The spatial tuning of "motion streak" mechanisms revealed by masking and adaptation

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We previously reported that fast-moving dot arrays cause orientation-tuned masking of static gratings (D. Apthorp, J. Cass, & D. Alais, 2010), which we attribute to "motion streaks." Using similar "streaky" dot motion, we describe spatial frequency tuning of grating threshold elevations caused by masking (Experiment 1) and adaptation (Experiment 2) to motion. To compare the streaks with psychophysical tunings, we Fourier analyzed time-averaged translating dots, which were bandpass (peaking at ~2.3 c/deg). Masking, however, was strongest at lower test frequencies (≤ 1 c/deg) and largely isotropic over orientation, although a small orientation-tuned effect occurred at ~1.2 c/deg. Results were broadly similar across monoptic and dichoptic conditions. Adaptation to fast motion produced spatially bandpass threshold elevations for parallel test gratings, peaking slightly lower than the peak Fourier frequency, with little elevation below 1 c/deg (unlike the low-pass elevation resulting from masking). Slow adaptation produced little elevation for parallel gratings. For orthogonal test gratings, fast motion adaptation produced low-pass threshold elevations and slow motion produced bandpass elevations, suggesting that separable mechanisms process fast (streaky) and slow motion. The different threshold elevation patterns over spatial frequency for masking and adaptation suggest that the adaptation effects are mainly within-channel suppression, whereas the masking effects may be mainly due to between-channel suppression.

Keywords: masking, contrast sensitivity, motion—2D, spatial vision, adaptation, motion streaks

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Introduction

In a constantly moving visual environment, human and animal visual systems have evolved to make use of multiple sources of information to compute the motion of objects through space. It is a long-standing challenge for vision science to infer these processes from the response properties of visual neurons. An enduring tenet of this approach is that single neurons tuned for direction of motion are maximally responsive to orientations orthogonal to their preferred motion (Hubel & Wiesel, 1962). This leads to several "problems" for the visual system to solve, such as the "aperture problem." That is, a moving edge that is larger than a neuron's receptive field has an ambiguous direction and can only be perceived as moving orthogonally, regardless of its true direction. Recently, it has been suggested that an aspect of vision previously thought of as merely another problem for the system to solve-motion blur or "motion streaks"-might actually be useful in solving the aperture problem and also for giving finer resolution to direction perception (Geisler, 1999). Motion streaks occur when an object moves rapidly across the visual field, leaving a trail of activation due to temporal integration in the visual system. The orientation of this trail is aligned with the motion trajectory and could, therefore, be detected by neurons tuned to static, oriented lines and combined with signals from motionsensitive neurons to help resolve directional ambiguities. Several studies have since supported this theory in the physiological (Geisler, Albrecht, Crane, & Stern, 2001; Krekelberg, Dannenberg, Hoffmann, Bremmer, & Ross, 2003), neuroimaging (Krekelberg, Vatakis, & Kourtzi, 2005), and psychophysical (Badcock & Dickinson, 2009; Burr & Ross, 2002; Edwards & Crane, 2007; Ross, Badcock, & Hayes, 2000) domains.

Classical psychophysical studies have often used a channel-based approach to study visual processing. An underlying assumption of this approach is that a number of separate channels process a given stimulus dimension (such as orientation or spatial frequency) and these can be inferred by selective elevations of threshold due to masking or adaptation (Braddick et al., 1978). For instance, Blakemore and Campbell (1969) inferred the existence of separate channels for processing spatial frequency by showing that prolonged exposure to a 1D sinusoidal luminance-defined grating (containing a single spatial frequency) maximally elevated detection thresholds for the adapted frequency, with elevations decaying monotonically with increasing separation between adapting

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Figure 1. (a) Schematic diagram of the procedure for Experiment 1 to measure the spatial tuning of grating masking by motion streaks. Four motion directions were randomly interleaved, with the orientation of the grating probe being either parallel or orthogonal to the direction of motion (designated 0°). A range of grating spatial frequencies was tested so that the spatial tuning of the masking function could be derived. The upper and lower windows always contained the same motion direction on a given trial, and test spatial frequency was blocked. Participants fused the left- and right-eye images with a mirror stereoscope. The dichoptic condition (shown in this figure) and the monoptic condition were run in separate blocks. (b) Examples of time-averaged motion mask stimuli. The upper image shows the fast translating dots averaged over 100 ms (10 video frames), and the lower image shows the slow motion mask averaged over 100 ms. The Fourier analysis of the motion streaks discussed below and shown in Figure 5 was based on 100-ms time-averaged stimuli.

and test frequencies. The shape of this function is typically assumed to be Gaussian with selectivity of the underlying channel defined as the half-width at half-height.

A paradigm known as overlay masking can also be used to explore basic attributes of cortical processing by examining the extent to which grating sensitivity is affected by spatiotemporal superposition with an irrelevant masking grating. By measuring thresholds over a range of spatial or temporal frequencies and/or orientations, the shape of the underlying channels can be inferred (Anderson & Burr, 1985; Baker & Meese, 2007; Baker, Meese, & Summers, 2007; Boynton & Foley, 1999; Campbell & Kulikowski, 1966; Cass & Alais, 2006; Cass, Stuit, Bex, & Alais, 2009; Hutchinson & Ledgeway, 2004; Legge, 1979; Phillips & Wilson, 1984; Ross & Speed, 1991; Snowden & Hammett, 1996; Snowden, 1991; Stromeyer & Julesz, 1972; Switkes, Bradley, & De Valois, 1988). Although the precise shape of channels varies from study to study, the overwhelming evidence from both masking and adaptation paradigms is that the visual system is composed of a number of retinotopically localized channels that are tuned to particular spatiotemporal frequencies and orientations.

