Motion and position coding

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Abstract

Motion contained *within* a static object can cause illusory position shifts toward the direction of internal motion. Here we present data suggesting this illusion is driven by modulations of apparent contrast. We observe position shifts at blurred stimulus regions without corresponding changes to internal structure, and find that low-contrast targets are more difficult to detect at the trailing, as opposed to leading, edges of movement. Motion induced position shifts are also shown to occur without conscious appreciation of motion direction. Our data suggests that motion can influence spatial coding via interactions that modulate apparent contrast, thereby changing the regions of the stimulus that are visible.
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Keywords: Motion; Spatial coding; Position shift; Retinotopy

1. Introduction

Cortical neurons typically respond to activation within a specific region of the retina (the cortical receptive field—RF) and adjacent neurons in the cortex are activated by the stimulation of adjacent positions on the retina (Daniel & Whitteridge, 1961; Morgan, 2003; Sereno et al., 1995; Tootell, Silverman, Switkes, & De Valois, 1982). However, it has recently been suggested that the retinotopic mapping of visual brain regions is dynamic and that motion can induce cortical RF shifts (Fu, Shen, Gao, & Dan, 2004; Sundberg, Fallah, & Reynolds, 2006).

Although motion and position coding are anatomically and functionally separable (Livingstone & Hubel, 1987; Zeki, 1974; Zihl, VonCramon, & Mai, 1983), to some extent motion can influence spatial coding (Bressler & Whitney, 2006; De Valois & De Valois, 1991; Nishida & Johnston, 1999; Ramachandran & Anstis, 1990; Snowden, 1998; Whitaker, McGraw, & Pearson, 1999; Whitney & Cavanagh, 2000). For instance, stationary objects that contain patterns

of motion can appear shifted in the same direction as the embedded motion (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990; see Fig. 1). Hypothetically, if motion changed the region of retina to which a population of cortical neurons respond, positions encoded by this population might appear shifted relative to positions encoded by other, unaffected, populations. We shall refer to this possibility as the *RF account*. Motion-induced RF shifts have been reported following observations in cat (Fu et al., 2004) and monkey (Sundberg et al., 2006) cortex.

The motion-induced RF shifts reported (Fu et al., 2004; Sundberg et al., 2006) seem inconsistent with data from human brain imaging suggesting that motion signals shift the locus of cortical activity in the direction *opposite* to the motion signal (Whitney et al., 2003). However interpretation of this data is not straightforward. Originally, these data were taken as evidence for motion-induced changes in RF mapping (Whitney et al., 2003). In contrast, Liu, Ashida, Smith, and Wandell (2006) have since argued that the difference is due to a motion-direction asymmetry in response amplitude.

Whitney et al. (2003) proposed that, in this context, the difference in BOLD signal might reflect a process that

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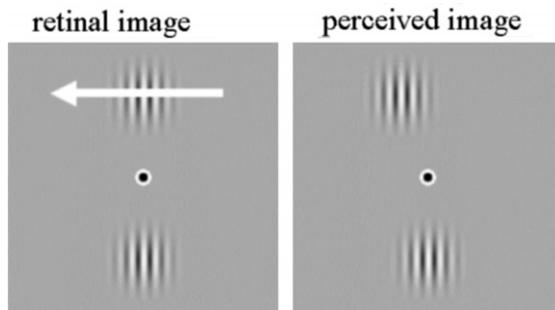 *E-mail address:* darnold@psy.uq.edu.au (D.H. Arnold).

Fig. 1. Schematic showing how motion can influence spatial perception. While both gratings are vertically aligned and do not change position, the upper grating has an internal carrier waveform drifting leftward whereas the lower grating has a static waveform. This physical configuration can make the upper grating appear shifted to the left.

suppresses visual responses—particularly at the trailing edges of movement. This proposal seems plausible as inhibitory interactions do not increase spiking rates but do increase blood flow (Mathiesen, Caesar, & Lauritzen, 2000). The functional role of the motion-induced suppression of visual responses might be to reduce luminance–contrast in order to diminish the blur that can occur at the trailing edges of movement (Burr, 1980; Whitney et al., 2003). We shall refer to this proposal as the *Contrast Modulation* account.

Of the two accounts described, *Contrast Modulation* seems more compatible with existing psychophysical evidence. For instance, position changes induced by internal motion are either reduced or eliminated by hard apertures (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990). There is no obvious explanation for this in terms of RF shifts. However, this observation is entirely consistent with the *Contrast Modulation* account. According to this account we would expect changes to be most apparent in blurred low contrast stimulus regions where slight contrast reductions or increments could, respectively, render the previously visible invisible and the invisible visible. Changes would be less apparent with hard apertures due to the absence of low contrast stimulus regions.

Thus, if motion induced position changes are driven by contrast modulations, we would expect the changes to be most apparent in blurred low contrast regions. Alternatively, if they are driven by RF shifts, we would expect all regions of the stimulus falling into shifted RFs to be equally effected. When the stimulus is small, this should include both the edges and centre of the stimulus. These possibilities will be tested in Experiment 1.

