Visual adaptation reveals asymmetric spatial frequency tuning for motion

Timothy Ledgeway

Claire V. Hutchinson

This study investigated the spatial frequency selectivity of the human visual motion system using the technique of adaptation in which motion aftereffect (MAE) duration was taken as an index of aftereffect magnitude. Eight observers adapted to two vertically oriented, oppositely drifting, luminance-defined gratings that were spatially separated in the vertical dimension. The spatial frequency of the adaptation patterns spanned a 3-octave range (0.25 to 2 c/deg) and drifted at 5 Hz. Following adaptation (20 s), two stationary test patterns were presented and MAE duration was measured. The spatial frequency difference between the adaptation and test patterns varied from −2.5 to 2.5 octaves in 0.5 octave steps. MAE tuning functions at the lowest adaptation frequency (0.25 c/deg) were bandpass and reasonably symmetric. However, as the spatial frequency of the adaptation patterns increased, overall MAE duration decreased and the shape of the tuning functions became markedly asymmetric. This asymmetry was characterized by a MAE peak that was centered ∼1 octave below the adaptation frequency. The results are consistent with recent masking studies (C. V. Hutchinson & T. Ledgeway, 2007) and may reflect either asymmetric spatial frequency selectivity of underlying motion units or frequency-specific interactions (e.g. inhibition) between motion sensors tuned to different spatial frequencies.

Keywords: motion-2D, temporal vision, spatial vision, adaptation, motion aftereffect, spatial frequency selectivity


Introduction

Prolonged exposure to a moving (adaptation) stimulus produces illusory opposite motion in a subsequently viewed (test) stimulus. This illusory motion in the direction opposite to that of the adaptation is referred to as the motion aftereffect (MAE) and occurs when the test pattern is stationary (static MAE), such as a stationary grating, and when it is moving (dynamic MAE), such as a directionally ambiguous counter-phasing grating. Although the MAE is a pervasive phenomenon in vision research, a relatively small number of studies have systematically examined its spatial frequency tuning. There is evidence for spatial frequency tuning of the static MAE using square-wave (Over, Broerse, Crassini, & Lovegrove, 1973) and sinusoidal (Ashida & Osaka, 1994; Cameron, Baker, & Boulton, 1992) gratings. In general, static MAEs are greatest when the adaptation and test patterns are the same spatial frequency and decrease as the spatial frequency difference between the adaptation and test patterns increases. The spatial frequency tuning of the dynamic MAE is not as clear-cut. Ashida and Osaka (1994) measured the dynamic MAE using counter-phasing gratings as the test stimulus and did not find any evidence of spatial frequency tuning. Bex, Verstraten, and Mareschal (1996) have also measured the spatial frequency tuning of the dynamic MAE using counter-phasing test gratings and did find evidence of spatial frequency tuning. Like the static MAE, dynamic MAE duration was greatest when the adaptation and test gratings were the same spatial frequency and decreased as the spatial frequency difference between them increased. These differences are easily reconciled and reflect the temporal frequency dependence of the dynamic MAE. Whereas the counter-phasing gratings employed by Ashida and Osaka (1994) had a temporal frequency of 5 Hz, those employed by Bex et al. (1996) had a temporal frequency of 2 Hz. In a follow-up study, Mareschal, Ashida, Bex, Nishida, and Verstraten (1997) found that the spatial frequency tuning of the dynamic MAE is somewhat labile and heavily dependent on temporal frequency. Specifically, MAE spatial frequency tuning broadened with increasing test temporal frequency and was virtually non-existent at temporal frequencies above about 2 Hz.

In a recent study (Hutchinson & Ledgeway, 2007), we measured the spatial frequency tuning of the mechanisms that underlie the detection of motion in the human visual system over a range of test spatial frequencies using the technique of visual masking. The findings of that study supported the existence of motion-detection mechanisms that are each selectively sensitive to a limited range of spatial frequencies. For low spatial frequencies (0.25 c/deg), we found similar results to those reported previously in the masking literature (e.g. Anderson & Burr, 1985) in that maximal masking (threshold elevation) occurred when the...
test and mask shared the same frequency, decreasing as the spatial frequency difference between the test and mask increased. However as test spatial frequency increased (≥1 c/deg) a striking asymmetry in spatial tuning was evident, in that maximal threshold elevation occurred when the mask spatial frequency was 1 octave below the test spatial frequency. This asymmetric tuning of the masking functions could reflect either asymmetric spatial frequency selectivity of underlying motion units that respond to particular frequency ranges, or an interaction between mechanisms (see De Valois & De Valois, 1990) such as some form of inhibition between motion detectors tuned to different spatial frequencies. Although it is currently not possible to distinguish between these two putative explanations, a fundamentally important first step is to establish the generality of this phenomenon and ensure that any principles gleaned from such investigations are not merely task specific (e.g. specific to the paradigm of masking). Thus in the present study we examined whether the asymmetric spatial frequency tuning revealed by visual masking is also apparent in the tuning of the motion aftereffect.

