Available online at www.sciencedirect.com

SCIENCE DIRECT®

Vision Research 46 (2006) 1120–1128

Vision Research

www.elsevier.com/locate/visres

Second-order motion shifts perceived position

David W. Bressler, David Whitney *

Department of Psychology and Center for Mind and Brain, University of California, Davis, CA 95616, USA

Received 25 May 2005; received in revised form 13 October 2005

Abstract

Many studies have documented that first-order motion influences perceived position. Here, we show that second-order (contrast defined) motion influences the perceived positions of stationary objects as well. We used a Gabor pattern as our second-order stimulus, which consisted of a drifting sinusoidal contrast modulation of a dynamic random-dot background; this second-order carrier was enveloped by a static Gaussian contrast modulation. Two vertically aligned Gabors had carrier motion in opposite directions. Subjects judged the relative positions of the Gabors' static envelopes. The positions of the Gabors appeared shifted in the direction of the carrier motion, but the effect was narrowly tuned to low temporal frequencies across all tested spatial frequencies. In contrast, first-order (luminance defined) motion shifted perceived positions across a wide range of temporal frequencies, and this differential tuning could not be explained by differences in the visibility of the patterns. The results show that second-order motion detection mechanisms contribute to perceived position. Further, the differential spatial and temporal tuning of the illusion supports the idea that there are distinct position assignment mechanisms for first and second-order motion.

Keywords: Motion; Position; Visual motion; Perception; Vision; Second order; Second-order motion; Illusion; Mislocalization; Perceived position

1. Introduction

A number of striking illusions show that visual motion influences perceived position (De Valois & De Valois, 1991; Durant & Johnston, 2004; Edwards & Badcock, 2003; Fang & He, 2004; Fu, Shen, & Dan, 2001; Matin, Boff, & Pola, 1976; McGraw, Walsh, & Barrett, 2004; McGraw, Whitaker, Skillen, & Chung, 2002; Mussap & Prins, 2002; Nishida & Johnston, 1999; Ramachandran & Anstis, 1990; Snowden, 1998; Whitaker, McGraw, & Pearson, 1999; Whitney & Cavanagh, 2000; Whitney et al., 2003; Zanker, Quenzer, & Fahle, 2001; for a review, see Whitney, 2002). However, only the first order, luminance-based motion-induced position shift has been characterized in detail. The illusion shows band pass temporal frequency tuning, peaking around 4–8 Hz (De Valois & De Valois, 1991; Whitney & Cavanagh, 2000). As well as showing relatively specific temporal frequency tuning, the motion-induced position shift is also sensitive to the relative timing of the motion and position information. For example, we found that if a moving texture reverses direction unpredictably, the perceived shift in the position of a nearby flashed object depends on the direction of the texture's motion approximately 200–300 ms later (Whitney & Cavanagh, 2000). Using a single moving object (rather than a field of moving texture), Durant and Johnston (2004) found that a nearby flashed stimulus appears shifted most when it precedes the position of the moving object by about 80–100 ms. Both of these temporal asynchronies indicate that assigning an object's position (or relative position) involves lengthy delays or integration periods (cf. Krekelberg & Lappe, 2001). In addition to being temporally tuned, the motion-induced position shift is low pass tuned to spatial frequency, peaking at less than 1 cycle/deg (De Valois & De Valois, 1991).

This spatial and temporal tuning only characterizes the influence of first-order motion on position, but does not say anything about the limitations or properties of other types of motion (non-first-order motion). The only studies

* Corresponding author. Tel.: +1 530 297 4451; fax: +1 530 297 4400.
E-mail address: dwhitney@ucdavis.edu (D. Whitney).

0042-6989/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2005.10.012

of the motion-induced position shift using non-first-order motion employed illusory motion (long-range apparent motion or inferred motion—motion behind occluders; Shim & Cavanagh, 2004; Watanabe, Nijhawan, & Shimojo, 2002; Watanabe, Sato, & Shimojo, 2003). One difficulty measuring the tuning properties of non-first-order motion, such as inferred motion and ambiguous apparent motion, is that the spatial and temporal frequency of the patterns cannot be easily manipulated.

One type of non-luminance-based motion whose temporal and spatial frequencies can be manipulated is second-order (contrast defined) motion. Here, we tested whether second-order motion influences perceived position, and measured the spatial and temporal tuning of this effect. We found that second-order motion does influence the perceived positions of static objects, and, moreover, we found that the second-order motion-induced position shift shows distinct tuning from the first-order motion-induced position shift.

2. Experiment 1: The influence of second-order motion on perceived position

2.1. Methods

The methods in the first experiment involved three stages: determining threshold contrast, measuring the equiluminance point using a minimum motion technique, and measuring the perceived positions of second-order defined drifting Gabors. (Hereafter, the term "second-order Gabor" refers to Gabors with contrast-modulated carriers—Fig. 1; "first-order Gabor," on the other hand refers to Gabors with luminance-defined carriers).

Three subjects with normal or corrected-to-normal visual acuity participated in Experiments 1 and 2. Stimuli were presented on a high-resolution CRT monitor (Sony Multiscan G520, 1024×768 pixels, 100 Hz refresh) using an Apple G4 Power Macintosh with OS9. Subjects were seated in a dark room and immobilized with a chinrest placed 49 centimeters from the screen.

To determine the threshold contrast (the first phase of the experiment), subjects fixated on a point (1.2 deg diameter) and reported the direction of motion within a Gabor located 10.7 deg above the fixation point (from center to center). The Gabor consisted of a dynamic random-dot pattern (each dot was 0.2 by 0.2 deg, refreshed every 10 ms) modulated by a contrast-defined sinusoid, which could be 0.71, 0.35, or 0.18 cycles/deg, determined randomly on each trial (Fig. 1). A static contrast-modulated Gaussian envelope blurred the edges of the Gabor (3.7 deg full width at half maximum amplitude).