2. General methods

Stimuli were either displayed on a 19 in. Sony Trinitron Multiscan 500PS monitor driven by a VSG 2/5 (Cambridge Research Systems) at a refresh rate of 100 Hz (Experiments 1 and 4) or on a Samsung SyncMaster 1100p+ monitor (1024 × 768 resolution; 120 Hz refresh rate) driven by a

ViSaGe stimulus generator (Cambridge Research Systems) at a refresh rate of 120 Hz (Experiments 2 and 3). All stimuli were viewed binocularly from 57 cm with the head placed in a headrest.

3. Experiment 1

3.1. Methods

Stimuli in Experiment 1 consisted of pairs of abutting stationary sinusoidal luminance-modulated gratings (see Fig. 2). The gratings had a width of 0.7°, s.f. 1.0 cpd, a peak contrast of 100% and were centred 0.35° to the left or right of fixation. The waveforms within the gratings drifted (7.5°/s) upward or downward. The top and bottom edges of test gratings, shown in Fig. 2 on the left, were blurred. The height of test gratings subtended 2.64° and the *SD*'s of Gaussian luminance–contrast envelopes were 0.44°. The height of standard gratings, which did not have blurred edges, subtended 1.76°. The background of the display was grey (Commission Internationale d'Eclairage (CIE) 1931 chromaticity chart: $x = 0.329$, $y = 0.329$ $l = 50.81$).

Observers completed two tasks. In one, observers adjusted the vertical position of the test grating until its visible top edge appeared aligned with the top edge of the abutting standard grating—an external border alignment task. During these tasks the initial phases of the waveforms within the abutting gratings were determined independently and at random. Initially the test grating was centred either 0.5° above or below the central position of the abutting standard grating, determined at random on a trial by trial basis. The vertical position of the test grating was then adjusted in steps of 0.05° by pressing one of two response
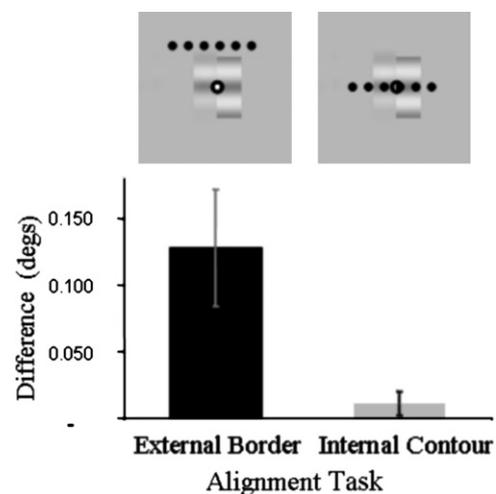

Fig. 2. Stimuli and results for Experiment 1. Results from the external border alignment task are shown in black. Results from the internal contour alignment task are shown in grey. Dotted lines in the schematics indicate the region of the stimulus judged for the data shown below. The schematics also illustrate how the stimulus appeared when the two gratings were physically aligned and contained upward motion. Error bars show ±1 standard error.

buttons. A third button was pressed when the observer felt that the top edges were aligned—at which point the trial was terminated. Each response, whether it terminated the trial or changed the position of the test grating during a trial, caused the screen to go blank for 500 ms. On each occasion that the stimulus was presented, the stimulus remained until the observer indicated a response. Trial runs consisted of 12 adjustments.

In the other task observers adjusted the phase of the drifting waveform within the test grating until it appeared aligned with the waveform in the abutting standard grating—an internal contour alignment task. The central positions of the abutting gratings were aligned. The initial phase of waveforms within standard gratings was 180° whereas the initial phase of waveforms within test gratings was either 90° or 270°. Test grating waveforms were then adjusted in steps of 10° of phase until the observer felt that the abutting waveforms were aligned. Trial runs consisted of 12 adjustments.

3.2. Results

Position shifts of external borders were given by differences between border alignments in trials containing upward movement relative to trials containing downward. As shown in Fig. 2, external border alignments in this task were influenced by motion direction ($t_4 = 2.90$, $p < .05$).

Position shifts of internal contours were calculated as the difference between grating phases within apparently aligned test and standard gratings, for abutting gratings moving upward relative to when they moved downward [(upward test–upward standard) − (downward test–downward standard)]. To aid comparison these estimates are expressed in degrees of visual angle rather than phase. As shown in Fig. 2, these judgments were not influenced by motion direction ($t_4 = 1.25$, $p = .278$). We were also interested in the range of physical offsets over which waveforms within the test and standard gratings appeared aligned, so we have reported the average standard deviation (*SD*) between all adjustments of phase completed by individual observers. When expressed in degrees of visual angle, the average *SD* was equal to $0.025 \pm 0.005°$. The average range, being the difference between the most positive adjustment of phase and the most negative, was equal to $0.075 \pm 0.018°$.

3.3. Discussion

Apparent alignments of the top edges of abutting gratings with blurred and non-blurred edges were influenced by motion direction. However, motion direction did not influence internal contours. This demonstrates that illusory changes in the position of the extremities of a contrast envelope can be observed without corresponding changes to the internal structure of the stimulus.

