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Distinct position assignment mechanisms revealed by cross-order motion

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ABSTRACT

Motion perception influences perceived position. It has been shown that first-order (luminance defined) motion shifts perceived position across a wide range of spatial and temporal frequencies. On the other hand, second-order (contrast defined) motion shifts perceived position over a narrow range of temporal frequencies, regardless of spatial frequency [Bressler, D. W., & Whitney, D. (2006). Second-order motion shifts perceived position. *Vision Research, 46*(6–7), 1120–1128]. These results suggest the presence of distinct position assignment mechanisms for first- and second-order motion. We investigated whether the first- and second-order systems independently encode and assign the position of a moving stimulus. To measure motion induced position shift we presented two horizontally offset Gabors placed above and below a central fixation point, with sine wave carriers drifting in opposite directions. Subjects judged the position of the top Gabor relative to the bottom one. We used both first-order Gabors (sinusoidal luminance modulation of a dynamic noise carrier enveloped by a static Gaussian) and second-order Gabors (sinusoidal contrast modulation of a dynamic noise carrier enveloped by a static Gaussian). Results showed a strong position shift in the direction of the carrier motion when both Gabors were first-order, a weak position shift when both Gabors were second-order, and no appreciable position shift when one Gabor was first-order and the other was second-order (cross-order motion). The absence of a position shift using cross-order motion supports the hypothesis that the two motion systems independently encode and assign the position of a moving object. These results are consistent with those of experiments investigating global spatial interactions between static first-order and second-order Gabor patches, indicating a commonality in the underlying spatial integration processes.

1. Introduction

Apparent motion influences the perceived position of an object. A striking number of studies have shown that when observing a moving object, its position appears shifted in the direction of motion (Chung, Patel, Bedell, & Yilmaz, 2007; De Valois & De Valois, 1991; Durant & Johnston, 2004; Edwards & Badcock, 2003; Fang & He, 2004; Fu, Shen, Gao, & Dan, 2004; Harp, Bressler, & Whitney, 2007; McGraw, Levi, & Whitaker, 1999; Mussap & Prins, 2002; Nishida & Johnston, 1999; Ramachandran & Anstis, 1990; Snowden, 1998; Whitaker, McGraw, & Pearson, 1999; Whitney, 2002; Whitney & Cavanagh, 2000; Whitney & Cavanagh, 2003; Zanker, Quenzer, & Fahle, 2001). It has been shown that both low-level and high-level motion processes can influence the perceived position of an object. For example, a moving stimulus can influence the perceived position of a stationary nearby flashed stimulus (the flash-lag effect: for a review see Bachmann & Poder, 2001; Baldo, Ranvaud, & Morya, 2002; Ichikawa & Masakura, 2006; Nijhawan, 1994; Nijhawan, 2002; Whitney & Murakami, 1998). Shim and Cavanagh (2004) measured the motion-induced position shift with a bistable quartet and found a shift in position for flashed stimuli in the direction of the perceived motion of the bistable stimuli. Such a result indicates that high-level motion processes that resolve ambiguity can produce a position shift in stationary objects, as well as low-level processes (Shim & Cavanagh, 2004; Whitney, 2006). These effects and other related phenomena (e.g. representational momentum; Freyd & Finke, 1984; Freyd & Finke, 1985; Thornton & Hubbard, 2002) suggest interactions between specialized visual areas that encode motion and position (Arnold & Johnston, 2005; Whitney et al., 2003).

Many studies, employing different paradigms, have examined the spatial and temporal properties of the motion-induced position shift of stationary objects (Arnold & Johnston, 2005; Bressler & Whitney, 2006; De Valois & De Valois, 1991; Durant & Johnston, 2004; Fu et al., 2004; McGraw, Whitaker, Skillen, & Chung, 2002; Mussap & Prins, 2002; Shim & Cavanagh, 2004; Sundberg, Fallah, & Reynolds, 2006; Watanabe, 2005; Whitaker et al., 1999; Whitney, 2005; Yokoi & Watanabe, 2005). De Valois and De Valois (1991) used pairs of first-order Gabor patterns (a sinusoidal luminance-modulated carrier enveloped by a static Gaussian) with sine wave carriers drifting in opposite directions, and found that the

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magnitude of the illusory motion-induced position shift depends on both the spatial and the temporal frequency of the stimulus, though they did not find a direct relationship between the magnitude of the motion-induced position shift and the carrier speed. However, McGraw et al. (2002) found that the motion-induced position shift for first-order Gabor patterns peaks at about 1 deg/s, regardless of carrier's spatial frequency. On the other hand, Bressler and Whitney (2006) found that the maximum position shift occurred at low spatial frequencies (less than 1 c/deg) for a wide range of temporal frequency. In addition, the magnitude of the first-order motion-induced position shift increased with increasing carrier speed. These findings suggest the presence of specific velocity tuned channels that play an important role in mediating the first-order motion-induced position shift.

Many studies suggest that separate mechanisms and neural substrates are responsible for detecting first- and second-order motion (e.g. contrast-defined motion; Ashida, Lingnau, Wall, & Smith, 2007; Cavanagh & Mather, 1989; Cowey, Campana, Walsh, & Vaina, 2006; Derrington & Badcock, 1985; Edwards & Badcock, 1995; Ledgeway & Smith, 1994; Lu & Sperling, 1995; Lu & Sperling, 2001; Mather, 1991; McCarthy, 1993; Nishida & Sato, 1995; Seiffert & Cavanagh, 1998; Vaina, Cowey, & Kennedy, 1999; Vaina, Makris, Kennedy, & Cowey, 1998; Vaina & Soloviev, 2004); so the detection of second-order motion patterns may involve different spatio-temporal channels from those involved in first-order motion. Bressler and Whitney (2006) examined whether second-order motion influences perceived position. Their results showed that second-order motion does influence perceived position, but with a different spatio-temporal tuning from that of first-order motion. Second-order motion shifts perceived position over a relatively narrow range of temporal frequencies, peaking at about 4 Hz, and this effect is roughly invariant with spatial frequency.

