps. Because the odd element differed in color from the other elements in the sequence, we reasoned that any such mislocalization would likely manifest itself in the responses of neurons in a color-selective visual area. We chose to record responses in area V4, a retinotopically ordered, color-selective visual area, at an intermediate stage in the ventral visual processing stream. V4 is a likely locus of such a shift because it is the final stage in ventral visual processing to have clearly defined retinotopy and because its receptive fields (RFs) have been found to undergo attention- and eye-movement-dependent shifts (Connor et al., 1996; Tolias et al., 2001).

We began with the assumption that V4 encodes the location of a stimulus with a labeled-line population code for position. If so, then a spatial shift in the pattern of activity evoked by the flash would be expected to lead to a change in the perceived flash location. Under a labeled line code, a shift would occur if the set of neurons responding to the flash changes to either include neurons whose RFs are centered along the motion trajectory beyond the flash location, exclude neurons whose RFs are centered along the trajectory preceding the flash location, or both. To test this, we recorded the responses of neurons in area V4 of two passively fixating monkeys as they viewed the flash-jump illusion. We found that under conditions that give rise to the illusion in human observers, V4 underwent the predicted retinotopic map distortion, and this distortion was commensurate in magnitude with the perceptual shift in humans. We also found that this distortion in V4 was unabated when the flashed element terminated the sequence, a condition that we found no longer induced a perceptual shift in humans. This second finding dissociates V4 responses from perception and suggests that although V4 may contribute to the shift, additional processing beyond V4 may be required to generate the full percept.

Results

Human Psychophysics

We replicated the findings of Cai and Schlag in eight human observers, seven of whom were naive to the purpose of the experiment. Observers maintained fixation while an apparent motion sequence composed of colored bars appeared in the lower visual field moving

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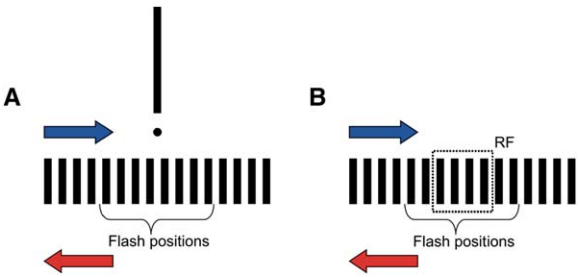

Figure 1. Stimulus Schematic

(A) For psychophysics, the apparent motion sequence was positioned 4° below fixation. Subjects reported whether the color change occurred to the right or left of center (marked by a bar in the upper field present throughout the trial).

(B) The stimulus was composed of an apparent motion sequence of sixteen bars spanning the neuron's RF (dotted line). On each trial, the flash occurred at one of the eight central "flash positions." On half the trials, the sequence was shifted by half the distance between the bars to test intervening positions. Each location was tested with rightward (blue arrow) and leftward (red arrow) motion sequences.

either leftward or rightward, as illustrated in Figure 1A. One of the elements in the sequence (the "flashed element") differed in color from the others. Observers were asked to report whether the flashed element appeared to the right or left of the center of the monitor, which was marked by a stationary vertical line in the upper visual field. In a comparison condition, a single bar replaced the motion sequence, and observers made the same judgment. This condition served to verify that observers were able to accurately report location in the absence of the apparent motion sequence.

We quantified the perceptual shift of the flashed element for each observer by computing a maximum likelihood fit of a cumulative Gaussian function to their reports, as illustrated for one (naive) observer, in Figure 2A. Here, the horizontal axis indicates the physical location of the flash, collapsed across direction of motion. Negative values correspond to flash positions along the apparent motion trajectory leading toward the midpoint of the monitor, and positive values correspond to positions along the trajectory beyond the midpoint. The vertical axis shows the proportion of times the subject reported the flash as being beyond the midpoint of the monitor. The black curve shows the subject's almost perfect performance at localizing isolated flashes. The red curve shows the subject's responses when the flashes were embedded in the motion sequence. The 50% crossing point of the fitted functions are illustrated by the dashed vertical lines. When the flashes were embedded in the motion sequence this subject's psychometric function was shifted to the left showing that they perceived the flashed element as shifted along the motion trajectory (shift = 0.36 dva). The mean shift across eight subjects was 0.22 dva (Figure 2B, one-tailed t test, p = 0.039).

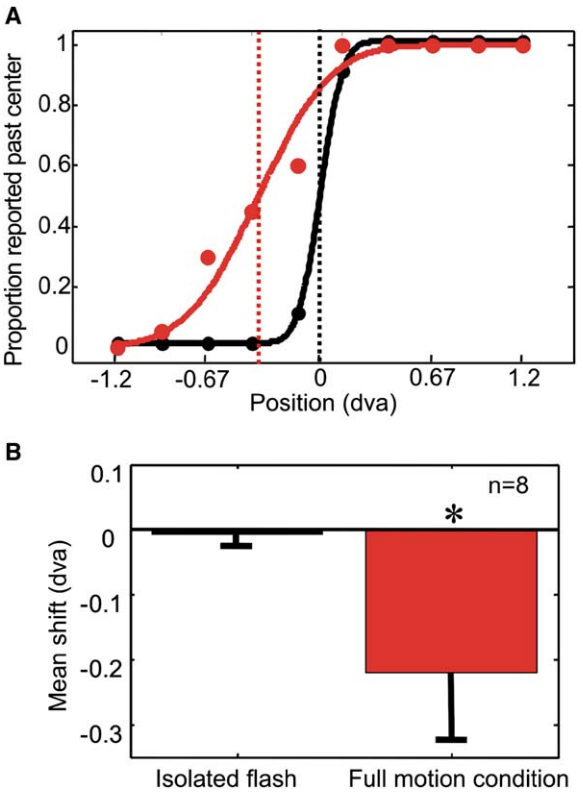

Figure 2. Psychophysics Results

(A) Single subject's performance in the isolated flash (black) and full-motion (red) conditions. Curves fitted to performance by a cumulative Gaussian function. Dashed vertical lines indicate the point where the fitted curves crossed 50%. Perceptual shift was measured as the distance of the 50% crossing point in the full-motion condition (red) from the center (zero). In this example the shift was 0.36 dva.

