Spatial non-homogeneity of the antagonistic surround in motion perception

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At high contrast, duration thresholds for motion direction discrimination deteriorate with increasing stimulus size. This counterintuitive result has been explained by the center–surround antagonism present in the neurons of visual area MT. Conversely, at very low contrast, direction discrimination improves with increasing size, a result that has been explained by spatial summation. In this investigation, we study the effects of stimulus shape and contrast on center–surround antagonism. Using adaptive Bayesian staircases, we measured duration thresholds of 5 subjects for vertically oriented Gabor patches of 1 cycle/deg with two types of oval Gaussian windows, one vertically elongated (S_x = 0.35, S_y = 2.5 deg) and other horizontally elongated (S_x = 2.5, S_y = 0.35 deg) moving rightward or leftward at a speed of 2 deg/s. We found that at high contrast (92%) duration thresholds were lower for vertically than horizontally elongated windows. However, at low contrast (2.8%), we found that duration thresholds were lower for horizontally than vertically elongated windows. These asymmetric results mirror the spatial non-homogeneity of the antagonistic surround found in MT neurons and suggest that the underlying center–surround antagonism is stronger along the direction of motion.

Introduction

A striking psychophysical result in motion perception is that when the size of the stimulus increases, the ability to discriminate the direction of motion depends differentially on the contrast of the stimuli. At high contrasts, as the size of the stimulus increases, more time is required in order to accurately report its direction of motion. At low contrast, as stimulus size increases, less time is required (Tadin, Lappin, Gilroy, & Blake, 2003). Consistent with these results, Pack, Hunter, and Born (2005) have reported that some MT neurons fire more intensely to a large stimulus presented at low contrast than to the same stimulus presented at high contrast. The impairment in direction discrimination at high contrast and big sizes has been explained by a perceptual effect called *surround suppression*, which is the psychophysical counterpart of the center–surround antagonism present in the receptive fields of motion sensors of the visual area MT (Allman, Miezin, & McGuiness, 1985a, 1985b; Born & Tootell, 1992; Tadin et al., 2003; Tanaka et al., 1986). This impairment has also been explained by suggesting that the response of the direction-selective filters, implicated in direction discrimination, saturates at modest contrast (Derrington & Goddard, 1989). Conversely, the improvement or facilitation in direction discrimination at low contrasts when the size of the stimulus is increased has been explained by a perceptual effect called *spatial summation* (Tadin et al., 2003). The physiological correlate of spatial summation is believed to be the increases in receptive field size which occur with decreasing contrast (Gilbert, Das, Ito, Kapadia, & Westheimer, 1996; Kapadia, Westheimer, & Gilbert, 1999; Nauhaus, Busse, Carandini, & Ringach, 2009; Sceniak, Ringach, Hawken, & Shapley, 1999). This result has also been found recently in psychophysics (Tadin & Lappin, 2005) where the authors reported that the optimal size for motion discrimination increases with decreasing contrast. However, this apparent change in receptive field size with contrast can be explained by shifts in the relative gain of fixed-size excitatory and inhibitory mechanisms (Cavanaugh, Bair, & Movshon, 2002). Recently, it has been found that MT surround modulation depends on the strength of the neuronal response: the surround antagonism (surround suppression) is stronger for stimuli that elicit larger responses, and the surround integration (spatial summation) is stronger for stimuli that elicit smaller responses (Huang, Albright, & Stoner, 2008).

In all these previous investigations, researchers have assumed that the antagonistic surround of MT neurons is spatially symmetric around the excitatory center. Recent models of center–surround organization also assume this

uniformity of the antagonistic surround (Cavanaugh et al., 2002; Huang et al., 2008; Sceniak et al., 1999; Tadin & Lappin, 2005). However, in fact, only 20% of MT neurons are circularly symmetric, so 80% of MT neurons present a non-homogeneity of the spatial organization of the inhibitory surround (Raiguel, Van Hulle, Xiao, Marcar, & Orban, 1995; Xiao, Raiguel, Marcar, Koenderink, & Orban, 1995; Xiao, Raiguel, Marcar, & Orban, 1997; see also Born & Bradley, 2005). The Orban laboratory, using eight small patches composed of moving random dots circularly distributed around a patch situated in the center (Surround Asymmetry Test), measured the effect of stimulating the surround on the response of the center receptive field. They found two types of asymmetric antagonistic surround: one confined to one side of the excitatory center, and the other bilaterally symmetric on opposite sides of the excitatory center.

