Asymmetric transfer of the dynamic motion aftereffect between first- and second-order cues and among different second-order cues

Andrew J. Schofield   School of Psychology, University of Birmingham, Birmingham, UK

Timothy Ledgeway   School of Psychology, University of Nottingham, Nottingham, UK

Claire V. Hutchinson   School of Psychology, University of Nottingham, Nottingham, UK

Recent work on motion processing has suggested a distinction between first-order cues (such as luminance modulation [LM]) and second-order cues (such as local contrast modulation [CM]). We studied interactions between moving LM, CM, and orientation modulation (OM) first comparing their spatial- and temporal-frequency sensitivity. We then tested for the transfer of the dynamic motion aftereffect (dMAE) between the three cues, matched for visibility. Observers adapted to moving, 0.5-c/deg horizontal modulations for 2 min (with 10 s top-ups). Relatively strong dMAEs were found when the adaptation and test patterns were defined by the same cue (i.e., both LM, both CM, or both OM); these effects were tuned for spatial frequency in the case of LM and CM. There was a partial transfer of the dMAE from LM to CM and OM; this transferred effect seemed to lose its tuning. The aftereffect transferred well from CM to OM and retained its tuning. There was little or no transfer from CM to LM or from OM to CM or LM. This asymmetric transfer of the dMAE between first- and second-order cues and between the second-order cues suggests some degree of separation between the mechanisms that process them.

Keywords: motion, aftereffect, first order, second order, luminance, contrast, orientation

Introduction

The human visual system is sensitive to motion conveyed by a range of cues including luminance modulations (LM, Movie 1; known as "first-order" or "Fourier" cues) and some modulations of visual texture, including local contrast (CM, Movie 2), orientation (OM, Movie 3), flicker rate, and element length/size (collectively termed "second-order" cues; Cavanagh & Mather, 1989). Chubb and Sperling (1988) termed the second-order cues "non-Fourier" to emphasize that, unlike first-order cues, they do not contain Fourier energy at the modulation frequency (although many examples do contain distinct energy peaks at other frequencies; Fleet & Langley, 1994).

The detection of second-order motion seems to require some form of nonlinear processing aside from the squaring implicit in the standard motion energy model (Adelson & Bergen, 1985) because this model followed by linear processes such as averaging cannot detect the direction of motion for CM stimuli (Benton & Johnston, 1997; Ledgeway & Hutchinson, 2006). The balance of evidence suggests that first- and second-order motion are detected, at least initially, by separate mechanisms (see Baker, 1999; Lu & Sperling, 1995, 2001; Smith, 1994; Sperling & Lu, 1998, for reviews). Accordingly, the filter-rectify-filter (FRF) model (Wilson, Ferrera, & Yo, 1992) proposes two mechanisms for motion detection: a standard motion energy mechanism that detects first-order motion and a parallel mechanism that is preceded by a nonlinear operator (to demodulate second-order cues) sandwiched between two filtering stages that exclude first-order signals from the second-order channel.

In contrast to the two-mechanism view, Benton (2002), Benton and Johnston (2001), Benton, Johnston, McOwan, and Victor (2001), Johnston, McOwan, and Benton (1999), and Johnston, McOwan, and Buxton (1992) have shown that first- and second-order motion (defined by CM) can be detected by a single mechanism that extracts motion gradients. However, it can been shown that some gradient models are equivalent to the energy model provided that the opponent motion energy signal is normalized by the amount of "static" energy in the stimulus (Adelson & Bergen, 1986; Benton, 2004; Bruce,
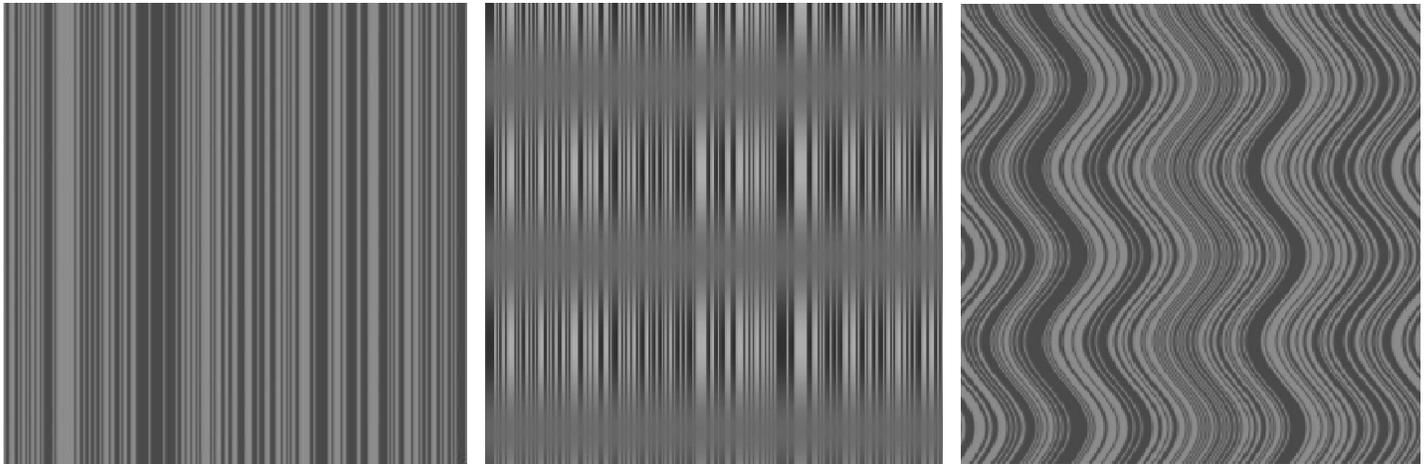
Movies 1–3. Sample stimuli: Movies 1–3 show motion sequences for the three cues used in this study. Left panel, Movie 1, LM; middle panel, Movie 2, CM; right panel, Movie 3, OM. Such sequences were used in Experiments 1 and 2 (duration = 1 s) and as the adapters in Experiment 3 (for duration see text). As static images, Movies 1–3 demonstrate the appearance of a single frame in our motion sequences. See text for details.