The static envelope remained centered above the fixation point, but contained contrast-defined motion (the sinusoidal carrier) randomized leftward or rightward across trials in either direction. The temporal frequency (either 1.6, 3.2, or 6.3 Hz) was also randomized across trials. The subjects' task was to report direction of motion for each trial.

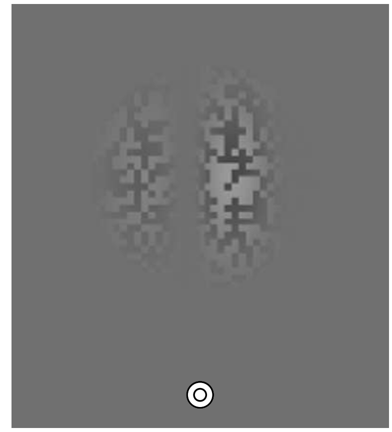

Fig. 1. Example second-order Gabor used in the first experiment. The Gabor consisted of a dynamic random-dot pattern, modulated by a sinusoidal contrast-defined carrier that drifted either leftward or rightward, and a Gaussian contrast-modulated envelope (to blur the edges). The sinusoidal carrier (visible here as random dots alternating with gray bars) was the only moving component. The Gaussian contrast-modulated envelope was always static. The dynamic random-dot background was updated every frame and produced a broadband noise (e.g., TV snow). The pictured pattern has a sinusoidal carrier with exaggerated contrast to reproduce in print; the actual Gabor had much lower contrast determined individually according to each subject's threshold (see Methods). Formally, the Gabor is described as: $L(x,y,t) = E + \left\{ V - E + \left[\frac{E-V+(R(x,y,t)*D)}{2} * (1+\sin\{[(SF*x)+(TF*t)]*2\pi\}) \right] \right\} * \exp\left(\frac{-r^2}{(\sigma M)^2}\right)$, where $L(x,y,t)$ is the luminance at any point at time t; E is physical equiluminance (mean luminance); V is subject's equiluminance value (see Methods); $R(x,y,t)$ is a random-dot array in time; D is the depth of the contrast modulation (the incremental contrast above and below E); SF is the spatial frequency of the carrier (pixels/cycle); TF is the temporal frequency of the carrier (cycles/degree); r is distance of (x,y) from the center of the Gabor; σ is the standard deviation of the static Gaussian contrast envelope; and M is the maximum radius of the Gaussian envelope. Because the monitor's refresh was 100 Hz, t is defined in 10 ms increments.

Subjects first encountered a high contrast display. The threshold contrast was determined by incrementally decreasing the contrast until subjects reported the direction of motion with 90% accuracy over 10 sequential trials (running average).

A minimum motion technique similar to that used by previous authors (Anstis & Cavanagh, 1983; Nishida, Edwards, & Sato, 1997; Seiffert & Cavanagh, 1998) was administered to find each subject's equiluminance value (the second phase of the experiment). Subjects fixated on a point 4.49 deg above a circular aperture (edge-to-edge) that was 11.2 deg in diameter. Inside the aperture, a luminance-defined sine wave (0.18 cycle/deg) was flickered in counterphase at 5 Hz. A second, contrast-defined grating (contrast determined above), was also presented in counterphase at 5 Hz. The luminance and contrast-defined gratings were interleaved in a four-frame sequence such that each sine wave was shifted by 90 deg (i.e., quadrature phase, luminance grating presented in even frames, contrast-modulated grating presented in odd frames). If only the luminance-defined grating were visible, there would be no directional motion percept; however, if the contrast-defined grating visibly deviates from equiluminance, the subject perceives unidirectional motion. On each trial (0.5 s duration), the luminance midpoint of the contrast-modulated grating was randomly varied (one of 11 values centered on physical equiluminance) and, using a method of constant stimuli task, subjects were asked to judge the direction of motion in the aperture (leftward/rightward). Each subject participated in 220 trials (20 trials for each of the 11 luminance values). The luminance midpoint (the relative luminance between the contrast-modulated segments of the second-order grating) that produced a percept of ambiguous motion (point of subjective equality) is the point of equiluminance (see Anstis & Cavanagh, 1983; Nishida et al., 1997; Seiffert & Cavanagh, 1998 for more details).

The main experiment (the third phase) utilized a subject's luminance threshold and equiluminance value to determine the effect of second-order (contrast defined) motion on the coding of location. Subjects fixated on a vertically centered point and made judgments about the relative locations of two vertically aligned Gabors (8.15 deg above and 10.1 deg below the fixation point). The Gabors were identical to those described above (sinusoidal contrast-modulated dynamic random noise with a contrast-modulated static Gaussian envelope). The contrast-modulated sine-wave carriers in the top and bottom Gabors always drifted in opposite directions (Fig. 2A). On each trial, the top and bottom Gabors were presented horizontally offset (misaligned) in opposite directions by one of six values. The Gabors were presented for 500 ms, after which subjects judged whether the one at the top of the display appeared to the left or right of the Gabor on the bottom (method of constant stimuli).

For each of three spatial frequencies (0.18, 0.35, 0.71 cycles/deg), there were six temporal frequencies tested (ranging from 0.4 to 37.5 Hz) for a total of 18 conditions. Each of the 18 conditions was tested 8 times for each of the 6 horizontal offsets, for a total of 864 trials per testing block. For each of the 18 conditions, a psychometric function was fit to the data from the logistic function $\{1/(1+\exp[-a(x-b)])\}$, where b estimates the physical misalignment between the Gabors that creates an apparent alignment (the point of subjective equality, PSE; (Finney, 1971; McKee, Klein, & Teller, 1985)). Each subject participated in 3 blocks for a total of 2592 trials, and the condition PSE was based on an average of the PSEs estimated in the 3 blocks of trials.

2.2. Results

Fig. 2A shows the stimuli used in the first experiment. The contrast of the Gabors pictured here is exaggerated to be clearly visible; in the actual experiment, the contrast was 33.1, 19.0, and 28.8% (Michelson contrast) for subjects DB, JS, and JL, respectively. Although the envelopes of the Gabors were always physically aligned, the drifting contrast-modulated carriers caused the static envelopes (i.e., the overall patterns) to appear shifted (as depicted in Fig. 2B).

