Motion streaks in fast motion rivalry cause orientation-selective suppression

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We studied binocular rivalry between orthogonally translating arrays of random Gaussian blobs and measured the strength of rivalry suppression for static oriented probes. Suppression depth was quantified by expressing monocular probe thresholds during dominance relative to thresholds during suppression. Rivalry between two fast motions or two slow motions was compared in order to test the suggestion that fast-moving objects leave oriented “motion streaks” due to temporal integration (W. S. Geisler, 1999). If fast motions do produce motion streaks, then fast motion rivalry might also entail rivalry between the orthogonal streak orientations. We tested this using a static oriented probe that was aligned either parallel to the motion trajectory (hence collinear with the “streaks”) or was orthogonal to the trajectory, predicting that rivalry suppression would be greater for parallel probes, and only for rivalry between fast motions. Results confirmed that suppression depth did depend on probe orientation for fast motion but not for slow motion. Further experiments showed that threshold elevations for the oriented probe during suppression exhibited clear orientation tuning. However, orientation-tuned elevations were also present during dominance, suggesting within-channel masking as the basis of the extra-deep suppression. In sum, the presence of orientation-dependent suppression in fast motion rivalry is consistent with the “motion streaks” hypothesis.

Keywords: binocular vision, masking, motion-2D, perceptual organization

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Introduction

Motion streaks

One influential view of visual cortical organization posited that the two major pathways through visual cortex—the dorsal and ventral steams—are specialized for distinct visual attributes (motion and form, respectively) and function largely independently (DeYoe & Van Essen, 1988; Livingstone & Hubel, 1988). There is, however, a growing body of evidence to suggest that these visual processing streams for motion and form are less independent than has often been assumed, with motion and form processes able to influence each other significantly (Cropper & Badcock, 2008; Francis & Grossberg, 1996; Giese, 1999; Kourtzi, Krekelberg, & van Wezel, 2008; Lorenceau & Shiffrar, 1992; Sincich & Horton, 2005; Treue, Husain, & Andersen, 1991). Geisler (1999) proposed a possible neural sensor for discriminating motion direction that explicitly combines form and motion signals. According to the model, the responses of oriented direction-selective cells are multiplicatively combined with those of orientation units selective for the orthogonal orientation. The rationale for this architecture is twofold. First, the bandwidth of direction tuning for motion-specialized units in primate MT and human MT+ is estimated to be rather broad at around 95° (Albright, 1984; Born & Bradley, 2005; Britten & Newsome, 1998), while units dedicated to detection of static orientation are more finely tuned with a bandwidth of about 35° (De Valois, Yund, & Hepler, 1982; Gur, Kagan, & Snodderly, 2005; Ringach, Shapley, & Hawken, 2002). Second, because early visual cortical units have a temporal integration period of about 100 ms (Burr, 1980; Snowden & Braddick, 1989), any translating object with significant speed should leave smeared trail, which Geisler termed a “motion streak”. The idea behind Geisler’s (1999) motion streak model is to exploit this inevitable smearing of spatial information to improve the precision with which motion direction can be encoded.

Evidence is accumulating, both in psychophysics and in single-unit neurophysiology, which supports the motion streak model. Geisler’s original proposal was backed by psychophysical data showing that one-dimensional

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dynamic noise masks raised the threshold for detecting a translating dot when the noise was oriented parallel to the dot's direction of motion, relative to noise masks oriented orthogonally to dot direction. Moreover, the threshold elevation only occurred for dots that translated above a critical dot speed—when the speed was sufficient to create elongated motion streaks. Thresholds measured in this way for a range of dot speeds and dot diameters showed that the critical speed at which streaks occurred, and were thus masked by the parallel noise masks, was a constant 1 dot width per 100 ms. Subsequent investigations found neurophysiological evidence consistent with the motion streak model (Geisler, Albrecht, Crane, & Stern, 2001; Krekelberg, Dannenberg, Hoffmann, Bremmer, & Ross, 2003), as well as further psychophysical support (Apthorp & Alais, 2009; Burr, 2000; Burr & Ross, 2002; Edwards & Crane, 2007; Ross, Badcock, & Hayes, 2000; Tong, Aydin, & Bedell, 2007).

One way of thinking of motion streaks is that they are a neural homologue of the "speed lines" used by artists to imply movement (Burr, 2000). Although this may seem a superficial similarity, it has been found that form that merely implies motion is sufficient to stimulate specialized motion processing areas in human cortex (Kourtzi, 2004; Kourtzi & Kanwisher, 2000; Krekelberg et al., 2003; Senior et al., 2000; Zeki, Watson, & Frackowiak, 1993) and that viewing static photographs implying unidirectional motion produce directionally opposite motion aftereffects (Winawer, Huk, & Boroditsky, 2008).

A curious aspect of the motion streak proposal is that it does not generally accord with our perception of moving objects. Except for very fast motions, well above the speed threshold for streaks, translating objects are not perceived to leave a streaky trail as they move across the retina. This may be due to "motion deblurring", a process that removes the spatial smear produced by temporal integration (Burr, 1980), and which may even cause objects to appear sharper when they are in motion than when static (Bex, Edgar, & Smith, 1995; Burr & Morgan, 1997). However, there is contradictory evidence about the visibility of streaks. A single target moving against a dark background may appear blurred if there are no surrounding targets in motion, but this visible blur decreases with increasing number of targets (Chen, Bedell, & Ogmen, 1995), as does visible persistence for static objects (Di Lollo & Hogben, 1987). This suggests that deblurring may be a process whereby streaks are suppressed from awareness but could still be available in early visual areas to assist with direction perception, as suggested by Geisler. However, other researchers (e.g., Georgeson & Hammett, 2002; Hammett, Georgeson, & Gorea, 1998) prefer a model in which "sharpening" of objects in motion occurs as a function of early contrast nonlinearities, and thus no special deblurring process is necessary. If this were the case, then deblurring would occur before the oriented streaks reached visual areas where they could be combined with motion information. In the experiments that follow, we used oriented probes in a motion rivalry paradigm to test whether oriented streaks are encoded at the level where rivalry occurs, and we use high dot densities to minimize the appearance of visible streaks in our displays.

Binocular rivalry

When two markedly dissimilar images are presented to each eye separately, an observer experiences stochastic alternations of perception between the two images, with switches between them occurring irregularly each second or so (Alais & Blake, 2005; Blake & Logothetis, 2002). Rather than seeing a fused binocular image, or a transparent combination of each eye's image, one of them dominates completely while the other image is suppressed from conscious awareness. A common technique for measuring the extent of binocular rivalry suppression involves delivering a probe stimulus to one of the eyes and measuring a contrast threshold for detection or discrimination. Thresholds are measured when the eye is in dominance and again when it is suppressed, and the ratio of threshold elevation is taken as a measure of suppression depth. Early experiments with rivaling gratings and contours showed that sensitivity to a probe presented during suppression is about 0.3 to 0.5 log units less than when presented during dominance (Blake & Fox, 1974; Makous & Sanders, 1978; Nguyen, Freeman, & Wenderoth, 2001), although probes can be much more deeply suppressed during rivalry between complex images such as faces and global motions (Alais & Melcher, 2007; Alais & Parker, 2006; Nguyen, Freeman, & Alais, 2003). To standardize suppression as an index, we define suppression depth as the base 10 log of the ratio of probe detection threshold during dominance to probe detection threshold during suppression.