Green, & Georgeson, 1996). The final normalization stage renders the unified model sensitive to CM signals (Benton, 2004). We note that the unified model splits the processing of LM and CM signals. One part of the model computes an unnormalized opponent motion energy signal and is blind to moving CM, whereas the other part provides the normalization signal and is sensitive to CM motion. One could argue that the notion of separate first- and second-order detection is preserved within the unified gradient/energy model provided that the observer has independent access to the two signals described above. However, the second-order signal would most likely require additional low-level processing prior to any higher stage motion analysis.

Lu and Sperling (1995, 2001) not only present considerable evidence in favor of separate first- and second-order motion-detecting mechanisms but also propose an additional (termed third-order) mechanism that processes motion based on figure-ground salience. The third-order system is characterized by (among other things) its poor temporal acuity relative to either the first-order or second-order motion-detecting systems (Lu & Sperling, 2001).

Most research on second-order vision has used CM noise textures as the second-order cue, and there is a tendency to assume that the second-order system can be characterized by its response to CM. However, some recent studies have considered other second-order cues and have shown that the second-order class may itself be heterogeneous. For example, spatiotemporal sensitivity for moving modulations of the length of carrier elements is very different from that for CM (Hutchinson & Ledgeway, 2006). Similarly, spatial-frequency sensitivity for static CM peaks at a higher frequency than that for static OM (compare Gray & Regan, 1998; Kingdom, Keeble, &

Moulden, 1995, with Schofield & Georgeson, 1999). Further, there is no subthreshold facilitation between static CM, OM, and frequency modulations (Kingdom, Prins, & Hayes, 2003; Schofield & Yates, 2005). Finally, Baker, Mortin, Prins, Kingdom, and Dumoulin (2006) found similar patterns of fMRI activity in response to static CM and frequency-modulated stimuli but a different pattern of activation for static OM. This evidence supports the notion that there is more than one second-order detection mechanism.

Although the responses of the human visual system to first- and second-order motion differ in many respects, we focus on just one aspect of this comparison here: the induction of motion aftereffects (MAE). Following prolonged viewing of a moving stimulus, a physically static stimulus will appear to move in the opposite direction (the static MAE [sMAE]; Wohlgemuth, 1911). A similar effect can be induced in a flickering test stimulus (the dynamic MAE [dMAE]; von Grunau, 1986), which can be regarded as directionally ambiguous rather than strictly static (Levinson & Sekuler, 1975). Moving first-order gratings induce both types of MAE, whereas second-order gratings induce only the dMAE (Nishida and Sato, 1995; see also Derrington & Badcock, 1985; Ledgeway, 1994). Further, a compound adapter with first- and second-order (CM) components moving in opposite directions induces a sMAE opposite to the first-order component and a dMAE opposite to the second-order component (Nishida & Sato, 1995).

Here, we assess the ability of moving first-order (LM) and second-order (CM and OM) gratings to induce a dMAE in themselves (within-cue adaptation) and in each other (between-cue adaptation). However, we first review the limited literature pertinent to the transfer of the dMAE

between cues and, for completeness, the transfer of other types of adaptation. Lu, Sperling, and Beck (1997, but see also Lu & Sperling, 2001) found selective MAEs for first-, second-, and third-order motion (LM, CM, and motion-from-motion respectively) with little transfer of adaptation between cue types. Nishida, Ledgeway, and Edwards (1997) measured direction-identification thresholds for LM and CM stimuli and found strong postadaptation threshold elevation that was direction, spatial frequency, and cue specific; the only transfer observed was very weak and not spatial frequency tuned.

In contrast to the studies above, some researchers have found good transfer of adaptation between cues. Nishida and Sato (1995) used a variety of second- and third-order adaptation stimuli but tested for the dMAE using flickering luminance gratings; their results suggest that the dMAE can transfer from higher order cues to the first-order motion system. Further, Georgeson and Schofield (2002) found good transfer of the tilt and contrast-reduction aftereffects between static LM and CM stimuli. Note that, as with their moving counterparts, there is considerable evidence to suggest that static LM and CM signals are detected independently (Georgeson & Schofield, 2002; Schofield & Georgeson, 1999). Similarly, Cruickshank (2006) and Cruickshank and Schofield (2005) have demonstrated partial transfer of the tilt and contrast-reduction aftereffects between CM and OM, despite evidence to support their independent detection (Kingdom et al., 2003; Schofield & Yates, 2005). However, Cruickshank was unable to find transfer of the contrast-reduction aftereffect between CM and disparity modulations or between OM and disparity modulations.

In this article, we test the spatial-frequency tuning of any observed aftereffects. Spatial-frequency tuning can be taken as the signature of a channel-like mechanism. Also, it can be informative to compare the tuning of any transferred aftereffects to the tuning of the within-cue effects. However, comparing spatial-frequency tuning across conditions presupposes that the dMAE is a tuned effect. Ashida and Osaka (1994) found that dMAE did not exhibit spatial-frequency tuning. In contrast, others have found that the dMAE can be well tuned for spatial frequency (Bex, Verstraten, & Mareschal, 1996), although the sharpness of this tuning reduces with increased (test) temporal frequency (Mareschal, Ashida, Bex, Nishida, & Verstraten, 1997). Accordingly, we tested at a relatively low temporal frequency (1 Hz).

Experiments 1 and 2: Spatial and temporal sensitivity

The spatiotemporal frequency response of the human visual system to moving OM stimuli has yet to be characterized. We now address this issue as a necessary prerequisite to our adaptation study. We also measured sensitivity for LM and CM so as to allow direct comparison with OM under the same test conditions. These functions facilitated our choice of spatial and temporal frequency in our adaptation experiment and allowed us to equate the visibility of our cues for each observer.

Methods

Observers

Four observers participated overall, with three observers in each experiment. All had normal or corrected-to-normal visual acuity. Observers A.J.S., C.V.H., and P.D.J. (the first two are authors of this study, whereas the latter is a paid volunteer who was naïve to the purpose of the experiment) participated in Experiment 1. In Experiment 2, observer P.D.J. was unavailable and T.L. (an author of this study) acted as the third observer.