The relative position changes observed in Experiment 1 are inconsistent with the RF account of motion-induced position changes. According to this account we would expect both external borders and internal contours to be shifted by the same amount. Instead, we observe a dissociation—external borders appear shifted whereas internal contours do not. These findings are, however, consistent with the *Contrast Modulation account* (Whitney et al., 2003). According to this proposal, slight contrast modulations at blurred stimulus edges could render previously invisible extremities visible and visible extremities invisible.

Theoretically, the dissociation in Experiment 1 could occur if all regions of the stimulus with blurred edges were influenced by RF shifts but the internal contours of the abutting gratings were then somehow drawn toward one another—a form of *phase capture* (Levi, Li, & Klein, 2003, 2005). This explanation seems unlikely. The mechanisms by which this hypothetical operation might work are unclear and in any case one would need to make a number of additional assumptions to explain why the stimulus envelope is not constrained by phase capture. We believe that a different explanation, based on established neural coding strategies, is more probable. Specifically, we suggest that our data could readily be explained by contrast modulations driven by interactions that influence neural firing rates without changing RF structure or topography.

According to the contrast modulation account, motion induced position shifts are driven by a process that has a functional significance—the regulation of retinal image blur (Whitney et al., 2003). The relationship between movement and blur can be illustrated by still photography. Photographs of moving objects taken with slow shutter speeds can appear blurred. In contrast, objects that move across the retina typically appear sharply defined, despite the fact that the human visual system is relatively slow and integrates information over a considerable time period (~120 ms; see Burr, 1980, and Barlow, 1958).

Previously, it has been shown that moving dots appear more blurred following brief (40 ms) as opposed to longer (~100 ms) stimulus presentations (Burr, 1980). This suggests that motion-blur is suppressed by an active time-dependent process. If illusory position changes are related to this process, they should evolve over a similar time span. In Experiment 2, we therefore decided to examine how illusory internal motion-induced position shifts develop with increasing stimulus exposure.

4. Experiment 2

4.1. Methods

Stimuli in Experiment 2 consisted of pairs of Gabors (width/height 2.4°, s.f. 1.5 cpd, *SD* of contrast envelope 0.4°; peak contrast 100%) placed 1.9° above or below a central fixation point. The background of the display was grey (Commission Internationale d'Eclairage (CIE) 1931 chromaticity chart: $x = 0.329$, $y = 0.329$ $l = 50.81$). Five observers participated in this experiment, the first author

and four observers who were naïve as to the purpose of the Experiment.

The contrast envelopes of the Gabors were physically static. Within one of the Gabor pairs, the grating carriers drifted toward one another whereas in the other pair they drifted away. Observers completed two tasks in this experiment. In one, observers indicated which of two pairs of Gabors were separated by the largest inter-stimulus gap—an apparent position task. In the other, observers indicated if a single pair of Gabors contained gratings that drifted toward or away from one another—a direction identification task. In the apparent position task we determined relative positions at which Gabor pairs containing inward drifting patterns of motion seemed aligned with Gabor pairs containing outward drifting patterns of motion. In the direction identification task we determined the minimal stimulus exposure duration at which observers could accurately identify motion direction.

During apparent position tasks, standard gabor pairs contained inward drifting patterns of motion and were separated by 1.5°. Test Gabor pairs contained outward drifting patterns of motion. Each trial began with the observer-maintaining fixation for 500 ms, while the rest of the screen was set to grey, before the test and standard gabors were displayed for a given duration. The trial finished when the observer indicated which of the two gabor pairs had the largest inter-stimulus gap. During a run of trials test gabor separation was manipulated (1.5 ± 0.8°) according to the method of constant stimuli. Each trial run provided a distribution of apparent test gabor separation relative to standard gabor separation. Weibell functions were fitted to these data and the 50% points were taken as estimates of the physical separation between test gabors that appeared aligned with standard gabors.

Different stimulus exposure durations were sampled in separate trial runs. The first author completed four trial runs for each of 9 different stimulus exposure durations, ranging from 10–500 ms. This was done with stimuli containing an internal drift rate of 7.5°/s. The first author also completed four trial runs for each of four stimulus exposure durations (10–70 ms) with stimuli containing internal drift rates of 3.75° and 15°/s. Four-naïve observers completed a single run of trials for each of four different stimulus exposure durations (10–70 ms) with stimuli that contained an internal drift rate of 7.5°/s.

During direction identification tasks, single Gabor pairs were shown and stimulus exposure duration was manipulated (12.5–112.5 ms) according to the method of constant stimuli. Gabor separation was randomly determined (1.5 ± 0.8°) so that motion directions were not signalled by apparent separation. Each trial run provided a distribution of direction identification success as a function of stimulus exposure duration. Weibell functions were fitted to these data to determine stimulus exposure durations at which the observer could identify embedded motion directions on 75% of trials—the minimal stimulus duration at which observers could accurately identify

directions of motion. The first author completed four runs of 180 trials with stimuli that contained three different rates of internal drift (3.75, 7.5 and 15°/s)—a total of 2160 individual trials. Naïve observers completed a single run of 180 trials with stimuli that contained an internal drift rate of 7.5°/s.