Binocular rivalry is easily elicited by presenting motion signals to the eyes, provided they drift in different directions or at different speeds (Alais & Parker, 2006; Blake, Zimba, & Williams, 1985; Fox, Todd, & Bettinger, 1975; Moutoussis, Keliris, Kourtzi, & Logothetis, 2005; van de Grind, van Hof, van der Smagt, & Verstraten, 2001; Wade, de Weert, & Swanston, 1984; Wiesenfelder & Blake, 1992). In these experiments, we generated rivalry by presenting observers with dichoptic random dot arrays drifting in orthogonal directions, using a mirror stereoscope. The dots moved either at a speed fast enough to produce motion streaks or moved at speeds below the threshold for streaks shown by Geisler (1999). By combining this rivalry configuration with suppression depth measurements made with an oriented probe stimulus, the purpose of this experiment was to determine whether there is an orientation-specific suppression in motion rivalry that is present only for fast "streaky" motion, and not for slow motion moving at sub-streak speeds. More specifically, if indeed there are motion streaks produced by the fast motion, and assuming that they are not already removed by a process such as motion deblurring (Burr & Morgan, 1997) or motion sharpening (Hammett et al., 1998), then the oriented probe should be hard to detect when aligned parallel with the orientation of the motion streaks but should not be affected when oriented orthogonally to the streaks. Experiment 1 tests these predictions.

Experiment 1

Methods

Subjects

Five observers took part in the experiment. Three were the authors and two were naive observers. All had emmetropic or suitably corrected vision.

Apparatus and stimuli

Stimuli were presented on a Mitsubishi DiamondView 22 inch CRT monitor with a resolution of 1024 × 768 and a 120-Hz refresh rate, controlled by a MacPro 1.1 computer with a dual-core Intel Xeon processor. Stimuli were programmed in Matlab v.7.4 using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The adjacent left- and right-eye rivalry displays were presented within virtual 3.6° diameter apertures and were viewed through a mirror stereoscope from a distance of 57 cm.

The rival stimuli (see Figure 1a) were two drifting random dot displays, each composed of 80 Gaussian blobs with standard deviations of 3 min arc, giving a dot diameter, defined as 4 × dot *SD*, of 12 min arc. 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/m^2 and background luminance was 33.5 cd/m^2. In separate conditions, the dots drifted at speeds of either 8.57 or 2.14°/s (designed to be well above and just below Geisler's critical streak speed for dots of this size), and directions were always upward to the right (45°) in the right eye and upward to the left (135°) in the left eye. Speed was controlled by manipulating the update rate and pixel step size: slower speed stimuli updated every second frame (60 Hz). The initial position of each dot was randomly determined and all dots wrapped around the aperture.

The probe stimuli (see Figure 1a, right) were static noise patterns that had been spatial frequency filtered with a bandwidth of 1 octave and a center frequency determined by assuming that the width of the Gaussian blob (defined as above, 4 × *SD*) corresponded to the half-cycle of a sine wave. This gave a center spatial frequency of 2.5 cyc/deg. Two kinds of probe were used, differing in their orientation content: one was filtered using a Gaussian orientation filter with a standard deviation of 7.5°, while the other was isotropic with respect to orientation. Both probe types were matched for mean luminance and RMS contrast. Probes were presented using a Gaussian-ramped cross-fading method (see Figure 1b) that mixed the rival and probe stimuli smoothly over time and maintained constant levels of luminance and RMS contrast to avoid transients and artifacts. The Gaussian had a standard deviation of 40 ms, and a full-width at half-maximum of 94 ms. Examples of the motion stimuli temporally integrated over 100 ms are shown in Figure 1c to illustrate the fast and slow conditions. Examples of these combined with the oriented parallel and orthogonal probe stimuli are shown in Figure 1d.

Procedure

We wished to use a task that involved choosing between oriented and unoriented probe types; however, pilot experiments showed that the oriented and unoriented probes were not equally visible in all conditions. We therefore measured contrast thresholds for detecting each probe type (oriented vs. non-oriented), in both dominance and suppression. From the thresholds and psychometric functions for these conditions, we were able to ensure that all probes were presented at equal levels of detectability in our experiment. Subjects viewed the rivaling motion signals and used a key press to initiate the probe when the eye to be probed was either completely dominant or completely suppressed. The probe was always presented in the individual subject's preferred eye and was initiated after the key press with a random delay of between 0 and 240 ms. The motion and probe stimuli were combined by varying the relative contrast of the probe and motion stimulus according to the same Gaussian cross-fade (Figure 1b) described above. Using a yes/no task, subjects responded with a key press to indicate whether the probe was present or absent, and the relative contrast of the probe and motion signal was controlled by a QUEST procedure. Three QUESTs of 25 trials each were combined and fitted with a cumulative Gaussian psychometric function to find the contrast detection threshold. This was done for each subject for the three different probes:

1. orientation-filtered noise parallel to motion direction;
2. orientation-filtered noise orthogonal to motion direction; and
3. isotropic noise.

Using the thresholds and slopes of the fitted functions, the three probe stimuli could be presented at contrasts standardized for detectability, and then modulated as a ratio of these two contrast thresholds.

In the suppression depth experiments, observers inspected the rival stimuli and waited until the eye to be probed (always the observer's preferred eye) was in a period of complete dominance or complete suppression, depending on condition.[1] At that moment, the observer pressed the space bar to initiate probe presentation, and