From previous studies we can conclude that two separate and independent mechanisms are involved in the detection of first- and second-order motion, with different spatio-temporal tuning. However, it is not clear whether two independent mechanisms also encode position or if a single, common mechanism is responsible for assigning the location of both first- and second-order moving stimuli. Since first- and second-order moving patterns are initially detected by separate and independent mechanisms, each type of motion could independently influence position. Alternatively, it is possible that the mechanism involved in position assignment could be the same for first- and second-order motion; for instance, at a stage where motion information is integrated and neurons respond both to first- and second-order motion patterns, such as area V5/MT. In this latter case the differential spatio-temporal tuning found for first- and second-order motion-induced position shift could reflect the differences between the two lower level detector systems.

The purpose of the present study was to investigate whether first- and second-order motion systems contribute to the same or different position assignment mechanisms. We first measured separately the motion-induced position shift for first- and second-order moving patterns. Subsequently, we conducted an experiment in which first- and second-order drifting Gabors were presented within the same trial, to see if cross-order motion shifts perceived position as well. The rationale was that if there is a common position assignment mechanism for both first- and second-order motion, one would expect a cross-order motion-induced position shift that reflects a contribution from both first- and second-order motion systems. So, we should observe an effect that is intermediate between the first-order and the second-order motion-induced position shifts. On the other hand, the lack of an effect for cross-order stimuli would indicate the presence of separate and independent position assignment mechanisms. To anticipate, our results support the hypothesis that first- and second-order processes encode position independently (Burr, 1980; Burr & Ross, 1982; Burr & Ross, 2002; Burr, Ross, & Morrone, 1986; Fahle & Poggio, 1981; Geisler, 1999; Nishida, 2004).

2. Methods

2.1. Subjects

The two authors and six subjects who were unaware of the purpose of the study participated in each experiment. Subjects sat in a dark room and were immobilized with a chin rest placed at 57 cm from the screen. Viewing was binocular. They were instructed to fixate a point at the center of the screen and were given training at the beginning of each experiment to familiarize them with the stimuli and task. All subjects had normal or corrected-to-normal visual acuity.

2.2. Apparatus

Stimuli were displayed on a Sony Trinitron G400 monitor with a refresh rate of 100 Hz and generated by a CRS VSG2/5 graphics system. The screen resolution was set at 1024 × 768 pixels. The mean luminance was 29.03 cd/m^2. Luminance was measured using a Minolta LS-100 photometer. A gamma-corrected lookup table (LUT) was used to insure stimulus linearity.

2.3. Stimuli

Stimuli were vertically oriented first- and second-order Gabor patterns. First-order Gabors consisted of sinusoidal luminance modulation of a dynamic noise carrier enveloped by a static Gaussian. The Gabors had a full width of 3.3 deg at half maximum amplitude. Formally the first-order Gabors used can be defined as

$$L(x,y,t) = L_{\mathrm{mean}}[\langle\{1 + m\sin(2\pi f_{\mathrm{x}}x + 2\pi f_{\mathrm{t}}t + \phi\} + C_{\mathrm{n}}R_{(x,y,t)}\rangle] \times \exp\left(-\left((x/\sigma)^2 - (y/\sigma)^2\right)\right), \tag{1}$$

where $L_{(x,y,t)}$ represents the luminance at each point of the stimulus at the instant t, L_{mean} is the mean luminance of the resultant pattern, m is the modulation depth (Michelson contrast) of the sine wave carrier (range 0–1 Michelson contrast), f_{x} is the spatial frequency (1 c/deg), f_{t} is the temporal frequency (4 Hz), φ is the phase shift of the sinusoidal carrier, C_{n} is the contrast (0.5 Michelson contrast) of the dynamic noise carrier $R_{(x,y,t)}$. The noise carriers were generated by assigning to each screen pixel (2.14 arcmin) the value of 0 (black dot) or 1 (white dot) with an equal probability, so in each noise carrier 50% of pixels were black and 50% were white and there was no luminance variation within each noise pixel. The noise carriers were updated every frame, resulting in dynamic noise. The Gaussian envelope is expressed by the exponential of the Eq. (1); x and y represent the respective horizontal and vertical distances from the Gaussian peak, σ is the spatial constant of the Gaussian (1.1 deg). The Gaussian envelope was always static, whereas the sine wave drifted at a constant velocity of 4 deg/s either leftwards or rightwards. Second-order Gabors consisted of sinusoidal contrast modulation of a dynamic noise carrier enveloped by a static Gaussian. A second-order Gabor can be defined as

$$L(x,y,t) = L_{\mathrm{mean}}[1 + \langle\{1 + E + m\sin(2\pi f_{\mathrm{x}}x + 2\pi f_{\mathrm{t}}t + \phi)\}C_{n}R_{(x,y)}\rangle] \times \exp\left(-\left((x/\sigma)^2 - (y/\sigma)^2\right)\right), \tag{2}$$

where $L_{(x,y,t)}$, L_{mean}, m, f_{x}, f_{t}, φ, C_{n}, $R_{(\mathrm{x,y,t})}$ and σ are the same parameters as in Eq. (1). E is the subject's equiluminance value (established using the technique described in the next section). Equiluminant stimuli were used in order to insure that contrast-defined motion did not contain any residual luminance (first-order) artifact.

