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Temporal dependence of local motion induced shifts in perceived position

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Abstract

It has been shown that a moving visual pattern can influence the perceived position of outlying, briefly flashed objects. Using a rotating bar as an inducing stimulus we observed a shift, in the direction of motion, of the perceived position of small bars flashed together on either side of the moving bar. The greatest shift occurred when the 13 ms flashes were presented 60 ms before the rotating bar came closest to their locations. By varying rotation speed we showed that the peak effect was determined by the temporal rather than the spatial interval. The motion induced shift could be attenuated by introducing background flickering dots. The perceived shift decreased with distance from motion when the eccentricity of the flashes was kept constant. We conclude that the shift reflects feedback to primary visual cortex from motion selective cells in extrastriate cortex with receptive fields that overlap the retinal location of the flash.
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1. Introduction

Functional mapping of cortical areas has led to a modular, distributed view of visual processing in humans, each module with its own function and temporal characteristics (Zeki, 1978; Zeki & Bartels, 1999). However, this view provides little insight into how modules interact with each other to form a temporally coherent percept (Johnston & Nishida, 2001; van de Grind, 2002). Area V1, the striate cortex, contains a retinotopically organized network of neurons with small visual receptive fields, whose aggregate activity is exquisitely sensitive to changes in spatial position (Bosking, Crowley, & Fitzpatrick, 2002). Area MT/V5, which has reciprocal connections with V1 (Ffytche, Guy, & Zeki, 1995; Kennedy & Bullier, 1985; Shipp & Zeki, 1989) contains neurons with larger receptive fields that are specialised for motion (Andersen, Snowden, Treue, & Graziano, 1990; Zeki, 1969, 1974, 1978). The perception of movement usually (but not always) coincides with a change in perceived position, implying coordinated activity in MT and V1, but it is not clear how these two areas interact. Nevertheless there is growing evidence that motion, temporal and spatial position mechanisms do not operate in isolation.

A classic example of an interaction between motion and spatial position is the flash-lag effect (MacKay, 1958; Mateeff & Hohnsbein, 1988; Nijhawan, 1994), the tendency to misjudge the position of a moving object as advanced in the direction of motion relative to the location of a briefly presented stationary object. There has been much debate over whether this is an effect of motion on perceived position or a relative delay of flashed compared to moving objects (Eagleman & Sejnowski, 2000, 2002; Krekelberg & Lappe, 2000, 2001; Nijhawan, 2002; Patel, Ogmen, Bedell, & Sampath, 2000; Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney, 2002; Whitney & Murakami, 1998).

Many purely spatial displacements induced by motion have also been described. It has been shown that motion within a stationary envelope can cause the envelope to appear shifted in the direction of motion (De Valois & De Valois, 1991). Similarly a motion after effect (MAE) can cause a stationary pattern to appear

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shifted in position in the direction of the after effect (McGraw, Whitaker, Skillen, & Chung, 2002; Nishida & Johnston, 1999; Snowden, 1998). Culham et al. (1999), using functional imaging, have shown that MT+ is not active during storage of the MAE but reactivates after presentation of a static test pattern. Nishida and Johnston (1999) found that the spatial shift increased over a 2 s period after the presentation of a static pattern. However, like the MAE, this build up does not occur over the storage period, suggesting that activity in MT+ is a necessary condition for the spatial shift. Of course, the effect may also correlate with activity in V1 itself. However, McGraw, Barrett, and Walsh (2002) found that the MAE induced spatial shift was much reduced after TMS applied over human area MT but not after TMS applied to area V1. These three studies taken together strongly suggest the spatial shift is a consequence of a feedback pathway from MT to V1.

The motion of a rotating or translating pattern can cause a spatial shift in the position of briefly presented, stationary, objects located some distance from the motion (Whitney, 2002; Whitney & Cavanagh, 2000a). Here we show that this spatial shift can be induced by a single moving object, generating locally changing motion signals and that the size of the mislocalisation is dependent on the relative timing of the moving object and the flash. The specific contribution of motion was further established by the introduction of background flicker, which greatly reduced the magnitude of the shift.

We then examine the effect of distance between a different moving stimulus and the test bars and find that when their eccentricity is kept constant, the size of the effect is reduced the further the flashes are from the motion. This indicates that there is a spatiotemporally localised effect of motion and suggests the spatial shift is mediated by low-level mechanisms rather than higher level/grouping mechanisms as has been suggested previously (Watanabe, Nijhawan, & Shimojo, 2002; Whitney & Cavanagh, 2000a).

2. Experiment 1: varying the presentation time of flashes

The first experiment determined the relative position (and corresponding relative time) over which a moving bar influenced the perceived positions of stationary flashes.