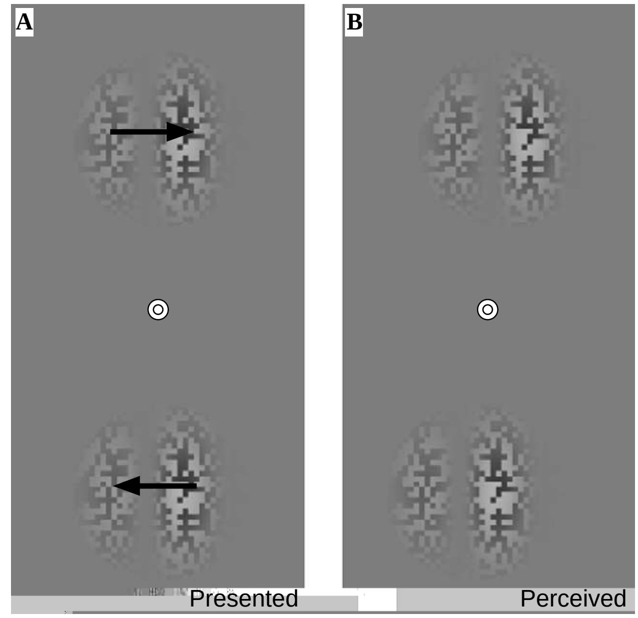

Fig. 2. Stimulus and percept in the first experiment. (A) Two vertically aligned second-order Gabors appeared misaligned (B) when the contrast-defined carriers drifted in opposite directions. The envelopes of the two Gabor patterns were physically stationary; only the carrier was moving.

The representative psychometric function in Fig. 3 shows the magnitude of the second-order motion-induced position shift for one spatial and temporal frequency. The inflexion point—the PSE—shows that the Gabors appeared shifted by 0.30 deg in the direction of the carrier's motion in this particular condition. The magnitude of the

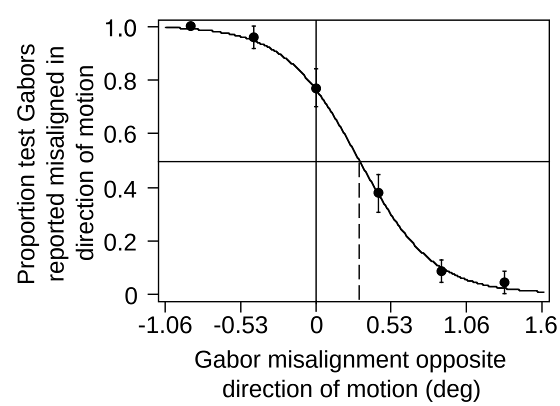

Fig. 3. Representative psychometric function for subject DB in the first experiment (3.2 Hz, 0.18 cycle/deg condition). The abscissa shows the physical misalignment between the second-order Gabors (positive values indicate that the Gabors were displaced opposite the direction of the carrier motion). The ordinate shows the proportion of responses in which subjects judged the Gabors as being misaligned (shifted) in the direction of the carrier motion. The point of subjective equality (PSE, the inflexion point) is the physical misalignment between the Gabors that created an apparent alignment; this estimates the magnitude of the illusory position shift. The PSE for this condition was 0.30 deg, which is one of the smaller effects but is still significant ($t_{(2)} = 3.49$, $P < 0.05$). Error bars ± SEM.

shift in this condition is one of the smaller of all the conditions tested, but is still significant ($t_{(2)} = 3.49$, $P < 0.05$). Fig. 4A shows that there was a significant and consistent shift in the perceived position of the Gabors (maximum effect for subject DB: 0.50 deg; the least significant overall effect was for subject JS, $F_{(17,36)} = 23.56$, $P < 0.01$), and the misalignment varied primarily as a function of the temporal frequency of the contrast-defined carrier (Fig. 4B; $F_{(7,36)} = 5.13$, $P < 0.001$). The effect did not vary as a function of spatial frequency ($F_{(2,36)} = 2.5$, $P > 0.05$), or at least the tuning is extremely broad (Fig. 4D).

One might be concerned that the second-order Gabors in this experiment may have inadvertently included luminance artifacts. To rule out this possibility we used dynamic random-dot patterns, which eliminate local first-order artifacts that can be present in static contrast-modulated displays (Smith & Ledgeway, 1997). We also used very low contrast stimuli (near threshold), which reduces luminance-based artifacts and also primarily drives second-order motion detectors (Seiffert & Cavanagh, 1999). Further, to test whether there were any residual first-order motion signals, we confirmed that our second-order drifting Gabors did not produce a static motion aftereffect (MAE; Mather, Verstraten, & Anstis, 1998). It is known that second-order motion does not elicit an MAE on static test patterns (Derrington & Badcock, 1985; McCarthy, 1993; Nishida & Sato, 1995), so this confirms that our contrast-modulated Gabors really were driving second-order motion processes alone.

3. Experiment 2: Comparing first- and second-order motion-induced position shifts

The first experiment revealed the tuning of second-order motion's influence on perceived position. The purpose of the second experiment was to compare these results to the tuning of the first-order motion-induced position displacement.