It has previously been shown that motion streaks produce similar orientation-dependent effects to those derived using luminance-defined grating patterns as masking and adaptor stimuli (Apthorp & Alais, 2009; Apthorp, Cass, & Alais, 2010; Apthorp, Wenderoth, & Alais, 2009). In this study, we used both masking and adaptation to study the spatial frequency selectivity of the visual system's response to motion streaks. Because motion streaks do not exist in the physical stimulus and arise only because the visual system integrates the trajectory of moving stimuli across a period of time (Burr, 1980; Snowden & Braddick, 1991), any analysis of the streak stimulus must assume a temporal blurring factor and average the motion stimulus over this duration to produce the motion streak stimulus. Guided by previous research, we assumed a temporal integration period of 100 ms for our fields of randomly plotted Gaussian blobs (Burr, 1980, 1981; Geisler, 1999; Snowden & Braddick, 1991). Note that even though these are fields of lowpass elements, the time-averaged streaky image tends to be spatially bandpass (see image of motion streaks in Figure 1b, together with its Fourier amplitude spectrum shown by solid symbols in Figure 5). In order to gain insight into the spatial frequency selectivity of the visual system's response to translating motion, we measured the spatial frequency tuning of grating threshold elevations due to streak masking (Experiment 1) and streak adaptation (Experiment 2) and compared these tunings with the spatial frequency content of the (temporally blurred) motion stimulus. This approach enables us to infer the nature of the psychophysical transformation from translating moving retinal image to oriented "streak" as it occurs simultaneously, as in masking, or across time, as in adaptation.

Experiment 1: Spatial frequency tuning of contrast masking of static stimuli by motion

Experiment 1 measured contrast masking of static grating targets by fields of translating Gaussian blobs as a function of target spatial frequency. In a 2×2 design, the masking motion was either fast or slow, and target gratings were oriented either parallel or orthogonal to the direction of the translating dots. Static dot masks were used to control for effects not related to motion. Assuming that target threshold elevation would be maximal when its spectral properties matched those of the (temporally blurred) masking stimulus, we predicted that masking (i.e., threshold elevation) would be greatest in the fast parallel condition, as the motion mask would contain elongated streaks that were co-oriented with the target grating. The fast parallel condition should also exhibit a spatial frequency tuning reflecting the spatial structure in the time-averaged motion mask (see Figure 1b). It was also of interest to compare dichoptic and monoptic masking, since previous studies (e.g., Legge, 1979) found differences in spatial tuning related to eye of origin, specifically broader tuning for monoptic than for dichoptic masking.

Methods

Participants

Participants were three experienced psychophysical observers, all of whom had normal or corrected-to-normal vision. Two were authors and the third was naive to the purpose of the experiment. All had normal stereoscopic vision as measured by the RanDot Stereo test.

Apparatus and stimuli

Stimuli were programmed in MATLAB version 7.4 using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Participants viewed the stimuli on a Sony Trinitron CPD-G500 22-inch CRT monitor with a screen resolution set to 1024×768 pixels and a vertical refresh rate of 100 Hz, controlled by a Mac Pro computer with a dual-core Intel Xeon processor. A Cambridge Research Systems Bits++ digital-to-analog converter was used to provide 14-bit resolution in order to enable precise measurement of low-contrast thresholds. The monitor was gamma-corrected in software to achieve linearity of output.

Observers viewed all stimuli through a mirror stereoscope with a total optical path of 57 cm.

The mask stimuli were two drifting random dot displays, each composed of 80 Gaussian blobs with a standard deviation (SD) of 0.08 degree, giving a dot diameter (defined as $4 \times \text{dot } SD$) of 0.32 degree. Half of the dots were dark and half were light, drifting with 100% coherence on a mid-gray background. Maximum and minimum dot luminances were 67.3 and 0.26 cd/m² and background luminance was 33.8 cd/m². Fast dots drifted at 13.02°/s, while slow dots drifted at 1.63°/s. Respectively, these speeds were well above and well below the speed of dot motion purported to be critical to the generation of motion streaks, known as Geisler's (1999) critical streak speed. This was the speed below which there was no difference between masking of a single dot's motion by parallel and orthogonal oriented random noise masks: the speed was found to be proportional to dot size and was estimated to be 1 dot width per 100 ms. Note that these critical speeds have also been psychophysically determined for dots of this size and luminance (Apthorp et al., 2009). Dot speed was controlled by manipulating the pixel step size for each video frame. We also tested a static mask condition in which one of the motion frames was chosen at random on each trial and presented for the entire mask duration (1000 ms).

Stimuli were presented within dark fusion squares in the upper and lower fields of the left- and right-eye views (see Figure 1), located 3.81° above and below a white fixation cross that appeared between the upper and lower fusion squares. Within the fusion squares (which were always present), stimuli appeared within virtual circular apertures 4.88° in diameter, located to the left and right of the center of the screen; these could be aligned by adjusting the stereoscope so that the left- and right-eye views were fused, to allow dichoptic or monoptic presentation of mask and target. The initial position of each dot was randomly determined and all dots wrapped around the aperture. During the test phase, the fixation cross changed to black and the test stimulus (a low-contrast sine-wave grating) appeared either in the upper or lower test aperture. The test grating could be either parallel or orthogonal to the direction of motion, and both dichoptic and monoptic masking were tested. The spatial frequency tuning of the masking effect was investigated by presenting test gratings at a range of spatial frequencies (from 0.27 to 4.31 c/deg, in half-octave steps). Spatial tunings were measured for both parallel and orthogonal test gratings, with fast, slow, and static masks at full contrast (see Figure 1).