We examined the spatial frequency selectivity of the static MAE using a protocol similar to that employed by Ashida and Osaka (1994) and Cameron et al. (1992). Cameron et al. (1992) examined the spatial frequency selectivity of the MAE over a range of adaptation spatial frequencies (0.25 to 4 c/deg). Observers adapted to two vertically oriented, oppositely drifting gratings that were separated in the vertical dimension by a blank field. After the adaptation period, the two drifting gratings were replaced by two stationary test gratings and the perceived velocity of the MAE was measured using a manual tracking procedure. This procedure required the observer to turn a potentiometer to match the perceived motion of the stationary test gratings. Results showed that in general, the magnitude of the MAE (average velocity) was greatest when the adaptation and test patterns shared the same spatial frequency and systematically decreased as the spatial frequency difference between the adaptation and test pattern increased. Using a similar protocol in which MAE duration was measured, Ashida and Osaka (1994) also found spatial frequency tuning of the MAE.

In the present study, we adopted the more conventional measure of MAE magnitude (duration) for a range of adaptation frequencies (0.25, 0.5, 1, and 2 c/deg) under similar conditions to those outlined above. Although it could be argued that duration is a somewhat subjective measure of MAE strength, it does correspond reasonably well with other measures of MAE magnitude (e.g. Keck, Palella, & Pantle, 1976; Pantle, 1974; Wade, 1994). Alternative techniques such as motion-nulling may yield more objective measures of the MAE under some conditions (Hiris & Blake, 1992), but they necessarily entail the use of dynamic (moving or flickering) tests which are not well-suited for measuring spatial frequency tuning of the MAE. As mentioned previously MAEs measured with dynamic (suprathreshold) test gratings, unlike static stimuli, may exhibit little or no spatial tuning even at relatively moderate rates of drift or flicker. This latter finding is consistent with the notion that static and dynamic test patterns differentially reveal adaptation at separate sites of motion processing (for a review see Culham et al., 1998). In addition Castet, Keeble, and Verstraten (2002) point out that the use of flickering or bistable test gratings in nulling paradigms can also lead to a large degree of inter- and intra-subject variability (Ashida & Osaka, 1995) because of the perceptual instability of the test stimulus. As there is some evidence to suggest that different measures of initial MAE strength (e.g. duration vs. motion-nulling) may well reveal different aspects of the phenomenon (Nishida & Ashida, 2000), there is little to be gained by debating which method is superior. Consequently we employed MAE duration as a measure of the spatial frequency tuning of the mechanisms that underlie the detection of motion in the human visual system.

Methods

Observers

Eight naïve observers (CLC, EJC, IL, JRM, ML, SJH, VC, and SH) participated in the study. All had normal or corrected-to-normal visual acuity and had no history of any visual disorders.

Apparatus and stimuli

Stimuli were generated using a Macintosh G4 computer and presented on a Mitsubishi Diamond Plus 73 monitor with an update rate of 85 Hz using custom software written in the C programming language. Stimuli were virtually identical to those employed by Cameron et al. (1992). The stimuli were presented within a rectangular window at the center of the display that subtended an angle of 10.1 degrees vertically by 25.8 degrees horizontally at the viewing distance of 70 cm. One screen pixel subtended 1.5 arc min. The mean luminance of the window and the remainder of the display area (which was homogenous) was approximately 15 cd/m². Viewing was binocular and a prominent fixation spot was located at the center of the display to aid stable fixation and prevent ocular tracking of the motion stimuli. A stimulus schematic is shown in Figure 1.