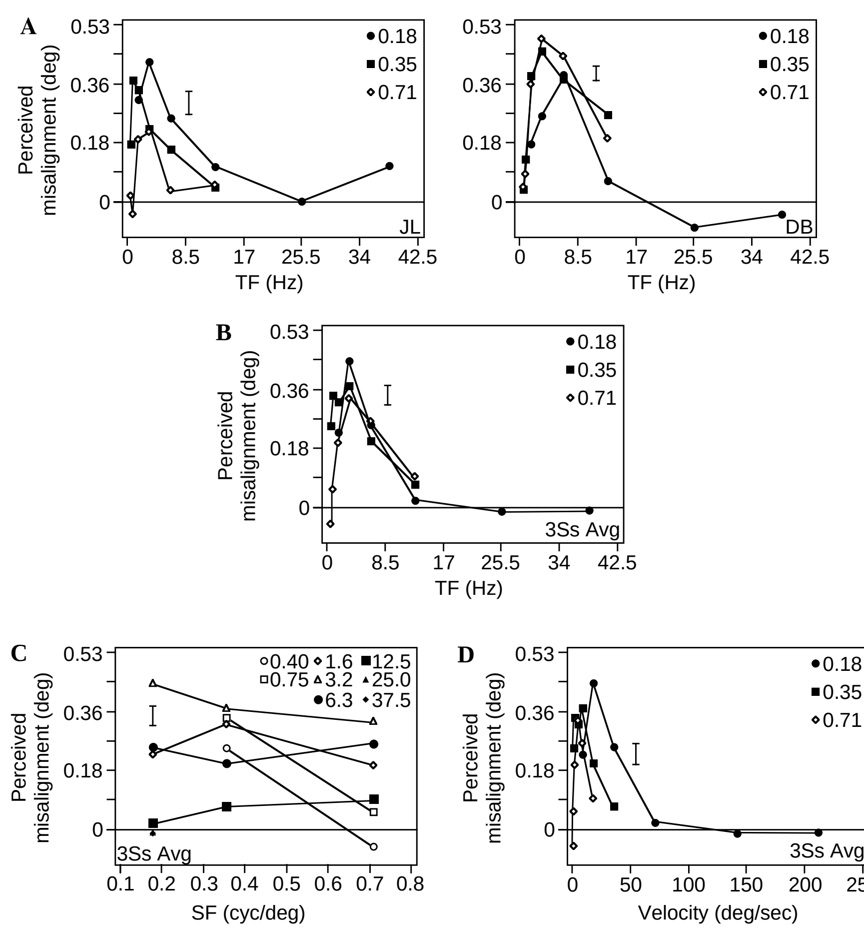

Fig. 4. Results for the first experiment. (A) The second-order motion-induced position shift as a function of the carrier temporal frequency for two representative subjects. Different symbols refer to three tested spatial frequencies (see legend). The effect is narrowly tuned, peaking at around 4 Hz, and falls to zero at higher temporal frequencies. (B) Averaging the data across all three subjects shows that the effect is well characterized by a temporal frequency selective mechanism. (C) The illusory position shift as a function of carrier's spatial frequency. Different symbols refer to tested temporal frequencies (see legend). The position shift is roughly invariant with spatial frequency ($F_{(2,36)} = 2.5$, $P > 0.05$). (D) Replotting the data from (B and C) shows the data as a function of carrier velocity, grouped by spatial frequency. Because of the narrow temporal frequency tuning, the effect is limited to lower velocities. There is a significant overall effect for each subject (JS: $F_{(17,36)} = 23.56$, $P < 0.01$; DB: $F_{(17,36)} = 218.8$, $P < 0.001$; JL: $F_{(17,36)} = 66.52$, $P < 0.001$). Representative error bars ±1 SEM.

3.1. Methods

The methods in the second experiment were identical to the third phase of the first experiment except that the Gabors contained first-order, luminance-defined carrier gratings. The carrier contrast was identical to that determined in the first phase of the first experiment. The carrier luminance midpoint (the average overall brightness of the carrier) was identical to that determined in the second phase of the first experiment (i.e., based on the minimum motion technique in the first experiment). For each of the three tested spatial frequencies (same as in Experiment 1), there were six temporal frequencies (ranging from 0.4 to 25 Hz), for a total of 18 conditions. The protocol, task, and analysis were identical to those in the first experiment.

3.2. Results

Consistent with previous studies, the luminance-defined drifting Gabors (Fig. 5) appeared shifted in position (see Whitney, 2002 for a review). Fig. 6 shows a representative psychometric function, which reveals the magnitude of the illusory position shift (0.75 deg illusory displacement in this condition). Fig. 7A shows that the motion-induced position shift varied as a function of the carrier's temporal frequency (across all three subjects, Fig. 7B reveals a significant effect; $F_{(6,36)} = 4.33$, $P < 0.01$). The peak misalignment occurred at lower spatial frequencies across every temporal frequency (Fig. 7C; $F_{(2,36)} = 7.97$, $P < 0.001$). This tuning is similar to the temporal contrast sensitivity function (Kelly, 1979), but is distinct from the motion sensitivity function, which is low pass (Nakayama, 1985). Replotting the data as a function of carrier velocity reveals that the first-order motion-induced position displacement generally increases with increasing velocity, but the peak effect at higher velocities always occurs for lower spatial frequencies (Fig. 7D). Velocity sensitive channels may therefore play an important role in mediating the first-order motion-induced position shift, and the illusion supports the existence of mechanisms that simultaneously code the motion and form of an object (Burr, 1979; Burr & Ross, 1982, 2002; Burr, Ross, & Morrone, 1986; Fahle & Poggio, 1981; Geisler, 1999; Morgan, 1976, 1980; Nishida, 2004).

There are some noticeable differences between first- and second-order motion's influence on perceived position. Comparing Figs. 4 and 7 reveals that the second-order motion-induced position shift is roughly invariant with the spatial frequency of the carrier, whereas the shift is much greater at low spatial frequencies for first-order motion. Moreover, the second-order motion-induced position shift is more narrowly tuned to temporal frequency.