Apparatus and stimuli

Stimuli were generated using a Macintosh G4 computer and presented on a Sony Trinitron GDM-520 monitor (refresh = 75 Hz) using custom software written in C. The number of intensity levels available was increased from 256 to 16,384 using a Cambridge Research Systems Bits++ attenuation device in its Mono++ mode to produce "grayscale" images on the color monitor. The monitor was gamma corrected using a sensitive, motion-nulling psychophysical task (Gurnsey, Fleet, & Potechin, 1998; Ledgeway & Smith, 1994a; Lu & Sperling 2001; Nishida et al., 1997). Stimuli were presented within a 5.3 deg square window at the center of the display. The mean luminance of the window and the remainder of the display area (which was homogeneous) was approximately 55 cd/m^2. The viewing distance was 2.08 m. Viewing was binocular, and a prominent fixation spot was located at the center of the display to aid stable fixation and discourage ocular tracking of the motion stimuli.

All stimuli were drifting sinusoidal modulations of either first-order or second-order motion that were oriented horizontally in space (see Movies 1–3). A dynamic noise carrier was used in all cases to allow direct comparisons between the results for each stimulus type. The carrier was a field of one-dimensional (1-D), vertically oriented, dynamic, random, binary visual noise. The noise had a Michelson contrast of 0.25 and was replaced with a new stochastic sample each time the position of the drifting modulation signal was updated, at a rate of 37.5 Hz. Noise stripes subtended 0.625 arcmin of visual angle.

First-order (LM) motion patterns were constructed by adding a drifting sinusoidal luminance grating to the field of dynamic noise. Second-order motion patterns were constructed as follows. For CM, the amplitude of the noise carrier was modulated by a drifting sinusoidal waveform (see Schofield & Georgeson, 1999). To generate OM

patterns, we spatially shifted each horizontal row of pixels in the noise carrier image in the horizontal dimension by an amount and direction (either leftward or rightward) that was determined by the drifting sinusoidal waveform. This resulted in a motion sequence in which the local orientation of the striped elements within the dynamic noise was modulated over space and time.

The modulation depth of all signals could be varied within the range 0 to 1 according to the following equations. The LM modulation depth (M_L) was given by $M_L = (L_{max} - L_{min})/(L_{max} + L_{min})$, where L_{max} and L_{min} refer to the maximum and the minimum luminances, respectively, averaged over adjacent noise stripes with opposite polarity in the image. For CM, $M_C = (C_{max} - C_{min})/(C_{max} + C_{min})$, where C_{max} and C_{min} refer to the maximum and the minimum local Michelson contrasts, respectively, in the image computed over adjacent noise stripes with opposite polarity. For OM, $M_O = (O_{max} - O_{min})/90$, where O_{max} and O_{min} refer to the maximum and the minimum local orientations, respectively, in the image computed relative to a reference orientation of 90° (corresponding to vertical).

The total stimulus duration was 1 s, although the on and off transitions were smooth with a raised cosine profile lasting 200 ms. Similarly, stimuli were spatially windowed in the vertical dimension according to a half cycle of a raised cosine function with a half period of 1 deg (not shown in the movies). These manipulations minimized the presence of spatial and temporal transients.

Procedure and analysis

Modulation thresholds for discriminating the direction of motion were measured over a range of spatial (Experiment 1) and temporal (Experiment 2) frequencies. Motion stimuli were presented in a single-interval, two-alternative forced-choice design where the observer had to indicate the direction of motion (up vs. down) using one of two response buttons. Stimulus modulation depth on each trial was chosen at random from a set of nine predetermined values, selected based on pilot studies. In Experiment 1, data were collected for spatial frequencies in the range 0.125–4 c/deg (maximum of 2 c/deg for P.D.J.) at a fixed temporal frequency of 1 Hz. In Experiment 2, data were collected for temporal frequencies in the range 0.5–9.5 Hz at a fixed spatial frequency of 0.5 c/deg. Conditions were blocked such that only one cue type and frequency were tested in a given session. Observers completed four sessions of 70 trials for each spatial and temporal frequency tested. Data were fitted with Weibull (1951) functions from which 75% correct thresholds were extracted. Sensitivity was calculated as the reciprocal of the threshold modulation depth.

Results
Experiment 1

Sensitivity curves for direction discrimination versus spatial frequency are plotted in Figure 1. Sensitivity for LM appears high pass because we did not test at high enough spatial frequencies to obtain the expected band-pass response. Sensitivity for LM was maximal at about 1–2 c/deg. Sensitivity for CM was band pass with a peak at 1 c/deg, but unlike LM, sensitivity reduced rapidly with further increases in frequency. Sensitivity for CM was considerably lower than that for LM across the range. Sensitivity for OM was more low pass than for CM with a knee between 0.5 and 1 c/deg (except for A.J.S.) with an acute reduction in sensitivity beyond the knee. These results are consistent with previous findings suggesting that sensitivity for second-order cues is much lower than that for first-order cues but that sensitivity curves for CM and LM have broadly similar shapes whereas those for some other types of second-order cue are more low pass (Hutchinson & Ledgeway, 2006; Lu & Sperling, 2001). However, we note that first-order sensitivity can depend on the type of noise used (Lu & Sperling, 2001; Schofield & Georgeson,
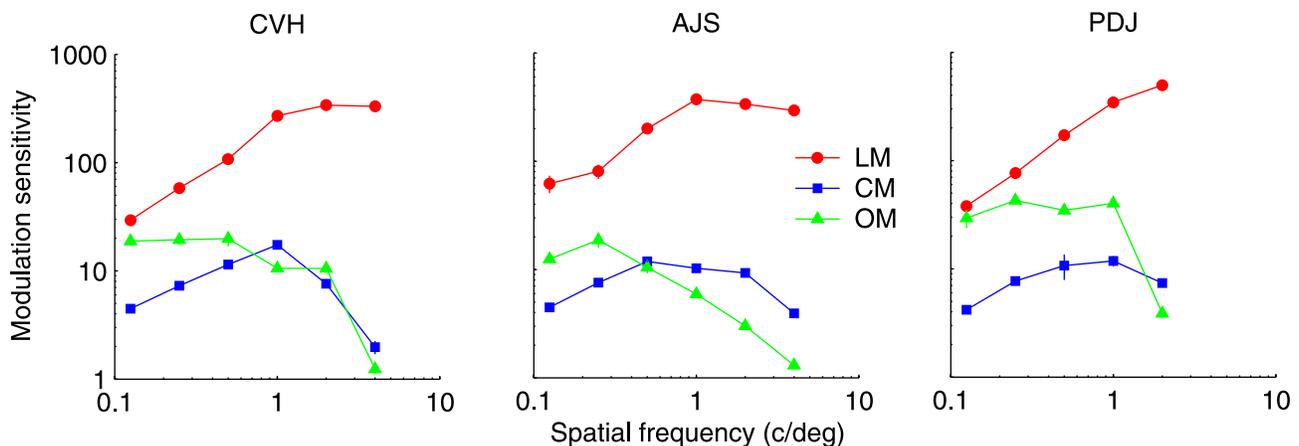