Procedure

Participants were given time to adjust the stereoscope to ensure correct fusion of the stimuli, using the fusion squares, after which they pressed a key to initiate trials. Conditions were blocked by spatial frequency and orientation difference from motion (parallel or orthogonal) for dichoptic and monoptic conditions, and the drifting Gaussian dot arrays were presented to the participant's dominant eye. During each session, four directions of motion (45°, 135°, 225°, and 315°) were randomly interleaved to prevent motion adaptation from affecting the results, and the grating's orientation was always defined relative to the motion trajectory (parallel or orthogonal). The motion was always present for 1000 ms, during which the probe grating ramped on and off briefly in a temporal Gaussian window with a standard deviation of 100 ms; there was a random lag of between 10 and 200 ms from motion to probe onset times. In separate blocks, the grating could appear in the subject's dominant eye (with the motion stimulus: monoptic presentation) or the nondominant eye (dichoptic presentation, as illustrated in Figure 1). In a spatial two-alternative forced-choice task, the subject was asked to indicate whether the grating had appeared in the upper or lower aperture, and contrast thresholds for grating detection were determined in four interleaved QUEST staircases (Watson & Pelli, 1983), one for each direction of motion. Measurements were also made in each eye for grating detection in the absence of masking dots (either moving or static) to provide an unmasked baseline threshold. The dependent variable was the elevation in grating detection threshold from the unmasked baseline, expressed in decibels:

$$M = 20 \cdot \log_{10} \left(\frac{T_{\text{masked}}}{T_{\text{unmasked}}} \right), \tag{1}$$

where M refers to the masking level and T refers to contrast detection threshold.

Results and discussion

The threshold elevation data from Experiment 1 are shown in Figure 2, which plots individual spatial tuning functions, together with group means, for test gratings masked by translating fields of Gaussian blobs. The test gratings were oriented either parallel or orthogonal to the motion trajectory, and the speed of masking motion was either fast or slow, or static in the control condition. The masking functions were collected under monoptic and dichoptic viewing conditions and are plotted separately. The data are plotted as contrast masking functions showing log elevation of grating detection thresholds from the baseline (unmasked gratings) due to the presence of the translating blob masks (see Equation 1) as a function of the spatial frequency of the test pattern. Evidence of masking in Figure 2 is indicated by the elevation of the data points above 0 dB. Spatial frequency (on the x-axis) was log transformed, and the data were fitted with skewed Gaussian functions with five parameters,

as shown in the following equation (solid lines show the best fits for each observer and for the mean):

$$f(x) = A \cdot \left[\exp\left(\frac{-(x_{(x_{\min}, x_{\mathrm{f}}]} - x_{\mathrm{f}})^2}{2 \cdot \sigma_{\mathrm{l}}^2} \right) + \exp\left(\frac{-(x_{[x_{\mathrm{f}, x_{\max})}} - x_{\mathrm{f}})^2}{2 \cdot \sigma_{\mathrm{r}}^2} \right) \right] + b, \qquad (2)$$

where x is log frequency, and A (amplitude), σ_1 and σ_r (standard deviations of the left and right halves of the distribution), and b (baseline offset) are the free parameters. A frequency offset (x_f) was added as a fifth free parameter so that the peak spatial frequency tuning of masking for each condition could be empirically determined. In effect, the function splits the data at x_f (which is a free parameter, not an arbitrary choice) and fits half-Gaussians with separate standard deviations to the left and right halves. Data fitting was performed using a custom routine written in MATLAB (version 7.4), which utilized a least-squares nonlinear fitting procedure.

Looking at the group mean data, several points emerge. The most important ones for our purposes are that, first, masking was greatest in the condition where fast motion overlaid gratings oriented parallel with the direction of motion (red curve, upper panels of group mean data), as predicted, and second, there is some evidence of spatial frequency tuning in this "fast parallel" condition, as indicated by the Gaussian amplitude (A) being well above zero with a combined bandwidth (i.e., the sum of the left and right standard deviations from Equation 2) being well defined with a width of 2.53 c/deg. The pattern of data in the fast parallel condition is similar under monoptic and dichoptic conditions, although masking is slightly weaker overall in the dichoptic case (peak amplitudes of 6.1 vs. 5.3 dB). The peak spatial frequencies of the functions fitted to the fast parallel data are also very similar across the monoptic and dichoptic conditions at 1.42 and 1.54 c/deg, respectively. These values are very similar to the nominal streak frequency we estimated using Geisler's blob width criterion (blob width is $4 \times SD$) and calculating the spatial period of a dark blob abutting a light blob, which yielded a value of 1.54 c/deg. Another clear result is that fastmoving mask stimuli only produced higher thresholds than slow masks at these peak spatial frequencies when motion was parallel to the test grating (compare red and green curves in parallel conditions with those in orthogonal conditions; see also Figure 3).

The static mask condition (purple curve) provides a useful point of comparison. When the slow motion functions are compared with the static functions, peak masking for slow motion is no different in magnitude or peak frequency from that produced by the static blob mask. This remained true whether the test grating was parallel or orthogonal to the slow motion mask, suggesting that our slow motion condition was indeed below the



Figure 2. Results showing the spatial frequency tuning of dichoptic and monoptic masking of frequency-varying target gratings by masking fields of Gaussian blobs translating at both fast (shown in red) and slow (shown in green) speeds and also by static dots (shown in purple). The smaller panels show results for individual participants, and the larger (lower right) panels show the group mean results. Masking strength is defined as the threshold elevation from unmasked baseline and is expressed in decibels (see Equation 1). Skewed Gaussian functions were fitted to the data (see Equation 2) and the error bars in the group mean data show ± 1 standard error. Log spatial frequency is shown on the lower *x*-axis, and spatial frequency is shown on the upper *x*-axis.

speed threshold for producing streaks. One interesting aspect of the static mask is that it exhibits a clear spatial frequency tuning, peaking at 1.18 c/deg and showing a rather tight tuning relative to the tunings produced by the motion masks, with a combined standard deviation of 1.7 c/deg, as compared to 2.53 and 2.95 for fast and slow motion, respectively (see Figures 2 and 3). This was unexpected, given that the static mask is simply an array of spatially low-pass elements, and it has not been shown before to our knowledge, although De Valois and Switkes (1980) showed spatial-frequency-specific adaptation effects on gratings after adapting to Glass patterns whose Fourier spectra bore no obvious resemblance to the grating patterns affected. One final point of interest in Figure 2 concerns the lowfrequency portions of the spatial tuning curves for the two motion conditions. For all mask stimuli, masking functions do not exhibit the classical symmetrical Gaussian decline to baseline on each side of the fitted peak. Instead, low-spatial-frequency thresholds remain disproportionately elevated, especially so for fast compared to slow motion and for slow motion compared to static stimuli. This low-frequency skew can be quantified by the difference in standard deviation between the left and right portions of our fits (respectively, σ_1 and σ_r in Equation 2; Figure 3). The higher standard deviations in the left half of the data confirm the skewed tunings and indicate that motion, especially fast motion, is a potent mask for static



