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Attraction of flashes to moving dots

Ozgur Yilmaz [a,*], Srimant P. Tripathy [a,c], Saumil S. Patel [a,b,d], Haluk Ogmen [a,b,c]

[a] *University of Houston, Department of Electrical and Computer Engineering, Houston, TX 77204-4005, USA*
[b] *University of Houston, Center for Neuro-Engineering and Cognitive Science, Houstan, TX 77204-4005, USA*
[c] *University of Bradford, Vision Science Research Group, School of Life Sciences, Bradford BD7 1DP, West Yorkshire, UK*
[d] *University of Houston, College of Optometry, Houston, TX 77204-2020, USA*

Abstract

Motion is known to distort visual space, producing illusory mislocalizations for flashed objects. Previously, it has been shown that when a stationary bar is flashed in the proximity of a moving stimulus, the position of the flashed bar appears to be shifted in the direction of nearby motion. A model consisting of predictive projections from the sub-system that processes motion information onto the sub-system that processes position information can explain this illusory position shift of a stationary flashed bar in the direction of motion. Based on this model of motion–position interactions, we predict that the perceived position of a flashed stimulus should also be attracted towards a nearby moving stimulus. In the first experiment, observers judged the perceived vertical position of a flash with respect to two horizontally moving dots of unequal contrast. The results of this experiment were in agreement with our prediction of attraction towards the high contrast dot. We obtained similar findings when the moving dots were replaced by drifting gratings of unequal contrast. In control experiments, we found that neither attention nor eye movements can account for this illusion. We propose that the visual system uses predictive influences from the motion processing sub-system on the position processing sub-system to overcome the temporal limitations of the position processing system.
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1. Introduction

Spatial localization of objects is one of the fundamental functions of vision. Determining the positions of objects is crucial in analyzing visual scenes, in deducing the spatial relationships between objects, and in interacting with the environment. In general, visual scenes consist of both stationary and moving objects, and the visual system is required to compute their position and motion information simultaneously. Several lines of evidence suggest that motion and position of objects are processed by largely separate substrates in the brain (for a review, see Whitney, 2002).

However, psychophysical, anatomical and physiological evidence for interactions between these two systems also exists. For example, when a stationary bar is flashed in the proximity of a moving stimulus, the position of the flashed bar appears to be shifted in the direction of nearby motion (Whitney, 2002; Whitney & Cavanagh, 2000). Other examples of motion signals influencing the perceived position of stationary targets were reported in Ramachandran and Anstis (1990) and in DeValois and DeValois (1991); the apparent position of a physically stationary window is shifted in the direction of the carrier motion inside the window. Motion-induced illusory position shifts suggest interactions between motion and position systems (McGraw, Whitaker, Skillen, & Chung, 2002; Nishida & Johnston, 1999). However little is known about the function and the details of the underlying mechanisms of these putative interactions.

* Corresponding author. Fax: +1 713 743 4444.
E-mail address: yilmazozgur81@yahoo.com (O. Yilmaz).

In this paper, we suggest that one type of interaction between motion and position systems is of a predictive kind. Predictive strategies for cortical cells (e.g., Kanai, Sheth, & Shimojo, 2004) and *within* the motion system have been previously studied (Grzywacz & Yuille, 1990; Verghese & McKee, 2002; Verghese, Watamaniuk, McKee, & Grzywacz, 1999; Watamaniuk, McKee, & Gryzywacz, 1995). According to the model proposed by Gryzywacz et al., motion detectors send facilitatory anticipation signals to other detectors lying along the predicted trajectory of motion. Thus, computed motion is used to enhance the speed and responsiveness of other motion detectors that are likely to be activated in the near future by the moving object. The model proposed and tested here is similar to these earlier models but has a different locus for the facilitatory signals. In our model, which consists of separate retinotopically organized motion and position systems, computed motion is used to enhance the speed and responsiveness of *position-encoding units* in the position system that are in the predicted path of the moving object. Accordingly, the speed of processing within the position system will be enhanced in the vicinity of moving objects. However, this improvement may involve a cost: under certain conditions, this merging of motion and position information may lead to motion-induced illusory position shifts. We conducted psychophysical experiments that aimed to measure these predicted motion-induced illusory shifts in perceived position.

2. Proposed model for motion–position interactions

In our model, motion and position information are computed in two separate retinotopic maps. Motion information is computed fast and the motion system has relatively low spatial resolution compared to the position-encoding map which has better spatial resolution and relatively lower temporal resolution. We hypothesize that in order to prepare the position system for the moving object, motion signals project to locations in the position map that lie ahead on the anticipated path of motion (see Fig. 1). Through this predictive influence, the speed and gain of the neuronal population in the neighborhood of the probable future trajectory are elevated in the position map.

Previous studies have suggested that illusory position shifts are due to an influence from motion-related brain areas to early areas that encode position (Berzhanskaya, Grossberg, & Mingolla, 2004; Fu, Shen, Gao, & Dan, 2004; Jancke, Erlhagen, Schoner, & Dinse, 2004). Our proposed mechanism and explanation for the illusory position shifts differs from these proposals. In our proposal, the predictive influence from the motion system changes the *gains* of neurons inside a cone as illustrated in Fig. 2a. As shown in Fig. 2b, these gain changes in turn cause a "distortion" in the position map which results in a two-dimensional illusory position shift for a flashed stationary stimulus. Whitney and Cavanagh (2000) reported an illusory position shift of a flashed stimulus in the direction of a nearby
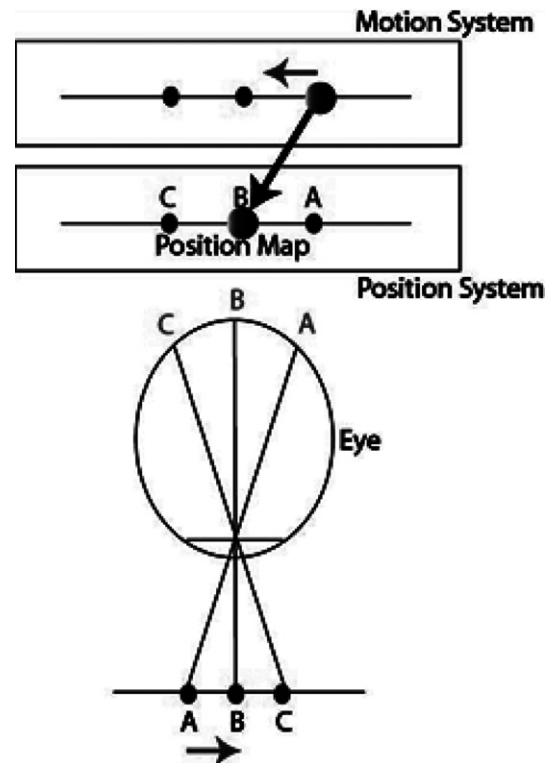