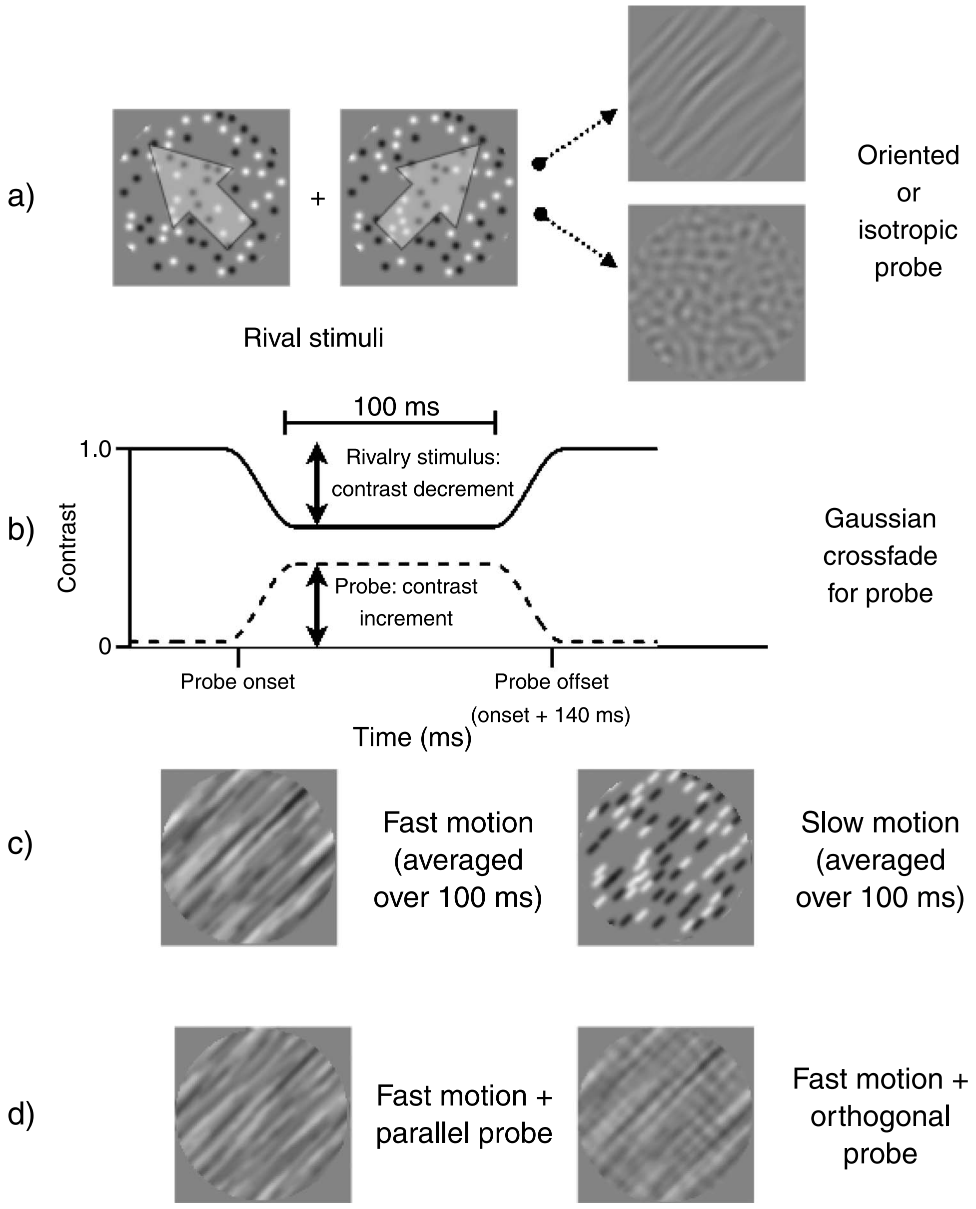

Figure 1. (a) Rival stimuli were Gaussian blob arrays drifting at fast (8.57 deg/s) or slow (2.14 deg/s) speed; probe was either isotropic, spatial-frequency-filtered noise or orientation-filtered noise. (b) Schematic illustration of the Gaussian cross-fade used to combine the probe with the probed eye's rival image. The probe increased smoothly in contrast, with a corresponding decrease in the contrast of the rival image to maintain total contrast and luminance. The magnitude of the contrast increment (and corresponding decrement) was varied adaptively using QUEST to determine the contrast threshold for the probe. (c) Example of fast and slow rival motions averaged over 100 ms. (d) Averaged fast motion with parallel and orthogonal oriented probes.

probe onset occurred after a random delay of between 0 and 240 ms. In a forced-choice discrimination task, subjects responded with a key press to indicate whether the probe was an oriented probe or not (see Figure 1a). A QUEST procedure was used to vary the relative amplitudes (contrast) of the probe and motion stimuli using a Gaussian cross-fade (see Figure 1b) to avoid transients in the stimuli, which might break suppression. Data for at least three QUEST staircases of 25 trials each were pooled and fitted with a cumulative Gaussian function for each subject to find the contrast threshold for discriminating the probes. Conditions were blocked (fast or slow motion, dominant or suppressed eye, parallel or orthogonal to motion direction) and randomly interleaved.

Results

Figure 2a shows the mean contrast thresholds and standard errors for the five observers on the probe discrimination task, with dominance and suppression

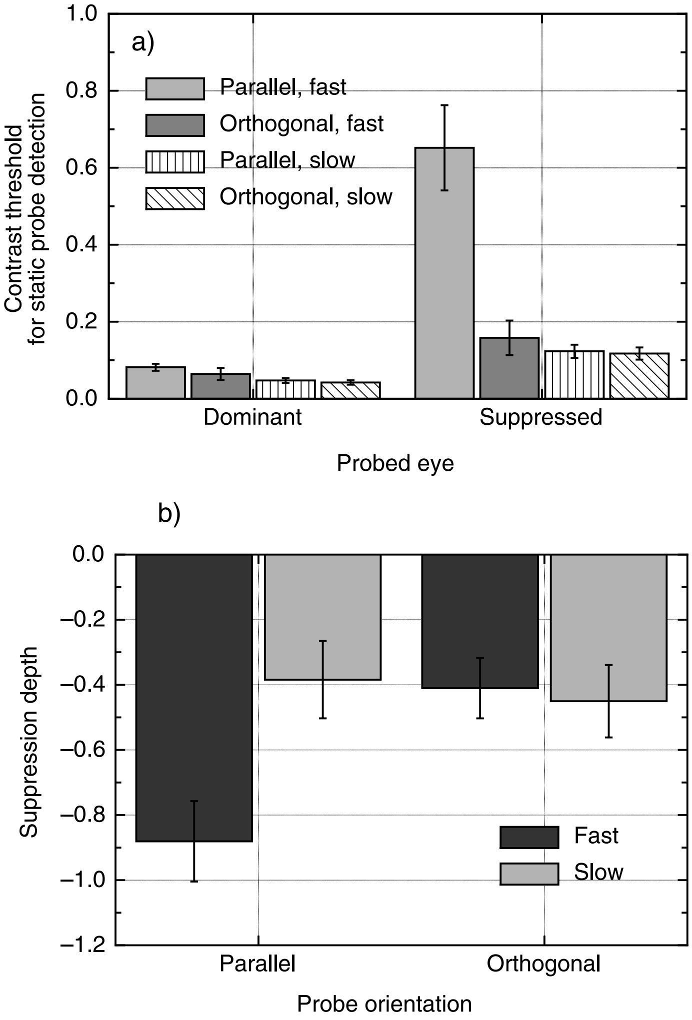

Figure 2. (a) Raw contrast detection thresholds for oriented probes for 5 subjects, shown in dominance and suppression for fast and slow motions, with probes either parallel or orthogonal to the direction of motion in the probed eye. Thresholds are expressed as a proportion of the maximum available contrast (99% Michelson contrast). (b) Suppression depth (expressed as the base 10 log of dominant/suppressed thresholds) graphed as a function of probe orientation. Error bars show ±1 standard error.

conditions shown separately. It is clear that contrast discrimination thresholds for suppression are elevated with respect to those measured during dominance—the effect of rivalry suppression—and that for three of the four conditions the threshold elevation is about a factor of two. Twofold increases in threshold are typical of the elevations reported in many rivalry suppression depth studies (Blake & Fox, 1974; Makous & Sanders, 1978; Nguyen et al., 2001). The most striking effect, however, is the sixfold increase in threshold when the parallel probe is presented during fast motion rivalry. This is a far greater threshold elevation than is usually measured in rivalry suppression experiments, and notably, it only occurred for probes oriented parallel to the direction of motion, and only when the motion was fast enough to produce motion streaks.

Suppression depth can be expressed as an index by taking the log of the ratio of dominance to suppression thresholds. This gives an index of suppression whereby no suppression would give a value of zero, and deeper suppression gives lower values. The advantage of this index is that the threshold elevation for each probe is standardized as a proportion of the dominance threshold for the same stimulus, controlling for variations in dominance threshold across conditions. These data are shown in Figure 2b: on a standardized index, suppression depth is greater for the parallel probe in fast motion rivalry than for the other three conditions. We carried out a two-way repeated-measures analysis of variance (ANOVA) on the suppression depth indices. The two-way ANOVA showed there were significant main effects of orientation, $F(1,4) = 17.01$, $p = 0.015$, and of speed, $F(1,4) = 16.06$, $p = 0.016$. Importantly, there was also a significant interaction between orientation and speed, $F(1,4) = 11.505$, $p = 0.027$, and a complex contrast showed that suppression depth for the parallel, fast condition was significantly greater than that for the other three conditions, $F(1,4) = 11.183$, $p = 0.029$.

Discussion

The suppression depth indices (Figure 2b) show that rivalry suppression was significantly non-zero in all conditions. This is as expected in any binocular rivalry condition and it simply quantifies the basic phenomenology of rivalry: that the failure of binocular fusion causes one eye's image to become perceptually suppressed. Typically, rivalry suppression studies report suppression indices (calculated as $1 - \text{dominant/suppressed}$ thresholds) of around 0.5 to 0.6 (Blake & Fox, 1974; Li, Freeman, & Alais, 2005; Nguyen et al., 2001). These scale to -0.3 to -0.4 when expressed in base 10 log units; for three of the four conditions in Figure 1b the suppression indices we report are in this range. However, the key result, as predicted, is that there was much greater suppression of the oriented probe, occurring only in the fast motion condition, and only when the probe's orientation was aligned with the motion direction. This appears to be an additional component of rivalry suppression, on top of the degree of binocular rivalry suppression normally reported, and the data show that this extra component is not simply due to probe orientation, nor solely to the probe being presented in fast motion rivalry, but to a specific combination of both factors.