In previous psychophysical research, the authors have used mainly Gabor patches with different contrast and sizes but with circular spatial envelopes (Betts, Sekuler, & Bennet, 2009; Lappin, Tadin, Nyquist, & Corn, 2009; Tadin & Lappin, 2005; Tadin et al., 2003). This type of circular spatial envelopes cannot discriminate between circular surround suppression or bilateral surround suppression. In this investigation, we will study the effect on perceived motion when the stimulus shape is elongated along the direction of motion and when the elongation is orthogonal to it. If there is a psychophysical correlate of the asymmetric surrounds found in MT cells, then we should observe different suppression and facilitation effects depending on the axis along which the window is elongated.

Methods

Subjects

Five human subjects (aged between 18 and 37 years) with experience in psychophysical experiments, two males (ISP, PFA), and five females (CH, VM, LH, JCAR, and NS) took part in the experiments (JCAR and NS only participated in the control experiment). The subjects PFA, CH, VM, and NS were not aware of the purpose of the study. All subjects had normal or corrected-to-normal refraction and normal visual acuity. Experimental procedures were approved by Newcastle University's Faculty of Medical Sciences Ethics Committee.

Stimuli

The stimuli used in Experiments 1 and 2 were Gabor patches of 512×512 pixels and 8-bit range, constructed using Matlab (MathWorks, Natick MA). The equation of a moving Gabor patch is given as follows:

$$L(x, y, t) = L_0 \left[1 + m(t) \exp\left\{ -\frac{\hat{x}^2}{2\sigma_x^2} - \frac{\hat{y}^2}{2\sigma_y^2} \right\} \cdot \cos(2\pi\rho_0(\hat{x} - vt) + \varphi_0) \right], \tag{1}$$

where $\hat{x} = x\cos(\theta_0) + y\sin(\theta_0)$, $\hat{y} = -x\sin(\theta_0) + y\cos(\theta_0)$; x and y are position on-screen; L_0 is mean luminance; ρ_0 is the spatial frequency; θ_0 is the orientation; σ_x and σ_y are the spatial standard deviations of the Gaussian window; v is the speed of the Gabor patch; and m is the Michelson contrast as a function of time given by

$$m(t) = M\exp\left\{ -t^2/(2\sigma_t^2) \right\}, \tag{2}$$

where σ_t is the temporal standard deviation, in milliseconds (ms); and M is the peak contrast.

In both experiments, the spatial frequency was $\rho_0 = 1$ cycle/degree, the speed was $v = 2$ deg/s, and the mean luminance was $L_0 = 28$ cd/m^2. The peak Michelson contrasts were $M = 92\%$ for the high-contrast condition and $M = 2.8\%$ for the low-contrast condition, and four types of spatial windows were tested: two oval windows, one vertically elongated ($\sigma_x = 0.35°$, $\sigma_y = 2.5°$, for $\theta_0 = 0°$) and other horizontally elongated ($\sigma_x = 2.5°$, $\sigma_y = 0.35°$, for $\theta_0 = 0°$), and two Gaussian windows: one small ($\sigma_x = 0.35°$, $\sigma_y = 0.35°$) and one big ($\sigma_x = 2.5°$, $\sigma_y = 2.5°$). In Experiment 1, the orientation of the grating was vertical ($\theta_0 = 0°$) so the stimulus was perceived moving leftward or rightward, and in Experiment 2, the orientation of the grating was horizontal ($\theta_0 = 90°$), thus, the motion was perceived upward or downward. The temporal standard deviation (σ_t) was varied as described below, so as to find the duration threshold. All stimuli were truncated to give an overall duration of 500 ms, with the maximum contrast occurring in the middle of this temporal window.

Equipment

The experiments were carried out in a dark room. In Experiments 1 and 2, the stimuli were presented on a 16" monitor (SONY Trinitron Multiscan G200) under the control of a PC running Matlab using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997, www.psychtoolbox.org) and Bits++ (Cambridge Research Systems), giving 14 bits of grayscale resolution. The monitor was gamma-corrected using a Minolta LS-100 photometer. It had a resolution of 800×600 pixels (horizontal $\times$ vertical) with vertical frame rate of 120 Hz, a mean luminance (L_0) of 28 cd/m^2, and was observed binocularly from a distance of 83 cm, resulting in 38 pixels per degree

of visual angle. A chin rest (UHCOTech HeadSpot) was used to stabilize the subject's head and to control the observation distance. Stimuli were presented at the center of the monitor screen in a square of 19.5 cm per side, subtending an area of $13.5° \times 13.5°$. The remainder of the screen was at the mean luminance.