Fig. 1. Illustration of the motion–position interaction postulated in our model. In our model, the position of objects is computed by interactions between two largely independent systems: a relatively slow position system and a faster motion system. Each system encodes information in a retinotopically organized map. When a moving object reaches the point A, it activates the motion detector at that location in the motion map. The motion detector at point A facilitates the position-encoding unit at point B before the moving object reaches the point B, thus speeding up the position system's processing of the moving object when it arrives at B.
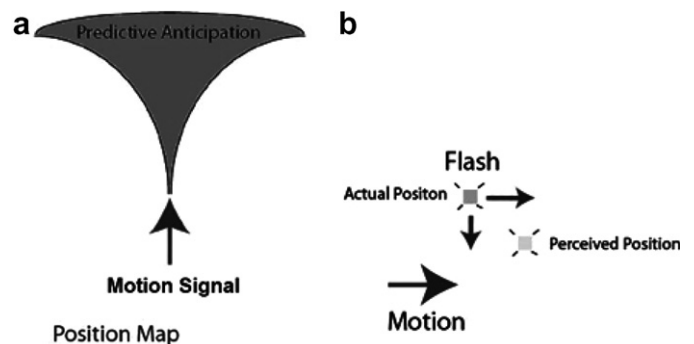

Fig. 2. Predictive anticipation and its influence on position. (a) In a two-dimensional position map, anticipatory signals from the motion system modulate the gain of the position-encoding units along the possible future trajectory of the moving object. The cone represents the spatial extent of gain-modulation in the position map. Within the cone, position encoders closer to the motion signals are more strongly modulated compared to those that are farther away. The arrow represents the retinotopic location of the motion signal in the motion map. (b) Due to the resulting imbalance in the gains of neurons in the position map, the perceived position of the flash is shifted in the direction of motion as well as orthogonally, i.e., in 2D. The large horizontal arrow represents the retinotopic location of the motion signal in the motion map. The perceived position of the flash is shifted along the direction of motion (small horizontal arrow) and attracted towards the motion signal (small vertical arrow).

motion stimulus. According to our model, this motion-induced illusory position shift of the stationary flashed object in the direction of motion is a side-effect of the predictive projections from the motion system to the position system. The two-dimensional influence of the motion signals on the position map also implies an additional illusory position shift *perpendicular* to the direction of motion. We describe below psychophysical experiments that measure this perpendicular component of the motion-induced illusory position shift of a flashed stimulus.

3. Experiment 1: Attraction of flashes to moving dots

If the influence of motion is to provide anticipation then it should distort the (future) locations in the position map that are ahead of the present location of the motion signal. The model implies that the distortion is two-dimensional. Hence, we expect to observe position shifts parallel to the direction of motion (Whitney, 2002) and perpendicular to the direction of motion, i.e., attraction towards the motion stimulus. In order to test the novel prediction of the model for the perpendicular position shift, we measured the illusory mislocalization of a stationary flashed dot in the direction perpendicular to the direction of nearby moving dots. To improve sensitivity, we used a differential measurement technique using two moving dots followed by a flashed dot. Two dots moved from left to right, terminated their motion at the center of the screen and disappeared. After the dots disappeared, a flashed dot was presented vertically midway between the two dots and horizontally to the right of the motion end-points (see Fig. 3).

It is known that high contrast stimuli produce stronger responses in the visual system (Albrecht & Hamilton, 1982; Boynton, Engel, Glover, & Heeger, 1996; Sclar, Maunsell, & Lennie, 1990). Thus, we expect that modulation of the saliency of a moving stimulus should alter the strength of the predictive projections from the motion system to the position system. We therefore measured the illu-

sory vertical position shift of the flashed stimulus as a function of the relative contrast of the two moving dots. The differential contrast of the moving dots is expected to cause a net gain bias in the position map which will be in the direction of the higher contrast moving dot. Consequently, as illustrated in Fig. 4, a flashed dot which is physically between the two moving dots should appear shifted towards the higher contrast moving dot.

3.1. Apparatus

All stimuli were generated via the Visual Stimulus Generator (VSG) card manufactured by Cambridge Research Systems (http://www.crsltd.com). This card was programmed using its driver library and the stimuli were displayed on a 19″ high resolution color monitor with a 160 Hz frame rate. A head/chin rest was used to aid the observer in keeping his/her head still while fixating at the center of the monitor. The distance between the monitor and the observer was 97 cm. Behavioral responses were recorded via a joystick connected to the computer driving the VSG card.

3.2. Methods and stimuli

A 31 ms flash (12.5 cd/sq-m) was presented 21 arc min to the right of the final position of the trajectory of two rightward horizontally moving dots (see Fig. 3; dot velocity = 9.5 deg/s, motion duration = 770 ms, vertical separation = 85 arc min). The moving dots and the flashed dot were squares of side 6.4 arc min. The flash was presented 19 ms after the offset of the moving dots and its vertical
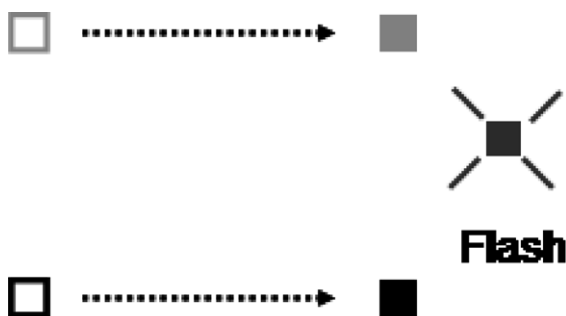

Fig. 3. Schematic of stimuli used in Experiment 1. Two horizontally moving dots (one having a higher contrast) terminated their motion at the center of the screen. On termination of the motion the dots disappeared and then a flash was presented to the right of the terminal locations of the dots and vertically between them. Observers judged which moving dot was perceived to be vertically closer to the flash.
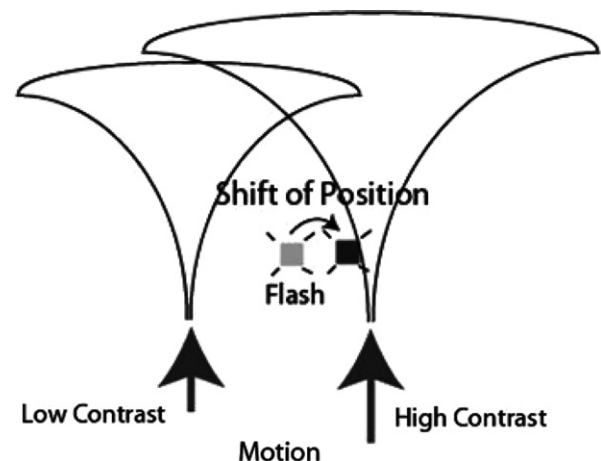

Fig. 4. The instantaneous anticipatory gain modulations due to low and high contrast moving dots on the position map are represented by the closed contours of smaller and larger extent, respectively. The contours represent the position encoders that have the same gain increase. Notice that the iso-gain contour due to the high contrast moving dot is closer to the flash than that due to the low contrast moving dot. The aggregate influence is that the position encoders to the right of the flash have a higher gain than those to the left thus causing a rightward shift in the perceived position of the flash relative to its physical position.

position was between the two motion trajectories. In many of the earlier studies that examined motion-induced position shifts (see Whitney, 2002, for a review) the flashed stimulus was presented during motion of the inducing stimulus. In the current study, the flash was presented after the inducers terminated and its location was to the right of the moving dots' last position because we were interested in the distortions in visual space ahead of the moving stimuli. One of the moving dots had a fixed luminance of 50 cd/sq-m and the luminance of the other dot varied from 50 to 10 cd/sq-m (i.e., contrast ratios ranged from 1 to 5). To minimize variability in the stimulus, the higher luminance dot was always presented below the lower luminance dot. This constraint was relaxed in Experiment 4 to ensure that the perceived mislocalizations did not result from potential biases from the fixed arrangement of the two dots. The background field was uniform and had a luminance of 5 cd/sq-m. From trial to trial, the vertical position of the flash was varied using the method of constant stimuli. Observers were asked to binocularly fixate the center of the screen where the flash was presented. A fixation target was not presented as this might have provided relative position cues that could be used to judge the flash's position. The observers' task was to indicate, by pressing one of two joystick buttons, which of the moving dots was perceived to be spatially closer to the flash. Two naïve observers and one author participated in this experiment. Observers in all experiments in this paper had corrected visual acuity of 20/20 or better and normal binocular vision and they participated after voluntarily granting informed consent.