Two high contrast (0.25 Michelson), oppositely drifting sinusoidal gratings were presented in two horizontal strips, each subtending 2.64 degrees vertically and 25.8 degrees horizontally. The gratings were separated by a blank field (of mean luminance) that subtended 4.86 degrees vertically by 25.8 degrees horizontally containing a central fixation spot. Following Cameron et al. (1992), the gratings appeared in a flat top raised cosine window in order to avoid artifacts due to abrupt spatial edges. Subsequently,
the stimulus was at a nominal eccentricity of 3.75 degrees measured from the fixation point to the midpoint of the grating strip, above and below fixation.

Following 20 s of adaptation to the oppositely drifting gratings, two stationary test patterns appeared in the same position as the adaptation stimulus and the duration of the MAE was measured. Spatial frequency selective adaptation was measured at adaptation frequencies of 0.25, 0.5, 1 and 2 c/deg. During the adaptation phase the gratings drifted at a temporal frequency of 5 Hz. The duration of the MAE was measured at test frequencies ranging from −2.5 to +2.5 octaves relative to each adaptation spatial frequency.

**Procedure**

Observers maintained their gaze on the central fixation spot during both the adaptation and test phases. In each run of trials, observers adapted to the two vertically oriented oppositely drifting gratings. Following adaptation two stationary test patterns appeared in the same position as the adaptation stimulus. The duration of the MAE was measured by instructing observers to press the space bar immediately when they were adamant the MAE had terminated. Each run of trials consisted of eleven adaptation phases (always 20 s) and eleven test phases. During each run of trials, the adaptation spatial frequency remained the same. After each adaptation phase, the test gratings were selected at random from eleven possible spatial frequencies using the method of constant stimuli ranging from −2.5 to +2.5 octaves from the adaptation spatial frequency in ½ octave steps. Each observer completed 20 runs of trials per condition (adaptation spatial frequency). On 10 runs of trials, the adaptation direction was leftward above fixation and rightward below fixation and on the other 10 runs adaptation direction was rightward above fixation and leftward below fixation.

**Results**

Figure 2 shows MAE magnitude (duration) for each adaptation spatial frequency (0.25, 0.5, 1, and 2 c/deg) as a function of the difference in spatial frequency (in octaves) between the test and adaptation patterns. Negative values on the abscissas indicate that the spatial frequency of the test grating was lower than that of the adaptation grating, positive values indicate the opposite state of affairs and 0 octaves refers to the case where the test and adaptation stimuli had the same spatial frequency. The results for each individual observer are plotted separately and the group mean data (*n* = 8) are also shown.

The first thing to note is that there are some differences between the results of the 8 observers, particularly in terms of overall MAE magnitude. For example MAE durations were uniformly much shorter for EJC than the remaining observers, indicating that she either adopted a more conservative response criterion or was less susceptible to motion adaptation. Nonetheless despite these individual differences it is readily apparent that the results of all observers exhibit a number of consistent features. First, in all cases the shapes of the MAE tuning functions, measured at each adaptation spatial frequency, are spatially bandpass. Second, with the exception of observer EJC, the location of the MAE peak (i.e. the spatial frequency difference producing the maximum MAE) is critically dependent upon the adaptation spatial frequency. It is evident that for the two lowest adaptation spatial frequencies (0.25 and 0.5 c/deg) the maximum MAE occurred around the point where the adaptation and test patterns shared the same spatial frequency and exhibited a steady fall-off as the spatial frequency difference between the adaptation and test pattern increased. However at the two highest adaptation spatial frequencies tested (1 and 2 c/deg), the maximum MAE did not occur when the adaptation and test patterns shared the same spatial frequency. Rather the adaptation tuning functions were markedly asymmetric. This asymmetry was characterized by a maximum MAE duration at test spatial frequencies below the frequency of the adaptation pattern. For an adaptation frequency of 1 c/deg, the maximum MAE occurred at approximately 0.5 c/deg and for an adaptation frequency of 2 c/deg, the maximum MAE occurred at 1 c/deg.

To quantify both the bandpass character of the MAE tuning functions and the position of the MAE peak at each adaptation spatial frequency, the results for each observer were fitted with a Gaussian function as follows:

\[
    y = \exp\{-[(x - a)/b]^2 \ln 2\}c + d
\]

where *x* is the spatial frequency difference between the test and adaptation stimuli (in octaves), *a* is the location of the MAE peak (in octaves relative to the adaptation spatial frequency), *b* is the bandwidth (half-width, half-height), and *c* and *d* are constants.
is the amplitude, and \(d\) is the minimum MAE duration. The values of the curve fit parameters and the associated \(R^2\) values, averaged across the eight observers, are given in Table 1.