Stimulus presentation

Each trial started with a fixation cross displayed at the center of the screen using a Gaussian temporal function (see Equation 2) with standard deviation of $\sigma_t = 80$ ms truncated to give an overall duration of 500 ms. The cross disappeared before the presentation of the stimulus. The Gabor stimulus (see Equation 1) was presented using a Gaussian temporal function (see Equation 2) with a temporal deviation controlled by an adaptive staircase procedure. The Gaussian temporal profile was truncated to give an overall duration of 500 ms so each trial including the fixation cross lasted 1000 ms. The motion direction of the Gabor patch, left or right (Experiment 1) or up or down (Experiment 2), was randomized and the observer's task was to indicate, by pressing a mouse button, the direction they saw on each presentation. A new trial was initiated only after the observer's response, thus the experiment proceeded at a pace determined by the observer. Feedback about correctness on individual trials was given by an auditory signal.

Data analysis

Duration threshold, the minimum presentation time that is needed in order to detect the correct direction of motion, was defined as the value of $2\sigma_t$ resulting in a performance of 82% correct. Duration thresholds were measured using adaptive Bayesian staircases (Treutwein, 1995) in a forced-choice direction discrimination task. The subject's task was to indicate the perceived direction of motion. In general, between 5 and 9 min were required per duration threshold estimation. The characteristics of the Bayesian staircases were given as follows: (1) the prior probability density function was uniform (Emerson, 1986; Pentland, 1980) with a starting duration of 200 ms; (2) we used the logistic function as the model likelihood function adapted from García-Pérez (1998, Appendix A) with a spread value of 1 (with delta parameter equal to 0.01, a lapse rate of 0.01, and a guess rate of 0.5); (3) the value of the temporal duration ($2\sigma_t$) in each trial was obtained from the mean of the posterior probability distribution (King-Smith, Grigsby, Vingrys, Benes, & Supowit, 1994); (4) the staircase stopped after 50 trials (Anderson, 2003; Pentland, 1980); and (5) the final threshold was estimated from the mean of the final probability density function. Three threshold estimations per condition were obtained for each subject. A total of 8 conditions

(4 spatial windows × 2 contrasts) in each experiment were tested in different sessions counterbalancing the conditions across subjects. Practice sessions were performed previous to the experiment.

To examine pairwise significant differences between conditions within a subject, a two-sample *t*-test was used to compare the 3 duration thresholds obtained for that subject in one condition with the 3 thresholds obtained for the same subject in the different condition. At the population level, we compared the *n* mean thresholds obtained for the *n* subjects in one condition with the *n* mean thresholds in the other condition.

Results

Experiment 1: Gabor gratings drifting horizontally

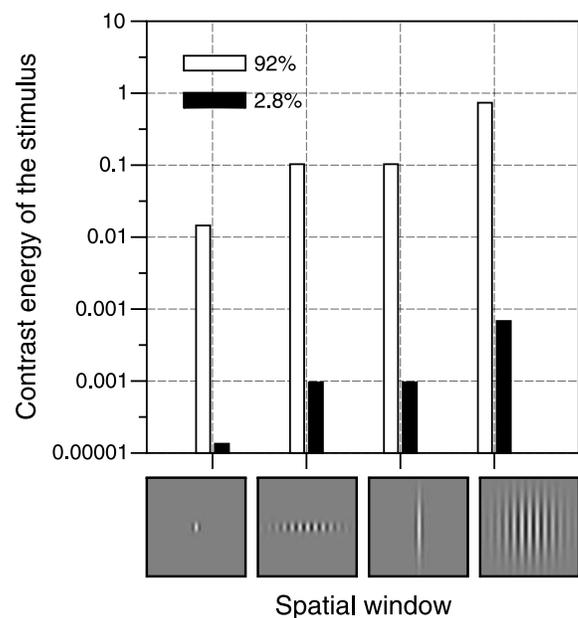In Experiment 1, we measured the duration thresholds (the minimum time that is needed to detect the correct