Some questions remain regarding the precise cause of the extra suppression in the fast, aligned condition. Because the effect is jointly dependent on fast speed and a probe orientation collinear with the motion trajectory, we take it as evidence that fast motion produces motion streaks, as reasoned in the Introduction section. That is, even though long oriented streaks are not perceptually obvious in the motion stimulus, they must nonetheless be encoded by orientation-selective mechanisms at the early stages of cortical processing where binocular rivalry is thought to be initiated (Blake, 1989; Blake & Boothroyd, 1985). We propose two possible explanations for this. The first is that the streaks in the stimulus are detected by orientation-selective units in early cortex and therefore give the fast rivalry stimulus a second rivalrous dimension: that of orientation rivalry. On this view, we suggest that the rivalry process is engaged over two stimulus dimensions, one due to the conflicting motion directions and one due to the conflicting orientation. The implication of the deepening of suppression in the fast parallel condition is that rivalry suppression can sum across stimulus dimensions such as motion and orientation when the interocular conflict involves more than one stimulus dimension (Knapen, Kanai, Brascamp, van Boxtel, & van Ee, 2007).

The second explanation we consider is also based on the assumption that there are motion streaks in the fast motion condition. The presence of elongated streaks would activate orientation-selective units in early cortex, such that when a probe stimulus was presented aligned with the streaks, the same units signaling the streaks would also be those required to judge whether the probe was oriented or not. Thus, an explanation could be formulated in terms of the oriented probe being masked by the streaks. In line with classical channel theory (Braddick, Campbell, & Atkinson, 1978; Graham, 1989), when two similar stimuli drive the same channel, there must be raised thresholds for detecting the stimulus that is nominally the target. On this view, the extra deep suppression observed in the fast parallel condition could be attributed to raised probe thresholds due to within-channel masking.

Experiment 2

The aim of Experiment 2 is to test between the competing explanations of deep suppression for parallel probes during fast motion rivalry outlined above. Both accounts are based on the presence of oriented streaks in the fast motion condition, and therefore both predict orientation-tuned effects, with threshold elevations maximal when the probe orientation matches the motion streak's orientation. Within-channel masking, however, predicts that orientation-tuned threshold elevations will occur regardless of whether the probed eye is dominant or suppressed, while summation of rivalry suppression predicts that tuned threshold elevations should only occur during suppression. The reasoning for the channel-masking explanation is that regardless of any change in a channel's baseline activity that may arise due to rivalry suppression, the presence of streaks will always elevate thresholds for similarly oriented probes. In contrast, the summation of rivalry suppression cannot occur if the probed eye is in a state of dominance. Experiment 2 tests these predictions.

Methods

Subjects

Four observers took part in the experiment, including two of the authors and two naive observers. All had emmetropic or suitably corrected vision.

Apparatus and stimuli

Apparatus was as in Experiment 1. The rival stimuli, dot speeds, luminances, and display sizes were also as in Experiment 1. However, probe stimuli were now solely orientation-filtered noise (spatial frequency bandwidth as in Experiment 1), oriented at 45 degrees, and ±7.5, 15, 30, and 60 degrees from 45 (the direction of dot motion in the dominant eye). Both fast and slow speeds were tested at each of these orientations, in dominance and suppression, in order to yield tuning functions for each condition.

Procedure

The experiment was run as a detection experiment. Observers initiated the probe stimulus with a key press when the motion in the eye to be probed was either completely dominant or completely suppressed. Probe timing was as in Experiment 1. In a yes/no paradigm, the observers reported whether the oriented probe was present or not. QUEST was used to adjust the relative contrast of the probe and motion stimuli in the cross-fade to obtain contrast thresholds for each condition. The QUEST data were fitted with cumulative Gaussian functions and contrast thresholds for probe detection were obtained, where threshold was defined as 75% correct.

Results

Contrast thresholds for probe detection showed clear orientation tuning for fast motion rivalry, both in dominance and in suppression (see Figure 3a). In the slow rivalry condition, some slight threshold elevation was seen in the suppressed condition, but no elevation was seen in the dominant condition (see Figure 3b); in fact, the data fit shows a slight threshold reduction near the orientation of the motion trajectory, perhaps due to sub-threshold summation. Gaussian functions were fitted to the data using a Monte Carlo bootstrapping technique: in the fast dominant condition, the fitted curve showed a full-width at half-height of 33 degrees, with an amplitude of 0.7411 log units and a baseline of −1.6. Chi-squared for

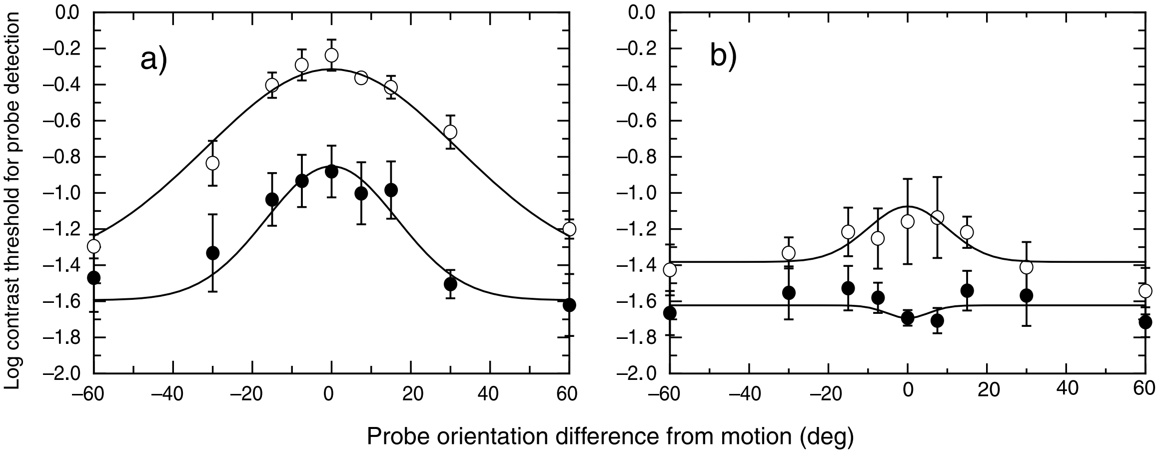

Figure 3. (a) Gaussian fits to log contrast detection thresholds for oriented probes in dominance (filled symbols) and suppression (open symbols) for fast motion, plotted against the orientation difference between the probe and the trajectory of motion. There is clear orientation tuning, shifted upward and broadened in suppression. (b) Thresholds for slow motion show shallow tuning in suppression. The curve for the dominance condition shows a suggestion of sub-threshold summation near the orientation of the motion trajectory.

this fit was 2.245. In the fast suppressed condition, the FWHH was 63.7 degrees, with an amplitude of 1.111 log units and a baseline of −1.43. In the slow condition, very slight tuning is seen in suppression (amplitude 0.3063, baseline −1.38, FWHH 20 degrees), but in dominance there is no threshold elevation; rather, there is slight sub-threshold summation (amplitude −0.007, width 10.4 degrees).