2.1. Methods

Stimuli were presented on a high resolution CRT monitor (800×600 pixels, 80 Hz refresh, SONY GDM-F520) controlled by a VSG graphics board (VSG2/3F www.crsltd.com) programmed in Matlab (www.mathworks.com) on a PC (www.dell.com). In all experiments subjects were seated 92 cm from the visual display. Subjects had normal or corrected-to-normal visual acuity. All parts of the stimuli were black (0 cd/m^2) and were presented on a white (53 cd/m^2) background.

The experiment took place in a dim ambient light. The rotating anti-aliased bar subtended $162' \times 12'$ of visual angle. The flashes were $11' \times 4'$ and separated from the bar by $24'$. Subjects were asked to fixate on the middle of the rotating bar. Each trial consisted of the clockwise or anticlockwise rotation (40 rpm) of the bar for 2.5 s (for 1.7 rotations), during which time the two flashes were presented horizontally either side of the bar—three times for one frame (13 ms) every half a rotation. From trial to trial the flashes were vertically offset from one another about the horizontal (the offset varied between $10'$ separation in the direction of motion to $21'$ against the direction of motion). Subjects judged which flash appeared vertically higher and responded left or right by pressing a button. The number of responses (out of 20) against the direction of motion were recorded for nine values of vertical offset. This data was used to establish the point of subjective alignment using probit analysis (Finney, 1971). Clockwise and anticlockwise presentations were interleaved randomly and since there was no noticeable effect of direction of rotation *per se* the results were combined together into 'with direction of motion' and 'against direction of motion'. The angle between the rotating bar and the vertical at the time of the flash was varied across blocks of trials to measure apparent flash alignment for 15 moving bar positions (every 12° from the vertical) at flash onset.

Flash lag for each subject was determined by presenting half a rotation of the bar, for on average 0.75 s and systematically varying the angle of the rotating bar at which a single instance of paired flashes were presented at the horizontal. Starting points and ending points were randomly jittered independently between 20° rotation about the vertical. Subjects were asked if the rotating bar was spatially ahead of the flashes or behind the flashes at the time of presentation. Four estimates (each based on 70 trials) of the 50% point on the psychometric function were averaged for each subject to determine subjective temporal coincidence of flash and bar along with associated standard errors. One of the authors SD, and two naïve subjects participated.

Experiment 1 was repeated, using the same method for 11 naïve subjects, with perceived misalignment measured for four relative positions of the bar to the flashes (60°, 90°, 150° and 180° past the vertical).

2.2. Results

At most positions of the rotating bar, two physically aligned flashes, presented horizontally on either side of the bar, appeared to be misaligned in the direction of bar motion (Fig. 1), but the magnitude of the effect varied significantly over different positions of the bar.

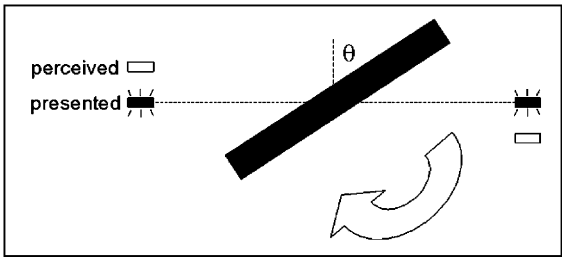

Fig. 1. The stimulus is a rotating bar (anticlockwise or clockwise) with flanking flashed bars. When aligned flashes are presented at a given value of θ, they are perceived to be misaligned, as illustrated, in the direction of the motion.

A typical psychometric function for one subject, SD is shown in Fig. 2a. We observe that there is a significant perceived misalignment in the direction of motion ($11'$, SE $= 0.7'$). The standard error of the approximated subjective point of alignment is calculated along with the probit fit (Finney, 1971). Fig. 2b shows the plots of perceived misalignment in the direction of motion against the angle of the rotating bar at which the flash was presented for three subjects. We find that the size of the effect varies significantly with the point in the trajectory of the moving bar at which the flashes were presented.

Importantly, at no point is a comparable misalignment observed in the opposite direction to motion. Only at one point does one subject see a significant misalignment of a $1.8'$ against the direction of motion (subject SD at 120°), whereas perceived misalignment in the direction of motion peaks for the same subject at $14.7'$. The fact that the perceived misalignment is almost