Figure 3. Mean estimated standard deviations (measured in c/deg) of the left and right halves of the skewed Gaussians fitted to parallel data in Figure 2 (see Equation 2), averaged across the individual fitted data from the three participants. This quantifies the skew in the data: there is a significant left skew (that is, the distribution is wider in the left half (i.e., lower spatial frequencies) than in the right) in the fast conditions but not in the slow or static conditions. For the orthogonal conditions, individual fits were not reliable enough to furnish a meaningful analysis.

low spatial frequencies. Moreover, this low-spatialfrequency motion masking is not tuned for orientation, as these low-frequency elevations are very similar across parallel and orthogonal test gratings. This aspect of the data is further explored below in Figure 4.

The reason for fitting skewed rather than conventional Gaussian functions to the data was to quantify an observed pattern in the data, whereby some thresholds remained elevated at the lower spatial frequencies rather than returning to baseline. By fitting skewed Gaussians, we were able to compare the estimated standard deviations for the left and right halves of the functions (see Figure 3), while the peak remained unaffected. From Figure 3, it is evident that this difference is present in the fast but absent in the slow and static conditions. This difference (between left and right) was statistically significant in both the monoptic (t(2) = 5.7, p = 0.03) and dichoptic conditions (t(2) = 7.85, p = 0.016). It is also interesting to note that the overall bandwidths were broader for monoptic than for dichoptic masking, consistent with the findings of Legge (1979). None of the other differences were statistically significant; unfortunately, the individual fits in the

orthogonal conditions were not reliable enough to enable a valid comparison. The remaining parameters for the parallel fits to the mean data (peak, baseline, amplitude, and goodness of fit) are shown in Table 1.

To quantify the effect of masking due to motion alone and not to the spatial characteristics of the Gaussian dot stimuli and to further explore any effects in the orthogonal conditions, we subtracted the threshold elevations for static stimuli from those for fast and slow motion for each participant, and again fitted skewed Gaussians to the data (see Figure 4). This clarifies the results presented in Figure 3 somewhat: it is evident that only in the monoptic, fast, parallel condition (where we would have expected to see the effect of motion streaks) is there a clear difference between fast and static stimuli, with a peak centered around 1.2 c/deg, close to the peak seen in the raw data and also close to the estimated spatial frequency of streaks, based on the dot widths. This peak has an amplitude of 2.5 dB, and the tuning curve has a standard deviation of 1.3 c/deg, with a baseline elevation of 2 dB. However, the fit is fairly weak and it is evident that there is a low-pass element in the data (shown by the elevated data points at the two lowest spatial frequencies). It is curious that difference between masking by parallel and orthogonal fast motion is not seen in the dichoptic data: this could indicate that the effect of any motion streak masking may be very early, perhaps pre-cortical, although it is also possible that the pattern in the dichoptic data is obscured by noise from individual results (see Figure 2). The other pattern that is clarified in this figure is the lowpass threshold elevation, which is clearest at the lowest two spatial frequencies (0.27 and 0.54 c/deg). Only in the slow dichoptic condition is this pattern absent, and it appears in both parallel and orthogonal conditions, around 3-4 dB for the fast conditions and 2 dB for the slow conditions. In addition to this, the elevated baseline of around 2 dB in the monoptic, fast, parallel condition reveals an overall threshold elevation that is not spatially tuned (or is very broadly tuned) and seems to be specific to that condition. This would be consistent with the notion that the effect of motion streaks, although tuned for orientation, is relatively broadband spatially and may be mediated by early, monoptic mechanisms.

To summarize the masking results, these data can be interpreted as revealing three aspects of masking. First, we can see that at least part of the masking is tuned to the oriented energy contained in "motion streaks," as seen in the orientation-dependent difference between masking due to fast motion and masking due to static dots (present for parallel gratings, absent for orthogonal gratings), shown in Figure 4. Although this showed tuning for orientation (as expected from previous results; Apthorp et al., 2010), the spatial tuning was relatively weak after controlling for spatial tuning due to the dots alone. In addition, the elevated thresholds for fast parallel motion appear only to occur in monoptic viewing. Again, this is consistent with previous results (Apthorp et al., 2010) where we have



Figure 4. Results from Experiment 1 showing the difference between masking due to motion and masking due to static stimuli, for monoptic and dichoptic conditions. Error bars show ± 1 standard error. Log spatial frequency is shown on the lower *x*-axis, and spatial frequency is shown on the upper *x*-axis.

shown clear orientation-tuned masking only in monoptic conditions. There are two other notable aspects of the data. The first is a spatially low-pass masking that is not tuned for orientation and appears to gain in strength with increasing mask speed, leading to skewed distributions that remain elevated at low frequencies (see Figures 3 and 4). Finally, we see masking that is spatially bandpass but not tuned to orientation, as revealed by the static mask condition (Figure 3, purple curves).