3.3. Results

Psychometric functions were obtained from each observer's responses and the bias in the perceived position of the flash was estimated using probit analysis. Because the background luminance was held constant in all our experiments, luminance ratios and contrast ratios are equivalent and are used interchangeably throughout this paper. For each value of the contrast ratio, a psychometric function was plotted with the vertical distance of the flash, measured relative to the high contrast dot, along the abscissa and the percentage of trials that the flash was perceived closer to the high contrast dot along the ordinate. The bias corresponds to the 50% point on these psychometric functions. As shown in Fig. 5, the results of Experiment 1 indicate that the perceived position of the flash averaged across the three observers is vertically shifted in the direction of the high contrast moving dot.

The average illusory vertical shift increases systematically as the contrast ratio of the moving dots increases. A linear regression analysis of the data pooled from all the observers indicates that the contrast ratio of the moving dots significantly affects the perceived position of the flashed dot (regression slope = 0.54, $p = .0003$, adj. $R^2 = .84$).
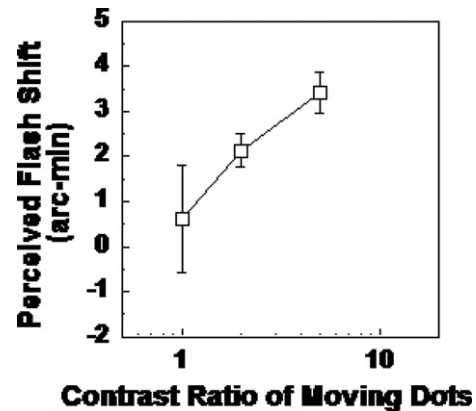

Fig. 5. Results of Experiment 1. The perceived position of the flash relative to its physical position is plotted as a function of the contrast ratio of the moving dots. Positive shifts correspond to attraction of the flash towards the high contrast moving dot. Data represent mean of three observers ± 1 SEM.

4. Experiment 2: Attraction of flashes to drifting gratings

We repeated Experiment 1 using drifting gratings instead of moving dots as our motion stimulus. The moving stimuli in the experiments of Whitney and Cavanagh (2000) were drifting gratings and they produced a position shift in a flashed stimulus, the shift being in the direction of motion. Thus showing a position shift in a flashed stimulus in a direction perpendicular to the direction of motion of a drifting grating is important for comparison and continuity. More significantly, it is important to investigate how the illusory position shift changes for spatially localized motion signals compared to spatially distributed motion signals (as in Experiment 1).

4.1. Methods and stimuli

As shown in Fig. 6, the moving dots in the previous experiment were replaced by drifting gratings with a spatial frequency of 1 cycle/deg and a temporal frequency 2.67 Hz. The duration of the drifting grating was 1 s. Each drifting grating was a square of side 3.5 deg. The gratings disappeared after their motion was terminated and 19 ms later a 31 ms duration flash (12.5 cd/sq-m) was presented 21 arc min to the right of the right edge of the gratings. The average vertical position of the flash was midway between the two moving stimuli with the actual position being varied between trials according to the method of constant stimuli. One of the drifting gratings had higher contrast than the other. The maximum and minimum luminance values of the high contrast grating was 50 and 5 cd/sq-m, respectively, and the Michelson contrast of the higher contrast grating was fixed at 0.82. The low contrast grating had also minimum luminance value of 5 cd/sq-m but the maximum luminance value varied between sessions. The contrast ratio of the two gratings varied from 1 to 2.5 between sessions. The uniform background field had a

Fig. 7. Results of Experiment 2. The perceived position of the flash relative to its physical position is plotted as a function of the contrast (Michelson) ratio of the moving gratings. Positive shifts correspond to attraction of the flash towards the high contrast drifting grating. Data represent means of three observers ± 1 SEM.
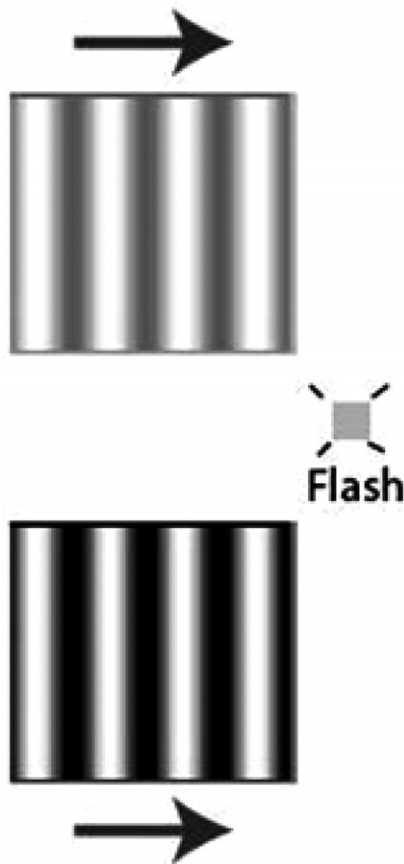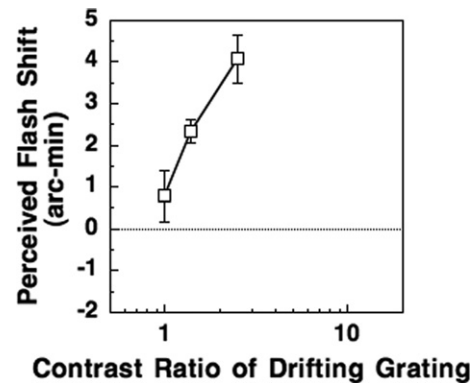

Fig. 6. Stimuli used in Experiment 2. After the two gratings (one having a higher contrast) stopped drifting and disappeared, a flash was presented to the right of the gratings and vertically in the middle. Observers judged which grating was perceived to be vertically closer to the flash.

luminance of 5 cd/sq-m. Observers fixated at the center of the screen where the flash was presented. No fixation stimulus was presented. The observers' task was to indicate which drifting grating was perceived to be closer to the flash. Three observers (two naïve) participated in this experiment.

4.2. Results

Psychometric functions were fit and the bias in the perceived position of the flash were estimated as in the previous experiment. The results of this experiment (Fig. 7) are similar to those of Experiment 1, but the slope of the linear fit is steeper (regression slope = 2.075, $p = .0007$, adj. $R^2 = .87$).