Figure 1. Sensitivity as a function of spatial frequency; circles, squares, and triangles show sensitivity to LM, CM, and OM, respectively. Error bars show 95% confidence intervals estimated from 5,000 iterations of a nonparametric bootstrap procedure.
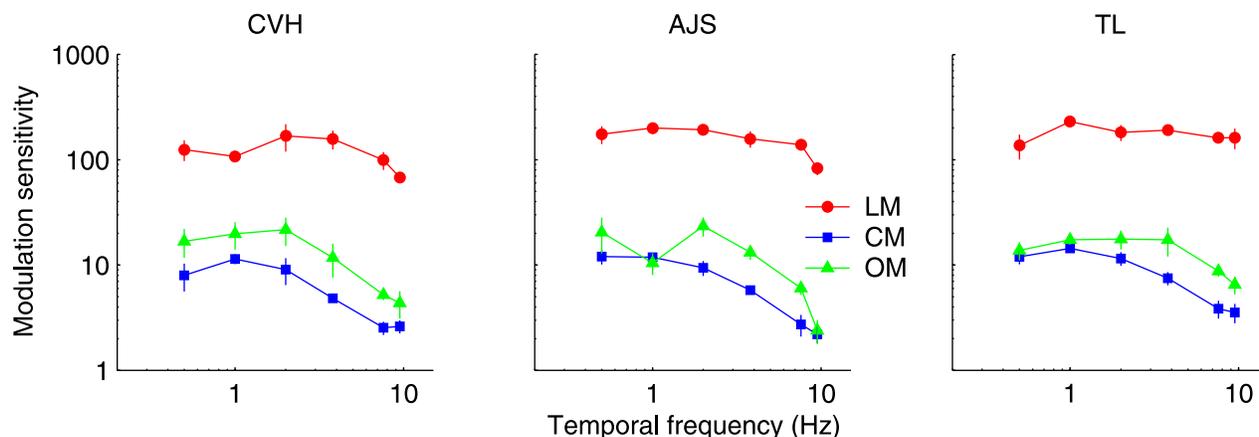
Figure 2. Sensitivity as a function of temporal frequency; details are as described in Figure 1.

2003). Further, Hutchinson and Ledgeway (2006) recorded low-pass sensitivity for CM stimuli using an isotropic dynamic.

Experiment 2

Sensitivity curves for direction discrimination versus temporal frequency are shown in Figure 2. Sensitivity for LM was quite flat, although it did decline at the highest frequencies tested (again, the range of test frequencies was not high enough to fully characterize the LM response). Sensitivity curves for CM and OM were more low pass, suggesting a low cutoff frequency for these cues relative to that for LM. Crucially, CM and OM produced very similar sensitivity curves in the presence of our 1-D noise, with OM having perhaps a marginally higher cutoff frequency. Thus, temporal acuity for OM is relatively high, suggesting that OM is not a third-order cue as defined by Lu and Sperling (2001).

Experiment 3: Motion aftereffect

Having first characterized the spatial- and temporal-frequency responses to LM, OM, and CM in Experiments 1 and 2, we investigated suprathreshold interactions between these cues using the dMAE paradigm.

Methods

Observers

Observers A.J.S., C.V.H., and P.D.J. participated in Experiment 3.

Apparatus and stimuli

The apparatus and stimuli were similar to those used in Experiments 1 and 2 with the following exceptions. Adaptation stimuli were drifting patterns composed of LM, CM, or OM (see Movies 1–3). The spatial and temporal frequencies of the modulation were 0.5 c/deg and 1 Hz, respectively, chosen based on the results of Experiments 1 and 2 to ensure that each variety of motion was readily visible and did not exceed its spatial and temporal acuity limits. Adaptation stimuli were presented at $10\times$ the appropriate threshold value for A.J.S. and C.V.H. and $8.5\times$ threshold for P.D.J. (it was impossible to generate adaptation stimuli at $10\times$ P.D.J.'s CM threshold at 0.5 c/deg). Threshold estimates were taken from Experiment 1.