Fourier analysis of "motion streaks"

Given the evidence for some orientation bias in the masking of static gratings by the motion of unoriented dot stimuli, it is of interest to know exactly what orientation information is contained in the motion streaks generated by our translating dots. To determine this, we took 10 consecutive animation frames (i.e., a motion sample of 100-ms duration) and summed them to reveal the motion streaks (see Figure 1b). We did this for both fast $(13^{\circ}/s)$ and slow $(1.6^{\circ}/s)$ motion stimuli, as well as static dots, and conducted Fourier analyses on the resulting images. Motion sequences of 100 ms were chosen as this is estimated to be the period of temporal integration in early visual cortex (Burr, 1980, 1981; Snowden & Braddick, 1991) that is presumed to produce motion streaks. From a previous psychophysical study, we also know that these fast and slow speeds are, respectively, above and below the threshold for producing motion streaks (Apthorp et al., 2009). Each summed image was transformed into frequency space using a fast Fourier transform (FFT) and was

	Peak (x _f , in c/deg)	Baseline (b, in dB)	Amplitude (A, in dB)	R^2
Monoptic, fast	1.42	5.16	6.12	0.96
Monoptic, slow	0.97	1.28	6.99	0.99
Monoptic, static	1.18	2.89	4.91	0.99
Dichoptic, fast	1.54	2.93	5.3	0.79
Dichoptic, slow	0.87	0.92	4.74	0.99
Dichoptic, static	1.22	0.81	3.25	0.98

Table 1. Fit parameters for the means of the parallel conditions.

then filtered in orientation and spatial frequency. Spatial filtering was done using a sliding log Gaussian with a 1-octave spatial bandwidth and 15-degree orientation bandwidth. By sliding the filter along the spatial frequency axis corresponding to the direction of streak modulation, it was possible to measure the spatial energy in the streaks at every point between the minimum frequency and the Nyquist limit. The distribution of the summed and squared energy from the filtered amplitude spectrum was then recorded for the parallel and the orthogonal orientations so that the oriented "streak" energy in the mask could be compared with the psychophysical masking functions. The same process was conducted for all three mask types: fast motion, slow motion, and static dots. Because the motion sequences were long, we repeated this process many times, randomly sampling a new starting point for each 100-ms motion sequence on every iteration and averaging the results. For the static dots, we generated a new set of random dots on each iteration. An average of 100 iterations of this procedure produced the results shown in Figure 5



Figure 5. Distributions of oriented energy in the amplitude spectra of time-averaged (100 ms) motion masks, compared with psychophysical masking results from Experiment 1. Filled dots show the spatial frequency energy in the Fourier amplitude spectrum, filtered with a log Gaussian filter with an orientation full bandwidth of 15 deg and a spatial frequency full bandwidth of 1 octave, at all possible spatial frequencies in the stimulus. Dashed lines show the group mean monoptic masking data from Figure 2. The upper panel shows Fourier and psychophysical tunings for test gratings parallel to the motion mask, and the lower panel shows the same for orthogonal test gratings. Spatial tunings are shown for fast and slow motion masks and for static masks. To allow comparison between Fourier and masking data, the fast, slow, and static amplitude spectra were normalized to the maximum overall value for Fourier energy, and masking data were normalized to the maximum value across all conditions. The Fourier tunings are very similar for all three mask stimuli in the parallel orientation but diverge in the orthogonal orientation where the fast mask contains very little energy (due to its elongated streaks). Overall, in all conditions, the psychophysical tuning functions show a slightly lower spatial frequency peak than is contained in the Fourier energy, particularly for orthogonal motion. Log spatial frequency is shown on the lower *x*-axis, and spatial frequency is shown on the upper *x*-axis.

(note that data are normalized to the maximum value for summed, squared energy in all conditions).

We compare the spatial tunings along the parallel and orthogonal dimensions of the Fourier amplitude spectra for the three "summed" (temporally blurred) mask stimuli with the psychophysical masking produced by the same stimuli (which are not blurred physically). The Fourier energy and psychophysical data are shown in Figure 5, where the Fourier amplitude spectra have been normalized so they can be compared on the same scale. In all conditions, the peak of the spatial frequency tuning is considerably higher in the Fourier energy (~ 2.3 c/deg) than observed in psychophysical masking ($\sim 1-1.5$ c/deg). In the parallel conditions (Figure 5, top panel), there is similar Fourier energy in all three masking stimuli (fast, slow, and static), whereas the psychophysical masking functions differ considerably between masking type, with greater threshold elevations for fast motion masks than for slow motion or static masks, in both monoptic and dichoptic conditions. In the orthogonal conditions (Figure 5, lower panel), the differences are even more pronounced: the Fourier amplitude spectrum for the fast motion mask shows very little tuning at all in the orthogonal dimension (and very low energy), yet there is clear low-pass tuning in the psychophysical masking function for this stimulus. Interestingly, this orientationuntuned (isotropic) low-pass threshold elevation increases with the mask speed (as noted above).

Interestingly, there is an asymmetry between the amplitude of the oriented energy in the stimulus and the amplitude of the masking functions. Although the energy in the fast stimuli is lower in amplitude than that in the slow or static stimuli in both conditions, fast motion produces substantially greater masking in both parallel and orthogonal conditions. Thus, the masking of static by moving stimuli cannot be purely a result of the oriented energy in the stimulus but must reflect some inherent underlying bias in the visual system, such as the inhibition of low temporal frequencies by high temporal frequencies (Cass & Alais, 2006).

What could explain the orientation-independent elevation of psychophysical masking thresholds at low spatial frequencies, given that there is little corresponding energy in the Fourier amplitude spectra of the masking stimuli? One possibility is that the translating dot mask could elicit excitatory responses in spatially low-pass and isotropic (possibly magnocellular-like) mechanisms. Assuming that target detection thresholds are determined by the ratio of target-relevant (signal) to target-irrelevant (noise) responses within target-relevant channels (Graham, 1989), a low-pass excitatory mask-driven response of the kind described above would effectively increase noise within low-spatial-frequency channels across the orientation spectrum, causing low-pass elevation of target thresholds.

Another possibility is that the low-spatial-frequency masking elevations result from a "between-channel" process, which selectively *suppresses* low-spatial-frequency responses across the entire orientation spectrum, particularly in the presence of high temporal frequencies (Cass & Alais, 2006).

Experiment 2: Spatial frequency tuning of static grating threshold elevation after motion adaptation

The aim of Experiment 2 is to use adaptation to fast and slow motion to shed light on what underlies the lowspatial-frequency and orientation-untuned threshold elevation observed in the masking data of Experiment 1 (see Figures 3 and 5). If these untuned low-frequency elevations were due to excitatory within-channel masking elicited by the motion mask (see Results and discussion section, Experiment 1), then adapting to fast motion should produce a similar orientation-independent lowspatial-frequency bias in threshold elevation to that observed with masking. If, however, the low-frequency elevations were due to between-channel suppression of low spatial frequencies, then we would expect to observe little or no threshold elevation at lower spatial frequencies following adaptation to fast motion, possibly even reducing thresholds via adaptation of the suppressive process. To investigate these possibilities, we carried out an adaptation experiment using stimuli with the same spatial parameters as those employed in Experiment 1.