5. Experiment 3: Is motion of dots necessary for the illusion?

Previous research has shown that attentional influences may cause illusory mislocalizations (Suzuki & Cavanagh, 1997; also see Suzuki & Cavanagh, 1998). It is therefore possible that attention could have created a distortion by modulating the position map around a high contrast target differently than a low contrast target. Because we always

presented the high contrast target below the low contrast target in Experiments 1 and 2, there could also be a vertical static bias in judging the position of the flash. In order to test these possibilities, we replaced the moving dots in Experiment 1 by either flashed dots (flash-inducer condition) or flickering dots (flicker-inducer condition) in two separate control experiments. Failure to find illusory shifts of a flashed target in flash-inducer and flicker-inducer conditions will provide evidence that motion of the inducers is necessary for the illusory position shifts observed in the first two experiments. It will also rule out the presence of a systematic vertical bias.

5.1. Methods and stimuli

As illustrated in Fig. 8, instead of motion stimuli (moving dots or gratings), in the first control experiment (flash-inducer condition) two flashes of 19 ms duration were used. In the second control experiment (flicker-inducer condition) flickering dots of 19 ms onset duration, 38 ms offset duration (i.e., 17.5 Hz with 33% duty cycle) and 1.1 s total duration were used. The location of each flashed or flicker-
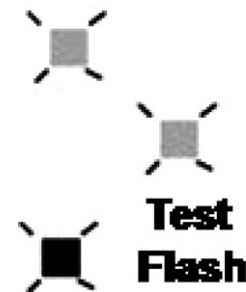

Fig. 8. The display configuration used in Experiment 3. For the control experiment, either flashed dots or flickering dots were presented at the terminal positions of the two-dot moving stimulus of the first two experiments. As in Experiments 1 and 2, the test flash was presented to the right of the inducing stimuli. The task of the observer was to report which dot was perceived to be vertically closer to the test flash.

ing inducer-dot matches the last position of the corresponding apparent motion stimulus in Experiment 1 and the closer right corners of the corresponding drifting grating in Experiment 2. A test flash was presented 19 ms after the termination of the flashing or flickering inducers as is the previous experiments. Only the highest contrast ratio of 5 was tested in both control experiments. Three observers (two naïve) participated in these experiments.

5.2. Results

As shown in Fig. 9, there is no evidence of an illusory position shift of the flashed dot in these control experiments, (t-test: $t = 1.394$, $df = 2$, $p = .3$ for flashed dots and $t = 1.075$, $df = 2$, $p = .4$ for flickering dots) which suggests that motion is necessary for the illusory position shift of nearby flashed objects and that contributions of factors other than motion are negligibly small.

6. Experiment 4: Do eye movements contribute to the illusion?

Eye movements are known to cause illusory mislocalizations (e.g., Ross, Morrone, & Burr, 1997). In Experiments 1 and 2, motion was always from left to right. This might induce involuntary eye movements in the horizontal direction. If there is a vertical drift towards the more salient stimulus at the time that the flash was presented, then the flash could be mislocalized closer to the salient stimulus. In addition, a fixation stimulus was not used in the first two experiments in order to avoid a static reference that might serve as a cue for position judgments. However, due to lack of a fixation stimulus, observers might fixate closer to one of the moving dots or drifting gratings (more likely closer to the high contrast stimulus) and previous studies (e.g., Mateeff & Gourevich, 1983) have suggested

that peripheral stimuli may appear closer to fixation than they actually are. Even though the lack of fixation might affect both motion experiments (1 and 2) and the control experiment (3), the amplitude of this effect might be larger when there is motion, since involuntary eye movements might influence the fixational focus. Thus, eye position bias towards the high contrast stimulus might be one possible source for the mislocalizations that we observed. We conducted an additional experiment to rule out this possibility.

6.1. Methods and stimuli

As illustrated in Fig. 10, there were four moving dots, two each on the left and right side of the screen, moving towards the center. A fixation cross was presented in the middle of the screen while the dots were in motion. The fixation cross disappeared when the dots finished their motion. The speed of the moving dots was the same as in Experiment 1 (9.5 deg/s) and the length of the trajectories was 1.78 deg. The vertical distance between each pair of moving dots was 0.7 deg. The moving dots terminated their motion and disappeared at 2.48 deg eccentricity. Nineteen milliseconds after the disappearance of the moving dots, two flashes were presented on either side of fixation at 2.13 deg eccentricity. The luminance of the two flashes was 6.25 cd/sq-m and their duration was 93 ms. As in previous experiments, the uniform background field had a luminance of 5 cd/sq-m. On each side, one of the moving dots had a higher luminance (50 cd/sq-m) than the other and the contrast ratio changed in different sessions. The high and low luminance moving dots were placed in reverse order for left and right sides of the screen. For example, when the high luminance moving dot was in the upper and the low luminance moving dot was in the lower portion of the left side of the screen, the opposite was true for the right side of the screen. In this experiment, if there is an attraction of flashes towards the high contrast moving dots, then we should observe a relative vertical offset between the flashes when their physical alignment is horizontal. Observers' task was to report which flash was perceived to be higher than the other. The method of constant stimuli was used and the offset between the flashes was var-

Fig. 10. Stimuli used in Experiment 4. Two moving dots (one having a higher contrast) were presented in left visual field and two moving dots were presented in the right visual field. The contrast configuration of the pair of dots in the left visual field was opposite of that in the right visual field. The pair of dots in the left (right) visual field moved rightward (leftward). Two flashes were presented when the dots finished their motion. The task of the observers was to fixate on the fixation cross and report which of the two flashes was perceived to be vertically higher in the display.
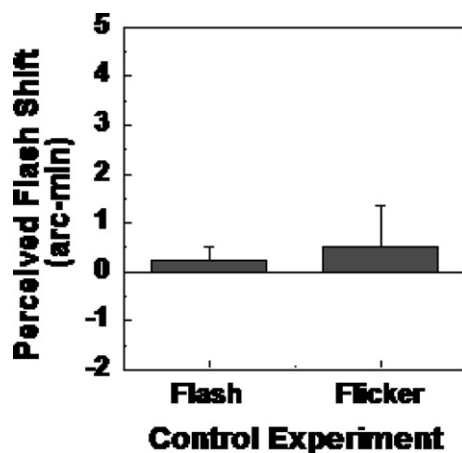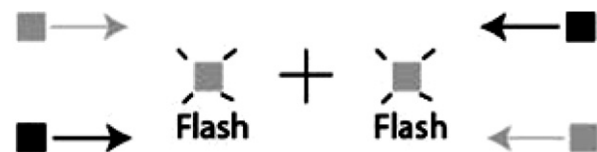

Fig. 9. Results of Experiment 3. The perceived position of the flash relative to its physical position is plotted for the flash and flicker control conditions. Positive shifts correspond to attraction of the flash towards the high contrast flashed or flickering dot. Data represent means of three observers ± 1 SEM.

ied between trials to obtain the psychometric function (the offset between the two flashes along the abscissa and the percentage of trials that the right flash was seen above the left flash along the ordinate). The point of subjective alignment was computed from the psychometric function. The placement of high and low luminance moving dots (which one will be above for left and right sides) was randomly changed from trial to trial to avoid biases, and the points of subjective alignment for the two conditions were averaged. Two observers (one naïve) participated in this experiment.