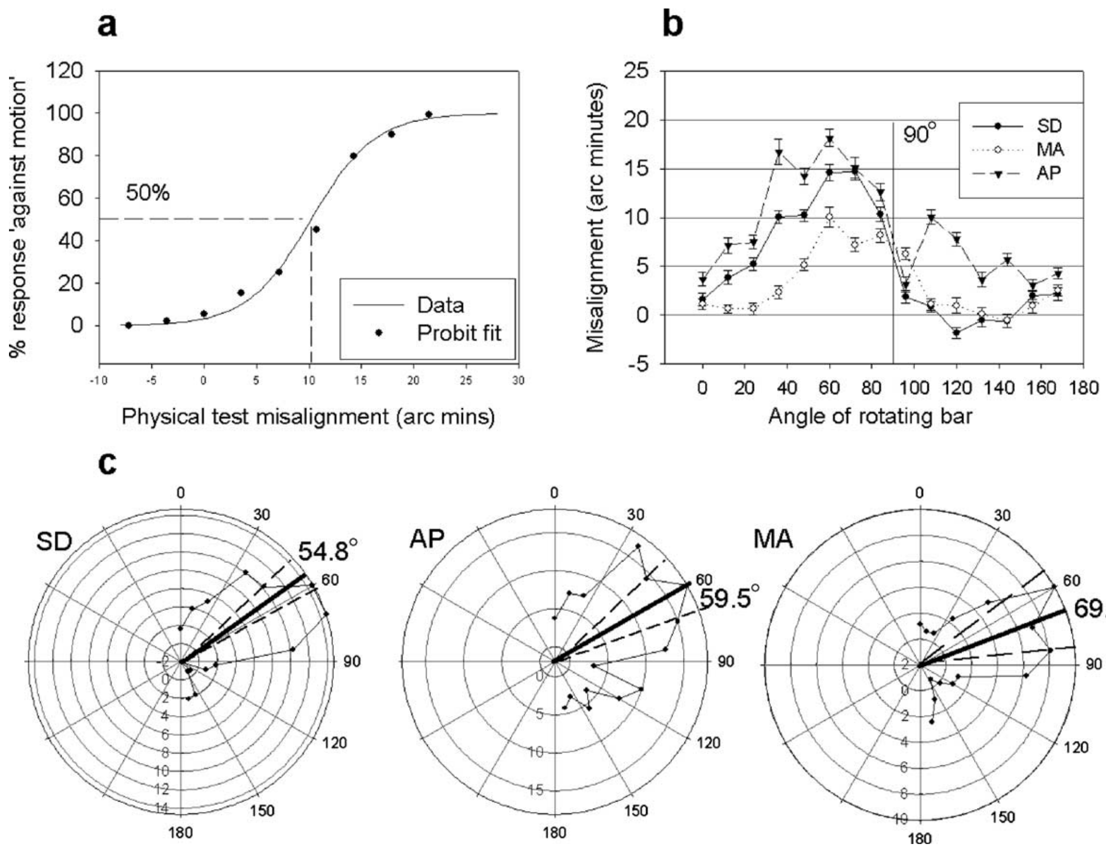

Fig. 2. Results for the first experiment, subjects SD (author), MA and AP (naïve). (a) Psychometric curve for subject SD. Flashes were presented when the rotating bar was 6° before the horizontal. Responses 'right' vs. 'left' higher are combined into 'with' or 'against' the direction of motion (percentage 'against' plotted). For the physical flash misalignment values, positive values represent flashes physically shifted against the direction of motion (nulling the effect). By checking the 50% point we see that subject SD perceived the flashes to be aligned when they were misaligned by about $11'$ all together against the direction of motion. (b) Plots of perceived misalignments for each subject against the angle from the vertical of the rotating bar at the time of the flash. A negative value corresponds to a perceived misalignment against the direction of motion. Error bars ±1 S.E. were found from the probit fit. (c) Data from (b) plotted on polar axes. Perceived misalignment is shown on the radial axis (arc min) and the angle at flash presentation on the angular axis. The zero circle indicates no misalignment and negative values indicate a misalignment against the direction of motion. Phase $= \tan^{-1}\left(\frac{\sum_{i=1}^{15} M_i \sin 2\theta_i}{\sum_{i=1}^{15} M_i \cos 2\theta_i}\right)$, Magnitude $= \frac{2}{15}\sum_{i=1}^{15}\sqrt{(M_i \sin 2\theta_i)^2 + (M_i \cos 2\theta_i)^2} + \overline{M}_i$. The phase was divided by 2 to find the peak angle. The error on this angle is calculated by drawing 1000 bootstrap samples from the normal distribution given by each psychometric function at each observed point and recalculating phase each time. Corresponding times between flash presentation and the bar reaching the horizontal are 147, 85 and 126 ms respectively.

always in the direction of motion means that the shift is not attributable to a simple spatial tilt illusion (Gibson & Radner, 1937; Wenderoth & Johnstone, 1988). A typical tilt illusion would result in equal and oppositely signed spatial shifts for opposite relative orientations of the bar with respect to the horizontally oriented flashes (Arnold, Durant, & Johnston, 2003).

In order to determine the angle along the trajectory of the moving bar at which the presentation of the flashes results in a peak misalignment, we calculated the phase of the second harmonic of the data for each subject (Fig. 2c). We used the second harmonic as the data necessarily repeats every 180° with each rotation of the bar. Effectively we are fitting a $\sin(2\theta)$ function to the data. We found that for each subject the peak misalignment (10′–18′) occurred when the rotating bar was about 30° before the horizontal or, equivalently, about 120 ms before the rotating bar reaches the position physically closest to the flashes (SD 147 ms; MA 85 ms; AP 126 ms). This temporal window lies within the temporal range of the flash-lag effect (Eagleman & Sejnowski, 2000; Krekelberg & Lappe, 2000; Nijhawan, 1994; Whitney & Murakami, 1998). This suggests that the size of the positional shift could be related to the *perceived* position of the rotating bar at the time of the flashes. However, the average flash-lag effect in this case, measured explicitly for the three subjects was only 24 ms (SD 41.1 ms; MA 13.9 ms, AP 17.6 ms).