Methods

Participants and apparatus

Participants and apparatus were as in Experiment 1, with the exception that the monitor used was a Mitsubishi DiamondView 22-inch CRT monitor.

Stimuli and procedure

Participants viewed the stimuli binocularly, using a standard chin rest. The adapting stimuli were the same drifting random dot displays as used in Experiment 1 (80 Gaussian blobs, SD = 0.08, half dark and half light on a mid-gray background of 33.5 cd/m², 100% coherent) and drifted at a speed 13.02°/s, well above the threshold for motion streaks. There was also a slow motion condition in which adapting dots drifted at 1.63°/s, as in Experiment 1. Adapting dots were presented in two virtual circular apertures 4.88° in diameter, 3.81° to the left and right of a white fixation cross, and always drifted directly upward. During the test phase, the fixation cross changed to black and the test stimulus (a low-contrast sine-wave grating) appeared either in the left or right aperture. Subjects initially adapted for 42 s to the motion stimuli,

200 ms after which the test grating appeared in either the right or left aperture for 10 ms, and the subject keyed their response ("left" or "right"). Subsequent trials involved 6 s of top-up adaptation. Contrast was manipulated in two interleaved adaptive staircases using the QUEST procedure (Watson & Pelli, 1983) to determine subjects' contrast thresholds for grating detection after adaptation. In a control condition, unadapted thresholds were obtained by removing the adapting dots.

Test stimuli were presented at a range of spatial frequencies in separate blocks so that the spatial tuning could be derived. Spatial frequencies were 0.54, 0.77, 1.09, 1.54, 2.18, 3.07, and 4.31 c/deg. The test grating was either parallel or orthogonal to the adapting direction of motion. Parallel and orthogonal conditions were blocked, as was spatial frequency, and all blocks were randomly interleaved (Figure 6).

Results

Contrast threshold elevation was measured as the ratio of unadapted to adapted contrast thresholds, expressed in decibels:

$$A = 20 \cdot \log_{10} \left(\frac{T_{\text{adapted}}}{T_{\text{unadapted}}} \right), \tag{3}$$

Adapt (42 sec)

Test - L or R?

where A refers to the adaptation level and T refers to contrast detection threshold.



Top-up adapt (6 sec)

with ± 1 standard error bars, normalized to the maximum value across conditions (solid lines), along with the monoptic masking data (dotted lines) and Fourier data (dashed lines), also normalized as in Figure 5. Following fast motion adaptation, thresholds for test gratings oriented parallel to the direction of adapting motion were strongly elevated (Figure 7a, continuous line), but unlike the masking condition, there was very little threshold elevation for orthogonal gratings (Figure 7c, continuous line). As in Experiment 1, the threshold elevations were fitted with skewed Gaussian functions (see Equation 2). For the parallel condition, threshold elevations peaked at a spatial frequency of 1.61 c/deg, with a bandwidth (standard deviation) of 1.3 c/deg. For the orthogonal condition (Figure 7b, continuous line), thresholds appear elevated at the lowest spatial frequencies tested, compared to the parallel condition, but this difference was not significant (p = 0.42, uncorrected). The fit appears to reveal a more low-pass tuning, so the peak value and standard deviations are not considered meaningful to report. Further information is provided by comparing fast to

Figure 7 shows the group mean data for three subjects

Further information is provided by comparing fast to slow adaptation and masking (Figure 7, lower panels). After adapting to parallel slow motion, in contrast to the masking data, very little threshold elevation is seen (Figure 7c). However, interestingly, when testing sensitivity to orthogonal gratings after adapting to slow motion, there is a small but clear bandpass tuning peaking at 1.4 c/deg, with a standard deviation of 1.33 c/deg, very similar to that seen in the parallel fast motion and similar to the stimulus content revealed by the Fourier analysis.

Discussion

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The aim of Experiment 2 was to adapt the motion streak mechanism and map the spatial tuning of this adaptation, with the goal of better understanding the masking results reported in Experiment 1, particularly the threshold elevations that were low spatial frequency biased and untuned for orientation (see Figure 5). Two models were outlined in the introduction to this experiment, one involving within-channel interactions and the other involving between-channel interactions. Assuming that adaptation and masking reflect the behavior of identical neural structures, adaptation provided a means of distinguishing between these possibilities. If the low-frequency elevations were due to between-channel suppression (i.e., due to motion activation causing suppression of static low spatial frequencies), then adaptation of this suppressive mechanism may serve to reduce its response. The question of what effect such suppressive adaptation would have in the absence of an otherwise suppressive stimulus (i.e., to the target alone) is unknown, although it is conceivable that it may produce a reduction in threshold elevation through disinhibition (Kohn & Movshon, 2003). This may explain the fact that while fast masking produced



Figure 7. Group mean threshold elevations for grating detection following adaptation to fast- and slow-translating dot motion, plotted as a function of grating spatial frequency. Results are shown separately for gratings oriented (left) parallel to the motion streaks and (right) orthogonal to the streaks, and error bars show ± 1 standard error. Group mean threshold elevations were fitted with a skewed Gaussian function (Equation 2) and were expressed in decibels (Equation 3). To facilitate comparison with the masking data from Experiment 1, the masking data from the corresponding conditions are replotted here (dotted lines). Finally, the unfilled circles show the spatial tuning of the Fourier amplitude spectra of these stimuli along the parallel and orthogonal dimensions (replotted from the fast conditions in Figure 5). To enable comparison of all the data on the same graph, masking and adaptation data were normalized to the maximum threshold elevation for the adaptation experiment, and Fourier data were normalized to the maximum value as in Figure 5. Maximum threshold elevation for the adaptation experiment was 8.5 dB (in the fast, parallel condition). Log spatial frequency is shown on the lower *x*-axis, and spatial frequency is shown on the upper *x*-axis.

profound threshold elevation of low spatial frequencies (which we propose are the result of cross-orientation masking), little adaptation was observed at these lower spatial frequencies. Alternatively, given the different tuning profiles of adaptation and masking, one should consider the possibility that masking and adaptation may be the result of distinct mechanisms.