2.4. Procedures

The experiment involved four different stages: (i) determining the contrast threshold for both first- and second-order drifting Gabors; (ii) estimating the subjective equiluminance point in second-order Gabors; (iii) measuring the perceived positions for first- and second-order drifting Gabors separately and in a cross-order stimulus; and finally (iv) measuring perceived positions of cross-order Gabors after having equated the saliency of second-order Gabors with respect to first-order Gabors. The procedure used in each phase is described below.

2.4.1. Contrast threshold

For first-order contrast thresholds, two Gabors were displayed at 9.7 deg above and below the fixation point, respectively (from fixation point to the center of the Gabor; same separation as used in the position-shift experiments). The two Gabors could drift either in the same or different directions; motion direction was balanced and randomized across trials. Using the method constant stimuli (MCS), subjects performed a discrimination task, pressing a response button to report whether the Gabors drifted in the same or different directions. Gabors had a spatial frequency of 1 c/deg and drifted at 4 Hz. Each subject performed 240 trials; 40 trials for each of the 6 contrast levels used (0.01, 0.015, 0.02, 0.025, 0.03 Michelson contrast). The procedure used to estimate the contrast modulation threshold for second-order stimuli was identical to that used for first-order stimuli, except for the 6 contrast modulation levels (0.20, 0.30, 0.40, 0.50, 0.60, 0.70 Michelson contrast). Contrast threshold (corresponding to 75% accuracy) was estimated by fitting a logistic function to the data. The contrast value used in subsequent experiments was obtained by multiplying the threshold value by three, in order to insure that all subjects could reliably perceive the motion direction of both first- and second-order patterns.

2.4.2. Minimum motion technique

A modified minimum motion technique (Anstis & Cavanagh, 1983; Nishida, Edwards, & Sato, 1997; Seiffert & Cavanagh, 1998) was used to find the subjective equiluminance value for second-order patterns. Subjects fixated a point at the center of the screen. First- and second-order Gabors were presented 9.7 deg above the fixation point and interleaved in a four-frame sequence such that each Gabor's sine wave was shifted by 90 deg, with first-order Gabors presented in odd frames and second-order Gabors presented in even frames. A first-order luminance modulation was added to second-order Gabors, and was varied from trial to trial according to a simple Up-Down staircase (Levitt, 1971). The rationale was as follows. Since successive frames are in quadrature phase, when second-order frames contain a residual luminance artifact subjects should perceive unidirectional motion in the four-frame sequence, either in one direction or the opposite depending on the contrast polarity of the artifact; when the luminance modulation added to second-order frames nulls or cancels out the artifact subjects should perceive no consistent apparent motion.

At the beginning of the procedure a very low contrast luminance modulation (0.01 Michelson contrast) was added to second-order frames in order to produce a unidirectional motion percept, and the initial staircase step size was chosen to be half this value. After the first, third, seventh, fifteenth and thirty-first reversal of apparent direction the step size was halved and after each halving of the step size the subsequent run was started with a value of the luminance artifact that was the average of the peaks and valleys for the preceding step size. On each trial (480 ms), subjects were asked to indicate perceived motion direction, either leftward or rightward, using a button press. Testing was terminated after a total of 40 runs and the average of peaks and valleys of all the runs was taken as an estimate the point of subjective equality (PSE; Finney, 1971; McKee, Klein, & Teller, 1985); this corresponds to the amplitude of the nulling luminance modulation added to second-order Gabors that produced a percept of ambiguous motion.

We assume that thresholds for second-order motion measured in phase (i) were not significantly affected by luminance artifacts because the nulling contrasts indicated in phase (ii) were so low that they would be vanishingly small at detection threshold.

2.4.3. Position shift

We used the contrast values and equiluminance points estimated in previous phases to measure the perceived position of first-, second-, and cross-order motion. As before, Gabors had a spatial frequency of 1 c/deg and drifted at 4 Hz. These values were chosen on the basis of data in Bressler & Whitney, 2006, to produce at least a moderate position shift for both first- and second-order Gabors. The spatial frequency we employed was higher than that used by Bressler and Whitney (2006). In pilot observations using the same spatial frequency as Bressler and Whitney (2006), namely 0.18 c/deg, we found that it was extremely difficult to discriminate the motion direction of second-order patches located 9.7 deg into the periphery. (Bressler & Whitney, 2006, reported relatively little difference between results at 0.18 c/deg and at 1 c/deg). Subjects fixated a point at the center of the screen and judged the relative position of two vertically oriented Gabors placed at 9.7 deg above and 9.7 deg below the fixation point. The sine wave carriers of the top and the bottom Gabor always drifted in opposite directions. On each trial, the two Gabors were presented horizontally offset in opposite directions by one of six values (−0.71, −0.43, −0.14, 0.14, 0.43, 0.71 deg of visual angle; positive values indicate rightward offset, negative values indicate leftward offset). Each trial was presented for 500 ms, after which the subject indicated with a button press whether the top Gabor appeared more to the left or more to the right of the bottom one. Each subject performed 240 trials in each the three stimulus conditions. MCS was used for all three conditions. A logistic function was fitted to the data in order to estimate the 50% corresponding to the physical misalignment between the Gabors required for apparent alignment (the point of subjective equality, PSE; Finney, 1971; McKee et al., 1985).