Figure 1. Contrast energy of the stimulus used in Experiment 1. The contrast energy (*E*) was calculated numerically using the equation: $E = \Sigma\Sigma\Sigma(f2(x, y, t)\Delta x \Delta y \Delta t$, where *f* is the contrast function of the stimulus image *L*, $f = (L(x, y, t)/Lave) - 1$, where Lave is the average of the stimulus image and $L(x, y, t)$ is defined in Equation 1. $\Delta x = \Delta y$ are the horizontal and vertical pixel sizes (0.0254 deg) and Δt is the duration of a frame (8.3 ms) We calculated the contrast energy of the stimuli for four types of spatial window, two contrasts (2.8%, black bars and 92%, white bars), spatial frequency of 1 cycle/deg, speed of 2 deg/s, and a temporal standard deviation of 50 ms for the temporal Gaussian envelope (see Equation 2).
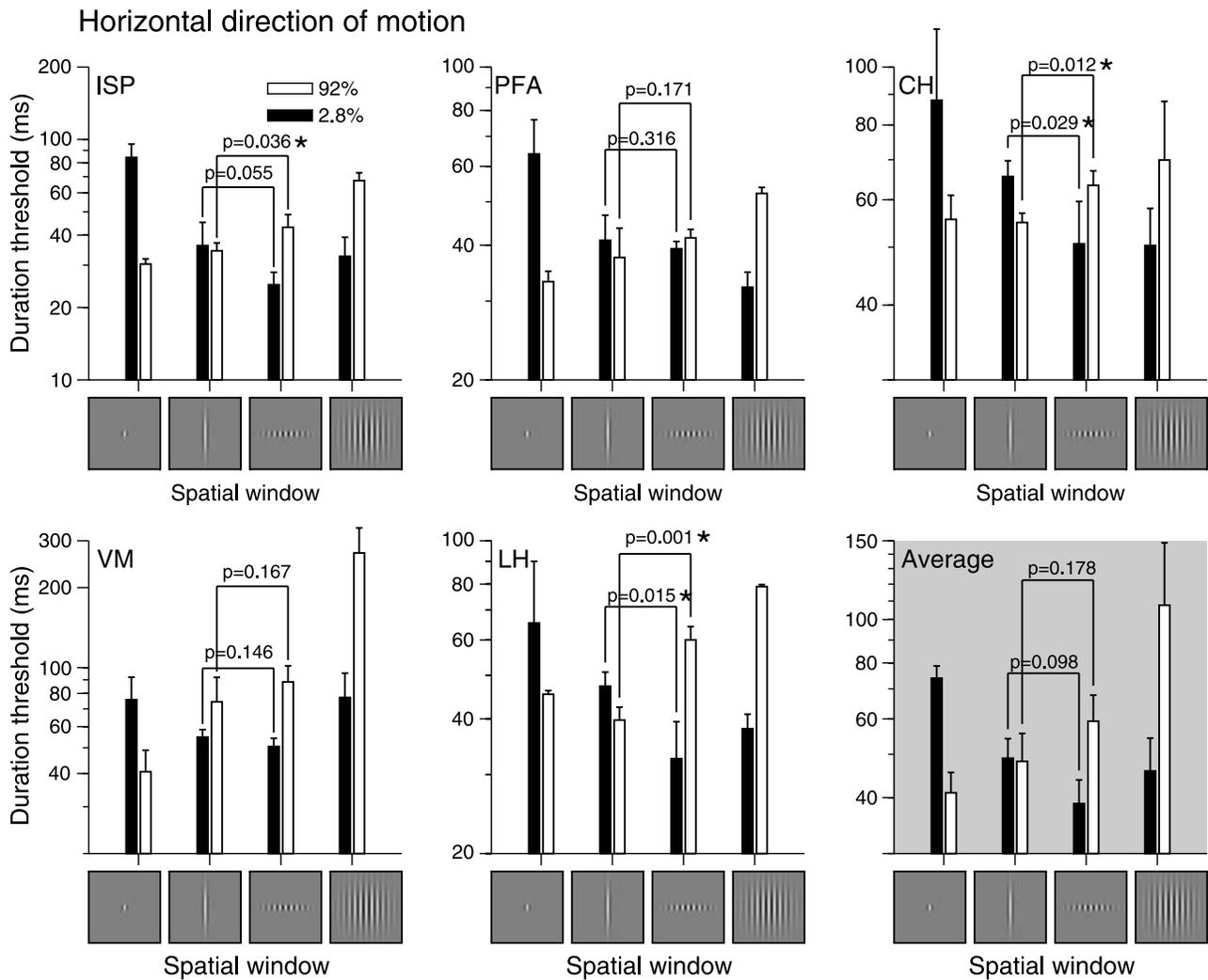
Horizontal direction of motion