To establish the reliability of the spatial shift effect, we repeated the experiment over a group of 11 naïve subjects for four positions of the moving bar (60°, 90°, 150° and 180° from the vertical). In Fig. 3a we can see that a significant misalignment occurs at all the angles except 150°, (60°: $t_{(10)} = 3.38$, $p < 0.05$; 90°: $t_{(10)} = 3.73$, $p < 0.05$; 150°: $t_{(10)} = -0.17$, n.s.; 180°: $t_{(10)} = 3.46$, $p < 0.05$), which is where we might expect the least effect from the first part of Experiment 1. The significant misalignment at 90° indicates that despite the relatively small size of the induced spatial shift (10′), position is still disrupted when the bar is physically aligned with the flashes. We fitted a $\sin(2\theta)$ curve to visualise how these four points might lie on a distribution over all angles (Fig. 3b). We can see that the data fit the shape of the distribution we found in over the first three subjects in Experiment 1 and the peak of the sin curve lies at 19° (74 ms) before the horizontal, reinforcing the estimate of the time-lag.

3. Experiment 2: varying the speed of rotation

In this experiment we tested whether it was the physical location of the bar at the time of the flashes or the timing of the flashes along the trajectory of the rotating bar that was crucial in determining the size of the perceived misalignment.

3.1. Methods

Using the same methods we repeated Experiment 1 (10 responses per test level), with the original speed of the rotating bar (40 rpm), and the original speed ×2 (80 rpm), ×3 (120 rpm) and ×4 (160 rpm). The frame rate remained the same and the bar rotated 3°, 6°, 9° and 12° on each frame respectively. Movement appeared smooth and continuous in each case. The flashes were again presented three times, so they were presented every 0.5, 1, 1.5 and 2 rotations of the bar respectively. One of the authors SD, and four naïve subjects participated.

3.2. Results

There is some variability across subjects but the peak of the misalignment tends to regress away from the horizontal as speed of rotation of the bar increases, i.e. at higher speeds the flashes need to be presented at an earlier point of the trajectory of the rotating bar to achieve the same size of effect (Fig. 4). If we average over the difference between the angle of greatest effect and the horizontal (Fig. 5a), we see an increase in peak angular difference with speed of rotation. We found a significant main effect of speed on the angular difference, $F_{3,12} = 12.84$, $p < 0.05$. If we plot the time between bar and flash position (rather than the rotation angle) that delivers the greatest spatial shift against the speed of the bar, there is no systematic change with bar speed for the five subjects, $F_{3,12} = 1.075$, $p = 0.396$ (Fig. 5b). The temporal difference averaged across subjects remains constant over all four speeds at a value of 62 ms. Following Whitney and Cavanagh (2000a) we found no overall change in the magnitude of the peak perceived misalignment as a function of speed, $F_{3,12} = 0.583$, $p = 0.637$ (Fig. 5c).

We have found that it is the relative motion over a fixed time after the flashes are presented that is crucial, not the spatial position at the time of the flash. Note the flash-lag effect behaves in a similar way, increasing in spatial extent with speed according to a constant time rule (Nijhawan, 1994).

The use of a spatially localised moving stimulus has allowed us to measure a spatiotemporal window over which movement can have influence on the bar. The critical determinant is motion introduced near the test bar locations after the flash. This is consistent with Whitney and Cavanagh's (2000a) finding that flashes presented at the time of a change in direction of rotation go with the following motion.