6.2. Results

The results of Experiment 4 are shown in Fig. 11. Qualitatively the results are similar to those obtained in Experiment 1: flashes are perceived to be closer to the high contrast moving dots. As the contrast ratio of the moving dots is increased, a significant increase in the position shift of the flashed dots is observed (regression slope = 0.352, $p = .003$, adj. $R^2 = .75$). On the other hand, the magnitude of illusory shift in this experiment is reduced compared to those in Experiments 1 and 2 (regression slopes of 0.54 and 2.075 in Experiments 1 and 2, respectively, vs. regression slope of 0.35 in this experiment). The results of this experiment therefore suggest that even though eye movements and lack of fixation target are not likely to be the factors causing the motion-induced illusory position shift of a nearby flashed object they may have contributed to magnify the illusion.

7. Experiment 5: Spatial extent of motion–position interactions

The same experimental paradigm that was used for Experiment 4 is used in this experiment. In this experiment,

the contrast ratio of the moving dots was fixed at 10 and the vertical separation between the moving dots was varied in order to map the spatial extent of the interaction between the motion and position systems, and to quantify the effect of distance on the illusory shift of the position of the flashes. As we propose that motion *locally* distorts the position map, a decrement in the illusory position shift is expected as the distance between the moving dots and the flash is increased. The results agree with this expectation. As shown in Fig. 12, there is a significant decrease in the amount of illusory position shift with increase in distance between the flash and the moving dots (regression slope = −0.04, $p = .009$, adj. $R^2 = .81$) and the illusory position shift is negligibly small when the distance between the two moving dots is approximately 2 deg. These data indicate that motion locally distorts the position map and they provide a quantitative constraint for our model.

8. Modeling the proposed predictive influence by motion signals

In this paper, we have proposed that the position computation system, which has high spatial resolution but is slow, is assisted by predictive signals from the fast motion computation system to improve the overall spatio-temporal resolution and signal-to-noise ratio of the visual system. This anticipatory motion influence enhances the responsiveness of the position-encoding units that lie in the predicted path of motion. In our model, this is achieved by direct connections from the retinotopic motion map to the retinotopic position map. Through these connections, the motion system stimulates the regions in the position map that are likely to correspond to the loci of the moving object's future trajectory (Figs. 1 and 2). A side-effect of this predictive strategy is suggested to be illusory position shifts for flashed objects. However, flashed objects are rare
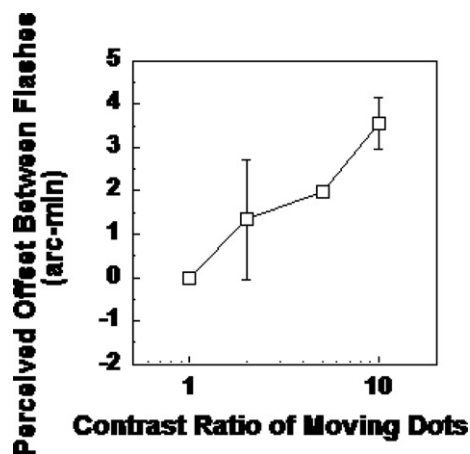

Fig. 11. Results of Experiment 4. The offset between the perceived positions of the two flashes is plotted as a function of the luminance ratio of the moving dots. Positive shifts correspond to attraction of the flash towards the high contrast moving dot. Data represent means of two observers ± 1 SEM. Note that the illusory offsets shown in this figure have to be halved for comparison with those in Figs. 5, 7 and 9.
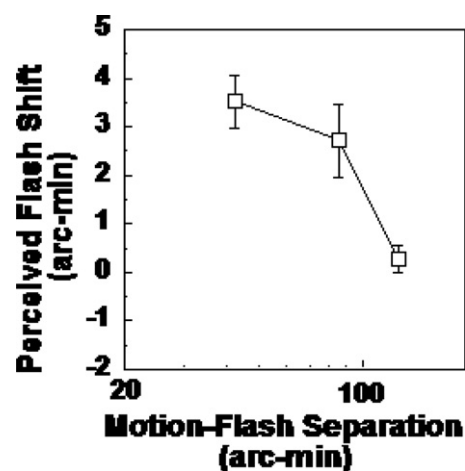

Fig. 12. Results of Experiment 5. The offset between the perceived positions of the two flashes is plotted as a function of the distance of the flash from the moving dots. The contrast ratio of the moving dots in Experiment 5 was 10. Data represent means of two observers ± 1 SEM.

in natural vision and this side-effect is not expected to have a large effect on the overall localization performance in humans. In the laboratory environment, motion-induced illusory mislocalizations can be measured and there are several studies that investigated the effect of motion on position. Whitney and Cavanagh (2000) reported that a flashed stimulus is shifted in the direction of nearby motion. Our model suggests that the nearby motion signals would distort the position map in two dimensions, thus we expected to see an illusory position shift of a flash perpendicular to the direction of motion as well as along the direction of motion (Fig. 2b).

We assume that the strength of the interaction from the motion system onto the position system depends on the saliency (contrast in our experiments) of the motion stimulus. We used an experimental design in which a flash was presented between two horizontal motion signals of different contrasts. If the influence of the motion signals on the position map extends in two dimensions, then the flash would be vertically misaligned in the direction of the higher contrast motion stimulus. In agreement with this prediction, we found that the flash presented between two moving dots of different contrasts is vertically mislocalized towards the high contrast moving dot (Fig. 3). Qualitatively, the same result was obtained when moving dots were replaced with drifting gratings.

Suzuki and Cavanagh (1997) have shown that attention can cause illusory mislocalizations and suggested that attention might distort the position map. We did two control experiments to determine if attention by itself can account for our results. We found that if motion is removed from the stimulus by just flashing or flickering the previously moving dots, there is no illusory vertical shift of a flash towards the high contrast dot. This is not contradictory to the findings of Suzuki and Cavanagh since the difference in luminance of the dots might not have caused a substantial difference in the underlying attentional signals, and two flashed or flickering dots in our experiments might not be differentially distorting the position map, hence their effects may be canceling each other out. However, this is not the case for motion stimuli and the contrast of the motion stimulus is an important parameter for its effect on the position map.

Two other issues that needed addressing were possible involuntary eye movements and the lack of a fixation cross in Experiments 1 and 2. Both eye movements and the location where observers fixate are known to influence position judgments (Mateeff & Gourevich, 1983; Ross et al., 1997). Because the first two experiments did not use a fixation stimulus, we designed another experiment to test if these two factors could account for our data. In this experiment, to minimize horizontal eye movements we used opposite directions of motion for the left and right visual fields and a fixation cross in the center of the screen (Fig. 10). Qualitatively, our results did not change: flashes were shifted towards the high contrast moving dot. However, the magnitude of the illusory shift in this experiment was

reduced compared to that in the first two experiments, probably because of the fixation cross supplying a steady position cue that may have partially nulled the illusory mislocalization. The results of the four experiments suggest that the illusory mislocalization that we report is caused by a two-dimensional influence of nearby motion signals, and this motion influence is localized in a finite neighborhood since the magnitude of illusory vertical mislocalization of the flash decreases as the separation between the flashes and the motion stimuli is increased (Fig. 12).

In our model, the interaction from the motion system modulates the gain of the position-encoding neurons residing in the position map. In Fig. 4, we illustrate how the modulation of neural gains within the position map can cause an illusory position shift of a stationary flashed stimulus.