Discussion

Since thresholds for fast motion exhibit clear orientation tuning in dominance, which is consistent with the tuning of early cortical channels (De Valois et al., 1982; Gur et al., 2005), it seems likely that within-channel masking is at least partly responsible for the extra suppression depth seen for probes oriented parallel to the direction of motion. If instead it were due to the combination of rivalry suppression over the two rivalrous stimulus dimensions (i.e., orientation and motion), then the extra suppression would only have been exhibited when the orientation and motion were undergoing rivalry suppression, so would not have been evident when the probe was presented to the dominant eye. Indeed, the masking account is consistent with Geisler's (1999) original data, in which it was shown that an oriented noise stimulus masked the motion of a single Gaussian dot if the noise was oriented parallel to the dot's trajectory, but only if the dot moved above the critical "streak" speed. Here we have shown the converse effect: that streaky motion can mask parallel orientations.

Experiment 3

The tuning curves obtained in the fast speed conditions of Experiment 2 show clear evidence of within-channel masking, which is orientation-tuned both in dominance and suppression. However, the slow speed condition also shows some evidence of tuning (although much weaker) in the suppression condition, suggesting that there may be some streak-related orientation energy present even in the slow motion condition. To quantify this, we Fourier analyzed the summed (temporally integrated over 100 ms) stimuli from the fast and slow motion conditions (as shown in Figure 1) to measure the oriented energy contained in each. Figure 4 plots the oriented energy for both stimuli, showing clearly that while energy in the slow stimulus is much more broadly distributed than in the fast stimulus, it still shows a small peak aligned with the direction of motion that is consistent with the presence of weak streaks.

To assess the importance of the orientation bias evident in the slow motion stimulus in Figure 4, we conducted a masking experiment for dots moving at various speeds to determine psychophysically the speed threshold for motion streaks. We replicated the design of Geisler's (1999) original masking experiment but used motion as the mask and an oriented grating as the target, with stimuli at the same contrast and average luminance as in Experiments 1 and 2. In Geisler's experiment, two subjects were tested in a 2IFC masking experiment where the task was to detect a moving dot in the presence of dynamic random noise either parallel or orthogonal to the dot's direction of motion. However, these experiments were performed at

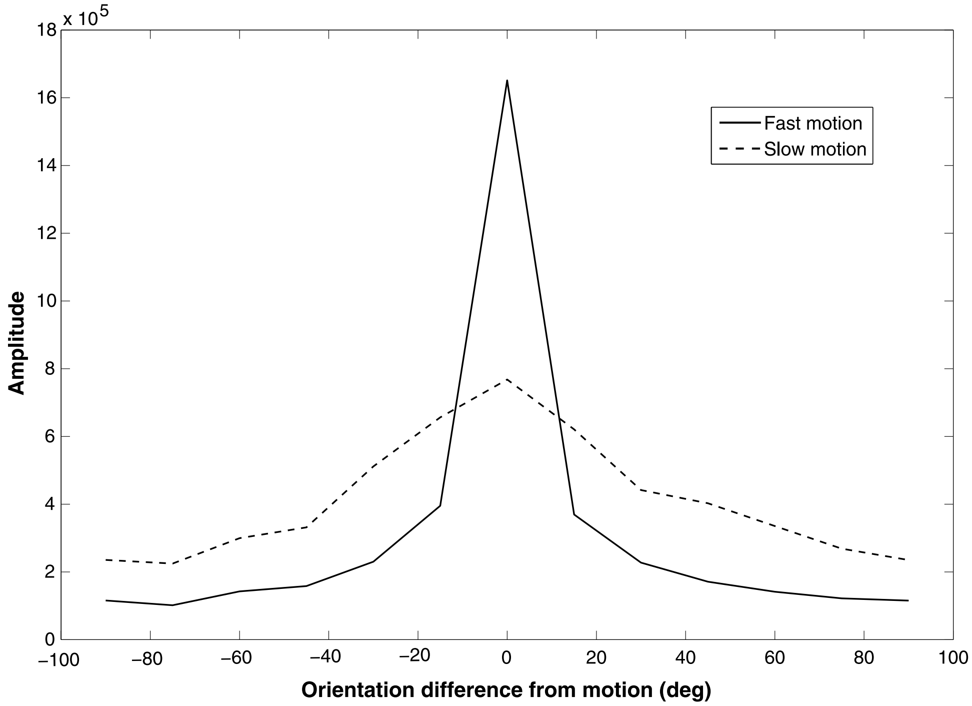

Figure 4. Orientation energy plotted for the long and the short streak stimuli averaged over 100 ms, as shown in Figure 1c. The energy in the amplitude spectrum was averaged over 15° sectors, centered on 0° (the orientation of the streaks). For fast motion, the energy at the streak orientation is 2.15 times greater than for slow motion. More importantly, only the fast motion stimulus has a sharply tuned distribution of oriented energy. For fast motion (long streaks), the energy at the streak orientation is 4.3 times higher than the mean energy at the flanking orientations (±15°). For slow motion, this ratio is only 1.2. The lack of tuning for the slow speed (short streaks) is reflected in the psychophysical data shown in Figure 5, which shows no significant advantage for parallel streaks at the speed (length) plotted here.

very low average luminance (1.36 cd/m^2), and luminance thresholds rather than contrast thresholds are reported. Since integration times tend to be shorter at higher luminances (Hogben & Di Lollo, 1985), it is more likely that the critical speed Geisler reported is below that which would have been seen with higher luminance stimuli such as ours.

Methods

Subjects

Four observers took part in the experiment, including one of the authors and three naive observers. All had emmetropic or suitably corrected vision.

Apparatus, stimuli, and procedure

Apparatus was as in Experiment 1. Observers viewed the stimuli monocularly in their preferred eye, using a mirror stereoscope as in Experiments 1 and 2. Dot contrast, number of dots, and mean luminance were as in the previous experiments, but observers now viewed motion in two apertures, 3.05 degrees above and below fixation, and the experiment was run as a 2AFC where the task was to detect whether the grating was in the upper or lower aperture. Probe stimuli were sine-wave gratings with a spatial frequency of 2.1 cycles/degree and were oriented either parallel or orthogonal to the direction of motion. Motion was either upward to the right or downward to the left, randomized to control for motion adaptation but always the same in both apertures. Probe timing was as in Experiment 1. QUEST was used to adjust the relative contrast of the probe grating. The QUEST data were fitted with cumulative Gaussian functions and contrast thresholds for probe detection were obtained, where threshold was defined as 75% correct.

Results and discussion

Figure 5 shows the mean contrast thresholds and standard errors for the four observers on the grating detection task at the nine speeds tested. It is clear that there is no significant difference between detection thresholds for parallel and orthogonal probes at speeds up to 3 degrees/s; at higher speeds, the thresholds begin to diverge. A two-way repeated-measures ANOVA showed a significant interaction between speed and streak length, $F(6, 18) = 5.344$, $p = 0.003$. Paired t-tests for the four