(B) Average data for eight subjects. The mean 50% crossing point of the fitted psychometric curve for the full-motion condition (right, mean = −0.22 dva) and isolated flash condition (left, mean = −0.005 dva). Error bars show the standard error of the mean.

Predictions of a Retinotopic Shift Model of Mislocalization

Such a perceptual shift might be mediated by a motion-dependent distortion of the retinotopic map at one or more stages of visual processing. Suppose that the position of a stimulus is encoded in a retinotopic map via a population vector code (Sparks et al., 1976; Georgopoulos et al., 1986; Groh et al., 1997). Each neuron encodes a particular location, which we assume to be the center of its RF, and the population estimate of position is the average of the positions encoded by all activated neurons, weighted by each neuron's firing rate. In order to form the basis of the perceptual mislocalization reported in human subjects, we would have to shift the vector average estimate of the flash position in the same direction as the motion sequence. This makes a simple prediction about how individual neuron responses should change with the direction of the apparent motion sequence. In order for the vector average estimate of the flash position to shift in the same direction as the motion sequence, we would have to shift the spatial profile of individual neurons' responses to the flash in the direction opposite to the motion direction. For example, if the motion sequence moves to the right toward the RF of an individual neuron, the neuron would respond to the flash at positions earlier in the motion sequence (further to the left) than it would when the flash appears within a leftward moving motion sequence.

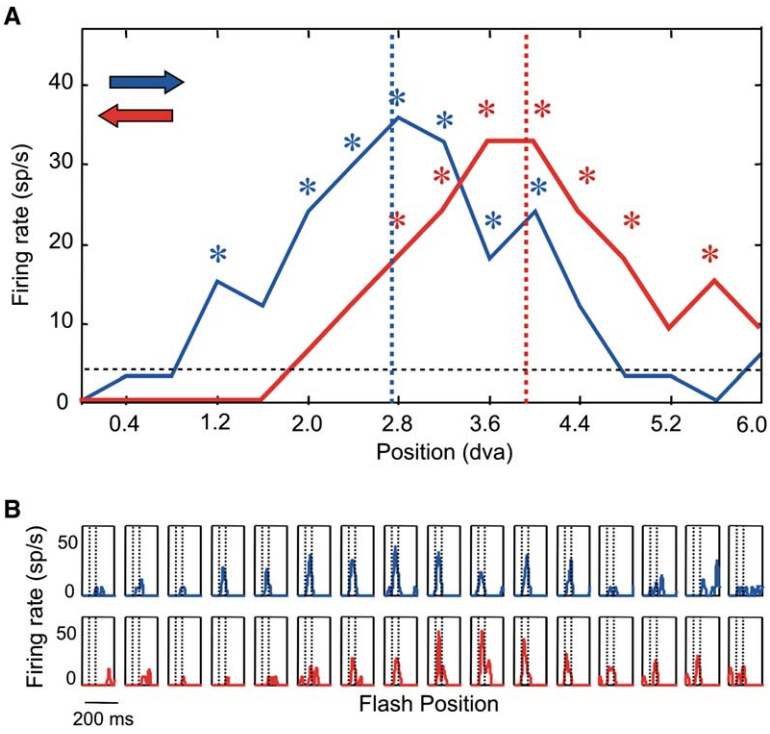

Figure 3. Single-Cell Response to Experiment 1 Rightward and Leftward Motion Trajectories

(A) Response profiles for flashes embedded in rightward (blue line) and leftward (red line) motion trajectories. Responses are calculated by taking the average firing rate in the 33 ms time window aligned with the onset of the flash after shifting by the neuron's latency (54 ms). Dotted black line indicates baseline firing rate. The weighted average positions are shown by blue (rightward motion sequence) and red (leftward motion sequence) dotted lines. Asterisks indicate those positions where the flash elicited a response significantly greater than baseline.

(B) Average response histograms for the flash occurring at each position in the rightward (blue) and leftward (red) trajectory. Dotted lines mark the 33 ms time windows over which the response was averaged.

Because the neuron is assumed to encode a position to the right of the flash location, this leftward shift in the response profile causes the neuron to bias the position estimate to the right of the veridical location. When the spatial profiles of individual neurons' responses to the flash shift in the direction opposite to the motion direction, this therefore leads to a population vector average estimate that assigns the flash to a position ahead of its retinal location, matching the mislocalization reported psychophysically in human subjects.

Experiment 1—Single-Unit Recording Experiment to Test the Predictions of the Retinotopic Shift Model

We tested this prediction by recording neuronal responses in area V4. After mapping the RF of a V4 neuron with a flashed bar, we arranged the elements of an apparent motion sequence so that they spanned the recorded neuron's RF and extended into the surround. As illustrated in Figure 1B, the motion sequence on each trial was composed of 16 bars. On each trial, one of the eight centermost bars of the sequence, labeled "flash positions," was the flashed element: a bar that differed in color from the other bars in the sequence. On half of the trials we shifted the position of the elements of the sequence by one half cycle. This enabled us to double the spatial resolution of our measurement, leading to a total of 16 tested flash positions. We computed the responses evoked by the 8.3 ms duration flashed element at each flash position, within a response-latency adjusted time window aligned to the flash onset. The width of the analysis window, 33 ms, was equal to the time period separating successive bar onsets. The direction of the apparent motion sweep was selected at random on each trial from the two possible directions. This enabled us to derive separate response profiles for flashes appearing within motion sequences sweeping across the RF in each direction. If the neuron responded to the physical location of the flash, these two response profiles should be identical. If, however, the pattern of activity evoked by the flash was shifted in accordance with the perceptual shift reported by human observers, then the set of positions where the neuron was activated by the flash should differ, depending on the direction of the apparent motion. Specifically, if the flash activated neurons with RF's further along the extrapolated motion trajectory, this would result in a shift in the response profile in a direction opposite to the direction of apparent motion.