The fit to the parallel data in Figure 7a shows that adaptation to parallel fast motion produces the characteristic bandpass shape that is typically reported in studies using static grating adaptation to reveal spatial tuning (Anderson & Burr, 1985; Blakemore & Campbell, 1969; Legge, 1979). Although the shape of the adaptation tuning is much narrower than that seen for masking in Experiment 1 (compare solid line in Figure 7a with the dotted line), this is broadly consistent with existing psychophysical studies comparing adaptation with masking for grating stimuli (Ross & Speed, 1991). The spatial tuning of the Fourier energy along the parallel dimension (dashed line) is also

plotted in Figure 7a. As was seen in Experiment 1, the peak of the spatial tuning in the Fourier analysis of the streak stimulus is again somewhat higher than what was revealed psychophysically by adaptation to the streak stimulus (although by less than half an octave), although the shape of the adaptation and Fourier tunings are very similar, both being bandpass. In the orthogonal adaptation condition (Figure 7b), by contrast, there is little similarity between the Fourier tuning (dashed line) and the adaptation tuning (continuous line). That is, there is virtually no energy oriented orthogonally to the motion streaks at any spatial frequency (dashed line), yet adaptation to this stimulus produced considerable threshold elevation with a spatially low-pass spatial tuning (continuous line). The origin of this effect is not clear, but since direction-selective neurons in early cortex are thought to be maximally sensitive to orientations orthogonal to their preferred direction, this may represent adaptation of more classical motion-selective units.

Interestingly, adaptation to slow motion produces considerably different results from masking by slow motion. In the parallel condition, there is almost no threshold elevation: the fit to the data appears to show low-pass tuning, but this fit is very noisy and may be skewed by the single data point at the lowest spatial frequency. In the slow orthogonal condition, however, there appears to be tuned threshold elevation centered around 1.4 c/deg, very similar to the spatial tuning revealed in the Fourier analysis of the stimulus. Tuning to orthogonal orientations for slow motion would be consistent with Geisler's (1999) suggestion that distinct mechanisms might be used for the processing of fast and slow motion.

General discussion

Overview

To review the results, in Experiment 1, we explored the spatial frequency tuning of threshold elevation caused by dichoptic and monoptic masking of static gratings by translating dot masks (fast vs. slow) and by static dots. The results reveal two (or possibly three) separate effects: first, an orientation tuned, spatially bandpass masking that can be attributed to motion streaks; second, a spatially low-pass element that is not tuned for orientation (i.e., orientationally isotropic) and that increases with masking speed; and third, a spatially bandpass element revealed in the masking by static dots that is not tuned for orientation.

The first effect, masking that we assume is due to the effect of motion streaks, is seen in the speed-dependent threshold elevation being more prominent when test gratings are oriented parallel to the direction of motion, relative to orthogonally oriented test gratings (see Figure 5a). The spatial tuning of this elevation, however, was relatively weak and broadband and was confined to the monoptic condition. A stronger anisotropy can be seen in the adaptation data (Experiment 2), where threshold elevations for parallel gratings were narrowly tuned following prolonged exposure to translating dots, whereas those for orthogonal gratings were not.

The second and most substantial aspect of the masking data is a spatially low-pass, speed-tuned (and/or possibly temporal frequency-tuned) threshold elevation that is isotropic with respect to orientation. It is also similar across dichoptic and monoptic conditions, although somewhat reduced in the dichoptic case. This effect is specific to masking, as it was not observed when sensitivity was measured after adaptation to the moving stimulus (Experiment 2), and so depends on simultaneous presentation of the stimuli.

In Experiment 2, we studied the effect of adaptation to fast- and slow-moving dot arrays on contrast threshold

elevations. In contrast to the relatively broadband threshold elevation from fast, parallel masking seen in Experiment 1, threshold elevations after adaptation to fast motion showed a bandpass pattern over spatial frequency but did not show the isotropic low-pass threshold elevation (see Figure 7a). This "streak-related" adaptation function showed a spectral profile that was relatively narrow and resembled the spatial content of the FFT of the temporally integrated stimulus (albeit narrower and slightly downshifted in frequency). This spatially band-limited threshold elevation seen in Experiment 2 is likely related to the spatial tuning of orientation-selective channels encoding the motion streaks. As to the absence of isotropic threshold elevation in the adapt-and-test paradigm, this clearly requires the simultaneous presentation of motion streaks and test grating (i.e., masking paradigm). Interestingly, a similar bandpass spatial tuning is seen for gratings orthogonal to motion direction after adaptation to slow motion (Figure 7d). This would be consistent with the notion that motion too slow to form streaks is processed by (and therefore adapts) mechanisms more similar to those of classical motion models, in which the units are maximally sensitive to orientations orthogonal to their preferred direction of motion (Adelson & Bergen, 1985; Adelson & Movshon, 1982; Watson & Ahumada, 1985).

Fourier analysis compared to masking and adaptation data

One very interesting finding is that the spatial frequency content of the (temporally blurred) streaky stimulus as revealed by Fourier analysis (see Figure 5) does not correspond directly to the spatial tunings of the masking and adaptation data (Figures 5 and 7). Although the motion streak stimulus contains a unimodal spatial frequency spectrum peaking at about 2.2 c/deg (Figure 5), the portion of masking thought to be due to streaks (Figure 4a), as well as the adaptation-induced threshold elevations (Figure 7a), peak at about 1-1.5 c/deg, considerably lower than the spatial frequencies contained in the temporally integrated stimulus. This shift toward low spatial frequencies in the masking functions, which occurred for both fast- and slow-translating dot masks, could be consistent with an early low-pass spatial filtering operation preceding the masking influence of the motion. It was proposed some time ago that a low-pass spatial filtering operation might take place before motion processing (Morgan, 1992). This form of filtering would mean that the transformation from stimulus to motion perception involves the attenuation of higher spatial frequencies. Although this kind of low-pass pre-filtering would account for the low-frequency shift in peak threshold elevation we observed, it does not account for the masking by static dot stimuli.