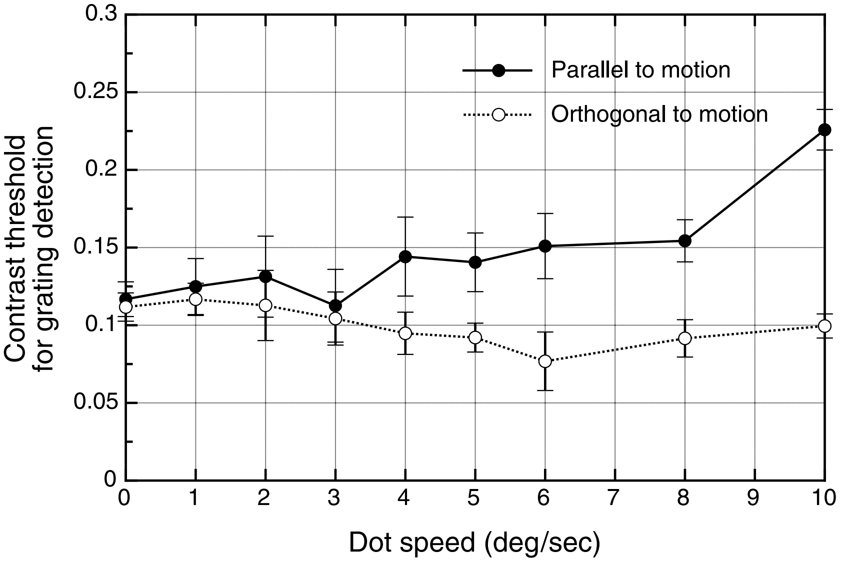

Figure 5. Contrast thresholds for detection of a static oriented grating either parallel or orthogonal to direction of motion of a dot field, plotted as a function of dot speed.

speeds near the point of divergence show that, at speeds below 5 deg/s, there was no significant difference between detection thresholds for parallel and orthogonal gratings (speed 2, $t(3) = 2.675$, $p = 0.075$; speed 3, $t(3) = 0.595$, $p = 0.594$; speed 4, $t(3) = 3.068$, $p = 0.055$), but at 5 deg/s, there was a significant difference, $t(3) = 3.381$, $p = 0.043$l. For our stimuli and conditions, therefore, the critical speed for masking by motion streaks is between 4 and 5 deg/s. This is somewhat faster than the critical speed reported by Geisler but is consistent with the much higher luminance values in our conditions reducing temporal integration times (Bair & Movshon, 2004; Hart, 1987) and therefore increasing the speed required to produce a given streak length. The important conclusion for our purposes is that the speeds used in Experiments 1 and 2 (2.14 and 8.57 deg/s) have been empirically determined to fall well below and well above the critical streak threshold for these stimuli.

General discussion

Motion streaks

Although we outlined two competing accounts in the introduction to Experiment 2 to explain the deeper suppression observed in the fast parallel condition (one based on masking, the other on summation of rivalry suppression), either explanation would be consistent with the idea that the visual system encodes orientation signals that result from spatial smearing of fast translating images. We will therefore discuss the implications for motion streaks first and discuss the questions of masking and suppression summation further below.

Our key finding in support of motion streaks is the orientation dependence of threshold elevations that only occur in fast motion conditions. As is clear in Figures 2a and 3, thresholds for detecting an oriented probe are greatly elevated when the probe is aligned with the orientation of the putative motion streaks. Importantly, this pattern only occurred in fast motion conditions and was absent in conditions where the motion was slow enough to be sub-threshold for streak formation. This pattern of results provides good evidence for motion streaks. Moreover, the orientation selectivity mapped out in Experiment 2 (see Figure 3) reveals, in the dominance condition, a tuning very similar to those of orientation-selective units in primary visual cortex (De Valois et al., 1982; Gur et al., 2005; Snowden, Treue, & Andersen, 1992). In sum, these results suggest that motion streaks are present in the neural representation of fast translating motions, that they are encoded by orientation-selective units, and that this occurs early in cortical processing. This is consistent with the physiological data of Geisler et al. (2001), where orientation-selective neurons in V1 of monkey cortex were shown to respond more strongly to fast motion *parallel* to their preferred orientation.

While our psychophysical data strongly imply that fast moving stimuli produce motion streaks at the neural level, the presence of these streaks was not perceptually obvious in the stimulus. Although this seems a curious anomaly, it is not unknown for perception to be influenced by stimuli outside awareness. Indeed, this has been demonstrated specifically in the case of orientation. He and MacLeod (2001) showed that tilt aftereffects, as well as orientation-specific elevations in contrast thresholds, could be produced by gratings whose spatial period was too fine to be perceived. Pearson and Clifford (2005) studied a version of the tilt illusion during binocular rivalry and found that the orientation of a vertical central stimulus in the dominant eye was systematically repelled by the tilted surround grating in the suppressed eye. Finally, Clifford and Harris (2005) used a backward-masking paradigm to suppress a surround grating from awareness and found that a tilt illusion could still be produced on a central grating. These findings show that the absence of awareness of orientation is not sufficient to preclude it having an influence on perception, as we also have shown regarding orientation aftereffects and illusions from motion streaks (Apthorp & Alais, 2009).

Binocular rivalry

What are the implications of these data for binocular rivalry? One possibility outlined above is that rivalry between fast streaky motions elicits rivalry in two stimulus dimensions, motion and orientation, and that the presence of interocular conflict in two dimensions would lead to stronger rivalry suppression than would occur with stimuli conflicting in only one dimension. There is an intuitive appeal in the idea that more vigorous suppression should occur when greater interocular conflict exists. It ties in with recent work showing that rivalry suppression depends upon the distance in multi-dimensional feature space between the rivaling images (Knapen et al., 2007) and on the level of shared features and stimulus complexity (Alais & Melcher, 2007). Rivalry between fast streaky motions would be more complex than slow motion, as the latter contains no above-threshold orientation signal, and would therefore engage a more widespread rivalry network. On this view, fast motion rivalry should lead to stronger suppression.

Although this interpretation appears to explain why the oriented probe was more strongly suppressed in fast motion rivalry than in slow motion rivalry, it does prompt some questions. For example, although it may be true that there would be more aggregate rivalry activity for fast motion rivalry relative to slow motion, because of rivalry in both motion and orientation networks, it is not clear how that would necessarily lead to deeper suppression of a probe that taps only the orientation dimension. This led us to consider a more parsimonious explanation: that the apparent increase in suppression depth for fast streaky motion may simply be due to within-channel masking of the probe orientation by the presence of orientated streaks. This explanation simply assumes that if there are elongated streaks in the fast motion stimulus, they should activate orientation-selective units in early cortex and therefore mask probes with the same or similar orientation. With the same units signaling both the streaks and the probe, thresholds for the probe must increase because the streaks effectively provide a source of noise, since the probe is the nominal signal. The rationale for within-channel masking when two similar stimuli drive the same channel is well established in classic channel theory (Braddick et al., 1978; Graham, 1989).

According to the masking account, the deepening of rivalry suppression in the fast parallel condition would arise primarily because the probe was harder to detect. Critically, this account stands independently of the rivalry process and therefore predicts that masking-related threshold elevations should occur irrespective of whether the probed eye is in a state of dominance or suppression. In contrast, explanations based on rivalry suppression processes are limited to the suppression state, since visual sensitivity, as assessed by probe detection, is equivalent during normal monocular vision and during the dominance state of binocular rivalry (Blake & Camisa, 1979; Fox & Check, 1972). It was for this reason that we measured the orientation tuning of threshold elevations in Experiment 2, to determine whether orientation-tuned elevations expected during rivalry suppression would also occur during rivalry dominance. Looking at the thresholds for fast motion (Figure 3a), there is clearly a strong orientation tuning for thresholds measured during suppression, as expected, yet there is also clear tuning for the dominance thresholds, lower in amplitude as would be expected since the stimulus is not suppressed. The most parsimonious explanation of this is that the loss of visibility due to rivalry suppression simply adds to the masking-related threshold elevations already present in dominance for fast motion rivalry.