Consistent with the latter hypothesis, flashes occurring at physically identical locations, but embedded in oppositely moving sequences, yielded profiles that were shifted in the direction opposite to the apparent motion. We quantified this shift for each neuron as follows. First, we determined the edges of the RF, for each direction. The two RF edges were defined as the two positions furthest from the center of the RF that elicited a response significantly above baseline in either of the two motion directions. We then computed the average position, weighted by firing rate, based on responses across all positions bounded by the edges of the RF. We quantified the magnitude and direction of each cell's shift as the difference between these weighted average positions for the two motion directions. Because this shift is calculated by comparing the response profiles between two directions of motion, this value must be halved to provide for a fair comparison with the human psychophysics, which measured the perceptual shift of a flash embedded within a single motion sequence. A positive value corresponds to the response profile being shifted in a direction opposite to the direction of motion, as predicted by the retinotopic shift model. Figure 3 shows a neuron with the

predicted shift (shift = 0.64 dva). 15 out of 17 cells (88%) recorded under these conditions showed RF offsets in this direction (mean shift = 0.18 dva, one-tailed t test, p = 0.015). This neuronal shift is comparable in magnitude to the mean psychophysical shift in humans of 0.22 dva. Thus, the RF shifts observed in this initial neuronal sample are consistent with a spatial shift in population activity that would result, through a labeled line code, in the assignment of the position of the flash ahead of its veridical retinotopic location, matching the perceptual mislocalization induced by the illusion in human subjects.

Experiment 2—Boundary Conditions of the RF Shift

In order to more fully characterize the conditions that give rise to the neuronal shift observed in Experiment 1, we recorded the responses of an additional 56 neurons (35 in the same and 21 in a second animal) with an expanded stimulus set. To accommodate these additional experimental conditions within the time constraints of a recording session without sacrificing spatial resolution, we reduced the number of tested flash locations from 16 to 8 and centered these on one border of the RF. Now, one motion trajectory began outside of the RF and moved inward, and the opposite trajectory began inside the RF and moved outward. A vector average position code is only valid if the full range of positions has been sampled because a biased sample of available positions will necessarily bias the vector average position estimate. Therefore, for each of these 56 neurons, we adopted another estimate of RF shift. We determined the positions at which the flash elicited a response that was significantly above baseline (positions within the RF) for inward and for outward trajectories. We then computed a shift index (SI) by subtracting the number of positions within the RF when the flash was embedded in an inward trajectory from the number of positions within the RF when the flash was in an outward trajectory. A positive SI indicates that the neuron's RF was shifted toward the incoming stimulus, relative to its position when the stimulus was outgoing, consistent with the finding in Experiment 1. This index is expressed in terms of the number of positions activated. To quantify this in degrees of visual angle (dva), we scaled this result by the distance separating adjacent flash positions. As with the vector average position estimate used in Experiment 1, this index must also be halved because it calculates the difference in response positions between two opposing directions of motion.

We first validated the new index by applying it to the data recorded in Experiment 1 and comparing the estimated shifts with both indices. For each neuron recorded in Experiment 1, we divided the set of tested positions in half, resulting in two sets of positions for each neuron, each of which spanned roughly half the RF (see Figure S1). We then calculated the shift index to be used in Experiment 2 for each neuron. The mean shift obtained in this manner was significant ($p < 0.01$) and was similar in magnitude to the shift obtained with the vector average index applied to the full RF's (0.17 dva, full RF vector average versus 0.18 dva, split RF shift index). Across the population, shift estimates by the two methods were not significantly different (two-tailed, paired t test p = 0.84).

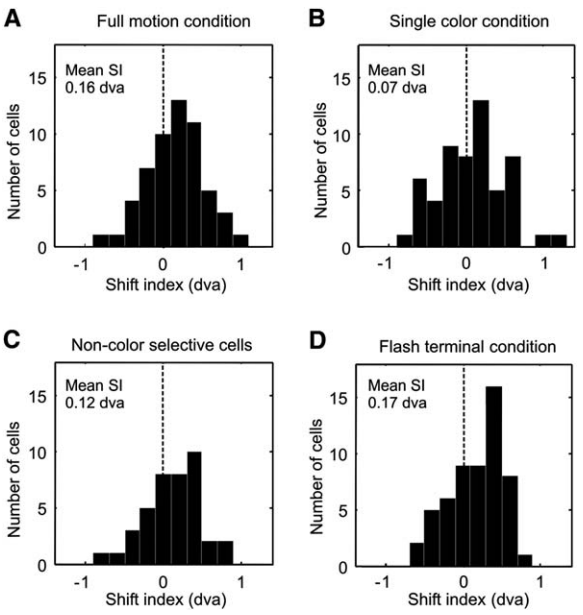

Figure 4. Distribution of Shift Indices for Experiment 2

(A) Full-motion condition (SI = 0.16).
(B) Single-color sequence (SI = 0.07).
(C) Non-color-selective subpopulation (SI = 0.12).
(D) Flash-terminal condition (SI = 0.17).

Having validated the shift index, we applied it to the responses recorded in Experiment 2 on trials in which a flashed element was embedded in the motion sequence (a condition we refer to as the "full-motion condition"). Figure 4A shows the distribution of SIs across the 56 neurons tested under this condition. The distribution was significantly shifted to the right (mean SI 0.16 dva, one-tailed t test, $p < 0.001$) and is similar in magnitude to the shift observed in Experiment 1. Thus, as in Experiment 1, the response profiles of the V4 neurons recorded in Experiment 2 were shifted opposite to the direction of motion, as would be expected if V4 neurons encode the perceived, not the veridical, location of the flash.

Single Color Sequences

In order to determine whether motion alone is sufficient to induce the shift, we tested the cells with a motion sequence in which all the elements were identical in color. Their color was the same as the flashed element in the full-motion condition. In all other respects, these sequences were identical to those that included the color change. Figure 4B shows the distribution of SIs across the same population of 56 neurons. The distribution was not significantly shifted from zero (mean SI = 0.07 dva; one-tailed t test, p = 0.12). Thus, motion without the transient color change was not sufficient to induce a significant distortion of the retinotopic map in V4.