It is possible that this narrower tuning—the temporal low pass characteristics of the second-order motion-induced position shift (Fig. 4B)—may be due to a reduction in the visibility of the contrast-defined Gabors (compared to the first-order Gabors in Experiment 1). While the physical contrast was equated for the first and second-order stimuli, it is possible that the illusory position shift may have varied as a function of salience or visibility, which was necessarily higher for the first-order Gabors. To address this possibility, we reduced the contrast of the first-order Gabors to psychophysically equate visibility (rather than equating physical luminance). To do this we used a variant of the minimum motion technique (Anstis & Cavanagh, 1983): we interleaved frames of first- and second-order carriers that drifted in opposite directions (using

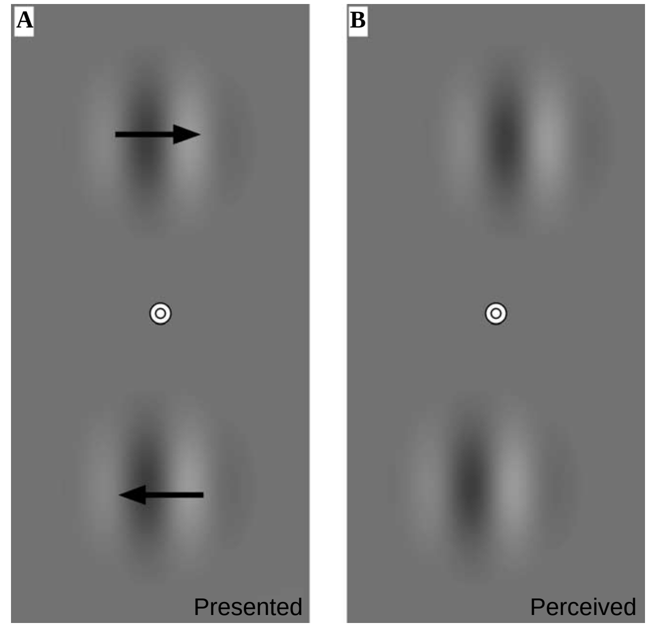

Fig. 5. Stimulus and percept in the second experiment. (A) Two vertically aligned Gabors (first-order drifting carriers with a contrast-modulated Gaussian envelope) were presented. (B) Consistent with previous studies, the luminance-defined drifting carriers caused the Gabors to appear shifted in position, creating an illusory misalignment. As with the second-order Gabors, the envelopes of the two Gabor patterns in this experiment were physically stationary; only the carrier was moving.

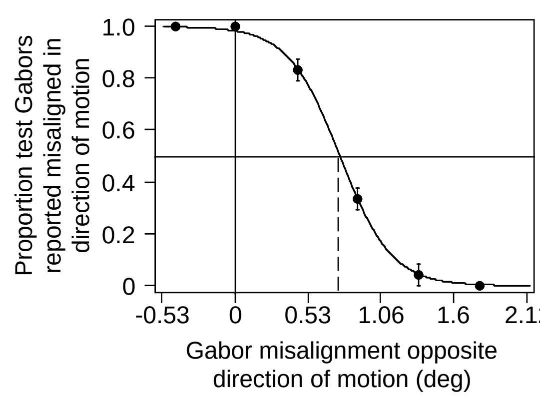

Fig. 6. Representative psychometric function for one subject in the second experiment (subject DB: 0.75 Hz, 0.18 cycle/deg condition). Format of the graph is identical to that in Fig. 3. The PSE (perceived misalignment between the Gabors) in this condition was 0.75 deg. Similar to Fig. 3, this is one of the smallest condition effects but is still significant ($t_{(2)} = 12.10$, $P < 0.05$). Error bars ± SEM.