In order to quantitatively test the idea illustrated in Fig. 13, we built a simple mathematical model and simulated that model in order to assess the mechanisms underlying the illusory position shifts obtained in previous experiments and experiments in this paper. To clearly understand the mechanisms underlying the illusory position shift, in our first simulation we used only one spatial dimension in the model. The position of a flash stimulus was represented by a scaled Gaussian type function (denoted by $P(x)$ with $\mu = 0$, $\sigma = 2$) in a one-dimensional position map denoted by x. The modulation in the gain profiles of the position encoders in the position map due to each motion signal were also modeled as Gaussian functions (denoted by $M_1(x)$ with $\mu = -4$, $\sigma = 3$ and $M_2(x)$ with $\mu = 4$, $\sigma = 3$), The net influence of two motion signals on the distribution of activity in the position encoders due to the flash was modeled as gain modulation

$$P_{\mathrm{mod}}(x) = \mathrm{Norm}\{P(x) + [M_1(x)P(x)]^2 + [M_2(x)P(x)]^2\} \quad (1)$$

where
$P(x)$: activity in position encoders due to the flash in isolation, i.e., solid curve in Fig. 13,
$P_{\mathrm{mod}}(x)$: activity in position encoders due to the flash and the two motion signals, i.e., dashed curve in Fig. 13,
$M_1(x)$, $M_2(x)$: the modulation in the gain profile of the position encoders due to the two moving dots, i.e., dotted curves in Fig. 13.
Norm{•}: it normalizes the peak of the activity in the position encoders to unity.

Note that in Eq. (1), since $M_1(x)$ and $M_2(x)$ simply serve as modulatory influences, afferent activity is required for their influence to be observed in the position computation process. The experiments reported in this paper were simulated by utilizing two modulatory influences, one of them being stronger than the other (compare dotted curves in Fig. 14). In this case, according to Eq. (1), the centroid of the modulated activity in the position encoders is biased towards the stronger modulatory influence, i.e., the higher contrast moving dot (see Fig. 13, dashed curve). The modulated activity in the position encoders also has a lower
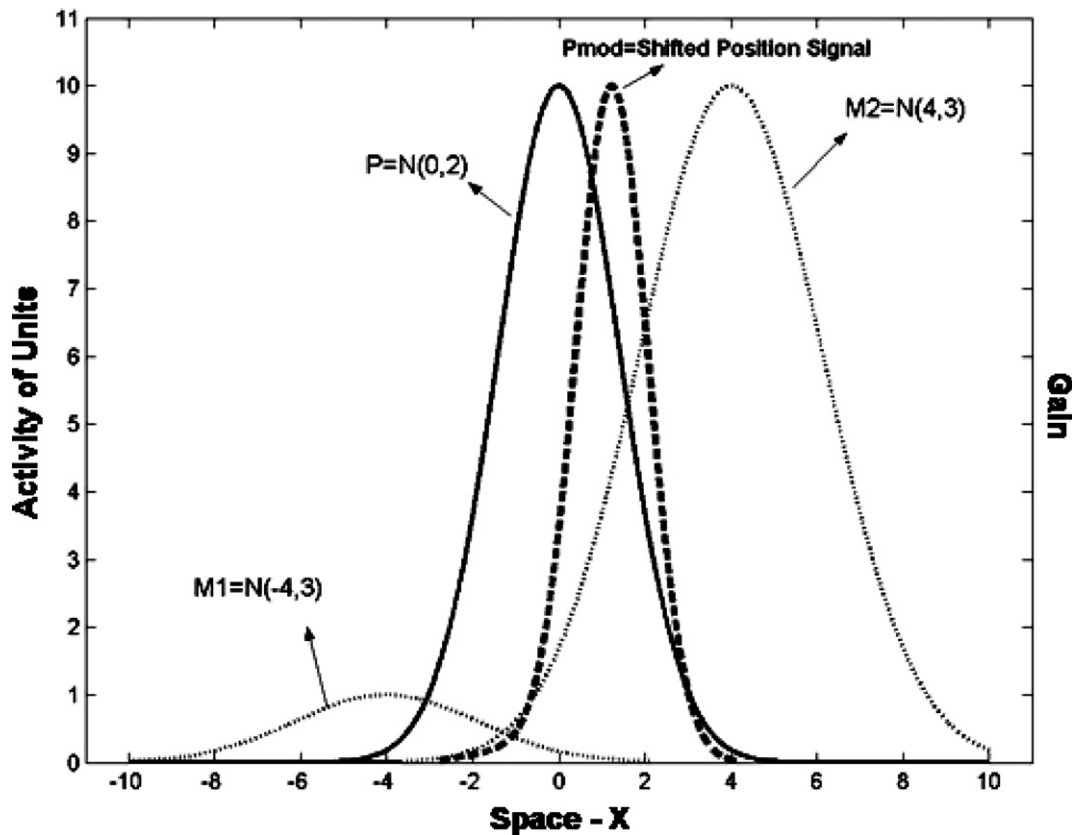
Fig. 13. Illustration of how our model explains illusory position shift of a flashed object towards a more salient moving object. In this plot the *x* axis represents the position map and the *y* axis corresponds to activity of neurons encoding the positions in the map as well as the gain of the position encoders. The solid curve ($P(x)$: Gaussian type function with $\mu = 0$, $\sigma = 2$) represents activity produced in the position encoders by a flash in isolation (i.e., without modulation by motion). The dotted curves ($M_1(x)$: Gaussian type function with $\mu = -4$, $\sigma = 3$; $M_2(x)$: Gaussian type function with $\mu = 4$, $\sigma = 3$) represent the modulation in gain profiles of the position encoders due to the two dots moving in a direction orthogonal to the dimension represented by the *x* axis. Note that the parameters of the Gaussian type functions are in arbitrary units and the predictions are qualitative rather than quantitative. The dashed curve ($P_{mod}(x)$) represents the activity in the position map corresponding to the flash after the net modulation by the two moving dots. Note that the modulation of gain profiles only occur due to dot motion and not due to dot flicker. Although, there might be gain modulations on the position map due to attentional influences when dots flicker, this is not part of our current model.

standard deviation, i.e., the population activity was sharpened. Even though squaring was used to combine the influences from the two motion signals in Eq. (1) and Fig. 13, we also tested other exponents (0.1–5). We found that, as the power gets higher, the magnitude of the position shift becomes greater. The exponent determines the nature of the competitive interactions among the modulatory influences on the position map. When the exponent is large, a winner-take-all type of computation is expected since the difference in the magnitude of the modulatory influences is magnified (Grossberg, 1988).

In order to test if the same model can explain the illusory position shift of a flash in the direction of nearby motion (Whitney & Cavanagh, 2000), we repeated the simulation using two spatial dimensions in the model. In the upper panels of Fig. 14, the two-dimensional (2D) gain profile of the position encoders in the position map and the activity in the position encoders due to a flash are represented separately. The 2D gain profiles due to the influence of the two moving dots (the predictive cones as in Fig. 2) are represented by slices of 1D Gaussians in the *x*

dimension with increasing standard deviation in the *y* dimension (see mathematical details in caption of Fig. 14). Note that the motion of the two moving dots is in the *y* direction. The activity of the position encoders due to the flash is represented by a two-dimensional (2D) Gaussian (Mean = 0, $SD_x = 2$, $SD_y = 2$). In the bottom panel of Fig. 14, the plots in the top panel are superimposed for comparison. A two-dimensional equivalent of Eq. (1) was used to compute the modulated position of the flash. Fig. 15 shows the effect of gain modulations on the representation of the flash. As seen in this figure, the modulated activity of the position encoders due to the flashed stimulus is shifted along the direction of motion, i.e., *y* axis and is attracted towards the high contrast moving dot.