Estimates of the MAE peak, derived from the mean of the individual curve fits, are also plotted in Figure 3a as a function of adaptation spatial frequency. As adaptation spatial frequency increased, the MAE peak shifted from about 0 at an adaptation frequency of 0.25 c/deg to 1 octave below the adaptation frequency at 2 c/deg. One-group \(t\)-tests confirmed that the MAE peak was not significantly different from 0 octaves when the adaptation spatial frequency was either 0.25 c/deg \([t(7) = 1.56, \text{ns}]\) or 0.5 c/deg \([t(7) = -2.26, \text{ns}]\), but differed significantly from

<table>
<thead>
<tr>
<th>Adaptation SF (c/deg)</th>
<th>a—MAE peak (octave)</th>
<th>b—bandwidth (octave)</th>
<th>c—amplitude (sec)</th>
<th>d—min. MAE duration (sec)</th>
<th>(R^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.25</td>
<td>0.25 (±0.17)</td>
<td>1.33 (±0.12)</td>
<td>8.39 (±1.16)</td>
<td>2.95 (±0.85)</td>
<td>0.94 (±0.02)</td>
</tr>
<tr>
<td>0.5</td>
<td>-0.37 (±0.16)</td>
<td>1.20 (±0.08)</td>
<td>10.09 (±1.09)</td>
<td>3.57 (±0.88)</td>
<td>0.96 (±0.01)</td>
</tr>
<tr>
<td>1</td>
<td>-0.82 (±0.20)</td>
<td>1.18 (±0.10)</td>
<td>8.93 (±0.86)</td>
<td>4.47 (±1.15)</td>
<td>0.97 (±0.01)</td>
</tr>
<tr>
<td>2</td>
<td>-1.26 (±0.25)</td>
<td>1.61 (±0.16)</td>
<td>6.38 (±0.86)</td>
<td>3.57 (±0.80)</td>
<td>0.91 (±0.05)</td>
</tr>
</tbody>
</table>

Table 1. Group average \((n = 8)\) curve fit parameters \((a, b, c, \text{and } d)\) and \(R^2\) values for each adaptation spatial frequency derived from fitting a Gaussian (Equation 1) to each observer’s MAE tuning functions. See text for further details.
0 at the two higher adaptation frequencies \( t(7) = -4.15, p < 0.01 \), and \( t(7) = -5.14, p < 0.01 \), respectively. This illustrates well the progressively asymmetrical nature of the MAE tuning functions at the highest adaptation frequencies tested. Interestingly, the masking data of Hutchinson and Ledgeway (2007) exhibit an almost identical pattern to the MAE data of the present study, when the masking peak is plotted as a function of the spatial frequency of the drifting test grating (Figure 3b).

### Discussion

The present study employed the conventional motion aftereffect (MAE duration) as a measure of the spatial frequency tuning of the mechanisms that underlie the detection of motion in the human visual system. Although there were inevitably some individual differences between the observers, most notably in terms of overall MAE magnitude, they generally exhibited qualitatively similar patterns of results.

A universal feature of the results shown by all observers is that MAE tuning functions at every adaptation spatial frequency tested (0.25 to 2 c/deg) were bandpass, supporting the existence of motion-detection mechanisms that are selectively sensitive to a limited band of spatial frequencies. Another important characteristic of the results is the finding that at an adaptation frequency of 0.25 c/deg, the MAE tuning function was reasonably symmetric, peaking when the adaptation and test patterns were the same frequency (i.e. both 0.25 c/deg). However for most observers (except EJC) as the spatial frequency of the adaptation pattern increased, the shape of the resulting tuning functions generally became markedly asymmetric, exhibiting a MAE peak that could be up to 1 octave below the adaptation frequency. The MAE durations reported by EJC were consistently much shorter than those of the other observers and the general brevity of her responses tended to obscure any potential differences between the adaptation conditions. Nonetheless the tendency of the MAE peak to shift toward progressively lower frequencies, as adaptation spatial frequency increased, was found to be statistically significant for the group of observers as a whole.