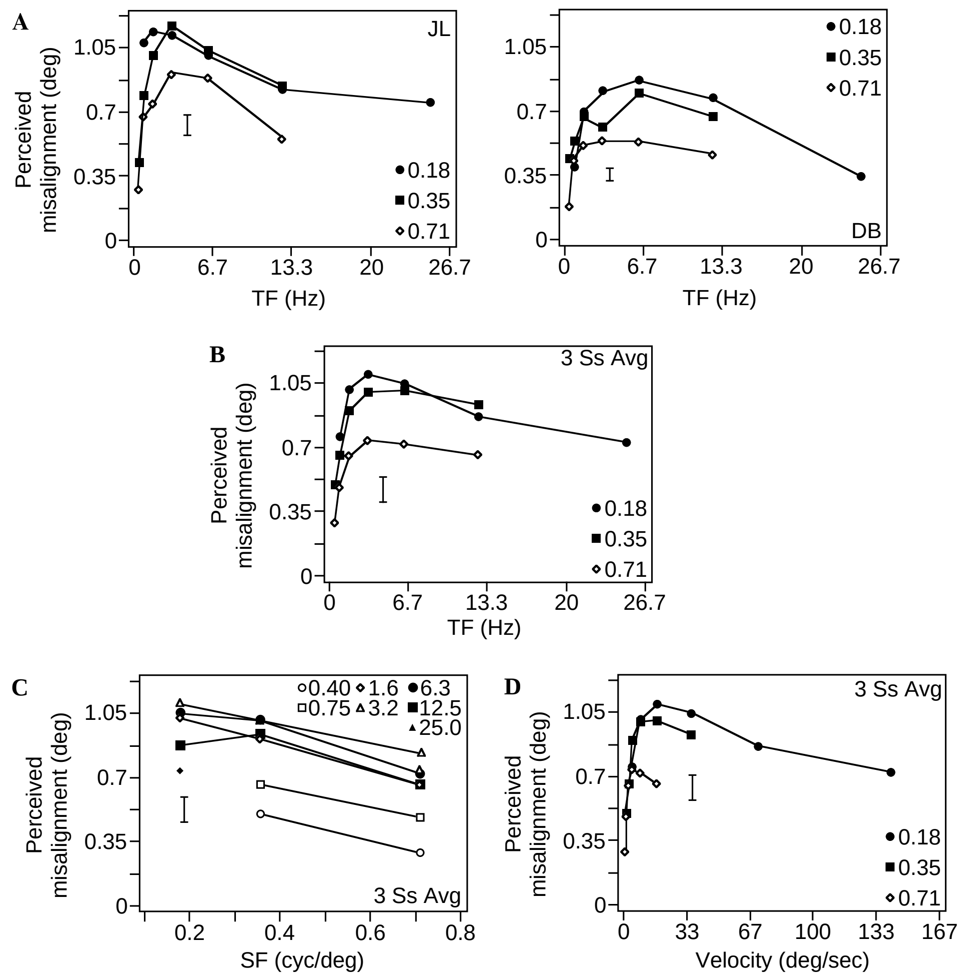

Fig. 7. Results for the second experiment. (A) The first-order motion-induced position shift as a function of the carrier temporal frequency for two representative subjects. Different symbols refer to three tested spatial frequencies (see legend). The effect peaks at around 7 Hz, but is band pass tuned to a broad range of temporal frequencies across every tested spatial frequency. The effect is significant at the highest tested temporal frequency (25 Hz) for both subjects (least significant effect was for subject DB, $t_{(2)} = 3.99$, $P < 0.05$). (B) The position shift, averaged across all three subjects, as a function of temporal frequency. (C) The illusory position shift as a function of spatial frequency across all three subjects. Different symbols refer to tested temporal frequencies (see legend). The position shift is greater at lower spatial frequencies ($F_{(2,36)} = 7.97$, $P < 0.001$). (D) Replotting the data from (B and C) shows the data as a function of carrier velocity, grouped by spatial frequency (see legend). At lower spatial frequencies, the peak shift in the apparent positions of the Gabors occurs at higher temporal frequencies. The least significant overall effect is for subject JS ($F_{(17,36)} = 1353.3$, $P < 0.001$). Representative error bars ±1 SEM.

a second-order Gabor whose contrast was defined in the first experiments). We then manipulated the contrast of the luminance-defined carrier. When the contrast of the first-order carrier was zero, the direction of motion perceived in the Gabor followed the second-order carrier; we measured the contrast of the luminance-defined carrier required to null the perceived motion of the second-order carrier. This level of contrast (6.2% Michelson for subject DB) ensured that the first-order carrier was as hard to detect as the second-order carrier in the first experiment, and allowed us to make a direct comparison between the magnitude of the effects for first- and second-order motion. Using this contrast, we measured the perceived shift in the positions of the Gabors with luminance-defined carriers (12.5 Hz, 0.18 cycle/deg). Fig. 8 shows that, even at this reduced contrast, subject DB still perceived a significant shift in the positions of the first-order Gabors (solid psychometric function). Whereas, at the same level of visibility, the second-order Gabor produced no shift (dashed psychometric function in Fig. 8). The first-order motion-induced position shift (Fig. 7B) therefore maintains its broad temporal frequency tuning even when the carrier's visibility is reduced. The dissociation here strongly suggests that the limiting factor (the narrower tuning for second-order motion) is not lower visibility, salience, or detectability. Rather, there appear to be independent position assignment mechanisms for the two types of motion.

4. Discussion

The results revealed that both first- and second-order motion can influence perceived positions of objects. First-order motion influences position assignment across a broad range of temporal and spatial frequencies and

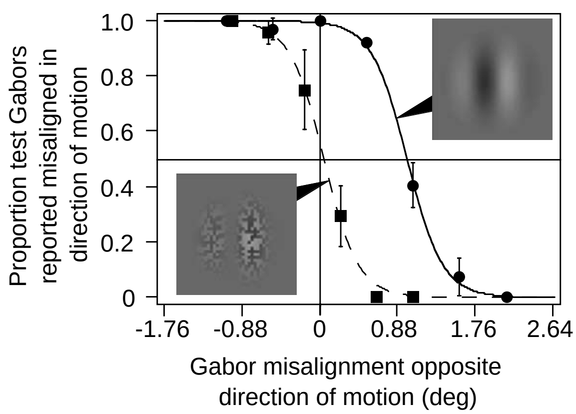

Fig. 8. Perceived shift in the position of first- and second-order Gabors with equated visibility. The luminance contrast of the first-order drifting Gabor (with a carrier of 0.18 cycle/deg, 12.5 Hz) that cancelled the motion of the original second-order drifting Gabor (the one used in the first experiment, also with a carrier of 0.18 cycle/deg, 12.5 Hz) was 6.2% Michelson contrast for subject DB. At this contrast, the visibility of the first-order Gabor was equated to that of the second-order Gabor. The psychometric function for this reduced contrast first-order Gabor (solid curve) reveals a PSE of 0.99 deg, showing that the first-order Gabor appeared shifted in position even when its visibility was equated to that of the second-order Gabor. The psychometric function for the second-order Gabor, on the other hand, reveals a perceived shift of only 0.074 deg (dashed curve); this is significantly less than the first-order effect (even with equated visibility; $t_{(28)} = 17.2$, $P < 0.001$). This suggests that the differential temporal frequency tuning for first- and second-order motion is not a product of visibility differences, but is due to independent position assignment processes for the two types of motion. Error bars ±1 SEM.

depends on both. Second-order motion, on the other hand, influences perceived position over a narrower range of temporal frequencies and is largely invariant with spatial frequency.

First- and second-order motion are thought to be processed by different mechanisms (Cavanagh & Mather, 1989; Derrington & Badcock, 1985; Edwards & Badcock, 1995; Ledgeway & Smith, 1994; McCarthy, 1993; Nishida & Sato, 1995; Seiffert & Cavanagh, 1998). For example, second-order motion could be detected by higher level passive (Edwards & Badcock, 1995; Nishida & Sato, 1995) or attentionally mediated processes such as attentive tracking or salience maps (Cavanagh, 1992; Lu & Sperling, 1995), whereas first-order motion is detected by low-level spatio-temporal energy sensitive mechanisms (Adelson & Bergen, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985). The differential tuning of first- and second-order motion found here may support this division, but the results also show that both types of motion influence perceived position. Since first- and second-order moving patterns (at least low contrast, low temporal frequency patterns) are initially detected by independent mechanisms, each type of motion may independently influence coded location. The stage at which location is coded could be the same for both first- and second-order motion (in which case it is the independent motion processing streams that causes the tuning differences in Figs. 4 and 7). Alternatively, position could be coded at different stages for first- and second-order motion. This interesting possibility needs to be tested in future experiments.