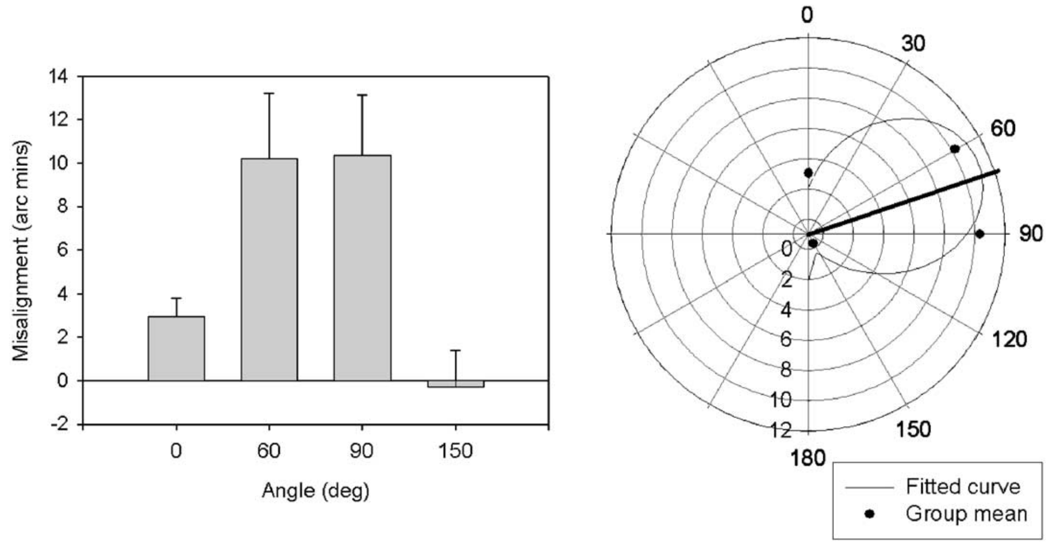

Fig. 3. Results of measuring perceived misalignment for 11 naïve observers. (a) We observe a significant difference over the four conditions. Error bars ±1 S.E. There is significant misalignment in the direction of motion at 90° (when the flashes are presented when the bar is horizontal). There is no significant misalignment at 150°. (b) The data from figure (a) plotted on a polar plot to illustrate how it can fit into a similar shaped distribution as in Experiment 1 (fitted with $a[b + \cos(2(\theta + p))]$), with a peak of 19° before the horizontal. Misalignment is presented on the radial axis (arc min); angle at flash presentation on the angular axis.

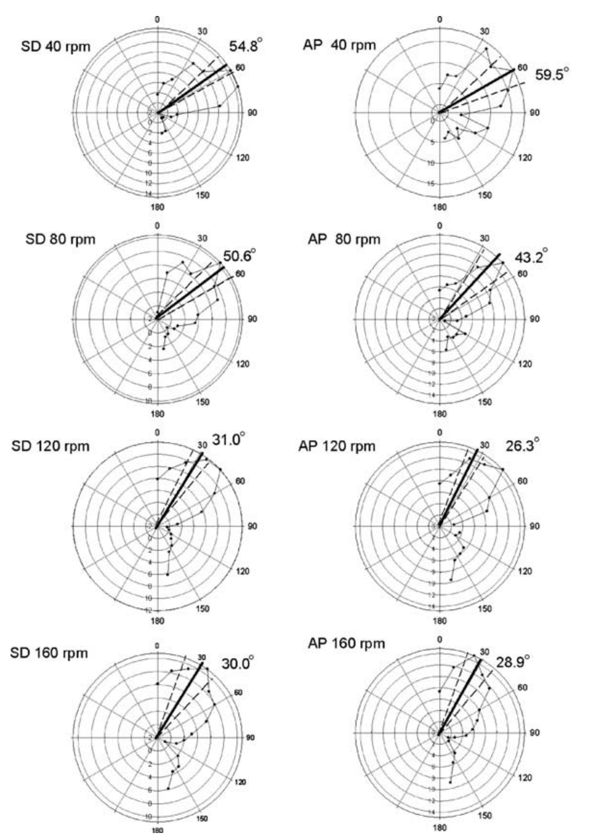

Fig. 4. Perceived misalignments for subject SD (author) and AP (naïve). As a function of the angle of the rotating bar the time of the flash. Data are shown for four different speeds on polar plots (misalignment on radial axis (arc min), angle of flash presentation on angular axis), with associated peak angles expressed in degrees from the vertical. With increasing speed, the peak angles move further away from the horizontal. S.E. bars calculated by bootstrapping as before.

4. Experiment 3: introducing background flicker

The action of motion on the target suggests the involvement of extrastriate motion selective cells with large receptive fields. In the third experiment we introduced dynamic noise into the area containing the stimulus by adding flickering noise dots in the background as a means of attenuating the influence of motion (Churan & Ilg, 2002).

4.1. Methods

Stimuli were all the same size and the speed of rotation of the bar was the same as in Experiment 1. The background was grey (19 cd/m^2). The experiment took place in dim ambient light with a chin-rest. The black flashed bars were presented at 1° separation from the central rotating bar and perceived misalignment between them about the horizontal was measured as in Experiment 1. A white fixation point was provided in the centre of the bar. The rotating bar was presented for half a rotation (0.8 s) from vertical. The flashed bars were presented once at the angle of maximal effect (60°) as found in Experiment 1. Subjective alignments and standard errors were calculated from the average of four estimates for each condition (60 trials per each alignment measurement). For the static dots condition on average 314 white (53 cd/m^2, $5' \times 5'$) dots were presented continuously during each trial (all within a circle of radius of 4° containing both the bar and flashes), at different randomly assigned locations. For the temporal frequency conditions, the dots were flickered on and off