Color Selectivity

Our failure to find a shift in the absence of a color change raises the question of whether the shift applies only to cells selective for color or applies across neurons regardless of color selectivity. Although we set the flashed element to be a preferred color and the other bars in the

sequence to be a nonpreferred color for one neuron in each recording session, we recorded multiple neurons simultaneously. Therefore, we recorded from a number of neurons whose responses did not distinguish between the two colors. Figure 5C shows the distribution of SIs for the full-motion condition from the population of neurons that were not selective for the two colors (n = 40, see Experimental Procedures). This population of neurons was still significantly shifted to the right (mean shift = 0.12 dva, one-tailed t test, p = 0.02). Further, we found no correlation across neurons between color selectivity and shift index (r^2 = 0.0001). Thus, although shifts were only observed when there was a transient color change, the shift did not appear to depend on the neuron responding differentially to the two colors appearing within the sequence.

Flash-Terminal Condition

One class of theories that has been advanced to explain a related motion-dependent mislocalization illusion, the flash-lag illusion, is that the mislocalization results from motion signals being integrated for a period of time after the flash (Eagleman and Sejnowski, 2000; Krekelberg and Lappe, 2000). This proposal is supported by psychophysical studies showing that the removal of motion after the flash reduces or eliminates the perceived mislocalization (Eagleman and Sejnowski, 2000, Kanai et al., 2004). To test whether the present illusion is similarly reduced by terminating motion upon appearance of the flash, we tested the ability of our human subjects to localize the flashed element when it terminated the motion sequence. The mislocalization error was no longer statistically significant (mean shift = 0.09 dva, one-tailed t test, p = 0.06).

If the shift in the V4 retinotopic map is sufficient to cause the perceptual shift, we would expect the shift in V4 to diminish in the flash-terminal condition. When the same population of V4 neurons tested with the full-motion condition was tested with this flash-terminal condition, however, the magnitude of the shift across the population was undiminished (Figure 5D, mean flash terminal SI = 0.17 dva, one-tailed t test, p < 0.001; mean full motion sequence SI = 0.16 dva). Though the flash was not mislocalized in humans observing the flash-terminal condition, the V4 shift persisted undiminished. Thus, either this dissociation represents a species difference, or the reduction in the perceived shift must be attributed to processes occurring outside of V4.

Eye Movements

It is important to consider whether eye movements could contribute to the observed shifts. The monkeys maintained fixation within a 0.75° radius square fixation window throughout each trial, limiting eye movements. All trials in which eye position deviated from this window were excluded from further analysis. Had the motion sequences triggered an ocular following response, this would have shifted RFs with the eye, in the direction of the motion sequence, resulting in RF shifts opposite to those we observed. Additionally, the neuronal shifts were only observed on trials when the flashed element appeared. Therefore, any contribution of eye movements would have to be contingent on the presence of the flashed element. Because the flash element was on for a very brief period of time (8.3 ms) and we examined the neural response to the flashed element within a very short window delayed only by the response latency of the cell, it is unlikely that an eye movement triggered by the flashed element could occur rapidly enough to affect our results. To directly rule out eye movements as a source of the shift, though, we performed the following analysis of eye position at the time the flashed element appeared. For each neuron, we determined which flash locations gave a significant response in one direction of the motion sequence but not in the other direction. We then compared eye position at the time the stimulus appeared at each of these differentially responding locations to determine whether the observed differences in neuronal response to flashes appearing at these locations could have resulted from differences in eye position at the time of the flash. A positive difference in eye position is a difference in the direction that could contribute to the differential neuronal response at the location. The mean eye position difference across all differentially responding locations was very small (<0.01 dva) and not statistically significant in any condition. We also verified that the standard deviation of eye position at the time of the flash was not significantly different between the responsive and nonresponsive direction at these differentially responding locations (mean difference in standard deviation <0.01 dva). Thus, the observed shifts in the retinotopic map are not artifacts resulting from eye movements.

Discussion

Summary

We find that the pattern of neuronal activity in area V4, the final retinotopically ordered area in the ventral visual processing stream, is spatially distorted when one element (the "flashed element") in an apparent motion sequence differs in color from the other elements in the sequence. We recorded V4 neurons whose RF's fell along the motion trajectory and found that the set of RF positions where the flashed element evoked a response was shifted in the direction opposite to the direction of motion. That is, the pattern of activity across the V4 retinotopic map was shifted in the direction of the apparent motion. Human observers viewing the identical stimuli perceived the flashed element to be shifted along the motion trajectory, in accordance with the neuronal shift. The magnitude of this perceptual shift was comparable to the magnitude of the neuronal shift. The shift disappeared when the color change was removed from the apparent motion sequence, demonstrating that motion alone was not sufficient to cause the neuronal shift. Additionally, despite being triggered by the color change, the V4 shift was not limited to neurons that were selective for the two colors present in the sequence. Thus, the presence of a flashed element appears to trigger a general shift in V4 spatial organization that is not sensitive to each neuron's particular color preference. The shift was quite rapid, manifesting itself within the first 33 ms of the response evoked by the flashed element. Finally, the shift was undiminished when the elements subsequent to the odd colored element were removed from the sequence, indicating that the V4 shift did not

depend on events occurring after the appearance of the odd colored element.

Possible Biophysical Mechanisms

Here, we consider various biophysical mechanisms that could potentially give rise to the shift. One possibility is that stimuli preceding the flash in the outward bound trajectory might lead to short-term adaptation (Maffei et al., 1973; Bonds, 1991; Muller et al., 1999; Priebe et al., 2002; Kohn and Movshon, 2003). Adaptation might cause positions near the edge of the RF to fail to elicit a response for outward bound trajectories. It is, in fact, known from studies of the retina (Berry et al., 1999) that a smoothly moving stimulus can cause changes in response gain that result in spatial distortions in the retinal map. Although the bars in our study were spaced far enough apart that they were unlikely to have induced a shift in the retina, it is possible that a similar adaptation mechanism might operate in the cortex, over a larger spatial scale. Adaptation is known to be largest when the adapting stimulus is identical to the subsequent stimulus evoking the adapted response (Movshon and Lennie, 1979). Therefore, if the observed shift resulted from adaptation, it should be larger when all bars in the sequence were of the same color. We find instead that the shift disappeared in this single-color condition. These data thus do not appear to be consistent with the proposal that the observed shifts in V4 are the result of known adaptation mechanisms.