4.1. High-level motion perception

The relatively narrow temporal frequency tuning for the second-order motion-induced position shift (Fig. 4) is similar to the range of temporal frequencies over which attention operates (the cutoff temporal frequency for the perceived shift in the second order Gabors is about 12 Hz). For example, position-based second-order motion detectors sensitive to low-contrast patterns are restricted to low temporal frequencies (e.g., below 8 or 10 Hz; Seiffert & Cavanagh, 1999). Moreover, attentively tracking items over space and time (Horowitz, Holcombe, Wolfe, Arsenio, & DiMase, 2004; Verstraten, Cavanagh, & Labianca, 2000), or attentively binding features across space (Holcombe & Cavanagh, 2001) both have a coarse temporal resolution. This raises the possibility that a slow attentional mechanism may be responsible for the reassignment (displacement) of perceived location in second-order moving patterns.

The involvement of attention in the second-order motion-induced position shift is supported by a number of demonstrations that high-level motion shifts perceived position (by high-level motion we mean the percept of motion, driven by top-down processes, in the absence of any physical movement or motion energy). For example, even without any physical motion in the scene, implied motion (e.g., motion behind an occluder) and ambiguous motion (e.g., a bistable quartet) can shift the positions of nearby static objects (Shim & Cavanagh, 2004; Watanabe et al., 2002, 2003). The perceived shift always follows the direction of the *perceived* motion. Another recent demonstration has shown that suppressing a moving stimulus with binocular rivalry eliminates the motion-induced position displacements, suggesting that awareness of motion may strongly modulate the position shifts (Watanabe, 2005).

If (low contrast, low speed) second-order motion is detected by a high-level mechanism (e.g., Seiffert & Cavanagh, 1998)—one that also detects implied/inferred motion as well as ambiguous motion—then perhaps a number of the motion-induced position shifts could be grouped as a single phenomena. Attentive tracking (Cavanagh, 1992), for example, may explain the perception of motion in ambiguous apparent motion displays as well as second-order motion. If there is a single top-down mechanism responsible for coding the motion that ultimately shifts perceived position, then we should observe the same kind of tuning found in Fig. 4 for other types of displays (such as those used by Shim & Cavanagh, 2004, and Watanabe et al., 2002, 2003).

4.2. Passive, low-level motion

Although top-down motion does influence perceived position, and second-order motion may be processed by such a mechanism, previous studies have shown that the awareness of first-order motion is not necessary to shift the perceived position (Whitney, 2005). This demonstrates that passive luminance-based motion detectors can code position without the involvement of top-down processes (top-down processes, based on object knowledge or attentional shifts, require an awareness or percept of motion). However, it is not clear if this is the case for second-order motion; future experiments are required to test whether the awareness of second-order motion is actually necessary to shift perceived position.

The dissociation found here between the tuning for first- and second-order moving patterns suggests that there is no single motion detector that also serves to (re)assign object position. Rather, it is likely that the location assigned to an object depends on multiple motion pathways, and may occur at multiple stages. It is conceivable that, for the sake of flexibility, we may have perceptual access to different position coding mechanisms or levels in the hierarchy. This may be a unique feature of position information because, unlike other features, there is a great deal of redundancy in the position information represented at multiple levels of the visual system (e.g., position is explicitly or at least implicitly registered in most early visual areas). The fact that position information is redundant may be a byproduct of efficient coding (e.g., maintaining retinotopic mapping may save wiring, or may ease binding of information), or it could reflect the importance of position information relative to other types of visual information. In any case, redundant position coding raises the possibility that we may have independent perceptual access to position information at multiple stages. This may help explain why so many different types of visual motion (first-order, second-order, and illusory motion) can all influence perceived position, but each in a slightly different way.

References

Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America. A, 2*(2), 284–299.

Anstis, S. M., & Cavanagh, P. (1983). A minimum motion technique for judging equiluminance. In J. Mollon & R. T. Sharpe (Eds.), *Color vision: Physiology and psychophysics* (pp. 155–166). London: Academic Press.

Burr, D. C. (1979). Acuity for apparent vernier offset. *Vision Research, 19*(7), 835–837.

Burr, D. C., & Ross, J. (1982). Contrast sensitivity at high velocities. *Vision Research, 22*(4), 479–484.

Burr, D. C., & Ross, J. (2002). Direct evidence that "speedlines" influence motion mechanisms. *Journal of Neuroscience, 22*(19), 8661–8664.

Burr, D. C., Ross, J., & Morrone, M. C. (1986). Smooth and sampled motion. *Vision Research, 26*(4), 643–652.

Cavanagh, P. (1992). Attention-based motion perception. *Science, 257*(5076), 1563–1565.

Cavanagh, P., & Mather, G. (1989). Motion: The long and short of it. *Spatial Vision, 4*(2–3), 103–129.

De Valois, R. L., & De Valois, K. K. (1991). Vernier acuity with stationary moving Gabors. *Vision Research, 31*(9), 1619–1626.

Derrington, A. M., & Badcock, D. R. (1985). Separate detectors for simple and complex grating patterns? *Vision Research, 25*(12), 1869–1878.

Durant, S., & Johnston, A. (2004). Temporal dependence of local motion induced shifts in perceived position. *Vision Research, 44*(4), 357–366.

Edwards, M., & Badcock, D. R. (1995). Global motion perception: No interaction between the first- and second-order motion pathways. *Vision Research, 35*(18), 2589–2602.

Edwards, M., & Badcock, D. R. (2003). Motion distorts perceived depth. *Vision Research, 43*(17), 1799–1804.

Fahle, M., & Poggio, T. (1981). Visual hyperacuity: Spatiotemporal interpolation in human vision. *Proceedings of the Royal Society of London. Series B. Biological Sciences, 213*(1193), 451–477.

Fang, F., & He, S. (2004). Strong influence of test patterns on the perception of motion aftereffect and position. *Journal of Vision, 4*(7), 637–642.

Finney, D. J. (1971). *Probit analysis* (3rd ed.). Cambridge [Eng.]: University Press.

Fu, Y. X., Shen, Y., & Dan, Y. (2001). Motion-induced perceptual extrapolation of blurred visual targets. *Journal of Neuroscience, 21*(20), RC172.

Geisler, W. S. (1999). Motion streaks provide a spatial code for motion direction. *Nature, 400*(6739), 65–69.