Figure 2. Results from Experiment 1 (horizontal motion) for five observers. Each white panel shows the duration threshold (mean $\pm$ *SD* of three estimated thresholds) for horizontal direction discrimination for one observer as a function of the type of spatial window. From left to right: Small window; elongated window along the direction of motion; elongated window orthogonal to direction of motion; and big spatial window. White bars: Results from moving Gabor patches of high contrast (92%). The spatial frequency of the grating was 1 cycle/deg and the speed was 2 deg/s. Black bars: Low contrast (2.8%). Gray panel shows the average $\pm$ *SEM* of the duration thresholds of five subjects. Asterisks (*) correspond to significant differences using a two-sample *t*-test (one-tailed and alpha = 0.05).

direction of motion) of drifting gratings moving horizontally. The gratings were presented embedded in four types of spatial windows (two isotropic windows, one small and one big, and two elongated windows, one along the direction of motion and the other orthogonal to it) and two contrasts (low and high, see Figure 1). Figure 2 shows the duration thresholds as a function of the spatial window and contrast for five subjects. The results obtained with isotropic windows replicate previous results in motion discrimination with drifting gratings (Tadin et al., 2003). Comparing the leftmost and rightmost bars in each panel, we see that in every case the white bars are higher on the right while the black bars are higher on the left. That is, direction discrimination is impaired with increasing size

of high-contrast stimuli (92%, white bars) and facilitated with increasing size of low-contrast stimuli (2.8%, black bars). The average threshold values (Figure 2, gray panel) obtained in this experiment for the isotropic conditions are also very similar to those obtained in Tadin et al. (2003).