2.4.4. Position shift with matched salience

A possible complication in the third phase of the study was that, while first- and second-order patterns were equated in terms of motion discriminability (both three-times discrimination threshold) they were not equated in terms of subjective pattern salience (the first-order pattern appeared much more salient), and this may have influenced position judgments. Therefore the position shift measurements and associated threshold measurements in previous phases were repeated (using a different set of eight subjects) so that we could employ a cross-order stimulus in which first- and second-order Gabors were equated for perceptual salience. In phase (iv) we reduced the contrast of first-order Gabors in the cross-order stimulus to psychophysically equate their salience with second-order Gabors. We used another variant of the minimum motion technique (Anstis & Cavanagh, 1983) to estimate the required level of contrast. Subjects fixated a point at the center of the screen. First- and second-order Gabors were presented at 9.7 deg above the fixation point and interleaved in a six-frame sequence, with first-order Gabors presented in odd frames and second-order Gabors presented in even frames. Each first-order Gabor's sine wave carrier was shifted by 90 deg (i.e. quadrature phase) on each appearance, and each second-order Gabor's sine carrier was shifted a corresponding distance in the opposite direction on each appearance. We then manipulated the contrast of the luminance-defined carrier in the first-order Gabor while keeping constant the contrast of the second-order Gabor. Initially the

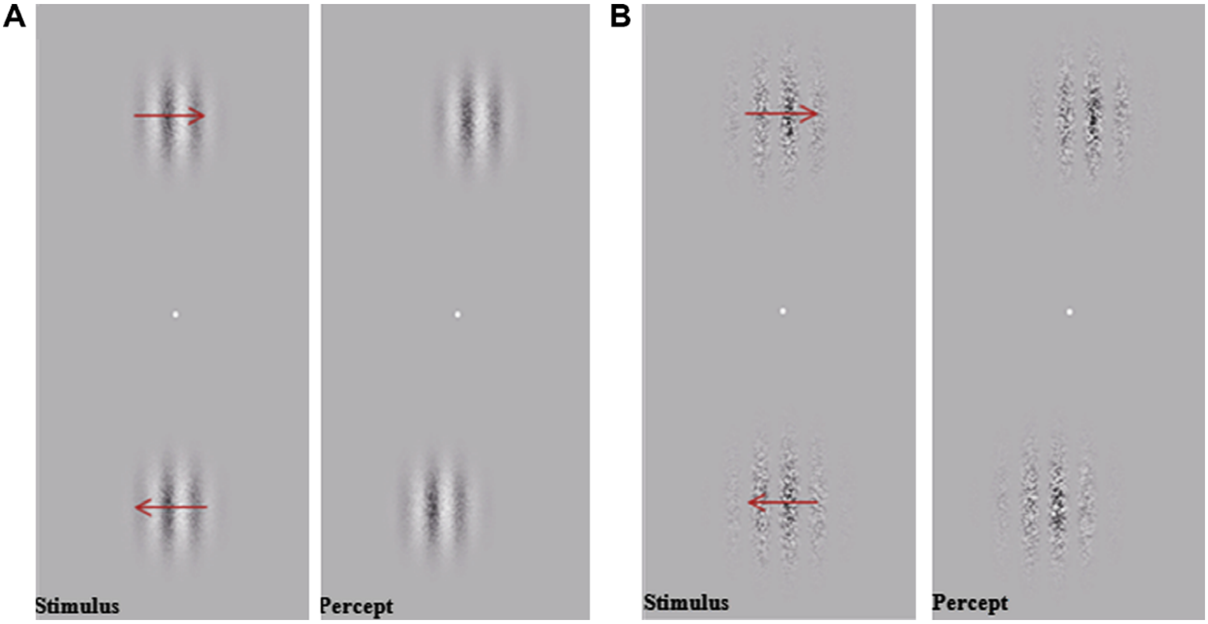

Fig. 1. (A) Stimulus and percept for first-order drifting Gabors (luminance-defined motion). (B) Stimulus and percept for second-order drifting Gabors (contrast-defined motion). The pictures show an example in which two first- and second-order Gabors are physically aligned (we did not include such a condition in our experiments; see Section 2) but when the luminance-defined carriers (A) and the contrast-defined carriers (B) drift in opposite directions the Gabors appear misaligned. For illustrative purposes the Gabors reported here have sinusoidal carriers with exaggerated contrast.

contrasts of the first- and second-order Gabors were set equal to those used in the previous phase for each subject. We then varied first-order contrast from trial to trial according to a simple Up-Down staircase (Levitt, 1971). When the contrast of the first-order carrier was very low or zero, the perceived motion direction of the six-frame sequence followed the second-order carrier; we measured the contrast of the first-order carrier required to null the unidirectional motion of the second-order carrier, assuming that this contrast equated the salience of first-order carriers with second-order carriers. We then measured the motion-induced position shift while first- and second-order Gabors were displayed within the same trial. In this last experiment we used the same parameters as in the previous experiments. Each subject performed 240 trials (40 repetitions for each of the 6 horizontal offsets). MCS was used, followed by computation of the best-fitting logistic function.

3. Results

Results showed that both first- and second-order motion shift the perceived position of the static envelopes in the direction of the moving carriers. For instance, if the envelopes of the two Gabors are physically aligned (Fig. 1A and B, left), they appear shifted towards the direction of the carriers (Fig. 1A and B, right).

Fig. 2 shows the psychometric functions for subject GM, illustrating the magnitude of the motion-induced position shift for first-order drifting Gabors (Fig. 2A), for second-order drifting Gabors (Fig. 2B) and for cross-order motion (Fig. 2C). The effect is marked for first-order Gabors (0.5 deg), small both for second-order drifting Gabors (0.06 deg) and virtually absent for cross-order motion (0.03 deg). Although some psychometric functions such as that shown (Fig. 2A) did not drop to zero (or alternatively reach 100%), they always spanned values that were significantly different from the mid-point, and all curve fits passed an X^2 goodness-of-fit test.

This pattern of results is consistent across all subjects. One subject was excluded from further analysis because their data never fell below 50%, indicating an extreme apparent misalignment between the Gabors (over two standard deviations larger than the remaining seven subjects).