Holcombe, A. O., & Cavanagh, P. (2001). Early binding of feature pairs for visual perception. *Nature Neuroscience, 4*(2), 127–128.

Horowitz, T. S., Holcombe, A. O., Wolfe, J. M., Arsenio, H. C., & DiMase, J. S. (2004). Attentional pursuit is faster than attentional saccade. *Journal of Vision, 4*(7), 585–603.

Kelly, D. H. (1979). Motion and vision. II. Stabilized spatio-temporal threshold surface. *Journal of the Optical Society of America, 69*(10), 1340–1349.

Krekelberg, B., & Lappe, M. (2001). Neuronal latencies and the position of moving objects. *Trends in Neurosciences, 24*(6), 335–339.

Ledgeway, T., & Smith, A. T. (1994). Evidence for separate motion-detecting mechanisms for first- and second-order motion in human vision. *Vision Research, 34*(20), 2727–2740.

Lu, Z. L., & Sperling, G. (1995). Attention-generated apparent motion. *Nature, 377*(6546), 237–239.

Mather, G., Verstraten, F., & Anstis, S. (1998). *The motion after-effect: A modern perspective*. Cambridge, MA: MIT Press.

Matin, L., Boff, K., & Pola, J. (1976). Vernier offset produced by rotary target motion. *Perception & Psychophysics, 20*(2), 138–142.

McCarthy, J. E. (1993). Directional adaptation effects with contrast modulated stimuli. *Vision Research, 33*(18), 2653–2662.

McGraw, P. V., Walsh, V., & Barrett, B. T. (2004). Motion-sensitive neurones in V5/MT modulate perceived spatial position. *Current Biology, 14*(12), 1090–1093.

McGraw, P. V., Whitaker, D., Skillen, J., & Chung, S. T. (2002). Motion adaptation distorts perceived visual position. *Current Biology, 12*(23), 2042–2047.

McKee, S. P., Klein, S. A., & Teller, D. Y. (1985). Statistical properties of forced-choice psychometric functions: Implications of probit analysis. *Perception & Psychophysics, 37*(4), 286–298.

Morgan, M. J. (1976). Pulfrich effect and the filling in of apparent motion. *Perception, 5*(2), 187–195.

Morgan, M. J. (1980). Spatiotemporal filtering and the interpolation effect in apparent motion. *Perception, 9*(2), 161–174.

Mussap, A. J., & Prins, N. (2002). On the perceived location of global motion. *Vision Research, 42*(6), 761–769.

Nakayama, K. (1985). Biological image motion processing: A review. *Vision Research, 25*(5), 625–660.

Nishida, S. (2004). Motion-based analysis of spatial patterns by the human visual system. *Current Biology, 14*(10), 830–839.

Nishida, S., Edwards, M., & Sato, T. (1997). Simultaneous motion contrast across space: Involvement of second-order motion? *Vision Research, 37*(2), 199–214.

Nishida, S., & Johnston, A. (1999). Influence of motion signals on the perceived position of spatial pattern. *Nature, 397*(6720), 610–612.

Nishida, S., & Sato, T. (1995). Motion aftereffect with flickering test patterns reveals higher stages of motion processing. *Vision Research, 35*(4), 477–490.

Ramachandran, V. S., & Anstis, S. M. (1990). Illusory displacement of equiluminous kinetic edges. *Perception, 19*(5), 611–616.

Seiffert, A. E., & Cavanagh, P. (1998). Position displacement, not velocity, is the cue to motion detection of second-order stimuli. *Vision Research, 38*(22), 3569–3582.

Seiffert, A. E., & Cavanagh, P. (1999). Position-based motion perception for color and texture stimuli: Effects of contrast and speed. *Vision Research, 39*(25), 4172–4185.

Shim, W. M., & Cavanagh, P. (2004). The motion-induced position shift depends on the perceived direction of bistable quartet motion. *Vision Research, 44*(20), 2393–2401.

Smith, A. T., & Ledgeway, T. (1997). Separate detection of moving luminance and contrast modulations: Fact or artifact? *Vision Research, 37*(1), 45–62.

Snowden, R. J. (1998). Shifts in perceived position following adaptation to visual motion. *Current Biology, 8*(24), 1343–1345.

van Santen, J. P., & Sperling, G. (1985). Elaborated Reichardt detectors. *Journal of the Optical Society of America. A, 2*(2), 300–321.

Verstraten, F. A., Cavanagh, P., & Labianca, A. T. (2000). Limits of attentive tracking reveal temporal properties of attention. *Vision Research, 40*(26), 3651–3664.

Watanabe, K. (2005). The motion-induced position shift depends on the visual awareness of motion. *Vision Research, 45*(19), 2580–2586.

Watanabe, K., Nijhawan, R., & Shimojo, S. (2002). Shifts in perceived position of flashed stimuli by illusory object motion. *Vision Research, 42*(24), 2645–2650.

Watanabe, K., Sato, T. R., & Shimojo, S. (2003). Perceived shifts of flashed stimuli by visible and invisible object motion. *Perception, 32*(5), 545–559.

Watson, A. B., & Ahumada, A. J. Jr., (1985). Model of human visual-motion sensing. *Journal of the Optical Society of America. A, 2*(2), 322–341.

Whitaker, D., McGraw, P. V., & Pearson, S. (1999). Non-veridical size perception of expanding and contracting objects. *Vision Research, 39*(18), 2999–3009.

Whitney, D. (2002). The influence of visual motion on perceived position. *Trends in Cognitive Sciences, 6*(5), 211–216.

Whitney, D. (2005). Motion distorts perceived position without awareness of motion. *Current Biology, 15*(9), R324–R326.

Whitney, D., & Cavanagh, P. (2000). Motion distorts visual space: Shifting the perceived position of remote stationary objects. *Nature Neuroscience, 3*(9), 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*(5646), 878–881, Epub 2003 Sep 2018.

Zanker, J. M., Quenzer, T., & Fahle, M. (2001). Perceptual deformation induced by visual motion. *Naturwissenschaften, 88*(3), 129–132.