4.2. Results

Position shift estimates were calculated as the difference between inter-stimulus gaps at which test gabors were either perceptually or physically aligned with standard gabors. As shown in Fig. 3a, for the first author the magnitude of illusory position changes increased gradually with stimulus exposure duration and saturated over a time scale of ∼180 ms. Fig. 3b shows the first four data points from this function along with data points determined with stimuli containing different speeds of motion. Fig. 3c is similar and shows data points calculated from trial runs completed by naïve observers. In all cases the initial increase of illusory position changes can be described as linear, as indicated by the high R^2 values of the linear fits. Minimal durations at which observers could identify directions of motion within Gabor patterns are shown in Fig. 3b and c as vertical dotted lines.

4.3. Discussion

Illusory position shifts increased, and then saturated, over a broad time scale (∼180 ms). These observations are reminiscent of the temporal integration period for motion (Braddick, 1973) and of the time-course of motion blur suppression (Burr, 1980). While these similarities might be coincidental, our findings demonstrate that, like motion and blur suppression, motion-induced position changes are driven by a neural mechanism that has a considerable integration period. The linear fits to illusory position changes as a function of stimulus exposure duration (Fig. 3b and c) also demonstrate that illusory position changes are not simply an implicit measure of internal motion as the extent of the change is only ever a small proportion of the position change actually signalled by motion.

Some of these observations have recently been confirmed, independently, in an elegant study that used similar stimulus manipulations (Chung, Patel, Bedell, & Yilmaz, 2007). This study (Chung et al., 2007) refers to the abstract form of the data set presented here in full (Arnold & Johnston, 2005). One substantial point of difference, however, concerned the development of illusory position shifts induced by rapid movement (16°/s). It was found that these first increased in magnitude (with increasing stimulus exposures up to ∼45 ms) before reducing (between exposure durations of 45 and 75 ms) and then increasing once more (for even longer durations up to ∼100 ms). In contrast here, using a similar drift rate (15°/s), we found a steady increase and then saturation of the effect. This discrepancy
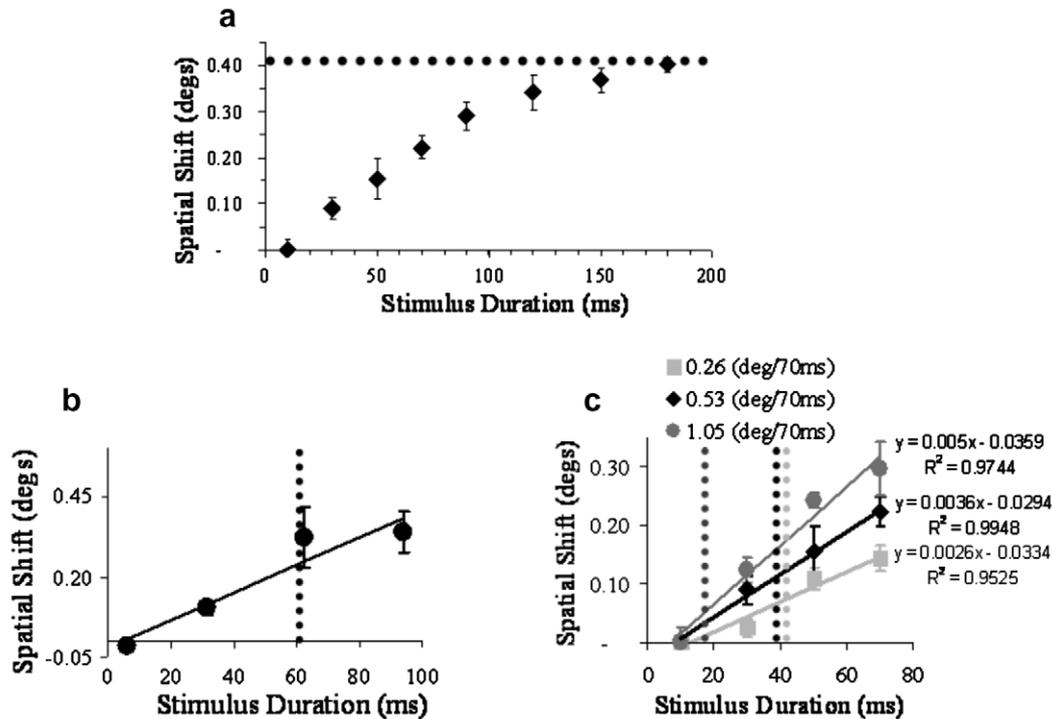
Fig. 3. Results for Experiment 2. All plots show apparent position shifts as a function of stimulus duration. Error bars show ±1 standard error. (a) Data points determined from four trial runs completed by the first author (stimulus speed 7.5°/s). (b) Data points determined from trial runs completed by four observers who were naïve as to the purpose of the study. The dotted vertical line shows the minimal stimulus duration at which motion directions could be identified on 75% of trials by these observers. (c) Data points determined from four trial runs completed by the first author. Three stimulus speeds (3.75, 7.5 and 15°/s shown as 0.26, 0.53 and 1.05°/70 ms) were sampled. Dotted vertical lines are coded (0.53°/70 ms black, 1.05°/70 ms dark-grey, 0.26°/70 ms light-grey) and show the minimal stimulus durations at which motion directions could be identified on 75% of trials by this observer.