For elongated windows, at high contrast (92%), duration thresholds were lower for windows elongated *orthogonal* to the direction of motion than for those elongated along it (see Figure 2, white bars). At low contrast (2.8%), we found the opposite result: the duration thresholds were lower for elongation *along* the direction of motion (Figure 2, black bars). Both these statements are true for each subject individually, though the difference does not always reach significance.
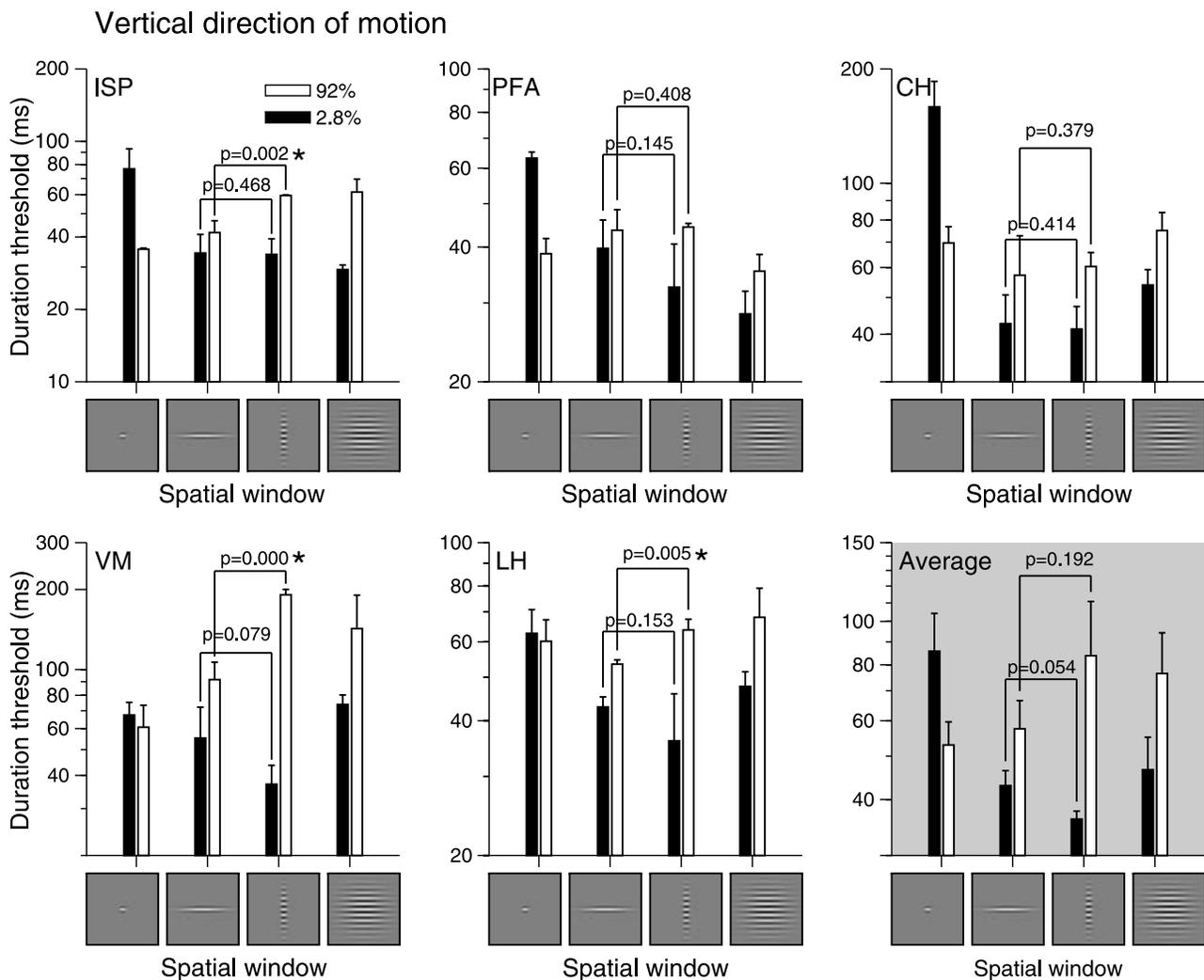
Figure 3. Results from Experiment 2 (vertical motion) for five observers. Each white panel shows the duration threshold (mean ± SD of three estimated thresholds) for vertical direction discrimination for one observer as a function of the type of spatial window. From left to right: Small window; elongated window orthogonal to the direction of motion; elongated window along the direction of motion; and big spatial window. White bars: Results from moving Gabor patches of high contrast (92%). The spatial frequency of the grating was 1 cycle/deg and the speed was 2 deg/s. Black bars: Low contrast (2.8%). Gray panel shows the average ± SEM of the duration thresholds of five subjects. Asterisks (*) correspond to significant differences using a two-sample t-test (one-tailed and alpha = 0.05).

Experiment 2: Gabor gratings drifting vertically

Experiment 1 confounds the effects of horizontal/vertical elongation and elongation parallel/orthogonal to the direction of motion. To discriminate between these, in Experiment 2, we changed the direction of motion from horizontal to vertical.

Figure 3 shows the results from Experiment 2 for the same five subjects. The results are qualitatively similar to those of Figure 2. Once again, comparing the isotropic windows, we find that, on average, duration thresholds become higher with increasing size for high-contrast stimuli and lower for low-contrast stimuli. However, for vertical motion, these differences are less dramatic,