Fig. 3 summarizes the mean position shift across all remaining seven subjects (±1 SE). The mean position shift found for first-order stimuli was 0.42 deg, whereas second-order motion shifted perceived position by 0.09 deg. There is a significant difference between first- and second-order results ($t_{(6)} = 4.60$, $P = 0.004$). Though the position shift found with second-order motion was very small, it was still significantly higher than that found for cross-order motion ($t_{(6)} = 2.69$, $P < 0.05$), for which we found a position shift of 0.039 deg. We also found a significant difference between the first-order and cross-order motion-induced position shift ($t_{(6)} = 4.43$, $P = 0.004$). Though the position shift found for cross-order patterns was significantly lower than that obtained for second-order patterns, it was still significantly different from zero ($t_{(6)} = 4.87$; $P = 0.003$). This result could be due to the different salience between first-order and second-order patterns; that is, the higher salience of first-order patches may have influenced the performance of the subjects. In the phase four of the experiment we addressed this issue.

In addition, in phase three we also found a significant difference between the slopes of the psychometric functions for the three stimulus conditions (Fig. 4); the slopes were calculated as the reciprocal of the standard deviation of the psychometric function. A paired-samples *t* test conducted on the slopes revealed a significant difference between first-order and second-order patterns ($t_{(6)} = 4.98$; $P = 0.003$), for which the mean slopes were 0.006 and 0.009 deg, respectively, and between second-order and cross-order motion patterns (0.007 deg) ($t_{(6)} = 4.64$; $P = 0.004$), but no significant differences between first-order and cross-order patterns ($t_{(6)} = 1.84$; $P > 0.05$). The difference in position sensitivity between first- and second-order stimuli could be due to the lower contrast employed for first-order than for second-order stimuli. Indeed the contrast thresholds estimated in phase one of the experiment were always much lower for first-order motion than for second-order motion. However, despite the difference in sensitivity, the shift in

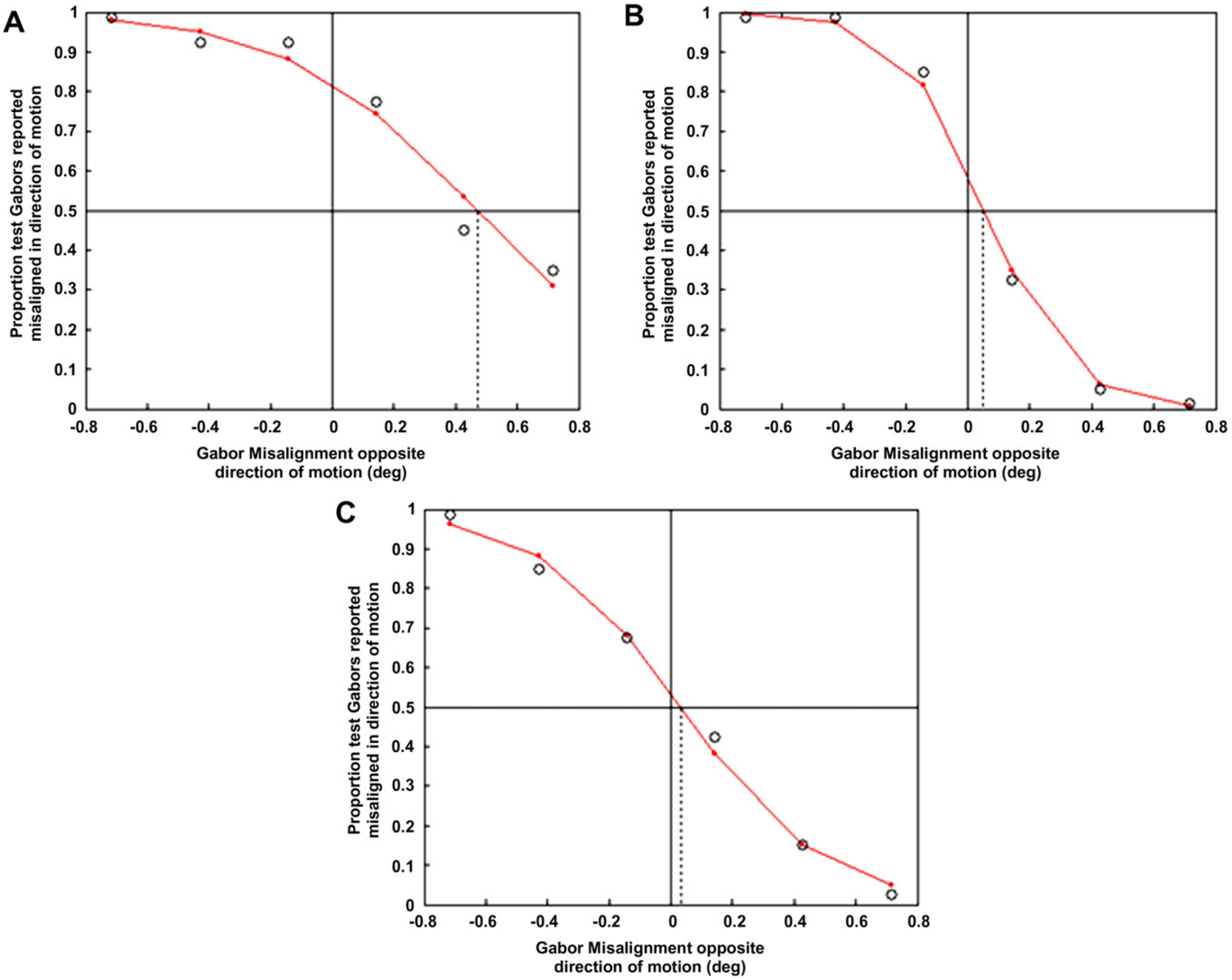

Fig. 2. Psychometric functions for subject GM using (A) first-order drifting Gabors, (B) second-order drifting Gabors and (C) cross-order motion. The abscissa shows the physical alignment between the Gabors in degrees of visual angle (positive values indicate that the Gabors were physically displaced opposite the direction of the carrier motion). The ordinate shows the proportion of responses in which subjects judged the Gabors to be shifted in the direction of the carrier motion. The point of subjective equality (PSE) is the physical misalignment between the Gabors that created an apparent alignment; this estimates the magnitude of the illusory position shift. The PSE of GM for first-order drifting Gabors was 0.5 deg, 0.06 deg for second-order drifting Gabors and 0.03 deg for cross-order motion.