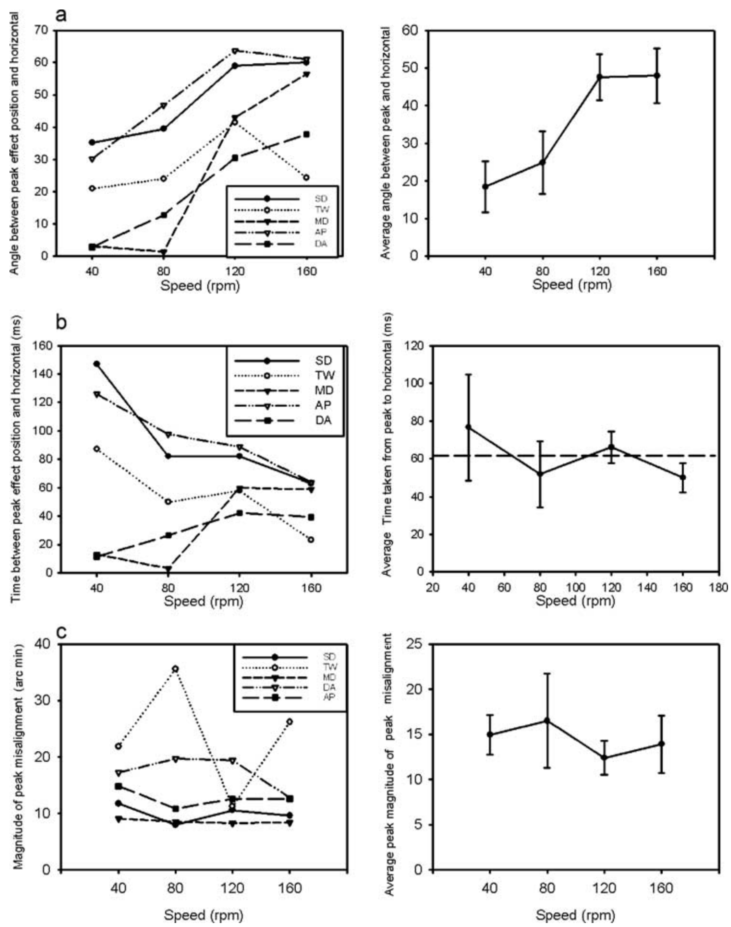

Fig. 5. Summary data for the fitted peaks of distributions of misalignments over all subjects. (a) The angle between peak misalignment and horizontal increases over the five subjects with speed shown along with the average angle. Error bars ±1 S.E. (b) The times taken for the rotating bar to travel from the angle of peak misalignment to the horizontal, plotted along with the average time. (c) The magnitude of the peak perceived misalignment. There is no overall effect of speed. Error bars ±1 S.E. There is no clear pattern over the three subjects. The average of all measurements is roughly constant around 62 ms over all speeds.

synchronously according to a square wave function at 20, 10, 5 and 2.5 Hz rates and the misalignment measured for each condition. The high contrast black moving bar always occluded the background. One of the authors (SD) and four naïve subjects participated.

4.2. Results

We found that static noise dots had no significant effect, indicating that the shift is robust with respect to the presence of a local spatial reference, $t_4 = 1.69$, $p = 0.166$. However, although there is again some variability between subjects in the size of the effect, perceived misalignment (see Fig. 6) was reduced as the rate of flicker increased. We treated the data as 4 conditions × 5 subjects factorial design, and found an effect of flicker, $F_{3,60} = 19.35$, $p < 0.05$. There was also an interaction between subject and flicker rate, $F_{12,60} = 6.963$, $p < 0.05$, indicating that the decrease is multiplicative rather than a constant size over subjects. The flickering

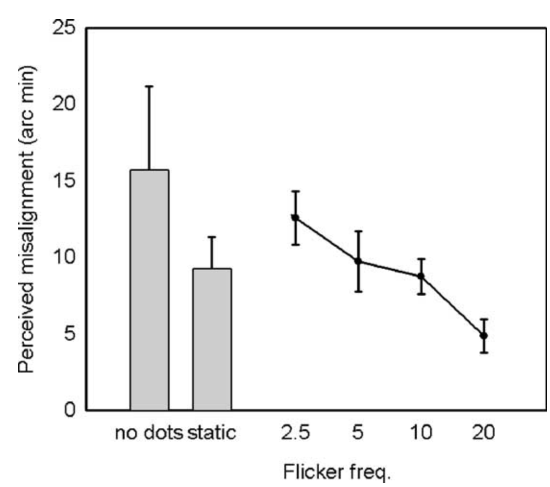

Fig. 6. Averaged results of Experiment 3. Error bars are ± the mean S.E. of the subjects, to illustrate the average error for each subject, rather than error over all subjects. There is no significant difference in perceived misalignment when static dots are presented in the background. However the size of the perceived misalignment decreases significantly when the dots are flickered. The spatial shift becomes more disrupted with higher rates of flicker.

dots did not appear to mask the motion of the bar although spatial misalignment was much reduced. This suggests activating transient mechanisms interferes with the effect of motion at a distance.