especially for high-contrast stimuli, and are not present in all subjects individually. Turning to the elongated windows, we see that just as for horizontal motion, at high contrast, duration thresholds were higher for windows elongated along the direction of motion than for windows elongated orthogonal to the direction of motion (Figure 3, white bars); whereas at low contrast, duration thresholds were lower for windows elongated along the direction of motion than for elongated windows orthogonal to the direction of motion (Figure 3, black bars). Once again, the signs of these differences are consistent across subjects, although for some subjects the differences are tiny. So these results confirm that different elongations with the same size produce opposite effects on motion discrimination depending on contrast. This suggests that the
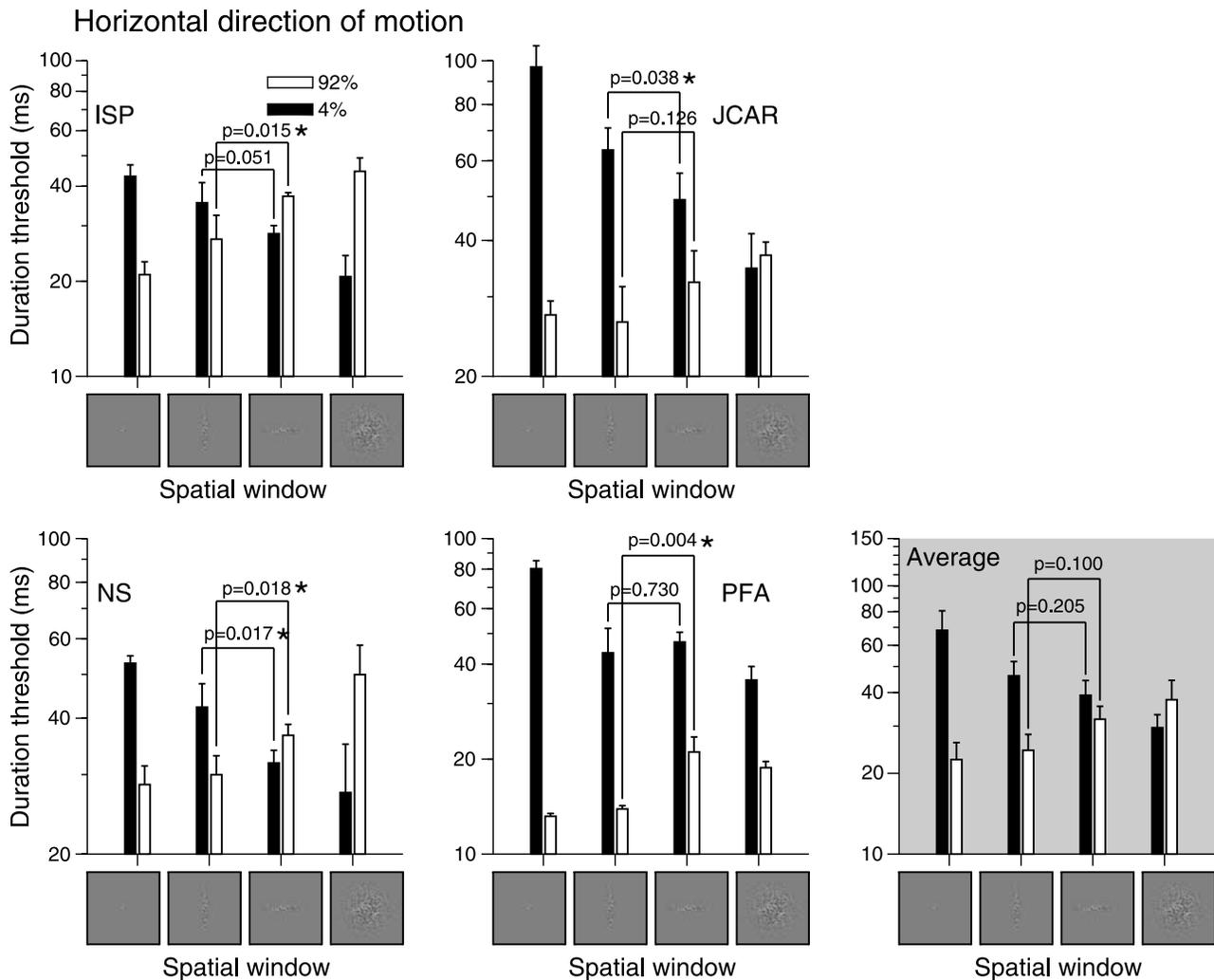
Figure 4. Results from the control experiment (horizontal motion using binary noise) for four observers. Each white panel shows the duration threshold (mean ± SD of three estimated thresholds) for vertical direction discrimination for one observer as a function of the type of spatial window. From left to right: Small window; elongated window orthogonal to the direction of motion; elongated window along the direction of motion; and big spatial window. White bars: Results from moving noise patches of high contrast (92%). The speed of the noise was 2 deg/s. Black bars: Low contrast (4%). Gray panel shows the average ± SEM of the duration thresholds of four subjects. Asterisks (*) correspond to significant differences using a two-sample *t*-test (one-tailed and alpha = 0.05).

difference between small and large isotropic windows may be driven largely by the increase in size orthogonal to the direction of motion. In the center–surround interpretation, our results imply that high-contrast drifting gratings with windows elongated along the direction of motion are suppressed more than the same stimuli with low contrast.