A potentially important issue concerning the pattern of results found in the present study is the degree to which they are influenced by “expectancy effects” or demand characteristics. Duration is a somewhat criterion-dependent measure of MAE strength and asymmetries in the MAE tuning functions might, in principle, reflect observer biases or expectancies. Although this is a possibility it seems highly unlikely for the following reasons: All observers were naïve with regards to the purpose of the experiment and had no prior knowledge of the conditions that were to be tested. The order in which the separate runs of trials for each adaptation spatial frequency were completed was randomized and so was the order of test patterns presented within any one run. On the basis of expectancy alone it is difficult to envisage why an observer would report longer MAEs for some test patterns that are lower in frequency than the adaptation pattern, but only when the two highest adaptation frequencies are tested. Furthermore there is absolutely no reason to suppose that different naïve observers would have similar expectations and thus respond in the same manner.

Previous studies (e.g. Ashida & Osaka, 1994; Cameron et al., 1992) that have measured the spatial frequency...
tuning of the static MAE have found that MAEs (measured in terms of perceived velocity or duration) were greatest when the adaptation and test patterns shared the same spatial frequency, across a range of adaptation spatial frequencies (0.25 to 4 c/deg). At first glance it might appear that these findings are at odds with those in the present study. Crucially, however, there are distinct differences between the stimulus dimensions used in previous adaptation studies and those employed in the present study. In Cameron et al.’s. (1992) study, two vertically oriented grating strips, each subtending 2.65 degrees vertically by 12.7 degrees horizontally, were presented above and below a blank field (4.85 × 12.7 degrees). Ashida and Osaka (1994) used a similar stimulus configuration to Cameron et al. (1992) except that the two grating strips subtended 1.5 degrees vertically by 6.5 degrees horizontally and the blank field subtended 2 degrees by 6.5 degrees. In the present study, the two gratings subtended 2.64 degrees vertically by 25.8 degrees horizontally and were separated by a blank field subtending 4.86 by 25.8 degrees. In our masking study (Hutchinson & Ledgeway, 2007) we found that for test spatial frequencies ≥1 c/deg, threshold elevation was maximal when the mask was 1 octave or so below the test spatial frequency (see Figure 3b). In that study we used an image size of 20 degrees vertically and horizontally. This meant that at a test frequency of 2 c/deg for example, 40 cycles of test grating were visible on-screen. Control experiments did however reveal that the peak at 1 octave below the test in our masking study was mediated by image size. Specifically, when masking effects were measured at 2 c/deg using a small image (2.5 × 2.5 degrees) maximal masking occurred when the test and mask shared the same spatial frequency. As such, our adaptation results, like those revealed by masking, appear to be mediated by image size. This suggests that asymmetries in the fine structure of MAE tuning functions may only be revealed when spatially extensive stimuli are employed. Although the reason for this is still puzzling, one intriguing possibility is that relatively small image sizes may be better for probing the properties of motion channels, while larger ones reveal more of the channel interactions.

Although masking and adaptation are undoubtedly complex phenomena and the processes underlying each may be very different, it is striking that when the adaptation and test patterns shared the same spatial frequency, across a range of adaptation spatial frequencies (0.25 to 4 c/deg) and the spatial frequency of the test grating was varied to derive the tuning function. In our previous masking study, however, to measure the equivalent tuning function the test spatial frequency was held constant (e.g. 2 c/deg) and the spatial frequency of the masking pattern was varied. Consequently despite differences in the labeling of the abscissas, the two sets of results are not in fact contradictory.

That the asymmetric spatial frequency tuning revealed by visual masking is also evident in the tuning of the MAE is important because, in the first instance, it serves to demonstrate that our findings are robust across different techniques and tasks. Moreover, the asymmetric tuning of our masking functions and the MAE may reflect either asymmetric spatial frequency selectivity of underlying motion units or inhibition between motion detectors tuned to different spatial frequencies. In terms of the latter possibility psychophysical studies investigating the selectivity of spatial vision, using adaptation and masking, have found evidence for the existence of inhibitory interactions between channels tuned for different frequencies (e.g. Barfield, 1976; De Valois, 1977; Henning, Hertz, & Broadbent, 1975; Nachmias, Sansbury, Vassilev, & Weber, 1973; Nachmias & Weber, 1975; Stecher, Sigel, & Lange, 1973; Stromeyer & Klein, 1974; Tolhurst, 1973; Tolhurst & Barfield, 1978). Furthermore physiological studies of the responses properties of some striate cells to compound gratings, support the psychophysical evidence that inhibitory interactions can occur between spatial frequency channels that are separated by several octaves (e.g. Albrecht & De Valois, 1981; De Valois, 1978; Movshon, Thompson, & Tolhurst, 1978). Inhibitory interactions of this kind may serve to increase the spatial frequency selectivity of mechanisms in vision.