could perhaps be related to differences in the stimuli used. We used stimuli with blurred edges, reduced to zero contrast at the extremities (above and Arnold & Johnston, 2005), whereas in the former study the stimuli had clearly visible edges (Chung et al., 2007). These differences can influence the magnitudes of illusory motion-induced position shifts (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990; Whitney et al., 2003) and might also alter the temporal dynamics of the phenomenon (Fig. 3).

The vertical dotted lines in Fig. 3b and c indicate the minimal stimulus durations at which observers could identify directions of motion within Gabor patterns. Some data points to the left of these lines indicate robust illusory position changes—showing that position changes can occur when stimulus presentations are too brief for directions of carrier drift to be identified. This finding is consistent with a recent demonstration that spatial shifts can occur when observers are not aware of the inducing motion direction because of crowding (Whitney, 2005). In combination, these results show that interactions between motion and position coding do not depend upon accurate identification of motion direction. The results of Experiment 3 also suggest that illusory motion-induced position changes can be a more sensitive direction cue than behavioural responses that are presumably based on analyses of motion signals *per se*.

While the results of Experiments 1 and 2 are consistent with the *Contrast Modulation* account (Whitney et al., 2003), a more stringent test of this proposal would be to determine objective measures of contrast sensitivity adjacent to static objects that contain movement. According to the *Contrast Modulation* account, low contrast stimuli located at the trailing edges of movement should be more difficult to detect than corresponding stimuli at leading edges. We tested this proposal in Experiment 3.

5. Experiment 3

5.1. Methods

Stimuli in Experiment 3 consisted of pairs of *inducing gratings* (widths 1.8° heights 0.5°, s.f. 2.5 cpd, contrast 100%) centred 0.6° above and below, and 1.075° to the left or right of a central fixation point (see Fig. 4a). The relative displacement of the inducing gratings, to the left or right of fixation, was determined at random on a trial by trial basis to help minimize the build-up of motion adaptation effects. A third, *target grating* (width 0.35° height 0.5°, s.f. 2.5 cpd) was horizontally centred but displaced vertically 0.6° above or below the fixation point (again determined at random on a trial-by-trial basis). The *target grating* therefore abutted one of the two *inducing gratings* (see Fig. 4a). During a
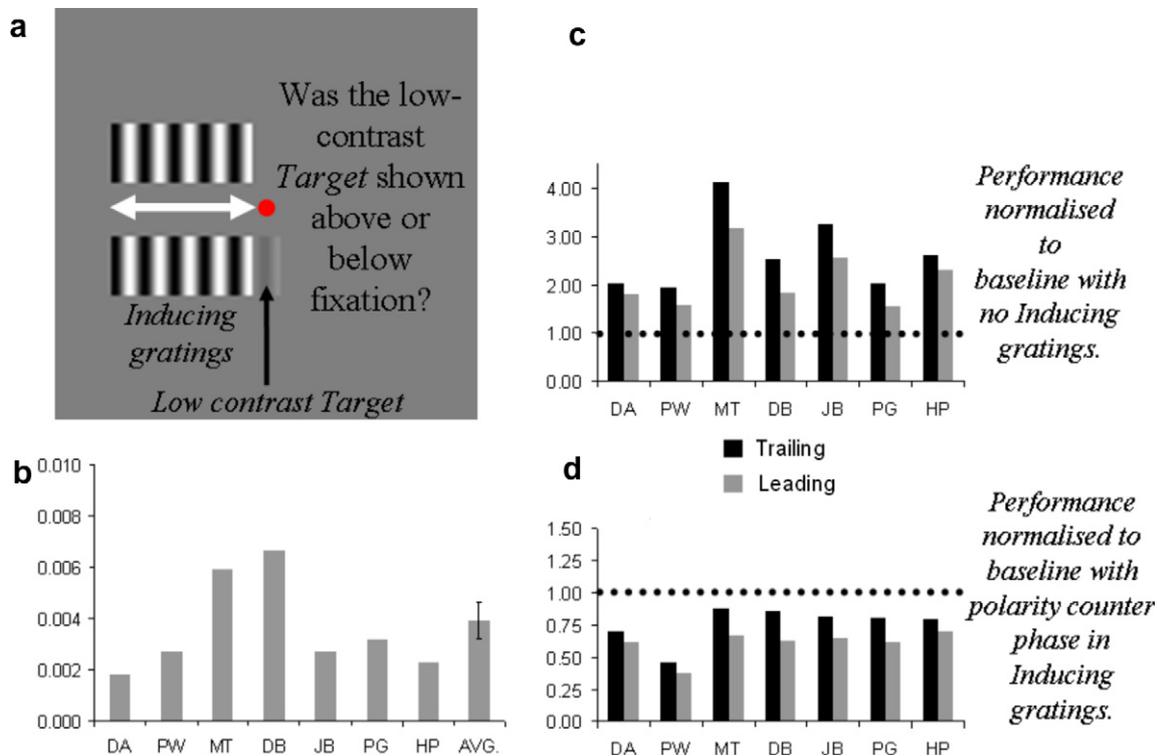
Fig. 4. (a) Graphic depicting stimuli used in Experiment 3. (b) Contrast detection threshold differences, thresholds for *target gratings* at leading edges minus thresholds for *target gratings* at trailing edges. (c) Contrast detection thresholds for *target gratings* at both leading *and* trailing edges, normalised to performance in the baseline condition without inducing gratings. (d) Contrast detection thresholds for *target gratings* at both leading *and* trailing edges, normalised to performance in the baseline condition in which the contrast polarity of *inducing gratings* was modulated to create sinusoidal luminance flicker.