The test stimuli (Movies 4–6) were directionally ambiguous motion patterns similar to those used in previous studies (e.g., Ledgeway, 1994; Ledgeway & Smith, 1994b) and were again composed of LM, CM, or OM. They were constructed from the sum of two horizontal sinusoidal modulations (components) of the same spatial and temporal frequency (1 Hz) drifting smoothly in opposite directions. The orientation of the drifting spatial modulation (horizontal) was always orthogonal to that of the 1-D dynamic noise (vertical) in all cases to ensure that any aftereffects of adaptation were due to the presence of the first- or second-order test structure and not the carrier (see Culham et al., 1998). The spatial frequency of the sinusoidal modulation could differ from that of the adaptation stimuli (0.5 c/deg) by -2, -1, 0, 1, or 2 octaves to measure the spatial-frequency dependence of the dMAE. The visibilities of the test stimuli were equated by presenting each pattern at the same multiple of threshold ($3.65\times$ threshold for A.J.S. and C.V.H. and $3.1\times$ threshold for P.D.J.). Thus, the modulation depths of the adaptation stimuli were $2.74\times$ higher than those of the test stimuli for all observers. Although equating stimuli in this manner has become conventional practice in the literature, it does assume that the magnitude of the internal (visual) response scales linearly with multiples of threshold in each case. However, presenting first- and second-order stimuli at equal multiples of threshold may not be unreasonable, as it often leads to quantitatively similar performance for the two
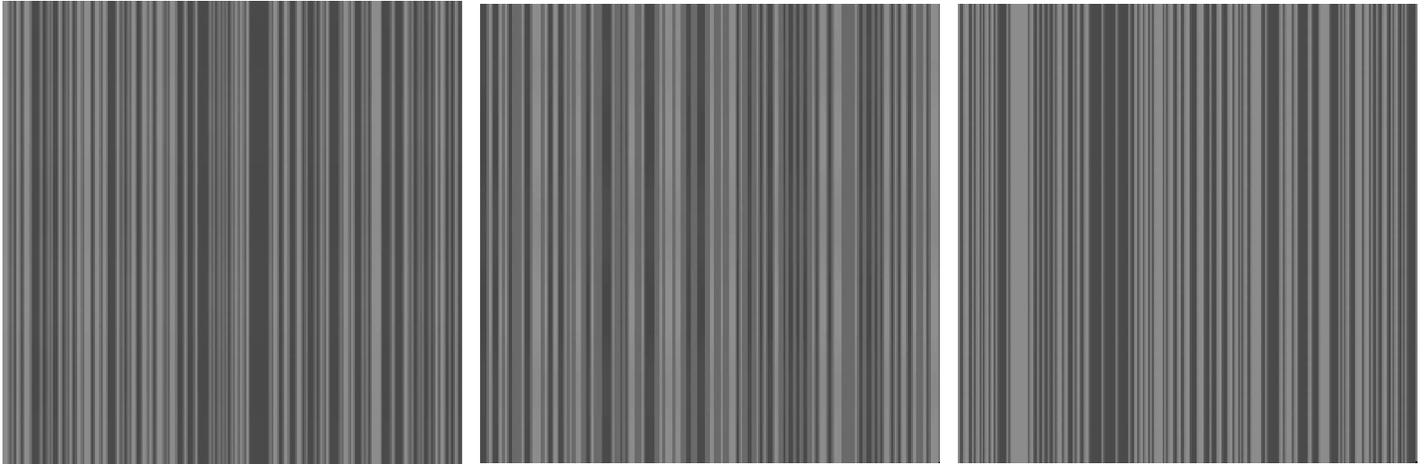
Movies 4–6. Sample test sequences for Experiment 3. Test sequences comprised two counterphasing components that are fully balanced in these examples so as to produce "flicker" rather than motion. Left panel, Movie 4, LM; middle panel, Movie 5, CM; right panel, Movie 6, OM. Test sequences lasted for 1 s. As static images, only the first unmodulated frame is shown. The reader is referred to Movies 1–3, which better illustrate our cues in a static presentation.

varieties of motion and at least goes some way toward controlling for gross differences in sensitivity.

A nulling technique was employed to measure the magnitude of the aftereffect. Specifically, the relative modulation depths of the oppositely moving components of the test stimuli could be manipulated in a "seesaw" (antagonistic) fashion to null the perception of unidirectional motion following adaptation. For example, if the modulation depth of the upward-moving component was increased by 10%, that of the downward component decreased by 10% accordingly. In this manner, the overall modulation depths of the test stimuli were kept constant. We express the relative modulation depths of the two motion components in terms of "motion contrast" (C), calculated as a Michelson ratio; specifically, $C = 100(M_a - M_u)/(M_a + M_u)$, where M_a is the modulation depth of the component moving in the direction of adaptation and M_u is the modulation depth of the opposite-moving component. Note that when the two components had equal modulation depth, motion contrast was zero.

Procedure

At the beginning of each run of trials, the adaptation stimulus (a sinusoidal modulation drifting either upward or downward) was presented for 2 min followed by the presentation of a blank field (except for the central fixation spot) to indicate to the observer that the test stimulus was to be presented 0.5 s later. The test stimulus was present for a total of 1 s, and the observer's task was to indicate its overall perceived direction of drift (i.e., either upward or downward). Adaptation was then "topped up" with a 10-s presentation of the adaptation stimulus before the test stimulus was presented again, and so on.

The motion contrast of the test stimulus was chosen at random from a set of seven predetermined values. These ranged from −100% (all motion was opposite adaptation) to 100% (all motion was in the same direction as adaptation) in equal steps of 33.3%.

Observers completed between two and six runs of 70 trials for each test spatial frequency, and all possible combinations of the first- and second-order adaptation and test stimuli were examined to investigate within-cue and between-cue adaptation effects. Adaptation cues were presented moving either up or down, in separate runs, with an equal number of runs per direction. We also measured the effects of adapting to the carrier only on each test cue. Observers were required to take a minimum break of 2 hr between runs with different adaptation stimuli to minimize any carryover of adaptation between conditions.

Analysis

Data were collapsed across direction of motion in the adaptation phase, and logistic functions were fitted to the resulting data for each observer and condition, plotted as the percentage of trials on which the observer perceived the test stimulus to drift in the same direction as adaptation as a function of the motion contrast of the test. From these fits, we determined the motion contrast, which produced no net perceived direction of drift (i.e., the point of subjective equality [PSE]).