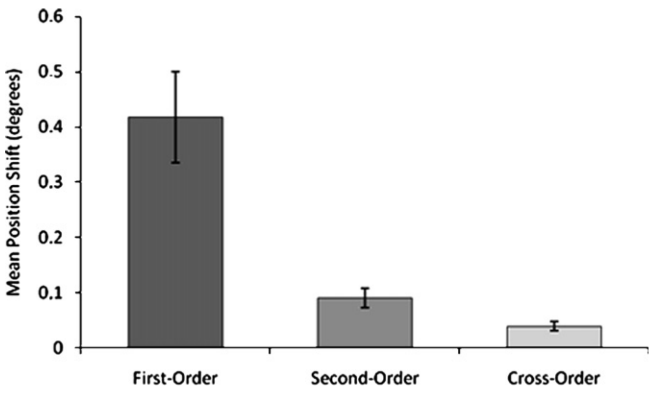

Fig. 3. Perceived misalignment for first-order, second-order and cross-order motion. The size of the offset for first-order stimuli is about 0.42 deg, whereas for second-order motion is 0.09 deg. The positional offset obtained for second-order stimuli, though very small, is higher than that obtained for cross-order motion (0.039 deg), for which we observed a lack of the effect. Error bars ± SEM.

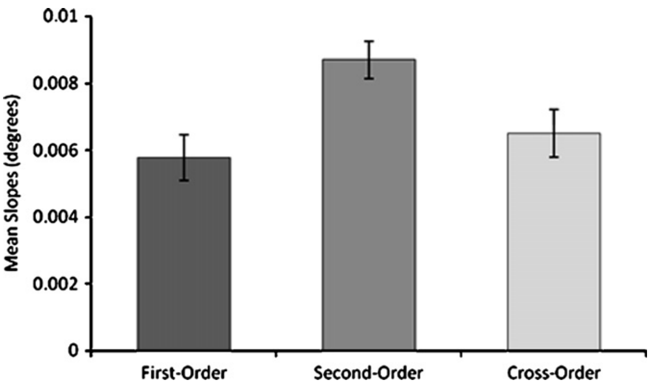

Fig. 4. Mean slopes for first-order, second-order and cross-order motion relative to the position shift experiments. The slopes were calculated as the reciprocal of the standard deviation of each psychometric function. The mean slope for first-order motion was 0.006 deg, 0.009 deg for second-order motion and 0.007 deg for cross-order motion. A paired-samples *t* test showed significant differences between first- and second-order motion, between second- and cross-order motion, and no between first- and cross-order motion patterns (see text for more details). Error bars ± SEM.

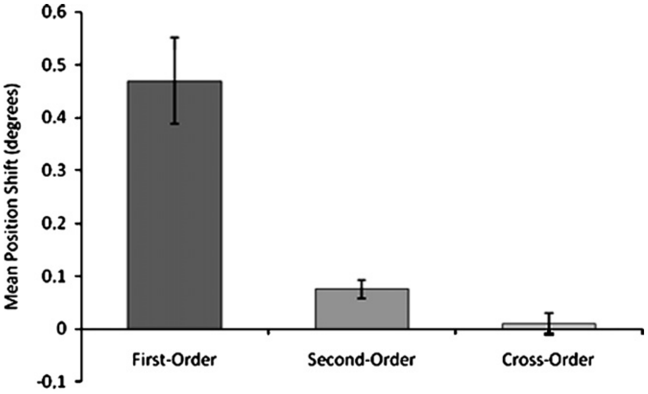

Fig. 5. Perceived misalignment for first-, second- and cross-order motion in phase four of the study, in which cross-order stimuli were matched for salience. The size of the offset for first-order stimuli is 0.47 deg, and it is significantly higher than that obtained for second-order Gabors (0.075 deg) ($t_{(6)} = 5.79$, $P = 0.001$). The positional offset obtained for second-order stimuli is still higher than that obtained for cross-order motion (0.01 deg) ($t_{(6)} = 4.67$, $P = 0.003$). A paired-samples t test showed no significant differences between the position shifts for cross-order stimuli calculated in phase three (i.e. without the match in salience) and in phase four of the study (i.e. with the match in salience) ($t_{(6)} = 1.14$, $P > 0.05$). Error bars ± SEM.

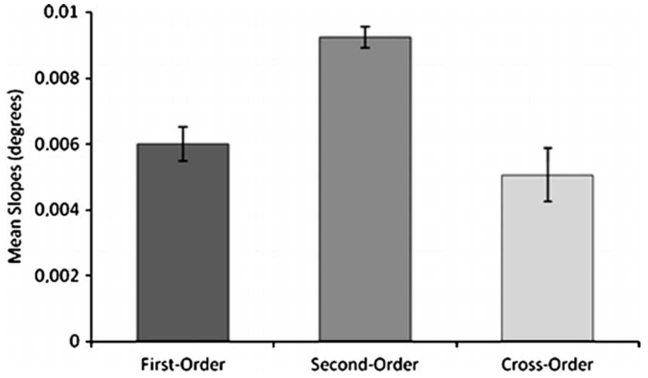

Fig. 6. Mean slopes for first-order, second-order and cross-order motion in four phase of the study. The slopes were calculated as the reciprocal of the standard deviation of each psychometric function. The mean slope for first-order motion was 0.006 deg, 0.009 deg for second-order motion and 0.005 deg for cross-order motion. A paired-samples t test showed significant differences between first- and second-order motion ($t_{(6)} = 7.92$; $P < 0.001$), between second- and cross-order motion ($t_{(6)} = 7.28$; $P < 0.001$), and no between first- and cross-order motion ($t_{(6)} = 1.26$; $P > 0.05$). In addition, were found no significant differences between the slopes for cross-order stimuli calculated in phase three and four of the study ($t_{(6)} = 1.38$; $P > 0.05$). Error bars ± SEM.

position obtained for first-order cues was significantly higher than that obtained for second-order cues.