run of trials, the contrast of the *target grating* was manipulated according to the method of constant stimuli (0–0.024, or 0–0.048%) The background of the display was grey (Commission Internationale d'Eclairage (CIE) 1931 chromaticity chart: $x = 0.28$, $y = 0.29$, $l = 66$). Each stimulus presentation persisted for 1 s. Seven observers participated in this experiment, two authors and five observers who were naïve as to the purpose of the Experiment.

All grating envelopes were physically static. Within the inducing gratings, both carriers either drifted toward (leading edge) or away from (trailing edge) fixation at a rate of 5 Hz. Trials sampling these two directions of carrier drift were interleaved, in a pseudo random order, during a run of trials to avoid any differences between the two conditions arising because of practise. The target grating carrier drifted in the same direction and at the same rate as the inducing grating carriers. On each trial, the observer was required to indicate if the target grating had been shown above or below fixation. A run of trials consisted of each contrast level being presented 20 times, both for target gratings located at leading edges of inducing gratings and for target gratings located at trailing edges—360 individual trials in total. Each observer completed two trial runs for each condition, so individual threshold estimates are based on 720 trials.

Each trial run provided a distribution of target grating detection as a function of luminance contrast. Weibull

functions were fitted to these data to determine contrast levels at which the observer could detect target gratings on 75% of trials—the contrast detection thresholds.

We also completed trial runs to provide baseline estimates of sensitivity. Details concerning these trial runs were similar to those described above with the following exceptions. Instead of having inducing gratings with carrier drift, in half of these trials target gratings were shown in the absence of inducing gratings. In the other half of the trials, the contrast polarity of carriers within the inducing gratings was sinusoidally counter phased at a rate of 5 Hz. These trials therefore provided baselines in which no motion was present in the target gratings but in which the spatial and temporal properties of the target gratings were matched as closely as possible to the standard stimulus configuration. The different types of trial run were completed in a pseudo random order to avoid practice effects.

5.2. Results

Fig. 4b shows differences between contrast detection thresholds measured abutting the leading and trailing edges of movement in inducing gratings. Positive values signify that observers were more sensitive to target gratings at leading edges relative to target gratings at trailing edges ($t_6 = 5.039$, $p = .002$).

Fig. 4c shows normalised contrast detection thresholds for target gratings located at both the trailing and leading edges of movement within abutting inducing gratings. These thresholds are normalised to the observers' performance in the baseline condition in which inducing gratings were absent. Normalised thresholds greater than 1 indicate that test grating detection was impaired by the presence of abutting gratings containing carrier drift ($t_{13} = 7.107$, $p < .001$).

Fig. 4d shows contrast detection thresholds normalised to the observers' performance in the counter phase baseline condition. Normalised thresholds less than 1 indicate that target grating detection was improved by the presence of abutting gratings with carrier drift relative to situations wherein the contrast polarity of abutting gratings was modulated at 5 Hz—generating considerable retinal blur but no smooth motion ($t_{13} = 8.185$, $p < .001$).

5.3. Discussion

The results of Experiment 3 allow us to comment on both the relative influences of motion direction and on the influence of dynamic change *per se*.

Low contrast targets were more difficult to detect at the trailing edges, as opposed to the leading edges, of movement in adjacent static high contrast gratings. This shows that motion direction can influence objective measures of contrast sensitivity in surrounding regions. These results compliment findings concerning subjective size distortions near blurred stimulus edges (De Valois & De Valois, 1991; Whitaker et al., 1999, 2003; Tsui, Khuu, & Hayes, 2007) and are consistent with the Contrast Modulation account. Together, these data suggest that low contrast regions at the leading edges of movement are more visible than corresponding regions at trailing edges.

To identify the influence of motion *per se*, we used a baseline condition in which inducing gratings were matched as closely as possible to those used in the experimental conditions. Spatial similarity was ensured by using static inducing gratings with static carrier waveforms of the same spatial frequency as those used in the experimental conditions. Temporal similarity was ensured by varying the contrast polarity of the waveforms to generate sinusoidal luminance flicker matched, in terms of temporal frequency, to the rate of carrier drift within the experimental stimuli. We therefore created an opportunity to compare spatially and temporally similar luminance modulations that do and do not generate smooth motion.