Although the presence of a clear tuning curve for dominance supports the masking interpretation, one complicating factor is that the tuning curve for suppression is not simply a uniform upward shift of the suppression curve, as would be expected from the simple addition of further suppression due to rivalry. Instead, the orientation-tuning curve for suppression is about twice as broad as that measured during dominance (33° vs. 63.7°). The reason for the broader orientation tuning in suppression is not clear, although another study recently reported broader orientation tuning during suppression for rivalry between static oriented stimuli (Ling & Blake, 2008). The most likely explanation can be found in models of cortical orientation selectivity. Recent models of orientation selectivity in primary visual cortex, based on recurrent cortical excitation (Carandini & Ringach, 1997; Somers, Nelson, & Sur, 1995) or inhibition of non-preferred orientations (Bonds, 1989; Ringach, Bredfeldt, Shapley, & Hawken, 2002), employ processes to actively sharpen orientation tunings (in contrast to the classical feedforward model; Hubel & Wiesel, 1962). Rivalry suppression may interfere with this sharpening process, possibly because the interocular suppression effected by the dominant orientation units in one eye may not be perfectly targeted on the rival orientation in the other eye. Any tendency for suppression signals to input to neighboring orientations would interfere with the sharpening process at a given orientation as it depends on activity in neighboring non-preferred orientations.

As a final observation, our data are instructive about where orientation encoding and motion deblurring are situated with respect to each other in the visual processing stream. Motion streaks are not generally seen; thus it is reasonable to conclude that some form of motion sharpening or streak suppression must take place (Burr, 1980; Burr & Morgan, 1997; Hammett et al., 1998). Our results indicate that streak suppression must occur subsequent to the point where orientation encoding occurs, since oriented streak information was an effective masker of oriented probes and so was clearly present at the stage of orientation coding in early cortex. Had the streaks already been suppressed at this stage, there would have been no orientation dependence in probe detection thresholds. Moreover, if motion streaks were suppressed prior to orientation encoding, it would be difficult to see how they could be exploited to augment motion processing, as the motion streak model proposes (Geisler, 1999).

In summary, we have found evidence for speed and orientation-dependent suppression of oriented probes in binocular rivalry. This supports the proposal that fast translational motion produces oriented motion streaks that activate orientation-selective channels in early cortical processing. We attribute the apparent deepening of suppression in fast motion rivalry for probes oriented parallel to the motion trajectory to masking. The orientation tuning of the thresholds we report in Experiment 2 closely match the tuning of orientation tuning previously shown in primary visual cortex, indicating that motion streaks are most likely to be encoded at this early stage.

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Footnote

[1] All participants were experienced observers of binocular rivalry and were given practice trials prior to the experiment. At this high dot density, observers reported long periods (in the order of several seconds) of complete dominance or suppression, and no percept of transparent motion during rivalry.

References

Alais, D., & Blake, R. (2005). *Binocular rivalry*. Cambridge, MA: MIT Press.

Alais, D., & Melcher, D. (2007). Strength and coherence of binocular rivalry depends on shared stimulus complexity. *Vision Research, 47,* 269–279. [PubMed]

Alais, D., & Parker, A. (2006). Independent binocular rivalry processes for motion and form. *Neuron, 52,* 911–920. [PubMed] [Article]

Albright, T. D. (1984). Direction and orientation selectivity of neurons in visual area MT of the macaque. *Journal of Neurophysiology, 52,* 1106–1130. [PubMed]

Apthorp, D., & Alais, D. (2009). Tilt aftereffects and tilt illusions induced by fast translational motion: Evidence for motion streaks. *Journal of Vision, 9*(1):27, 1–11, http://journalofvision.org/9/1/27/, doi:10.1167/9.1.27. [PubMed] [Article]

Bair, W., & Movshon, J. A. (2004). Adaptive temporal integration of motion in direction-selective neurons in macaque visual cortex. *Journal of Neuroscience, 24,* 7305–7323. [PubMed] [Article]

Bex, P. J., Edgar, G. K., & Smith, A. T. (1995). Sharpening of drifting, blurred images. *Vision Research, 35,* 2539–2546. [PubMed]

Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review, 96,* 145–167. [PubMed]

Blake, R., & Boothroyd, K. (1985). The precedence of binocular fusion over binocular rivalry. *Perception & Psychophysics, 37,* 114–124. [PubMed]

Blake, R., & Camisa, J. (1979). On the inhibitory nature of binocular rivalry suppression. *Journal of Experimental Psychology: Human Perception and Performance, 5,* 315–323. [PubMed]

Blake, R., & Fox, R. (1974). Binocular rivalry suppression: Insensitive to spatial frequency and orientation change. *Vision Research, 14,* 687–692. [PubMed]

Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews, Neuroscience, 3,* 13–21. [PubMed]

Blake, R., Zimba, L., & Williams, D. (1985). Visual motion, binocular correspondence and binocular rivalry. *Biological Cybernetics, 52,* 391–397. [PubMed]

Bonds, A. B. (1989). Role of inhibition in the specification of orientation selectivity of cells in the cat striate cortex. *Visual Neuroscience, 2,* 41–55. [PubMed]

Born, R. T., & Bradley, D. C. (2005). Structure and function of visual area MT. *Annual Review of Neuroscience, 28,* 157–189. [PubMed]

Braddick, O. J., Campbell, F. W., & Atkinson, J. (1978). Channels in vision: Basic aspects. In R. Held, H. Leibowitz, & H.-L. Teuber (Eds.), *Perception* (vol. VII, pp. 3–7). Berlin, Germany: Springer-Verlag.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10,* 433–436. [PubMed]

Britten, K. H., & Newsome, W. T. (1998). Tuning bandwidths for near-threshold stimuli in area MT. *Journal of Neurophysiology, 80,* 762–770. [PubMed] [Article]

Burr, D. (1980). Motion smear. *Nature, 284,* 164–165. [PubMed]

Burr, D. (2000). Motion vision: Are 'speed lines' used in human visual motion? *Current Biology, 10,* R440–R443. [PubMed] [Article]

Burr, D. C., & Morgan, M. J. (1997). Motion deblurring in human vision. *Proceedings of the Royal Society of London B: Biological Sciences, 264,* 431–436. [PubMed] [Article]

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

Carandini, M., & Ringach, D. L. (1997). Predictions of a recurrent model of orientation selectivity. *Vision Research, 37,* 3061–3071. [PubMed]

Chen, S., Bedell, H. E., & Oğmen, H. (1995). A target in real motion appears blurred in the absence of other proximal moving targets. *Vision Research, 35,* 2315–2328. [PubMed]

Clifford, C. W., & Harris, J. A. (2005). Contextual modulation outside of awareness. *Current Biology, 15,* 574–578. [PubMed] [Article]

Cropper, S. J., & Badcock, D. R. (2008). Perception of direction of motion reflects the early integration of first and second-order stimulus spatial properties. *Journal of Vision, 8*(4):12, 1–10, http://journalofvision.org/8/4/12/, doi:10.1167/8.4.12. [PubMed] [Article]

De Valois, R. L., Yund, E. W., & Hepler, N. (1982). The orientation and direction selectivity of cells in macaque visual cortex. *Vision Research, 22,* 531–544. [PubMed]

DeYoe, E. A., & Van Essen, D. C. (1988). Concurrent processing streams in monkey visual cortex. *Trends in Neurosciences, 11,* 219–226. [PubMed]

Di Lollo, V., & Hogben, J. H. (1987). Suppression of visible persistence as a function of spatial separation between inducing stimuli. *Perception & Psychophysics, 41,* 345–354. [PubMed]

Edwards, M., & Crane, M. F. (2007). Motion streaks improve motion detection. *Vision Research, 47,* 828–833. [PubMed]

Fox, R., & Check, R. (1972). Independence between binocular rivalry suppression duration and magnitude of suppression. *Journal of Experimental Psychology, 93,* 283–289. [PubMed]

Fox, R., Todd, S., & Bettinger, L. A. (1975). Optokinetic nystagmus as an objective indicator of binocular rivalry. *Vision Research, 15,* 849–853. [PubMed]

Francis, G., & Grossberg, S. (1996). Cortical dynamics of form and motion integration: Persistence, apparent motion, and illusory contours. *Vision Research, 36,* 149–173. [PubMed]

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

Geisler, W. S., Albrecht, D. G., Crane, A. M., & Stern, L. (2001). Motion direction signals in the primary visual cortex of cat and monkey. *Visual Neuroscience, 18,* 501–516. [PubMed]

Georgeson, M. A., & Hammett, S. T. (2002). Seeing blur: 'Motion sharpening' without motion. *Proceedings of the Royal Society of London B: Biological Sciences, 269,* 1429–1434. [PubMed] [Article]

Giese, M. A. (1999). Evidence for multi-functional interactions in early visual motion processing. *Trends in Neurosciences, 22,* 287–290. [PubMed]

Graham, N. V. S. (1989). *Visual pattern analysers*. New York: Oxford University Press.