5. Experiment 4: separating the effect of eccentricity and motion distance

Whitney and Cavanagh (2000a) found that motion influences position with no effect of distance between moving stimulus and flashes, suggesting a higher-order binding effect, rather than an effect of local motion. However we observed that for a given speed of rotation relative position determines the size of the effect. Previous work on motion influence on positional judgments has shown that the effect size can increase with peripheral viewing (De Valois & De Valois, 1991). In Whitney and Cavanagh's (2000a) experiment increased distance from the inducer was correlated with an increase in visual eccentricity. In this experiment we separated the influence of motion over distance from retinal eccentricity. For this we used a stimulus previously utilised by Whitney and Cavanagh (2000a), but manipulated the stimulus configuration so that separation from motion varied independently of the eccentricity of the flashes (Fig. 7).

5.1. Methods

Two gratings were presented drifting vertically in opposite directions. The gratings were 100% contrast on a grey background and had a spatial frequency of 2 cycles/deg and temporal frequency of 0.85 cycles/s. The gratings were separated by 32′ and had a black fixation point (14′ × 14′) between them. The experiment took place in ambient light and subjects made use of a chinrest. The gratings were presented for 850 ms before the first flash and flashes occurred every 850 ms until a judgement was made. Flashes were presented horizontally either side of the gratings on an arc of equal eccentricity (5° 2′) from the fixation point. The perceived misalignment was measured at 3°, 4° and 5° horizontal distances from the midline. There were 90 trials per measurement and four measurements were averaged to determine the misalignment at each distance. One of the authors (SD) and three naïve subjects participated.

5.2. Results

We treated the data as a 3 conditions × 4 subjects factorial design and found a significant effect of distance from motion, $F_{2,36} = 51.59$, $p < 0.05$, and again found an interaction between subject and distance from motion, $F_{6,36} = 19.64$, $p < 0.05$. The averaged data is shown in Fig. 7.

This data demonstrates that by controlling for the eccentricity of the flashes there is a decrease in the size of the perceived misalignment as the flashes are placed further away from motion, indicating that the extent of the influence of motion on spatial position is spatially localised and stronger the closer the flashed objects are to movement.

6. Discussion

We showed that the local motion of an object can influence the perceived position of a spatially dissociated flashed stationary object. Using a rotating bar allowed us to examine the spatiotemporal dependence of the displacement effect. Whitney and Cavanagh (2000a) showed, using their direction reversing inducing stimulus, that it is the direction of motion present around 200 ms after the presentation of the bar that determines the direction of the spatial displacement. We have shown that it is the presence of motion on the path to the flash location over a period of 60 ms after flash onset that maximizes the magnitude of the perceived spatial displacement.

Discussions of the spatiotemporal localization of flashed and moving objects often proceed as if the visual system has access to a snapshot of the visual stimulus on each time frame. However the neural representation is

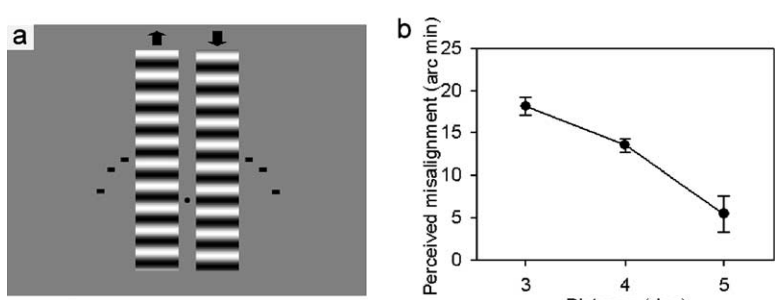

Fig. 7. Effect of distance from motion on perceived misalignment. (a) The configuration of the stimulus, with the three possible positions of the flashes. (b) Perceived misalignment is plotted against distance of flashes from motion. Error bars are ± the mean S.E. of the subjects.

subject to the spatiotemporal blurring specified by the spatiotemporal impulse response function for the human visual system. From the data of Hess and Snowden (1992) the peak latency for a realistic low-pass temporal filter can be calculated to be around 80 ms (Johnston & Clifford, 1995). Therefore it will take around 80 ms for the flash to maximally activate low level neural representations and in this time span its position will already be affected by motion. We can explain our data if the spatial encoding is influenced by cells centred on the flash with large enough receptive fields to be activated by distant inducing objects concurrently with the neural response to the flash. We can think of a spatiotemporal window around the flash presentation, with the maximal shift occurring when the moving bar is spatially close and at a fixed temporal interval from the peak of the response to the flash. In order to arrive at the right place at the right time a faster moving bar will need to 'set off' from a more distant spatial position (Fig. 8). The right place would appear to be around the horizontal and the right time, 60 ms after the flash. Since motion selective cells with large receptive fields are located in extrastriate areas such as MT and MST but fine position judgments are likely to require the precision of V1, the position shift is likely to result from feedback connections from extrastriate to striate cortex (Nishida & Johnston, 1999; Whitney & Cavanagh, 2000a). Motion analysis and feedback to a cell encoding spatial location will take time. Thus we need to include an small delay to account for the time it would