We found that observers could more easily detect target gratings when they abutted static gratings containing carrier drift (the experimental conditions) as opposed to static gratings that contained luminance flicker (the baseline condition). It is important to note that sensitivity to low contrast targets was generally enhanced by motion relative to luminance flicker—motion both toward and away from the target was beneficial in this context.

Both luminance flicker and motion can generate retinal image blur. This blur could be alleviated, to some extent, by modulating contrast in regions surrounding the motion (and or flicker) signal. This could be achieved by modulating neural firing rates via interactions between cortical neurons. Our data suggest that the firing rates of neurons with RFs located at the trailing edges of motion must be reduced to a greater extent than are neurons with RFs located at leading edges. Recently, other labs have independently arrived at similar conclusions (Chung et al., 2007; Liu et al., 2006; Tsui et al., 2007). These suggestions could readily be tested using traditional single unit neurophysiological methods.

6. General discussion

In general, our data do not support the *RF shift* account of motion induced position shifts (Fu et al., 2004). The specificity of apparent shifts (Experiment 1) is inconsistent with a simple re-mapping of cortical RFs. Instead, our data suggests that position shifts occur because of a process of *Contrast Modulation* (Whitney et al., 2003). Such a process would be particularly apparent at blurred low contrast stimulus regions where slight contrast modulations could render previously visible regions invisible and invisible regions visible.

Recently, it has been argued that motion induced position shifts could be driven by flexible retinotopy (Fu et al., 2004; Sundberg et al., 2006; Whitney et al., 2003). We believe that our data are inconsistent with this proposal. If cortical RFs were simply shifted, all stimulus properties encoded by effected neurons should seem equally displaced. However, we have observed that motion induced position shifts can be selective; while visible stimulus extremities appear relatively shifted, waveforms *within* the stimulus do not. This dissociation precludes the possibility that RF shifts might provide an adequate explanation for motion-induced position shifts. How then can we account for this dissociation?

It has been observed that firing rates, as a function of retinal location, can be modulated by motion direction in cat (Fu et al., 2004) and monkey (Sundberg et al., 2006) visual cortex. It has also been shown that peak activity in human visual cortex, as measured with fMRI, is modulated by motion direction (Whitney et al., 2003). While both observations have been attributed to flexible retinotopy, they are also consistent with response gain modulations (see Liu et al., 2006). By implication, apparent position shifts would occur because of gain modulations that directly influence visibility (Whitney et al., 2003).

Response gain modulations can be driven by lateral interactions between neighbouring neurons. For instance, motion selective lateral interactions can influence response gain in rabbit and salamander retinal ganglion cells (Berry, Brivanlou, Jordan, & Meister, 1999). These modulations do not necessitate a change in the location of the cells' RF. Response gains could be modulated, such that neurons encoding regions toward the leading edges of movement become more active relative to neurons encoding trailing edges. This would enhance the relative visibility of regions at leading edges, thereby inducing an apparent position shift. However, modulating response gains would not

influence activity as a function of waveform phase—so the apparent positioning of this 1st order stimulus attribute would be unaffected.

Other papers have recently drawn similar conclusions to those proposed here (Chung et al., 2007; Liu et al., 2006; Tsui et al., 2007). Concentrating on the encoded position of the 2nd order stimulus attribute (the envelope), these papers have pointed out that gain modulations could shift the centroid of activation in cortex, and thereby presumably the perceived position encoded by that activity (Chung et al., 2007; Liu et al., 2006; Tsui et al., 2007). Our data here are in broad agreement with these conclusions, but they also highlight the selectivity of this sort of motion-induced position shift. This selectivity could easily be tested using standard electrophysiological techniques. We predict that, because of gain modulations, the centroid of activity in primary visual cortex will be slightly shifted in the presence of motion (Fu et al., 2004; Liu et al., 2006; Sundberg et al., 2006). However, neural responses as a function of waveform phase will be unaffected. This latter hypothesis has not yet been assessed.

We believe that our data also clarifies the dynamics of the process by which contrast is modulated—thereby creating a motion induced position shift. We have found that the magnitudes of motion induced position shifts can increase linearly with increasing stimulus exposures up to exposure durations of ~180 ms. This suggests that the process might be driven by the temporal integration of a constant motion signal.

While our discussion of response gain modulations has focussed on interactions between neighbouring neurons, they could also be driven by intra cortical region interactions. Recently, it has been shown that illusory motion induced position shifts correlate with increased fMRI bold responses in human occipital cortex (Whitney et al., 2003). It has also been shown that illusory shifts can be reduced by applying TMS to V5, but not to the primary visual cortex (McGraw, Walsh, & Barrett, 2004). This pattern of results is consistent with the suggestion that specific patterns of feedback, from V5 to V1, can modulate V1 response gains and thereby influence apparent contrast and perceived position.