The center-surround organization of V4 neuron RF's could also potentially give rise to the observed shift. The most prominent type of surround modulation that has been documented in V4 is response suppression (Schein and Desimone, 1990). Although that study employed surround stimuli that appeared simultaneously with the center stimulus, there is evidence that surround suppression can be induced, with diminished strength, when the surround stimulus appears prior to the center stimulus (Kondo and Komatsu, 2000). In the present study, inward bound sequences activated the surround before reaching the RF. Surround suppression would be expected to have its most pronounced effect on single color trials because response suppression has been found to be strongest when the center and surround stimuli are identical in color (Schein and Desimone, 1990). This would have led to a reduction in response on inward bound trajectories on single color trials, resulting in a negative shift index. We found no significant shift in this condition, suggesting that center-surround effects are not robustly induced by the briefly presented, asynchronous stimuli used in the present study. Although surround suppression is most commonly reported, surround facilitation has also been reported to occur in V4 when a surround stimulus that differs in color from the center stimulus is used. This type of surround facilitation could result in the response to a flashed element appearing near the edge of a cell's RF being facilitated by the bars comprising the inward bound motion sequence preceding the flashed element. We find it unlikely that this type of surround facilitation explains our results because we did not find evidence of surround suppression in the single color sequences and because suppression has been found to be greater in magnitude than facilitation. Our findings thus do not appear consistent with adaptation and center-surround findings previously reported in the literature. The mechanisms underlying these two phenomena, however, are not fully understood and it remains possible that as-yet-unknown properties of these underlying mechanisms may also give rise to the observed shifts.

Dependence of the Estimated Shift on Latency Estimation

The retinotopic shift was measured on the basis of responses occurring over brief windows that were aligned in time to the flashed element allowing for each cell's response latency. By using the same brief time window, we could meaningfully compare shifts across different experimental conditions. This brief analysis window also enabled us to link the shift to the presentation of the flashed element and to determine that the shift was present within the first 33 ms of the cell's response to the flash. It is worth noting that the responses in area V4 to the 8.3 ms flashed element are sometimes longer than this brief analysis window. Although it might seem advantageous to extend the window to include the full period of the response, this would have included the response evoked by the subsequent bar, resulting in a measured shift even if none had actually occurred. Our window may also have included the tail end of the response evoked by the preceding bar, resulting in a somewhat larger response estimate for outward than inward bound trajectories. This is opposite to the shift we observed. Therefore, our estimate of the shift may slightly underestimate the actual shift of the V4 map.

Because the analysis window is shifted by each cell's latency, it is important to consider whether an error in estimating latency could bias our shift estimate. Consider a flash appearing just outside the RF, embedded within a motion sequence moving into the RF. Had we overestimated latencies, our estimate of the response evoked by the flash might inadvertently have included part of the response evoked by bars presented further along in the sequence, deeper within the RF. This might cause us to erroneously conclude that the flashed element had elicited a response. On trials in which the flash was presented at the same location embedded within an outward bound trajectory, our hypothetical shifted window would correspond to stimuli appearing further outside the RF and would not elicit a response. Observing that the cell had responded to the flash on the inward trajectory and not on the outward trajectory, we would be led to conclude that the RF had shifted in a direction opposite to the apparent motion direction, even if no such shift actually occurred.

This explanation cannot account for data collected from highly selective neurons such as the one illustrated in Figure 3, in which the only element to elicit a response was the flash element. A latency error might misalign the response window so that it excluded part or all of the response, but this would lead to an underestimate of the stimulus-evoked response in both directions. The clearest evidence that an error in latency estimation did not contribute to our shift estimate comes from our findings in the flash terminal and single-color conditions, which used the same latency estimates as the full-motion condition. Consider first the flash-terminal condition. Suppose that, as outlined in the hypothetical

case above, the observation of a shift in the full-motion condition were due to inadvertently registering responses evoked by stimuli appearing after the flashed element. Then, the shift should have disappeared in the flash-terminal condition because there were no stimuli subsequent to the flashed element. We found instead that the shift in the flash-terminal condition was present. It did not, in fact, diminish at all relative to the full-motion condition. Now consider the single-color condition. Suppose again that we had overestimated latencies. As outlined above, this would have caused the response window to include elements appearing further along the motion trajectory, resulting in responses on inward trajectories not present on outward bound trajectories. Therefore, if we had overestimated latencies, we should have found a shift in this condition. We find no evidence of a shift in the single-color condition. These data are thus inconsistent with the possibility that the observed shifts are artifacts of misestimating response latency.

Relevance of the Present Findings to Models of Motion-Dependent Mislocalization

Various theories have been advanced to explain the motion-induced perceptual mislocalization that is observed in a related illusion, the flash-lag illusion. In this illusion, a stationary stimulus is presented briefly, spatially aligned with a moving stimulus, and the moving stimulus is perceived to be further along its trajectory when the stationary stimulus appears. Although the stimuli differ, some insight can be gained from a consideration of the relationship between our physiological findings and the theories that have been advanced to account for this illusion. Nijhawan (1994) postulated that the flash-lag illusion illustrates that the visual system extrapolates the motion of the moving stimulus forward so as to compensate for delays in neural processing. This theory predicts that all moving stimuli should be extrapolated forward. Physiological evidence for such an extrapolation mechanism has been reported in the retina where the peak of activity evoked in response to a sweeping bar leads the bar's veridical location (Berry et al., 1999) and in V1 (Jancke et al., 1999). Our results are compatible with an extrapolation of the flashed element position along the motion trajectory in the full-motion condition. We do not find, however, that this extrapolation applies to motion in general within V4 because we did not find a significant shift when all elements in the motion sequence were identical in color.

The temporal integration and postdiction models posit that the visual system collects information over a period of time in order to make a judgment about the position of an object (Krekelberg, and Lappe, 2000; Eagleman, and Sejnowski, 2000). These theories differ in terms of the time period over which this integration occurs, but a common component of these theories is an integration window that extends beyond the time of the flash. This allows the position judgment to be biased by the moving object after the flash occurs. We find that the shift in V4 was apparent in the first 33 ms of neuronal responses evoked by the flash, leaving little time to integrate motion over subsequently appearing flashes. Further, the shift in V4 persists in the flash-terminal condition. Thus, the initial shifted response in V4 does not appear to depend on events occurring subsequent to the appearance of the flashed element.