Results

Figure 3 shows the PSEs for each observer and all combinations of adapter and test cue. Results for LM,
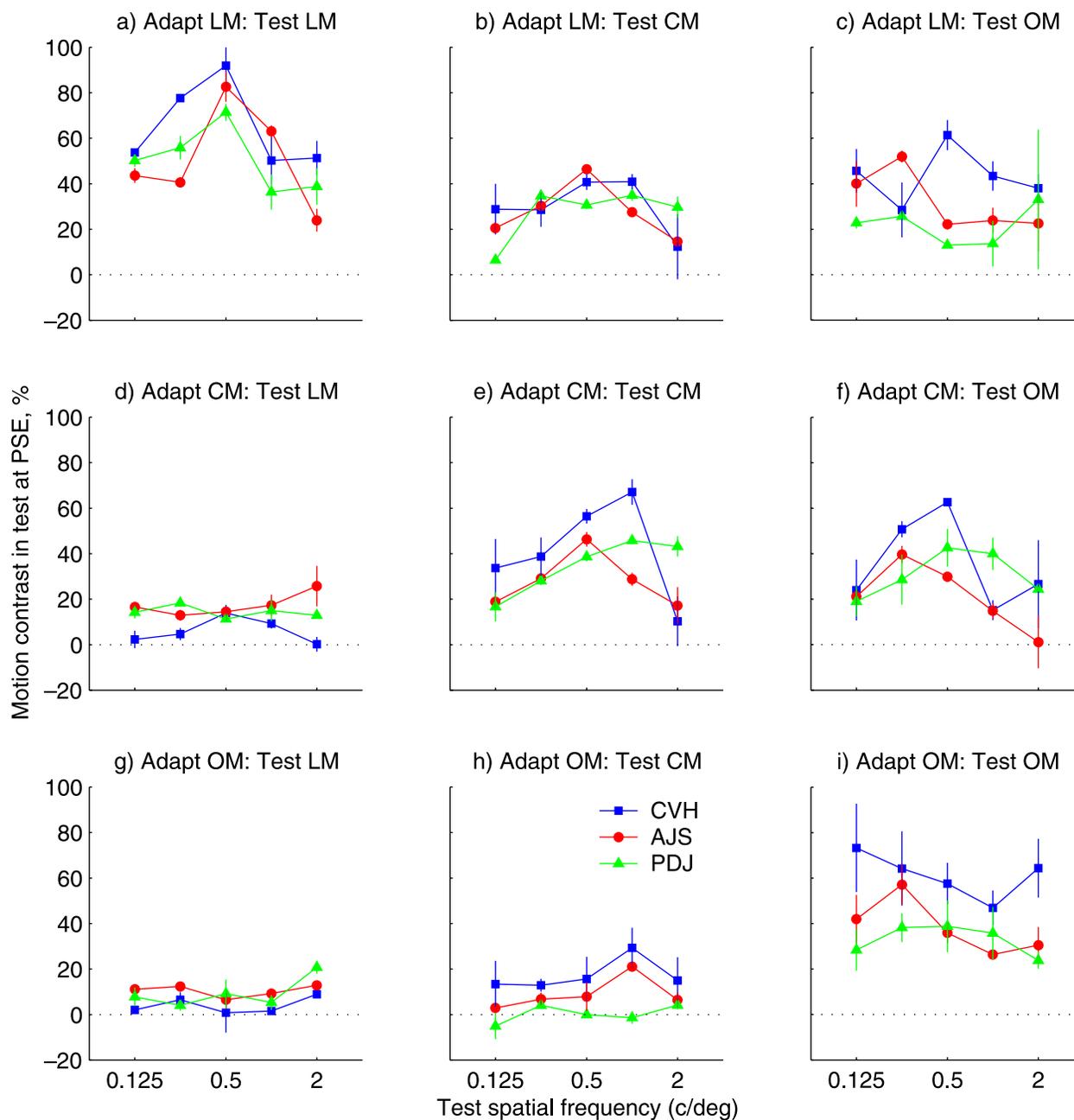
Figure 3. Adaptation results. The motion contrast required to null any aftereffect. (a–c) Adaptation to LM; (d–f) adaptation to CM; (h–j) adaptation to OM. Symbols: circles, squares, and triangles represent data for observers A.J.S., C.V.H., and P.D.J., respectively. Dotted lines show position of zero aftereffect. Error bars are as described in Figure 1.

CM, and, OM adapters are shown on the top, middle, and bottom rows, respectively. Within-cue adaptation is shown on the leading diagonal. Each plot shows the PSE at the adaptation frequency (0.5 c/deg) and test frequencies of up to 2 octaves on either side of this. The strength of the aftereffect is given as the motion contrast at the PSE. Values >0% indicate that the observer required extra signal in the same direction as the adaptation cue (less in the opposite direction) to perceive a stationary stimulus and that their aftereffect was therefore in the direction opposite the adaptation motion. We confirm that adapting

to the carrier alone produced no significant aftereffect for any test cue (data not shown).

Adaptation to LM produced large shifts in PSE for LM tests (Figure 3a, LM:LM). The aftereffect was very strong at the adaptation frequency (motion contrast at PSE [C_{PSE}] ≈ 80%). The effect was tuned, reducing to around 40% when the spatial frequency of the adaptation and test patterns differed by 2 octaves. Adaptation to LM induced a considerably weaker but nonetheless significant shift in PSE (C_{PSE} ≈ 40%) for CM test patterns (Figure 3b, LM: CM). This aftereffect was broadly tuned for spatial
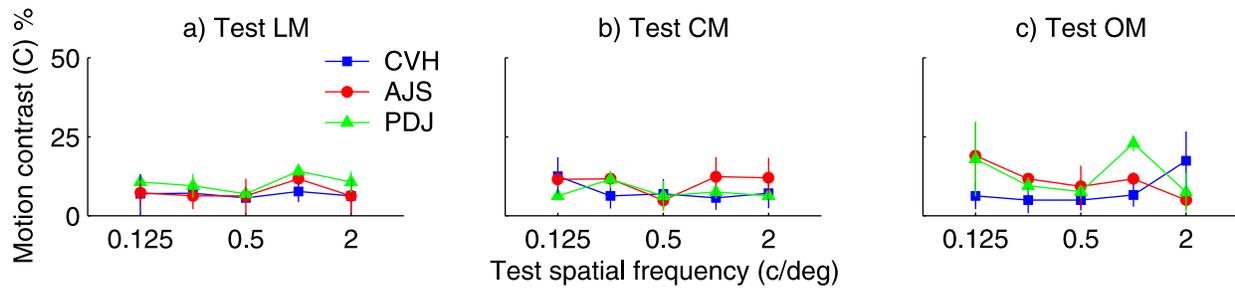
Figure 4. Sensitivity to motion contrast in test. Circles, squares, and triangles represent data for observers A.J.S., C.V.H., and P.D.J., respectively. Error bars are as described in Figure 1.

frequency. Adaptation to LM also induced an aftereffect ($C_{PSE} \approx 40\%$) onto OM tests (Figure 3c, LM:OM), although, in the case of P.D.J., this was very weak. The effect was much less well tuned for spatial frequency than either the LM:LM or the LM:CM interaction.