Acknowledgments

References

Arnold, D. H., & Johnston, A. (2005). Sub-threshold motion influences apparent position [Abstract]. *Journal of Vision, 5*(8):202, 202a, http://journalofvision.org/5/8/202/, doi:10.1167/5.8.202.

Barlow, H. B. (1958). Temporal and spatial summation in human vision at different background intensities. *Journal of Physiology, 141*, 337–350.

Berry, M. J., Brivanlou, I. H., Jordan, T. A., & Meister, M. (1999). Anticipation of moving stimuli by the retina. *Nature, 398*, 334–338.

Braddick, O. (1973). The masking of apparent motion in random-dot patterns. *Vision Research, 13*, 355–369.

Bressler, D. W., & Whitney, D. (2006). Second-order motion shifts perceived position. *Vision Research, 46*, 1120–1128.

Burr, D. (1980). Motion smear. *Nature, 284*, 164–165.

Chung, S. T. L., Patel, S., Bedell, H. E., & Yilmaz, O. (2007). Spatial and temporal properties of the illusory motion-induced position shift for drifting stimuli. *Vision Research, 47*, 231–234.

Daniel, P. M., & Whitteridge, D. (1961). *Journal of Physiology, 159*, 203.

De Valois, R. L., & De Valois, K. K. (1991). Vernier acuity with stationary moving gabors. *Vision Research, 31*, 1619–1626.

Fu, Y., Shen, Y., Gao, H., & Dan, Y. (2004). Asymmetry in visual cortical circuits underlying motion-induced perceptual mislocalization. *The Journal of Neuroscience, 24*, 2165–2171.

Levi, D. M., Li, R. W., & Klein, S. A. (2003). "Phase capture" in the perception of interpolated shape: Cue combination and the influence function. *Vision Research, 43*, 2233–2243.

Levi, D. M., Li, R. W., & Klein, S. A. (2005). "Phase capture" in amblyopia: The influence function for sampled shape. *Vision Research, 45*, 1793–1805.

Livingstone, M. S., & Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *Journal of Neuroscience, 7*, 3416–3466.

Liu, J. V., Ashida, H., Smith, A. T., & Wandell, B. A. (2006). Assessment of Stimulus-Induced Changes in Human V1 Visual Field Maps. *Journal of Neurophysiology, 96*, 3398–3408.

Mathiesen, C., Caesar, K., & Lauritzen, M. (2000). Temporal coupling between neuronal activity and blood flow in rat cerebellar cortex as indicated by field potential analysis. *Journal of Physiology (London), 523*, 235–246.

McGraw, P. V., Walsh, V., & Barrett, B. T. (2004). Motion-sensitive neurones in V5/MT modulate perceived spatial position. *Current Biology, 14*, 1090–1093.

Morgan, M. (2003). *The space between our ears*. London: Weidenfeld & Nicolson.

Nishida, S., & Johnston, A. (1999). Influence of motion signals on the perceived position of spatial pattern. *Nature, 397*, 610–612.

Ramachandran, V. S., & Anstis, S. M. (1990). Illusory displacement of equiluminant kinetic edges. *Perception, 19*, 611–616.

Sereno, M. I., Dale, A. M., Reppas, J. B., Kwong, K. K., Belliveau, J. W., Brady, T. J., Rosen, B. R., & Tootell, R. B. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science, 268*, 889–893.

Snowden, R. J. (1998). Changes in apparent position following adaptation to visual motion. *Current Biology, 8*, 1343–1345.

Sundberg, K. A., Fallah, M., & Reynolds, J. H. (2006). A motion-dependent distortion of retinotopy in V4. *Neuron, 49*, 447–457.

Tootell, R. B., Silverman, M. S., Switkes, R. L., & De Valois, R. L. (1982). Deoxyglucose analysis of retinotopic organization in primate striate cortex. *Science, 218*, 902–904.

Tsui, S. Y., Khuu, S. K., & Hayes, A. (2007). The perceived position shift of a pattern that contains internal motion is accompanied by a change in the pattern's apparent size and shape. *Vision Research, 47*, 402–410.

Whitaker, D., McGraw, P. V., & Pearson, S. (1999). Non-veridical size perception of expanding and contracting objects. *Vision Research, 39*, 2999–3009.

Whitney, D. (2005). Motion distorts perceived position without awareness of motion. *Current Biology, 15*, R324–R326.

Whitney, D., & Cavanagh, P. (2000). Motion distorts visual space: Shifting the perceived position of remote stationary objects. *Nature Neuroscience, 3*, 954–959.

Whitney, D., Goltz, H. C., Thomas, C. G., Gati, J. S., Menon, R. S., & Goodale, M. A. (2003). Flexible retinotopy: Motion-dependent position coding in the visual cortex. *Science, 302*, 878–881.

Zeki, S. M. (1974). Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. *Journal of Physiology (London), 236*, 549–573.

Zihl, J., VonCramon, D., & Mai, N. (1983). Selective disturbance of movement vision after bilateral brain damage. *Brain, 106*, 313–340.