This does not imply that localization of the flash by the visual system as a whole cannot benefit from information that is present after the flash. Indeed, our human observers apparently did so because they did not perceive a shift in the flash-terminal condition, indicating that perception is modified by events occurring after the flashed element. Thus, we find an interesting dissociation between the conditions that give rise to the illusion and the conditions that cause a shift in V4: the magnitude of the illusory shift is markedly diminished when the flashed element terminates the motion sequence, but the retinotopic shift in V4 was undiminished in this flash-terminal condition.

Taken together, the present results show that V4 undergoes a shift that occurs regardless of events occurring subsequent to the flashed element. We suggest that this shift could play a role in extrapolating the position of the flashed element. The match between the V4 and perceptual shift in the full-motion condition suggests that the V4 shift may contribute to the perceived shift. The dissociation between perceptual and V4 shifts in the flash-terminal condition, however, shows that the V4 shift is not the full neural correlate of the perceptual shift. Rather, the effect of the V4 shift on perception appears to depend on events occurring after the flash, likely mediated by areas beyond V4.

Comparison across Species

It is important to note a key limitation of the present study: that we have compared psychophysics in the human to physiology in the monkey. Ideally, we would have preferred to make both sets of measurements in the monkey, but there are several pitfalls that made this problematic. First, had we rewarded the monkeys for making accurate judgments about the veridical location if the flashed element, the monkeys would have had an incentive to correct for the perceptual shift, possibly leading us to wrongly conclude that monkeys are not subject to the shift observed in humans. We might have avoided this by rewarding the monkeys for reporting any position falling within a wide range of positions around the veridical one, but this would reward the monkey for providing a sloppy response. It would thus be difficult to reliably quantify the shift, and we might, again, conclude that monkeys do not perceive the shift that is observed by humans, even if they did, in fact, perceive the shift. Even if we were able to train the monkeys to reliably report their percepts, we would then have to be concerned that the physiological shift might have resulted from extensive training on the task (Bichot, et al., 1996). By imposing no behavioral constraint beyond accurate fixation, we believe we have derived a pure estimate of the physiological shift. Given the similarities between the physiological and psychophysical shifts in the full-motion condition, we conclude that the most parsimonious explanation is that the V4 shift in this condition contributed to the perceived shift.

A Possible Conceptual Model to Reconcile the Dissociation between Physiology and Perception

We propose a framework that offers a way to reconcile the dissociation between perception and area V4

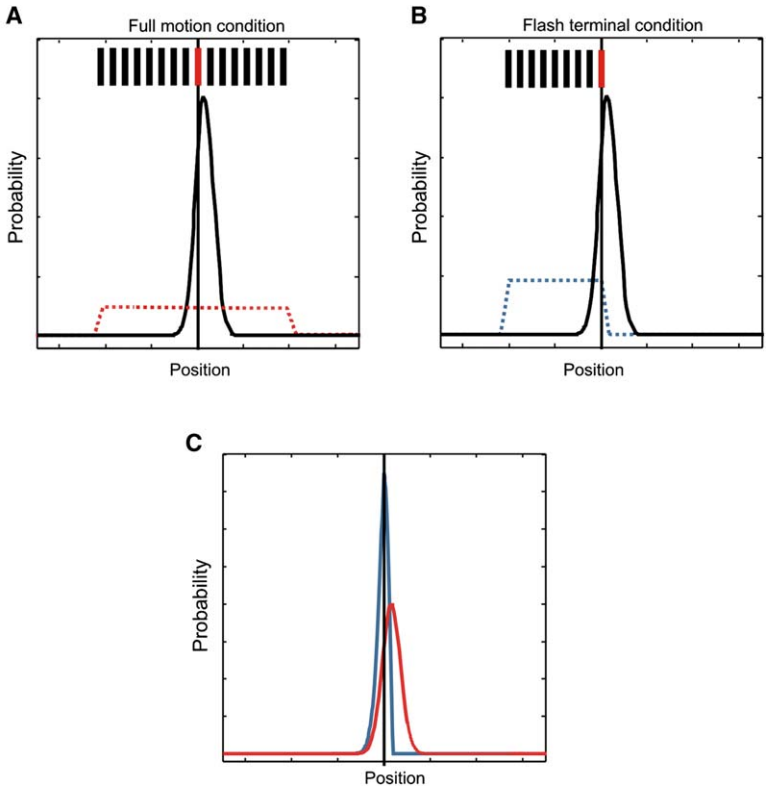

Figure 5. Illustration of Bayesian Model

(A) The black curve shows a hypothetical probability density function for the position of the flash, based on V4 responses in the full-motion condition. The red curve shows the probability density function for the hypothetical color-insensitive area in the full-motion condition. The black vertical line marks the veridical flash location.

(B) The same curves for the flash-terminal condition.

(C) Joint posterior probability for the full motion (red) and flash-terminal (blue) conditions. Note the peak of the curve is shifted in the full-motion condition but not in the flash-terminal condition.

physiology and that holds the potential to account for key properties of related illusions. The bars comprising the apparent motion sequences of the flash-jump illusion are represented across multiple visual areas, some color selective and others color insensitive. Color-insensitive areas would, by definition, be unable to indicate the location of the color change occurring within the motion sequence. Such areas would, however, be able to signal the location of the motion sequence as a whole. In contrast, color-selective areas, such as area V4, can signal the presence of the color change in the motion sequence. Our data, however, indicate that V4 provides a distorted estimate of the position of the color change. Let us consider how the position estimates derived from these different areas might optimally be integrated to form a conjoint estimate of the position of the color change. A Bayesian framework is useful in thinking about how this integration might be achieved. This framework has been effectively applied to account for sensory integration under conditions in which conflicting stimulus representations exist in different feature spaces or sensory modalities (Battaglia et al., 2003; Deneve and Pouget, 2004; Jacobs, 1999).