Adaptation to CM induced a moderate aftereffect ($C_{PSE} \approx 50\%$) in CM tests (Figure 3e, CM:CM). This effect was reasonably well tuned for spatial frequency, but this tuning was broader than that found in the LM:LM case. Although the effect peaked at 1 c/deg (+1 octave) for two of three observers, the tuning was asymmetric for at least one of these observers, suggesting that their peak may have been poorly estimated. However, we cannot rule out the possibility that the adaptable CM channels are more widely spaced than those for LM and that we adapted to one side of the center frequency of the nearest channel for two of our three observers. Adaptation to CM induced a moderate aftereffect ($C_{PSE} \approx 40\%$) onto OM tests (Figure 3f, CM:OM). This effect showed some spatial-frequency tuning. Adaptation to CM induced only a very weak shift in PSE for LM tests (Figure 3d, CM:LM). With the exception of one point (2 c/deg for A.J.S.), the PSE did not exceed a motion contrast of 20%. This very small effect was clearly not tuned for spatial frequency.

Adaptation to OM induced a moderate aftereffect ($C_{PSE} \approx 50\%$) onto OM tests (Figure 3i, OM:OM). The effect was, at best, very broadly tuned and possibly low pass. Adaptation to OM induced only very weak and broadly tuned aftereffects ($C_{PSE} \leq 20\%$) onto CM (Figure 3h, OM:CM) and LM (Figure 3g, OM:LM) tests.

We also assessed observer sensitivity to our test cues by extracting just-noticeable differences (75% correct thresholds) from the logistic fits for the control conditions where observers adapted to the carrier only. These data (shown in Figure 4) confirm that observers were quite sensitive to changes in motion contrast.

We estimated the transfer of adaptation between cues for each observer. The percentage transfer (T) was calculated from the equation $T = 100\ (x/w)$, where x is the between-cue PSE at 0.5 c/deg and w is the within-cue PSE at 0.5 c/deg for the adapter. We used the central PSE rather than those for all spatial frequencies as otherwise estimated transfer was very sensitive to the relative tuning of the aftereffects being compared. Table 1 shows the estimated percentage transfers for each observer. These results confirm the subjective impression gained from inspecting Figure 3 that adaptation to an LM signal transfers only partially to CM and OM tests, whereas adaptation to CM transfers well to OM but only very weakly to LM and adaptation to OM transfers only very weakly to LM and CM.

| | | Test (%) | | |
		LM	CM	OM
Adaptation	Observer			
LM	C.V.H.		44.33	66.77
	A.J.S.		56.22	26.79
	P.D.J.		42.97	18.21
CM	C.V.H.	24.56		110.91
	A.J.S.	31.34		64.48
	P.D.J.	29.28		100.61
OM	C.V.H.	1.44	27.16	
	A.J.S.	18.23	21.93	
	P.D.J.	23.63	0	

Table 1. Percentage transfer of adaptation between cues. See text for details.

Discussion

We have characterized the spatial- and temporal-frequency responses of human vision to moving OM stimuli and compared these to sensitivities measured for LM and CM under similar test conditions. OM sensitivity curves are both spatially and temporally low pass, but OM detection has reasonably high temporal acuity and, thus, OM is unlikely to be a third-order cue as defined by Lu and Sperling (2001). We have also tested the ability of our motion cues to induce the dMAE onto patterns of a similar type and assessed the degree to which the dMAE

transfers between the three cues. We measured the spatial-frequency tuning of each aftereffect. The within-cue effect was strongest for LM:LM but was clearly present for CM:CM and OM:OM. The aftereffect seen with an LM test after adaptation to LM was narrowly tuned. The CM:CM effect was also tuned, although less sharply than the LM:LM case, whereas the OM:OM aftereffect was untuned, although there was some evidence for low-pass tuning suggesting that the system for processing OM motion may have only a single low-pass channel.

The transfer of aftereffects was clearly asymmetric. Aftereffects were seen with both CM and OM tests following adaptation to LM, although we note that the percentage transfer was relatively low (especially for P.D.J.) in these cases and that the spatial-frequency tuning of the transferred aftereffects was relatively broad and less consistent than that for the LM:LM aftereffect. In contrast, adaptation to CM produced strong aftereffects only for CM and OM tests with only a very weak effect noted for LM tests. However, we note that the CM:OM effect was strong and that this effect showed more spatial-frequency tuning than the OM:OM case. Finally, only very weak aftereffects were found with LM and CM tests following adaptation to OM.

Our finding that the dMAE transfers asymmetrically between cues is at odds with the findings of both Lu et al. (1997), who found no transfer, and Nishida and Sato (1995), who found that higher order cues can impose a dMAE on LM tests. We note, however, that our stimuli differ markedly from those used in these previous studies, making direct comparisons difficult. Our results are also somewhat at odds with the symmetric transfer of the tilt and contrast-reduction aftereffects found for similar (but static) cues (Cruickshank & Schofield, 2005; Georgeson & Schofield, 2002), but we should not necessarily expect all aftereffects to follow the same pattern of transfer.

We now consider—but reject—the possibility that our asymmetric transfers are artifactual; we then go on to discuss the implications of our findings for models of first- and second-order motion processing.

One possibility is that our asymmetric transfers arise from the relative potency of the cues as adapters. For example, if CM and OM adapt the motion system less well than LM, then we might not expect to observe an aftereffect, using LM tests, following adaptation to the weaker cues. We can reject this criticism on two counts. First, our transfer metric normalizes each between-cue effect by the within-cue effect for the adaptation cue, thus taking the potency of each adapter into account. Second, CM and OM adapt the motion system equally well, but transfer between these cues is asymmetric.

Next, we consider the relative visibility of our cues. Adaptation is known to transfer better from strong cues to weak ones than it does from weak to strong (Gibson & Radner, 1937). In their study of the tilt aftereffect, Cruickshank and Schofield (2005) noted that OM is often

perceived as weaker than CM when both are presented at the same multiple of detection threshold. Accordingly, Cruickshank and Schofield used CM and OM stimuli based on thresholds for discriminating small differences in the orientation of the modulation, as such stimuli were deemed to be of the same apparent strength in a pilot study. We followed Cruickshank and Schofield by basing our signal levels on discrimination thresholds rather than on detection thresholds, but unlike them, we used a rather gross discrimination task. However, our 1-D binary noise carriers convey OM better than the oriented Gabor patterns used by Cruickshank and Schofield. We tested with a Gabor noise carrier in a pilot study and found, unlike 1-D noise, that the OM signal was too weak to support reliable direction discriminations. We are, thus, confident that our OM adapters were strong enough, in principle, to produce strong aftereffects. Finally, Georgeson and Schofield (2002) registered no difficulty in balancing the perceptual strength of LM and CM cues based on multiples of detection threshold and found good, symmetric transfer of both the tilt and contrast-reduction aftereffects. We thus conclude that relative signal strength is unlikely to account for the asymmetric transfer of the dMAE between our cues.