9. Discussion

The proposed interaction from the motion system to the position system could increase the processing speed for computation of position and could be useful for computing
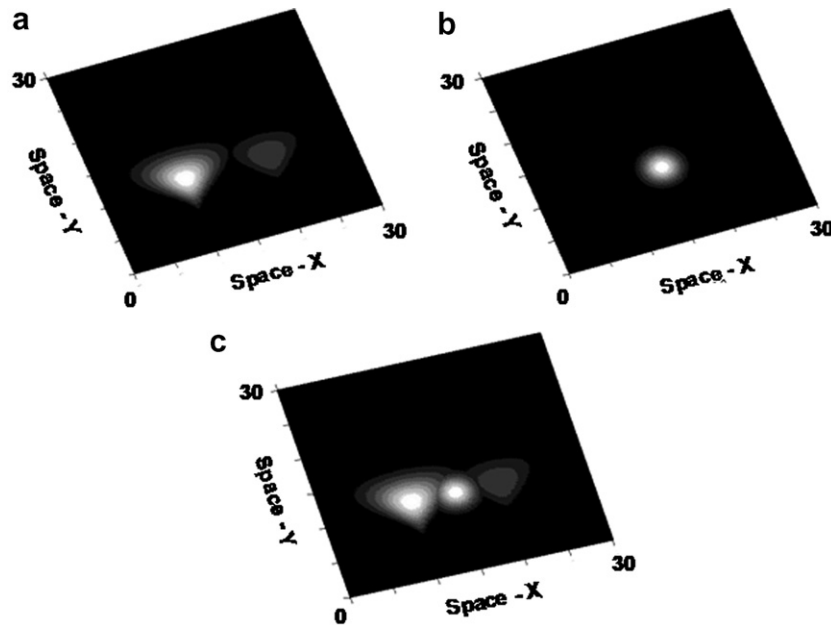
Fig. 14. Illustration of the instantaneous two-dimensional predictive influence from the motion system onto the position map. (a) The two cone like shapes (up-left) represent change in gains (from a baseline gain) of the neurons in the position map, due to the two dots moving in a direction orthogonal to the dimension represented by the x axis. The cones are described by the function: $M(x,y) = G(\text{contrast}) * e^{\left(\frac{-x^2}{\sigma_x^2} - \frac{-y^2}{\sigma_y(x)^2}\right)}$ where, $\sigma_y(x) = \sigma_0 + 0.2\sigma_0 x, \sigma_x = \sigma_0 = 3$, $G(\text{contrast})$ is 10 for high contrast and is 1 for low contrast moving dot. (b) The Gaussian represents a flash and is modeled as a two-dimensional Gaussian ($\mu = 0, \sigma_x = \sigma_y = 2$). (c) The cone and the flash are superimposed in this plot in order to facilitate visualization of the different elements modeled.

the position of moving objects. While the anticipatory mechanism speeds up the responses of position-encoding neurons, it might be producing two-dimensional illusory mislocalizations for briefly flashed objects (Whitney & Cavanagh, 2000; Yilmaz, Patel, Tripathy, & Ogmen, 2006) as well as moving objects (Chung, Patel, Bedell, & Yilmaz, 2007; DeValois & DeValois, 1991; Ramachandran & Anstis, 1990). The model proposed here differs from the previous models (Berry, Brivanlou, Jordan, & Meister, 1999; Fu et al., 2004; Ogmen & Gagne, 1990; Whitney, Cavanagh & Murakami, 2000) in that our source of position-anticipation comes from a distinct system directly tuned to the direction of motion; anticipation is not due to asymmetric connections/dynamics or gain control mechanisms inside the system that computes position. This separation provides flexibility in the adjustment of anticipation according to the needs of the visual task or the environmental conditions.

Could contrast adaptation have contributed to the illusory position shift reported in this paper? Adaptation is likely to be larger for the high contrast moving stimulus than the low contrast moving stimulus (Blakemore & Campbell, 1969), thus the effective gain of the neurons that encode the position of the high contrast stimulus should be reduced relatively more. Therefore, a contrast adaptation effect would predict a flash mislocalization in the opposite direction, i.e., the flash should be shifted towards the low contrast stimulus.

Attraction of flashed stimuli towards stationary salient objects in a memory task has been shown by Sheth and Shimojo (2001). Recently Watanabe and Yokoi (2006) also found two-dimensional mislocalizations of flashed dots around a moving object. A flashed white disk was presented at various locations with respect to a moving black disk. After the presentation of the flashed and moving disks in a given trial, a stationary black and a stationary white disk appeared on the screen. The stationary black disk was placed at the center of the screen. The relative position of the stationary white disk with respect to the stationary black disk was equal to the relative position of the white flashed disk with respect to the position of the black moving disk during the motion sequence. The task of the observers was to adjust the position of the stationary white disk "to indicate the perceived position of the flash relative to the black disk" (Watanabe & Yokoi, 2006). The perceived position of the flashed disk relative to the black disk was found to be displaced in two dimensions: in a direction parallel and perpendicular to the direction of motion. While there are some similarities between their findings and ours, it is difficult to compare their results directly to ours: when comparing the relative position of the flash with respect to the moving target, differential latencies (Ogmen, Patel, Bedell, & Camuz, 2004; Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney & Murakami, 1998) are likely to induce significant relative offsets parallel to the direction of motion influencing the horizontal components of their findings. Our data would be relevant to the vertical component of their findings. Observers in Watanabe and Yokoi's experiments had to memorize the relative positions of the flash with respect to the moving dot, and adjust the relative positions of two static reference targets presented after the motion sequence to match the memorized offset.
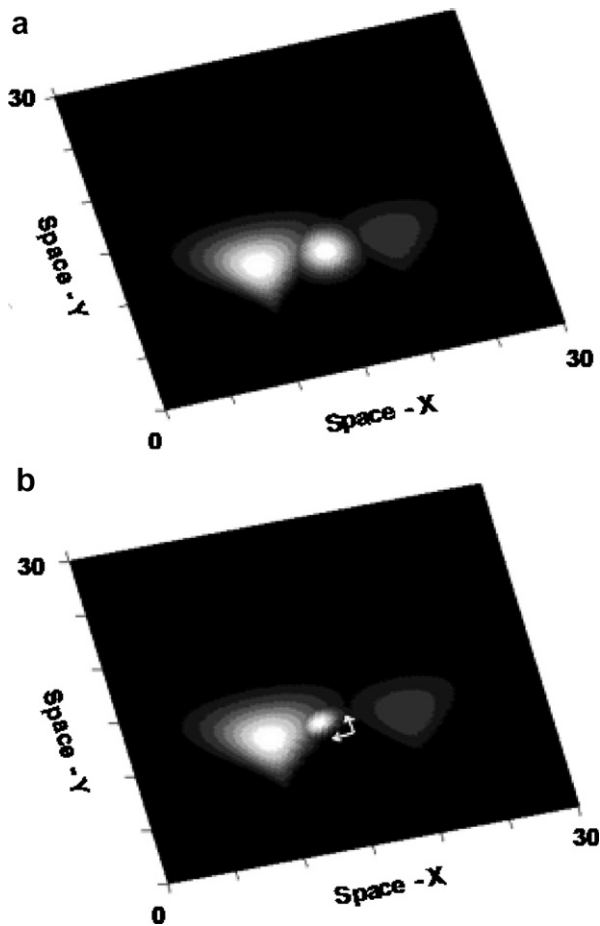
Fig. 15. Illustration of the model's prediction of the illusion. (a) Fig. 14c is replotted to show the representation of the flash before the modulation due to motion. (b) The representation of the flash after modulation due to motion is shown. When compared to the activity of the flash in (a), the centroid (also peak location) of flash's activity is shifted along the direction of motion (arrow parallel to *y* axis) and attracted towards the high contrast moving dot (arrow parallel to *x* axis). The population activity that represents the flash is also sharpened.