The outline of this approach in the present case is illustrated in Figure 5. The solid black curve in Figure 5A shows a hypothetical probability density function of the flash location, based on sensory information available in area V4. This distribution is shifted along the direction of the motion trajectory, as it is assumed to be derived from the shifted representation we find in V4. The red dashed curve indicates the probability density function derived from color-insensitive neurons, which are assumed to be blind to the isoluminant color difference that defines the flashed element but are able to signal the presence of the bars comprising the sequence. For simplicity, we illustrate the color-insensitive area estimate as having a flat probability density function, and we assume a flat a priori distribution. Either of these assumptions could be changed so as to favor the positions of bars occurring around the time of the flash without qualitatively changing the result. The solid vertical line shows the actual position of the color change. Under these assumptions, the most likely location of the flash is the product of the two probability functions (Knill and Richards, 1996). This joint posterior probability distribution is illustrated for the full-motion condition by the red curve in Figure 5C. The peak of this joint posterior probability distribution occurs at a location shifted from the veridical flash location, which is indicated by the solid vertical line. Because the color-insensitive area cannot distinguish the flashed element from the other bars in the sequence, the shifted V4 response dominates the joint posterior probability distribution leading to a shifted position estimate.

Now consider the flash-terminal condition. As we have shown, the shift in the V4 responses was undiminished in the flash-terminal condition. Therefore, the solid black curve in Figure 5B, which illustrates the probability density function derived from hypothetical V4 responses, is assumed to be shifted as it was in Figure 5A. The dashed blue curve in Figure 5B illustrates the probability density function derived from hypothetical color-insensitive neurons. These neurons are assumed to unambiguously signal that no bars, of any color, appeared at locations beyond the flash location. The blue curve in Figure 5C illustrates the joint posterior probability distribution derived by multiplying the two probability density functions in Figure 5B. In contrast to the full-motion condition, this

estimate peaks at the veridical bar location, consistent with our psychophysical results that human observers do not perceive a shift in the flash-terminal condition.

Although very simplified, this conceptual framework provides an intuitive way of reconciling our V4 physiology results with perception. The framework is also appealing because it can flexibly incorporate additional data as they become available, such as potential latency differences between color-selective and color-insensitive areas, the effect of prior knowledge about the possible locations of the color change, and the effect of altering stimulus parameters that influence the spatial uncertainty of position estimates (Kanai et al., 2004; Vreven and Verghese, 2005). Future experiments, including collecting behavioral data from monkeys trained to report the perceived location of the flashed element and recording from color-insensitive areas, will be necessary to test the validity of this account. This framework highlights the importance of considering the generation of a sensory percept in terms of processing across neural areas and not simply as resulting from a single mechanism working at one stage of processing.

Experimental Procedures

Electrophysiology

Preoperative magnetic resonance imaging (MRI) was used to identify the stereotaxic coordinates of V4 in two adult male monkeys (*Macaca mulatta*). Each monkey was prepared for recording by implanting a head holding device and a V4 recording chamber, placed over the prelunate gyrus. At the beginning of the study, several penetrations were made in each chamber to ensure that the electrode was in area V4 by RF sizes, topographic organization, and feature preferences.

In each experimental session, electrodes were advanced via a multielectrode drive (Mini-05 microdrive, Thomas Recording, Inc.; 3NRMD-3A microdrive, Crist Instruments). Neuronal signals were recorded extracellularly, and waveforms were stored with the Multichannel Acquisition Processor system (Plexon, Inc.). Single neurons were isolated online for analysis with Rasputin software (Plexon, Inc.) and again offline with Plexon Offline Sorter (Plexon, Inc.). RFs were initially plotted by hand with a flashed bar of the neuron's preferred color. For many neurons, this hand plotting was followed by an automated RF border plotting procedure in which preferred color bars were flashed at eight locations straddling the border that had initially been estimated by hand plotting. Experimental and surgical procedures were approved by the Institutional Animal Care and Use Committee and conformed to NIH guidelines for the care and use of laboratory animals.

Stimuli and Task

Stimuli were presented on a computer monitor (Sony Trinitron Multiscan, TC, 640 × 480 pixel resolution, 120 Hz, background luminance 4.5 cd/m^2) placed 57 cm from the eye. Eye position of humans and monkeys was continuously monitored with an infrared eye tracking system (240 Hz, ETL-400; ISCAN, Inc.). Experimental control was handled by Cortex (http://www.cortex.salk.edu/). The monkeys maintained gaze on a fixation point (0.25 dva) within a 0.75° radius square fixation window. Juice reward was delivered if fixation was maintained throughout the duration of the trial.

The stimulus appeared 200 ms after fixation was attained. The stimulus was an apparent motion sequence: a series of 3° by 0.2° bars presented one after another at equal intervals arranged along a straight trajectory. These motion sequences swept across the cell's RF in each of two opposite directions on separate trials (either up and down or left and right). Two colors from a set of six photometrically isoluminant colors (44 cd/m^2) were chosen: a preferred color that caused the strongest neuronal response when presented alone and a nonpreferred color that elicited a smaller response. On each trial, a single bar within the motion sequence was set to the preferred color, and the other bars in the sequence were set to the nonpreferred color. The locations where the preferred color bar could appear were called the "possible flash locations." Because multiple neurons were recorded simultaneously, stimulus color was optimized for one isolated neuron, and the stimulus was positioned to cross the border of all isolated neurons, if possible. The "flash-terminal" condition was identical to the flash condition, except that the bars after the flashed element were never presented. In the "single-color conditions," the bars were all identical in color.

In Experiment 1, the motion sequence on a single trial was composed of 16 bars. The eight center bars in the sequence were the possible flash locations. The bars were spaced 0.8° apart and presented for one frame each (8.3 ms) with three frames (24.9 ms) of blank time between bar presentations. In order to test with greater spatial resolution, on half the trials, the entire motion sequence was shifted by half the distance between the bars, enabling us test the intervening positions. This interdigitation allowed 16 possible flash locations to be tested at a resolution of 0.4°.

In Experiment 2, two different spatiotemporal configurations were used. In some recording sessions, the motion sequence was composed of 12 bars with the four center bars being the possible flash locations. Spatial and temporal spacing on single trials was identical to the full RF case. Again, on half the trials, the interdigitated positions were tested, resulting in a total of eight possible flash locations tested. In the other configuration, the sequence was composed of 16 bars with the eight center bars being the possible flash locations. On a single trial, the bars were spaced 0.4° apart. The blank time between successive bars was reduced to 8.3 ms to equate velocity across experiments. In this configuration, interdigitation was not used. Results for these two spatiotemporal configurations were similar, and the data have therefore been pooled.