An artifactual asymmetric transfer of aftereffects might also arise from one of the many luminance artifacts that are associated with second-order stimuli (especially CM, see Schofield & Georgeson, 1999). If weak first-order artifacts were to be present in our second-order stimuli, these might be susceptible to adaptation by LM signals but would not be strong enough to produce an aftereffect in the reverse direction. However, we are confident that this was not the case. Our noise samples were wide enough, and our monitor was of sufficiently high bandwidth, to avoid problems with the adjacent pixel nonlinearity (Klein, Hu, & Carney, 1996). Although the use of a 1-D carrier is not ideal for CM, its dynamic nature should have prevented problems due to "clumping" (Smith & Ledgeway, 1997), as the stimuli were drift balanced (Chubb & Sperling, 1988). Our OM stimuli and unmodulated carriers would have had identifiably different Fourier amplitude spectra. However, following Cruickshank and Schofield (2005), we conclude that although these Fourier components may have been detectable by a first-order mechanism, that mechanism would not have been able to reveal the spatiotemporal properties of the modulating signal as would be required to support discrimination tasks. Finally, if our transferred aftereffects were due to luminance artifacts, we should expect them to have the sharp spatial-frequency tuning found when the adaptation and test stimuli were both LM. In fact, when adaptation is transferred from LM to CM or OM, it is relatively broadly tuned.

Having established that our asymmetric transfer of aftereffects is unlikely to be artifactual, we now consider the implications of our findings for models of motion processing.

The classical view of adaptation aftereffects holds that if two cues are, at some point, processed by the same population of neurons, then aftereffects should transfer between them. Thus, adaptation has been used to test for spatial-frequency channels (Blakemore & Campbell, 1969). If our cues were rendered equivalent within the motion-processing system due to some relatively early nonlinear processing, then we would expect strong, symmetric transfer of the dMAE. To the extent that dMAE transferred weakly and asymmetrically, we can conclude that our cues are not treated as equivalent within the motion-processing system. That is, the cues are not processed by the same population of neurons.

However, our results are consistent with two alternative schemes: (a) they could be the result of processing within separate mechanisms that share adaptation selectively, or (b) they could be due to a single generalized mechanism that extracts the cues at different stages. For example, it can be argued that Benton's (2004) unified motion model extracts second-order motion later than first-order motion. Perhaps, signals that are extracted early affect those extracted later but not vice versa.

Although adaptation to LM transfers to CM and OM, the percentage transfer is relatively low (about 40%). Further, the transferred effect loses its spatial-frequency tuning. This pattern of results suggests a degree of separation between first- and second-order cues that goes beyond the split implied in Benton's (2004) model. Given the body of evidence to suggest that LM and CM are processed separately, we hypothesize that adapting to LM influences the processing of other motion cues at a relatively late cue-independent stage. In support of this idea, we note that MAEs induced by luminance gratings transfer liberally to stimuli with a very different composition.

The asymmetric transfer of adaptation between CM and OM suggests that these cues are also processed separately. To this extent, our results add weight to those of Baker et al. (2006), Kingdom et al. (2003), and Schofield and Yates (2005), suggesting a separation between the encoding of OM and CM. However, the fact that adaptation to CM does not transfer to LM suggests that this effect is not mediated by a cue-independent process. The strength of the CM:OM transfer and the fact that it was relatively well tuned suggest a strong but one-sided link between these cues. Further, the results of the studies by Kingdom et al. and Schofield and Yates can be explained by a generalized FRF-like system (similar to the texture segmentation model proposed by Landy & Bergen, 1991; but see also Schofield & Yates, 2005) that computes a CM-only signal alongside OM-sensitive orientation-opponent mechanisms and uses the CM signal to normalize the OM response. Under such a model, the CM channel sums inputs from all first-stage orientation channels and is, thus, blind to OM. Conversely, the OM mechanism (as described by Schofield & Yates, 2005) is initially sensitive to CM but gains immunity from it via the normalization process. In such a mechanism, transfer of adaptation from CM to OM would be more likely than transfer from OM to CM.

Conclusion

We tested the spatial- and temporal-frequency response of the human visual system to moving OM stimuli and have shown that these functions are both low pass but that temporal acuity for OM is a little better than that for CM given the same carrier.

We have also tested for the dMAE within and between the three cues. We found within-cue dMAEs for all three cues. For LM, the within-cue dMAE was narrowly tuned for spatial frequency, CM tuning was a little wider, whereas the dMAE for OM was untuned. The broad spatial-frequency tuning of the OM aftereffect might be a reflection of the spatial-frequency tuning of the OM mechanism itself.

There was evidence for a relatively weak transfer of dMAE from LM to CM and OM but little transfer of aftereffect in the opposite direction. When the aftereffect transferred from LM to the other cues, it seemed to lose its spatial-frequency tuning. The aftereffect transferred strongly from CM to OM but not vice versa and, in this case, seemed to retain its tuning.

These results could be taken to suggest that LM, CM, and OM motion are processed in three separate mechanisms. This conclusion in turn implies that there are multiple second-order motion mechanisms—a notion that already has some support in the literature. However, noting that the apparent independence between CM and OM can arise from a single generalized mechanism (Kingdom et al., 2003; Schofield & Yates 2005), and given the strength and tuning of the CM to OM effect, we feel that it may yet be premature to propose separate mechanisms for CM and OM.

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Corresponding author: Andrew Schofield.
Email: a.j.schofield@bham.ac.uk.
Address: School of Psychology, University of Birmingham, Birmingham, UK, B15 2TT.

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