Inhibition between motion detectors maximally sensitive to different spatial frequencies has also been proposed as a mechanism to explain other phenomena such as misperception of the direction of compound gratings at suprathreshold stimulus levels. Derrington and Henning (1987) reported that observers often misjudge the direction of a drifting 3 c/deg grating superimposed upon a 1 c/deg stationary background when the stimulus presentation is brief. They tentatively suggested that motion detectors responding to the 3 c/deg grating inhibit those tuned to the same direction, but lower spatial frequencies, that are stimulated by the directional noise resulting from the transient presentation of the 1 c/deg background grating. This inhibition could bias the perception of the net motion energy present in the stimulus in the direction opposite that of the drifting grating resulting in errors in direction judgements. Indeed Serrano-Pedraza, Goddard, and Derrington (2007) have recently shown that an explicit model of motion perception, that incorporates a stage in which the outputs of motion sensors tuned to different spatial frequencies but the same direction are subtracted from one another, can readily predict such impairments of motion perception.

To investigate this further, we measured performance for three observers for judging the motion direction
(leftward vs. rightward) of a 2 c/deg grating drifting at 5 Hz, in the presence of a temporally jittering (directionally ambiguous) grating that was superimposed at various spatial frequency intervals ranging from 3 octaves below to 3 octaves above the drifting grating. The suprathreshold contrasts of the drifting grating and jittering grating were identical and were both 0.25. Our findings are shown in Figure 4 where it is evident that observers consistently judged the motion direction of the 2 c/deg drifting grating correctly (approximately 100% of the time) when the spatial frequency of the superimposed jittering grating was 2 c/deg (0 octaves) or higher than the drifting grating (up to 3 octaves away). Direction discrimination was also possible (roughly 80% correct) when the spatial frequency of the jittering grating was 3 octaves below that of the drifting grating. However when the jittering grating was positioned 1 octave below the drifting grating (1 c/deg), performance dropped to around chance levels (50%).

These additional observations are not inconsistent with the existence of some form of asymmetric inhibition between motion sensors tuned to different spatial frequencies, but the same direction, as suggested by Derrington and Henning (1987). Furthermore Cleary and Braddick (1990) have also suggested that motion detectors sensitive to relatively high spatial frequencies may inhibit those tuned to lower spatial frequencies, when both are simultaneously active. However an alternative explanation of Figure 4 is that because the jittering grating was temporally broadband, there was a greater range of velocities present in the stimulus when the jittering grating was of relatively low spatial frequency than when it was of higher spatial frequency. Consequently it is conceivable that if motion mechanisms are tuned for velocity, then the lower spatial frequency jittering grating may have been more effective at disrupting (masking) performance because it contained more velocities. Although this is an elegant idea (we thank an anonymous reviewer for this suggestion), it cannot be the sole explanation as it incorrectly predicts that the greatest disruption in direction identification should occur in the presence of the very lowest spatial frequency jittering grating tested and this was clearly not the case. Nonetheless it remains to be seen if the shapes of the MAE tuning functions found in the present study are, at least in part, a consequence of inhibitory interactions between motion detectors.

Conclusions

In summary, we have shown asymmetric tuning functions for discriminating the direction of motion using the techniques of spatial-frequency-selective visual masking (Hutchinson & Ledgeway, 2007) and adaptation (the present study). We have also shown that the ability to accurately judge the direction of a suprathreshold 2 c/deg grating was markedly impaired in the presence of a jittering grating, but only when the spatial frequency of the jittering grating was less than that of the drifting grating. Thus our findings are robust across different techniques and tasks and are likely to reflect frequency-specific interactions (e.g. inhibition) between low-level motion sensors tuned to different spatial frequencies and/or asymmetric spatial frequency selectivity of underlying motion units.

Acknowledgments

TL acknowledges the support of the BBSRC. Some of the findings described have been reported previously in abstract form (Ledgeway & Hutchinson, 2007).

Commercial relationships: none.
Corresponding author: Timothy Ledgeway.
Email: Timothy.Ledgeway@Nottingham.ac.uk.
Address: Visual Neuroscience Group, School of Psychology, University of Nottingham, University Park, Nottingham, NG7 2RD, UK.
References