Data Analysis

Each neuron's response to each flashed element was quantified as follows. First, an estimate was made of the neuron's response latency. For highly selective cells, the response to the flashed element was clearly visible and was similar to the latency of responses to the identical element appearing alone at the center of the RF. We therefore used the response to the flashed element appearing alone in the RF center to estimate response latency for each neuron. Latency was estimated as follows. We first computed the average spontaneous firing rate for the neuron by averaging firing rates across all trials over the 100 ms period preceding the onset of the first element in each trial. We fit a Poisson distribution to this mean response and used this fit to determine the 95% confidence bounds for the neuron's spontaneous activity level. Response latency was then defined to be the first 5 ms bin, after the appearance of the isolated flashed element, for which three successive bins were above the 95% confidence level for spontaneous activity.

The neuron's mean firing rate to the flashed element was then computed over a latency-adjusted time window beginning with the onset of the flashed element and ending with the onset of the subsequent element. In the single-color conditions, the latency-adjusted time window was aligned with the onset of each element appearing at one of the eight flash locations. We compared trial-by-trial responses within this time window to the neuron's baseline rate (one-tailed t test, $p < 0.05$) to determine which locations responded significantly ("responsive positions"). The same computation was performed for each flash location and across the two directions of motion.

Receptive field shifts were computed as follows. In the full receptive field experiment (Experiment 1), we first determined the edges of the RF in each tested direction as the positions furthest from the center of the RF that elicited a response significantly above baseline. We then computed the average position, weighted by firing rate including all positions bounded by the edges of the RF. The average in the right or upward-moving sequence was subtracted from the average in the left or downward-moving sequence. In the single-border experiment, the shift was quantified by calculating a comparable Shift Index (SI), which was defined as the number of significantly responsive positions in the inward sequence minus the number of significantly responsive positions in the outward sequence, multiplied by 0.4 (the distance between tested flash positions). Because these shifts are calculated by comparing the response profiles between

two directions of motion, the shift was halved to represent the shift for a single-motion trajectory. This provides a fair comparison with the human psychophysics, which measured the perceptual shift of a flash embedded in a motion sequence versus a stationary comparison bar.

A cell was included for analysis if the following criteria were met in either the full-motion condition or the single-color condition. (1) There were at least two contiguous responsive positions in one motion trajectory and at least one responsive position in the opposing trajectory. (2) There was at least one nonresponsive end position in one motion trajectory. For most neurons recorded in Experiment 2, direction tuning was assessed by comparing responses to a bar sweeping in the two trajectory directions. Neurons were excluded from analysis if they showed significant difference in firing rate to the bar sweeping in these two directions. Seven neurons were excluded from analysis for showing direction tuning. 18 out of 56 neurons were included in the analyzed population even though direction tuning was not measured. When these neurons are excluded from the population the results are unchanged (full motion shift = 0.17 dva, $p = 0.007$; truncated shift = 0.18 dva, $p = 0.002$; single color shift = 0.05 dva, $p = 0.44$).

Color selectivity was calculated by taking the response to the first four bars of the single-color sequences (64 ms or 132 ms depending on the spatiotemporal stimulus parameters used) starting within the cell's RF for both the colors used in the main experiment. Cells were categorized as color-selective if an unpaired t test between the responses for the two colors was significant (two-tailed, $p < 0.05$). To determine the correlation between selectivity and shift index, a selectivity index was calculated as the difference between the preferred and nonpreferred response divided by the sum of the preferred and nonpreferred response. This index was then correlated with the shift index, across neurons.

Psychophysics

Motion sequences were identical to the interdigitated single border experiment except that the sequences were shifted by 1/3 and 2/3 the distance between successive bars, allowing us to sample the shift more densely. This allowed us to test ten possible flash locations with a spatial resolution of 0.266°. The bars in the motion sequence were blue, and the flashed element was an equiluminant red, 44 cd/m^2. All subjects had normal, or corrected to normal, acuity and gave informed consent for participating. Subjects were required to maintain fixation within a 1° radius square fixation window. The sequence was presented 4° below fixation with five possible flash locations occurring in the left hemifield and five in the right. A gray stationary bar (12° by 0.2°, centered 6.5° above fixation, 15 cd/m^2) was present throughout the trial and response period. At the end of the trial, subjects pressed a key to indicate whether the flash occurred to the right or left of center. Subjects were also tested with single isolated flashes to verify their ability to localize flashed bars. If the subject did not perform at least 80% correct at every position with isolated flashes their data was excluded from further analysis. For each position, we computed the percentage of trials on which the subject reported the flash as occurring further along the motion direction than the comparison line at the center. These data were fit with a cumulative Gaussian function, and the position where this function crossed 50% was determined. Perceptual shifts were measured as the distance of this crossing point from 0 (the physical center location).

Eye Movements

We determined eye deviation from fixation at the time the flash occurred on a trial-by-trial basis by averaging the eye position during the 8 ms the element was present on the monitor and subtracting the average eye position during the 8 ms immediately before the onset of the apparent motion sequence. To determine whether eye movements could be the source of our recorded neuronal shifts, we analyzed eye position specifically at locations where the presentation of the flash induced a significant response in one direction but not in the opposing direction (differentially responding locations). For each of these differentially responding locations, we calculated the mean eye position difference across the two directions of motion and defined this to be positive if the eye difference was in the direction that could contribute to the response difference at that location and negative if it was in the opposite direction. We looked at eye position in the dimension that the stimulus was moving (x eye position when rightward and leftward moving stimuli were used and y eye position when upward and downward moving stimuli were used). We then used a one-tailed t test across the population of differentially responsive locations to test whether there was a significant difference in eye position that could contribute to the neuronal shift we recorded. We also calculated the standard deviation of the eye position in each of the two directions of motion at each differentially responding location and compared the standard deviation of the eye position in the responsive and nonresponsive directions. We used a paired t test across all differentially responding locations to test whether responsive and nonresponsive directions differed in the eye position standard deviation.

Supplemental Data

The Supplemental Data for this article can be found online at http://www.neuron.org/cgi/content/full/49/3/447/DC1/.

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