Another point of interest is the difference between masking and adaptation data with respect to the Fourier analysis (Figure 7). For two of the conditions (fast parallel and slow orthogonal), the adaptation threshold elevations correspond relatively closely to the stimulus content: threshold elevations are narrower and slightly downshifted, but they fall within the bandwidth of the oriented Fourier content. By contrast, no threshold elevation is seen for parallel gratings after adaptation to slow motion, in spite of the clearly spatially tuned Fourier component of the time-averaged stimulus. The tunings for fast orthogonal motion are not dissimilar for masking and adaptation, and both appear to show a low-pass spatial tuning. However, the adaptation data in this condition is noisy and these low-frequency threshold elevations do not differ significantly from those seen in the parallel condition. Apart from this, the low-pass threshold elevations seen consistently in all masking conditions are absent after adaptation, suggesting that these are related to a mechanism such as cross-orientation masking and that this is more closely related to the temporal energy in the moving stimulus than its time-averaged spatial content. Thus, it could be that the spatial tuning thought to be related to motion streaks, seen in the adaptation conditions, is obscured in the masking conditions because of temporal frequency masking, or it could be that the two paradigms tap different processes.

Isotropic masking of static gratings by motion

Whereas orientation-dependent (i.e., streak-related) masking and adaptation are probably due to temporal blurring (which is greater at high speeds and reflect the narrow spatial tuning of the stimulus seen in Figure 5), the isotropic masking we observe that increases with speed and acts over parallel and orthogonal orientations is difficult to reconcile within a simple low-pass temporal integration framework thought to underlie motion streaks. We prefer an alternative account based on the response of local temporal frequency-selective filters. Transient (high temporal frequency) events such as fast motion or flicker are known to impair sensitivity to sustained (low temporal frequency) patterns (Anderson & Burr, 1985; Boynton & Foley, 1999; Burbeck & Kelly, 1981; Cass & Alais, 2006; Cass, Alais, Spehar, & Bex, 2009; Hess & Snowden, 1992; Meier & Carandini, 2002) and can even render otherwise salient suprathreshold patterns invisible. Examples of this include motion-induced blindness (Bonneh, Cooperman, & Sagi, 2001; Wallis & Arnold, 2009) and adaptation-induced blindness (Motoyoshi & Hayakawa, 2010). Consistent with the isotropic effects we observe with fast motion masks, these transient masking phenomena act isotropically with respect to orientation and require high temporal rates of mask modulation.

Transient isotropic masking may serve to suppress temporally low-pass motion streaks (known as deblurring;

Burr, 1980; Cass & Alais, 2006; Wallis & Arnold, 2009). Moreover, it may dampen or suppress the statistically more dominant low temporal frequency structure of natural scenes, whose temporal amplitude spectra fall off with a characteristic slope of approximately 1/f (Dong & Atick, 1995), a phenomenon known as temporal whitening.

What is the source of this isotropic masking effect, which appears at low spatial frequencies and increases with the speed of the masker? We suggest two possibilities: one based on noise and one based on suppression. According to the noise account, the low-spatial-frequencybiased threshold elevation we observe may simply reflect broad "within-channel" noise arising due to excitation of isotropic magnocellular-like mechanisms (Meese & Hess, 2004). Alternatively, the suppression account holds that strong responses in transient (motion-driven) temporal channels may elicit an active suppression of sustained temporal mechanisms (such as our static tests; Cass & Alais, 2006; Cass, Alais et al., 2009) and that the suppression is isotropic with respect to orientation (Cass & Alais, 2006). It is possible that the physiological mechanism underpinning this isotropic masking is related to cross-orientation suppression (Allison, Smith, & Bonds, 2001; Cass, Stuit et al., 2009; DeAngelis, Robson, Ohzawa, & Freeman, 1992; Li, Thompson, Duong, Peterson, & Freeman, 2006; Meese & Holmes, 2007, 2010). With respect to the recent proposal that cross-orientation masking may arise pre-cortically (Cass & Alais, 2006; Li et al., 2006; Meese & Baker, 2009; Meier & Carandini, 2002), the similarity between our monoptic and dichoptic masking results would suggest that the underlying mechanism is probably cortical (Allison et al., 2001; Cass, Stuit et al., 2009; Morrone, Burr, & Maffei, 1982). By contrast, recent findings indicate that isotropic adaptation-induced threshold elevation effects are purely monocular (Cass, 2010), suggesting an early pre-cortical locus, possibly LGN (Solomon, Peirce, Dhruv, & Lennie, 2004).

Conclusions

Overall, the findings of these experiments show that exposure to translating image motion has a profound effect on contrast sensitivity for static oriented images, producing threshold elevations across the spatial frequency spectrum. Threshold elevations for parallel gratings were narrowly tuned following exposure to fast adapting motion (Experiment 2), with a bandwidth similar to the spatial content of the adapting stimulus. For slow adapting motion, threshold elevations for orthogonal gratings were similarly tuned. By contrast, simultaneous exposure to translating motion (Experiment 1: masking) produced a complex pattern of threshold elevations that was broad over spatial frequency and that revealed both oriented and unoriented aspects of masking. Together, these experiments complement our previous work showing that the spatial elongations caused by temporally integrating a translating stimulus ("motion streaks") are encoded by orientation-selective mechanisms, probably within V1 (Geisler et al., 2001) and are able to produce orientationspecific masking and adaptation effects (Apthorp & Alais, 2009; Apthorp et al., 2010, 2009; Burr & Ross, 2002; Geisler, 1999).

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