Gur, M., Kagan, I., & Snodderly, D. M. (2005). Orientation and direction selectivity of neurons in V1 of alert monkeys: Functional relationships and laminar distributions. *Cerebral Cortex, 15,* 1207–1221. [PubMed] [Article]

Hammett, S. T., Georgeson, M. A., & Gorea, A. (1998). Motion blur and motion sharpening: Temporal smear and local contrast non-linearity. *Vision Research, 38,* 2099–2108. [PubMed]

Hart, W. M., Jr. (1987). The temporal responsiveness of vision. In R. A. Moses & W. M. Hart (Eds.), *Adler's physiology of the eye, clinical application* (pp. 429–457). St. Louis, MO: The C. V. Mosby Company.

He, S., & MacLeod, D. I. (2001). Orientation-selective adaptation and tilt after-effect from invisible patterns. *Nature, 411,* 473–476. [PubMed]

Hogben, J. H., & Di Lollo, V. (1985). Suppression of visible persistence in apparent motion. *Perception & Psychophysics, 38,* 450–460. [PubMed]

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in cat's visual cortex. *The Journal of Physiology, 160,* 106–154. [PubMed] [Article]

Knapen, T., Kanai, R., Brascamp, J., van Boxtel, J., & van Ee, R. (2007). Distance in feature space determines exclusivity in visual rivalry. *Vision Research, 47,* 3269–3275. [PubMed]

Kourtzi, Z. (2004). "But still, it moves". *Trends in Cognitive Sciences, 8,* 47–49. [PubMed]

Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience, 12,* 48–55. [PubMed]

Kourtzi, Z., Krekelberg, B., & van Wezel, R. J. (2008). Linking form and motion in the primate brain. *Trends in Cognitive Sciences, 12,* 230–236. [PubMed]

Krekelberg, B., Dannenberg, S., Hoffmann, K. P., Bremmer, F., & Ross, J. (2003). Neural correlates of implied motion. *Nature, 424,* 674–677. [PubMed]

Li, D. F., Freeman, A. W., & Alais, D. (2005). Contrast sensitivity of form and motion discrimination during binocular rivalry. *Vision Research, 45,* 1255–1263. [PubMed]

Ling, S., & Blake, R. (2008). Suppression during binocular rivalry broadens orientation tuning [Abstract]. *Journal of Vision, 8*(6):246, 246a, http://journalofvision.org/8/6/246/, doi:10.1167/8.6.246.

Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science, 240,* 740–749. [PubMed]

Lorenceau, J., & Shiffrar, M. (1992). The influence of terminators on motion integration across space. *Vision Research, 32,* 263–273. [PubMed]

Makous, W., & Sanders, R. K. (1978). Suppression interactions between fused patterns. In A. C. Armington, J. Krauskopf & B. R. Wooten (Eds.), *Visual pyschophysics and physiology* (pp. 167–179). New York: Academic Press.

Moutoussis, K., Keliris, G., Kourtzi, Z., & Logothetis, N. (2005). A binocular rivalry study of motion perception in the human brain. *Vision Research, 45,* 2231–2243. [PubMed]

Nguyen, V. A., Freeman, A. W., & Alais, D. (2003). Increasing depth of binocular rivalry suppression along two visual pathways. *Vision Research, 43,* 2003–2008. [PubMed]

Nguyen, V. A., Freeman, A. W., & Wenderoth, P. (2001). The depth and selectivity of suppression in binocular rivalry. *Perception & Psychophysics, 63,* 348–360. [PubMed] [Article]

Pearson, J., & Clifford, C. W. (2005). Suppressed patterns alter vision during binocular rivalry. *Current Biology, 15,* 2142–2148. [PubMed] [Article]

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10,* 437–442. [PubMed]

Ringach, D. L., Bredfeldt, C. E., Shapley, R. M., & Hawken, M. J. (2002). Suppression of neural responses to nonoptimal stimuli correlates with tuning selectivity in macaque V1. *Journal of Neurophysiology, 87,* 1018–1027. [PubMed] [Article]

Ringach, D. L., Shapley, R. M., & Hawken, M. J. (2002). Orientation selectivity in macaque V1: Diversity and laminar dependence. *Journal of Neuroscience, 22,* 5639–5651. [PubMed] [Article]

Ross, J., Badcock, D. R., & Hayes, A. (2000). Coherent global motion in the absence of velocity signals. *Current Biology, 10,* 679–682. [PubMed] [Article]

Senior, C., Barnes, J., Giampietro, V., Simmons, A., Bullmore, E. T., Brammer, M., et al. (2000). The functional neuroanatomy of implicit-motion perception or representational momentum. *Current Biology, 10,* 16–22. [PubMed] [Article]

Sincich, L. C., & Horton, J. C. (2005). The circuitry of V1 and V2: Integration of color, form, and motion. *Annual Review of Neuroscience, 28,* 303–326. [PubMed]

Snowden, R. J., & Braddick, O. J. (1989). The combination of motion signals over time. *Vision Research, 29,* 1621–1630. [PubMed]

Snowden, R. J., Treue, S., & Andersen, R. A. (1992). The response of neurons in areas V1 and MT of the alert rhesus monkey to moving random dot patterns. *Experimental Brain Research, 88,* 389–400. [PubMed]

Somers, D. C., Nelson, S. B., & Sur, M. (1995). An emergent model of orientation selectivity in cat visual cortical simple cells. *Journal of Neuroscience, 15,* 5448–5465. [PubMed] [Article]

Tong, J., Aydin, M., & Bedell, H. E. (2007). Direction and extent of perceived motion smear during pursuit eye movement. *Vision Research, 47,* 1011–1019. [PubMed]

Treue, S., Husain, M., & Andersen, R. A. (1991). Human perception of structure from motion. *Vision Research, 31,* 59–75. [PubMed]

van de Grind, W. A., van Hof, P., van der Smagt, M. J., & Verstraten, F. A. (2001). Slow and fast visual motion channels have independent binocular-rivalry stages. *Proceedings of the Royal Society of London B: Biological Sciences, 268,* 437–443. [PubMed] [Article]

Wade, N. J., de Weert, C. M., & Swanston, M. T. (1984). Binocular rivalry with moving patterns. *Perception & Psychophysics, 35,* 111–122. [PubMed]

Wiesenfelder, H., & Blake, R. (1992). Binocular rivalry suppression disrupts recovery from motion adaptation. *Visual Neuroscience, 9,* 143–148. [PubMed]

Winawer, J., Huk, A. C., & Boroditsky, L. (2008). A motion aftereffect from still photographs depicting motion. *Psychological Science, 19,* 276–283. [PubMed]

Zeki, S., Watson, J. D., & Frackowiak, R. S. (1993). Going beyond the information given: The relation of illusory visual motion to brain activity. *Proceedings of the Royal Society of London B: Biological Sciences, 252,* 215–222. [PubMed]