In our task, the observers reported directly which of the two moving stimuli appeared closer to the flash. Therefore, Watanabe and Yokoi's task is likely to be more sensitive to memory effects which are known to distort spatial judgments (Sheth & Shimojo, 2001). Because the magnitude of the illusory displacement perpendicular to the motion (vertical) in Watanabe and Yokoi's study was substantially smaller than that for the horizontal direction, it is likely that their method was not sufficiently sensitive to reliably measure small offsets that we report.

The existence of separate systems for motion and for position is supported in the vision literature. Thus in our model we assume that distinct specialized sub-systems analyze the position and motion of objects. Receptive field (RF) sizes of neurons get larger as one goes higher in the hierarchy of the stages of visual processing. Since RF size plays an important role in determining the spatial resolution of the information encoded by a neuron, the neural substrate that encodes fine spatial position is likely to be located at the early stages of the visual system (Hupe, James, Girard, Lomber, Payne, & Builler, 2001; McGraw et al., 2002). Lesioning, imaging and physiological studies indicate the involvement of area MT in the brain (among others) for the processing of some forms of motion (Allman, Miezin, & McGuinness, 1985; Dubner & Zeki, 1971; Maunsell & Van Essen, 1983; Newsome & Pare, 1988; Parker & Newsome, 1998; Salzman, Britten, & Newsome, 1990). Neurons in MT are direction/speed tuned, some of which signal local motion inside their relatively small RFs and some signal global motion with much wider RFs. MT is one of the most extensively studied areas in the brain, and the neuronal activity in MT has been correlated with motion perception in many separate studies (e.g., Parker & Newsome, 1998).

Hupe et al. (2001) investigated the timing of the influence of area MT on V1, V2 and V3 neurons. They showed that inactivation of MT neurons affected even the first 10 ms of the responses in lower order neurons. It has been known that the early wave of activity coming from magno LGN layers reaches V1 on average 20 ms earlier than activity from parvo neurons. During these 20 ms, the activity from magno neurons can be passed to higher cortical areas (e.g., MT) and the results of the computation can be fedback to V1 in time for the arrival of parvo wave of activity (Bullier, 2001). Also, recent studies have indicated a direct projection from LGN to MT bypassing V1 (Sincich, Park, Wohlgemuth, & Horton, 2004). Parvo-related cortical sites are more suitable candidates for encoding position with their small RFs. The interaction of early feedback from higher motion-related areas with late feed-forward activity from parvo neurons may be essential for the high fidelity computation of position particularly for moving objects.

Several studies have investigated the influence of MT feedback on LGN neural responses. Jones, Wang, Andolina, Salt, and Sillito (2002) enhanced the activity in MT and recorded from LGN neurons. They observed marked changes in the responses of magno, parvo and konio cells. Based on the transmission times, they concluded that LGN parvo neurons might be influenced by MT feedback before their activity reaches the cortex. Rockland and Knutson (2000) used retrograde tracers to unravel the feedback connections from MT to V1. In central vision they found that, MT feedback terminates only in layers 4B and 6. Labeling studies of Anderson, Martin, and Whitteridge (1993) suggest layer 6 of V1 projects only onto parvo layers of LGN. Thus, via V1 (layer 6) MT can affect the responses of LGN parvo neurons. Layer 6 neurons in V1 are known to show direction selectivity (Livingstone & Hubel, 1984), which further suggests that LGN parvo neurons may receive motion-related feedback. Andolina, Wang, Jones, Salt, and Sillito (2002) inactivated all feedback coming to LGN and recorded the responses of LGN neurons to flashing spots and drifting gratings. They reported no change in response to flashing spots, but significant change to drifting gratings. This finding is in agreement with the nature of feedback connections to LGN: directionally selective neu-

rons in V1 send back axons to LGN, which makes the motion an essential dimension in MT feedback to LGN. Based on these studies, the neural correlates for the interactions between the motion and position systems in our model could be either the projections of MT to LGN via layer 6 in V1 or the projections from MT to layer 4B.

Physiological findings suggest that the fast dynamics of the motion system may result in early emergence of activity in MT and the influence of MT on early visual areas might be critical for position computation. We suggest that early computed motion information supplies prediction to the position system in order to enhance its processing speed. The possible effect of motion on responses in early visual neurons is investigated in Andolina et al. (2002). A moving bar stimulates the neighboring neurons in LGN that have RFs lying along the bar. Synchronization of responses between these neighboring neurons is shown to be enhanced by feedback from the primary visual cortex in cats. This synchronization in turn enhances the input to V1 cells. In this scheme, higher order areas signal the existence of motion via feedback, after which the position input to primary visual cortex becomes more prominent by temporally overlapping feed-forward input. Stimulus driven synchronization of LGN cells by motion-related feedback might speed up the computation of the position of moving objects. The shorter latency for perceiving a moving object's position compared to a stationary object's position is consistent with this possibility (Jancke et al., 2004; MacKay, 1958; Metzger, 1932; Ogmen et al., 2004; Orban, Hoffmann, & Duysens, 1985; Patel, Ogmen, Bedell, & Sampath, 2000; Purushothaman et al., 1998; Whitney & Murakami, 1998; Whitney, Murakami, & Cavanagh, 2000).

MT is suggested to have a role in the anticipatory influence on the position map, however MT neurons' responses saturate at low contrasts (Kohn & Movshon, 2003) and contrast dependent gain modulations due to motion require additional neural substrates. Therefore the motion system modeled here might be better characterized as a lumped representation of various brain regions[1] including areas V1 (Movshon & Newsome, 1996) and V3 (Gegenfurtner, Kiper, & Levitt, 1997). Gain modulations due to attention are suggested to vary with stimulus contrast (Martinez-Trujillo & Treue, 2002; Reynolds, Pasternak, & Desimone, 2000), and motion-induced gain modulations originating from multiple neural substrates may also show contrast dependence.

10. Conclusion

We suggest that when localizing moving objects, the motion system assists the position system to enhance its processing speed. This may be achieved by anticipatory sig-

nals from the motion system that prepares the position system by elevating the gain and responsiveness of the neurons lying along the predicted trajectory of motion. We present further evidence of motion-related position illusions and suggest that these might be side-effects of differential gains among position-encoding neurons that are induced by anticipatory motion signals.

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