Figs. 5 and 6 show mean position shifts and psychometric function slopes in phase four of the study, in which cross-order stimuli were matched for perceptual salience. The pattern of results is very similar to that shown in Figs. 3 and 4. However, with stimuli matched for salience an important difference emerges; that is, the position shift obtained for cross-order patterns is not significantly different from zero ($t_{(6)} = 0.50$; $P > 0.05$). In the previous phase of the experiment (in which first- and second-order stimuli were not matched for salience) the position shift obtained for cross-order stimuli, though smaller than that obtained for second-order motion, was significantly different from zero. The match in salience between first- and second-order patterns may have canceled any possible influence of the first-order pattern.

Moreover, in both phases of the experiment, the shifts in position for first- and second-order patterns were significantly different from zero ($t_{(6)} = 5.06$; $P = 0.002$, $t_{(6)} = 5.18$; $P = 0.002$, respectively, for first- and second-order patterns in the phase three, $t_{(6)} = 5.79$; $P = 0.001$, $t_{(6)} = 4.49$; $P = 0.004$, respectively, for first- and second-order patterns in the phase four of the experiment).

4. Discussion

The magnitude of the motion-induced position shifts obtained for first-order motion are broadly consistent with the findings of previous studies (Bressler & Whitney, 2006; Whitaker, McGraw, & Levi, 1997), but we obtained a relatively small second-order position-shift (0.09 deg in phase three and 0.075 deg in phase four of the study) compared to those reported previously. For instance, Bressler and Whitney (2006), in a similar condition in which they used a spatial frequency of 0.71 c/deg and a temporal frequency of 4 Hz, obtained a mean second-order position of about 0.36 deg, three or four times larger than our effect. A contributory factor in the present experiment may be the slightly higher spatial frequency carrier employed, which is less than optimal for second-order patterns. However, we conducted pilot observations employing optimal spatial and temporal frequencies for second-order patterns based on Bressler and Whitney (2006) (i.e. 0.18 c/deg and 4 Hz, respectively). We did not obtain any appreciable position shift; indeed, displaying second-order patches at 9.7 deg above and below the fixation point made the task very hard to perform because it was very difficult to discriminate the relative motion direction of the second-order Gabors. It is possible that the greater second-order effect reported by Bressler and Whitney (2006), and their success at a lower spatial frequency, reflects incomplete removal of luminance artifacts in their stimulus. While Bressler and Whitney (2006) employed a minimum motion technique similar to that used in our experiments, their minimum motion stimulus was not a Gabor patch but a grating windowed by a circular aperture 11.2 deg in diameter, with fixation 4.49 deg above the edge of the aperture. Our minimum motion stimulus was a Gabor patch matching that used in our position shift experiments, viewed at the same peripheral location. Perhaps equiluminance settings in the near periphery of Bressler and Whitney's (2006) windowed stimulus (just inside the edge of the grating aperture, 4.5 deg from fixation) were not appropriate for their Gabor patches which were centered at up to 10 deg into the periphery (actually 8.15 deg above and 10.1 deg below fixation in Bressler and Whitney's experiment). So residual luminance artifacts may have contributed to performance for second-order Gabors (they reported a strong position shift with luminance-defined Gabors even at low contrast, so it is possible that the luminance artifact could contribute to position shifts).

An anonymous reviewer suggested the possibility that our results are due to spatial-frequency tuning within a single motion system. That is, detectors sensitive to both first- and second-order motion stimuli should be stimulated with the optimal spatial frequencies respectively for first- and second-order motion stimuli, in order to test for an interaction between these two motion cues. However, O'Keefe and Movshon (1998) showed that MT neurons responsive to both first- and second-order motion tend to prefer roughly similar directions and spatial frequencies for first- and second-order motion stimuli and tend to prefer lower temporal frequencies for second-order motion. On the basis of these findings, if first- and second-order motion position shifts are detected by a common mechanism employing detectors that respond to both first- and second-order motion, we should expect to obtain a reliable cross-order effect using the same spatial and temporal frequencies for first- and second-order stimuli.

The most interesting feature of the data is the absence of apparent position shift with cross-order stimuli, once first- and second-order stimuli have been carefully matched for salience. This result clearly indicates that first- and second-order motion are processed by different mechanisms (Cavanagh & Mather, 1989; Derrington & Badcock, 1985; Edwards & Badcock, 1995; Ledgeway & Smith, 1994; Mather, 1991; McCarthy, 1993; Nishida & Sato, 1995; Seiffert & Cavanagh, 1998), as indeed does the differential spatio-temporal tuning of first- and second-order motion-induced position shifts reported in previous studies. But it also implies separate and distinct position encoding mechanisms. The simplest account of position coding by a single mechanism shared between first- and second-order patterns would predict a cross-order position shift that is the average of the position shifts obtained using first- and second-order patterns presented separately. Yet there is hardly any apparent position shift at all with cross-order stimuli, even though the first-order patterns generated a large position shift. The effect cannot be due to unequal salience between the first- and second-order patches, since they were matched for salience in the data of Fig. 5. If judgments were nevertheless dominated by the first-order patch in cross-order stimuli, one would expect a cross-order position shift equal to half that obtained using only first-order patches. Moreover, the slope values plotted in Figs. 4 and 6 indicate that subjects did not find the judgement any more difficult for cross-order stimuli than for first-order stimuli which produce much larger position shifts. We conclude that the effect is due to a real difficulty faced by the visual system when it attempts to compare the position of first- and second-order stimuli, reflecting a segregation of position encoding mechanisms for the two classes of stimulus.