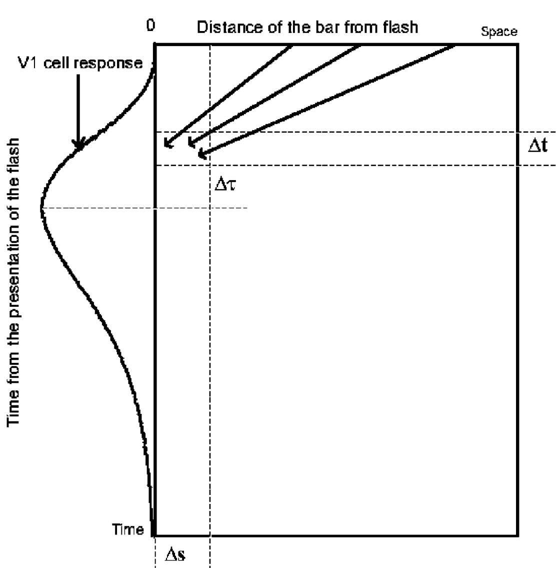

Fig. 8. A space–time plot depicting the traces of the bar moving at different speeds as a function of angle from the horizontal (flash location) and time from the flash. Faster moving bars need to start further from the horizontal if they are to reach the spatiotemporal window ($\Delta s, \Delta t$) of maximum influence 60 ms after the flash. We also need to include a motion calculation and feedback interval ($\Delta\tau$) giving a total delay of $(60 + \Delta\tau)$ to match the peak development of the temporal impulse response of the flash.

take for feed back to influence V1 spatial codes (Fig. 8). Adding a delay of 20 ms for this process would provide feedback at 80 ms from the onset of the flash i.e. when we would expect the response to the flash to peak.

Our stimulus resembles the configuration used by Nijhawan (1994) to measure flash lag, but in our perceptual alignment experiment subjects are not asked about the relative positions of the bar and the flashes. The 24 ms flash lag we measured is smaller than the typical temporal offset for the spatial shift. Nevertheless, it might be suggested that have we have obtained an implicit measure of the flash-lag effect.

This proposal raises some interesting issues. For instance in temporal explanations of the flash-lag effect such as the differential latency model (Mateeff & Hohnsbein, 1988; Patel et al., 2000; Purushothaman et al., 1998; Whitney & Cavanagh, 2000b; Whitney & Murakami, 1998), the position of the flash is established after a delay and then compared to the new position of the moving bar. However, if the flashed bar is simply delayed by 60 ms relative to the moving bar, there should be no opportunity for the moving bar to influence its position, since the moving bar would be closest to the flash when the flash first activates its neural representation. The flashed bar should initially appear in its proper retinotopic location. This does not occur as it has previously been found that for durations longer than 120 ms a flashed bar does not appear to move (Whitney & Cavanagh, 2000a) but still appears spatially displaced.

The spatial extrapolation model (Khurana & Nijhawan, 1995; Nijhawan, 1994, 2002) proposes that we extrapolate the position of moving objects to correct for neural delays. One might argue that the moving bar is shifted forward by 60 ms and therefore is perceptually aligned with the flashed bar at flash onset. However we would need to extrapolate not only the position of the bar, but also the motion field, since it is the motion not the bar position that influences the flashed bars (the effect does not reverse after the bar passes the horizontal). This goes further than current extrapolation theory.

Further explanations of the flash lag suggest that it is the side effect of a mechanism invoked to decide on a given relative spatial position at a given time for a moving object. The location of a moving object could be determined by a slow average of relative position over time (Krekelberg & Lappe, 2000, 2001), or positional sampling (Brenner & Smeets, 2000) or by post-dictive position integration after the flash presentation (Eagleman & Sejnowski, 2000, 2002). These theories do not bear on the spatial shift effect since subjects are never asked about the relative position of the flash and the moving bar.

The influence of motion was dramatically reduced by the introduction of flicker in to the background. This is an indication that flicker can counteract the influence of motion on spatial localisation.

It has been shown that similar motion induced spatial shift effects increase with greater eccentricity (De Valois & De Valois, 1991). The decrease in the size of the shift with distance from motion described here implies a local effect of motion since we ensured that the flashes have a constant eccentricity.

What is the reason for the existence of a motion-based feedback mechanism (Bullier, 2001; Pascual-Leone & Walsh, 2001)? It is possible that it could be a verification mechanism, testing whether motion calculations are correct by checking that the spatial displacement of an object is consistent with computed motion. The akinetopsic patient L.M., who suffered bilateral lesions to human V5 (Zihl, von Cramon, & Mai, 1983), reported spatial position change without experienced motion. This suggests feedback might support the perception of smooth motion. Updating spatial position may be what enables us to see smooth progression between temporally sampled locations, associating motion with the relevant visual location.

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