A large number of recent papers have investigated the properties of visual processes that mediate global operations across space, such as the detection of a virtual spatial contour linking a series of Gabor patches (Field, Hayes, & Hess, 1993). Field et al. (1993) proposed a model of global integration based on 'association fields' which link together information from different local spatial filters or receptive fields. Such a process could be implemented by long-range lateral connections between cortical cells with widely separated retinal receptive fields. The experimental task employed to measure motion induced position shift also requires the subject to integrate information across space, in effect linking together two Gabor patches by extracting the orientation of a virtual line joining them. Important differences have been reported between static first- and second-order Gabors in tasks requiring global interactions, which are consistent with our position shift results. Ellemberg, Allen, and Hess (2004) found weaker lateral spatial interactions between second-order Gabor patches compared to first-order Gabor patches. In a task involving orientation discrimination in Gabor patches, Allen, Hess, Mansouri, and Dakin (2003) found that subjects were unable to combine information between first-order and second-order Gabors. They concluded that there are separate global integration mechanisms for first-order and second-order attributes. These results are consistent with our failure to observe a cross-order position shift since, in order to judge the relative positions of first- and second-order patches it is necessary to integrate information between them. Huang and Hess (2007) recently studied collinear threshold facilitation with first- and second-order Gabor patches. In this paradigm, the detectability of a central target patch is improved in the presence of collinear flanking patches. Huang and Hess (2007) found weaker facilitation when both target and flanker patches were second-order than when both patches were first-order, but no facilitation at all when one patch was first-order and the other was second-order. They favoured an account of facilitation involving long-range, cross-channel interactions that occur only between patches that match in order. Their results are consistent with the pattern of results we obtained. Although the task used in Huang and Hess's (2007) study is very different from that employed in the present paper, their inferences about the processing constraints imposed on first- and second-order attributes are consistent with ours.

Distinct mechanisms seem to be involved for first- and second-order motion stimuli, but it is not clear yet if the stage at which location is coded is the same, or if position is coded at different stages for first- and second-order motion. Recent studies point out that the stage at which motion could strongly influence perceived position is situated at the level of area V5/MT (Ashida et al., 2007; McGraw, Walsh, & Barrett, 2004); an important motion-sensitive area with a strong retinotopic organization, in which many direction-sensitive neurons respond only to first-order motion and others to both first- and second-order motion (Albright, 1992). McGraw et al. (2004), using a motion adaptation paradigm (for review see Mather, Verstraten, & Anstis, 1998), found that area V5/MT is involved in modulating the positional representation of objects presented after the adaptation period. They disrupted the V5/MT cortical activity using transcranial magnetic stimulation (TMS) immediately after motion adaptation. When TMS was delivered to V5/MT the perceived misalignment of the test stimulus was greatly reduced. On the other hand, disruption of V1 had no effect on the perceived position after motion adaptation. This result demonstrates that the locus at which motion and positional information interact is situated in V5/MT rather than in V1/V2. However, this result is based only on adaptation to first-order motion patterns. Ashida and colleagues (2007), using a fMRI technique with motion adaptation, examined whether a single and common mechanism is responsible for detection of first- and second-order motion in V5/MT or whether two separate but co-localized mechanisms might exist within the same neural substrate. The results showed direction-selective adaptation independently for each type of motion in area V5/MT. Moreover, they did not found cross-order adaptation between first-order and second-order motion patterns. The results provide strong evidence for separate neural populations responsible for detecting first- and second-order motion that co-exist within the same neural substrate, and independently could encode and assign the position of moving objects. Consistent with this perspective, Edwards and Badcock (1995) provided psychophysical evidence for the independence of first- and second-order motion systems at the level of V5/MT in relation to global-motion pooling. They showed that adding a second-order motion signal (consisting of contrast-modulated dots) equal in strength and moving in an opposite direction (i.e. transparent motion) to a first-order global-motion signal (consisting of luminance-defined dots) had no effect on the extraction of the first-order global-motion signal, while adding a first-order motion signal to a second-order global-motion signal had an effect on extracting the second-order global-motion signal. These results suggest the presence of a system that responds only to first-order motion, and an independent system that encodes both first- and second-order motion. Moreover, these motion systems seem to remain separate up to and including the level at which global-motion signals are extracted.

Other studies, employing different experimental paradigms provide further evidence for the existence of distinct but co-localized mechanisms for first- and second-order motion. In a recent study, Campana, Pavan, and Casco (2008), using a visual repetition priming paradigm, found that priming for motion direction with either first- or second-order motion was much stronger if the spatial position was repeated as well, suggesting a retinotopic representation of motion priming with both types of motion. However, when priming was tested using cross-order motion (i.e. when first-order primed second-order motion and vice-versa), priming for motion direction was independent of spatial position, suggesting a higher locus of representation. Thus results on short-term memory for motion direction indicate that, at least until a certain level of the visual hierarchy, priming might be subserved by different neural populations in the same or similar neural structures for both first- and second-order motion.

The dissociations found between the tuning for first- and second-order moving patterns and the results from cross-order motion suggest that object position is not assigned by a single, common mechanism. Rather, it seems that multiple channels and motion processing streams are involved in the assignment of an object's location. Psychophysical, TMS and fMRI results (Ashida et al., 2007; Campana, Cowey, & Walsh, 2002; Cowey et al., 2006; McGraw et al., 2004) support the notion that different mechanisms may exist for the detection and position assignment of different types of motion, and that they could be co-localized in the same cortical area.

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