Control Experiment 3: Binary noise drifting horizontally

This asymmetry cannot be explained by differences in the stimulus contrast energy, which is exactly the same for both types of elongation (see Figure 1). However, the stimuli with elongated windows differ in the number of

visible cycles. For example, in the window elongated orthogonal to the direction of motion, only one cycle is visible, and in the window elongated along the direction of motion, 10 cycles are visible, i.e., 10 nearly identical white bars. This raises the possibility that the different effect of elongation along the two axes reflects changes in the number of features visible. In order to discard any window/ feature size confound, we performed a control experiment using a binary noise stimulus (we thank an anonymous referee for this suggestion). We repeated Experiment 1, horizontal motion discrimination, using noise made up of black and white squares, each 3.2 × 3.2 arcmin (2 × 2 screen pixels). The experimental conditions, speed, distance to the screen, apparatus, etc., were exactly the same as in the main experiment. For the high-contrast condition, we

again used a peak Michelson contrast of 92%. For the low-contrast condition, we found that two subjects could not perform the task with a small window and a peak Michelson contrast of 2.8%, presumably because in this broadband stimulus the available contrast energy is spread over many spatial frequencies. For this experiment, we therefore increased the contrast of the low-contrast condition to 4%. Four experienced psychophysical observers (ISP, JCAR, PFA, and NS) performed the experiment (PFA and NS were not aware of the purpose of the study). Figure 4 shows the results.

With binary noise, the different effect of elongation along the two axes is still present. At high contrast, duration thresholds were higher for the window elongated along the direction of motion than for a window elongated orthogonal to it. This difference was present for all of our 4 subjects and significant in 3/4 individually (see Figure 4, white bars). At low contrast, the duration thresholds for the window elongated along the direction of motion were usually lower than those obtained with a window elongated orthogonal to it. Although this difference was not significant for the population (Figure 4, black bars), the direction of the difference is in the same direction as for Experiments 1 and 2 and the magnitude of the effect is very similar between gratings and noise for the two subjects who were tested with both. These results obtained with binary noise confirm the results obtained with gratings and suggest that the relevant factor is indeed the spatial shape of the window relative to the direction of motion, rather than the number of features contained in it.

Discussion

The results with isotropic Gaussian windows replicate the results obtained in previous work (Tadin & Lappin, 2005; Tadin et al., 2003): at high contrast, the time required to discriminate the direction of motion gets longer as the stimulus increases in size. This counterintuitive result could be due to the center–surround antagonism displayed by neurons in cortical area MT (Allman et al., 1985a, 1985b; Born & Tootell, 1992; Tanaka et al., 1986). At low contrast, we have again replicated the opposite result: as the stimulus increases in size, direction discrimination improves (Tadin et al., 2003). This result could also be explained by the behavior of MT neurons, where their spatial summation increases for stimuli with low contrast (Gilbert et al., 1996; Kapadia et al., 1999; Sceniak et al., 1999).

Here, motivated by the known anisotropies in MT neurons, we asked whether increases in size along different axes have the same effect. Our results show very clearly that elongations along and orthogonal to the direction of motion have very different effects, even though the stimulus area and total contrast energy is identical in the two cases. At high contrast, thresholds were always *longer* for the elongation along the direction of motion than for the orthogonal elongation. At low contrast, on the other hand, thresholds were *shorter* for the elongation along the direction of motion. Our data contain 28 such comparisons, and these statements hold for 27/28 of them (the exception being subject PFA with low-contrast noise). Thus, this result is extremely reliable both within and across subjects. Similar results to ours have been reported in abstract form (Rajimehr, 2005), although details about the size of the elongations, the contrasts used, or the value of the duration thresholds have not yet been published.

Our results indicate that increases in stimulus size are most relevant when they occur along the direction of motion. This is so even though size increases have opposite effects for high vs. low contrast, suggesting that both spatial summation and surround suppression may act predominantly along the direction of motion. Van Doorn and Koenderink (1984) investigated coherence thresholds necessary to perceive coherent motion in random-dot kinematogram and found that for stimuli of a given area, the lowest thresholds are obtained for narrow stimuli elongated in the direction of motion. Given other psychophysical results suggesting that human motion sensors have roughly isotropic receptive fields (Anderson, Burr, & Morrone, 1991), this may indicate that in conditions of low contrast or coherence, information is summed across several motion sensors along the axis of their preferred motion direction. For high contrast, we suggest that our results may reflect anisotropy in the center–surround antagonism of MT neurons (Raiguel et al., 1995; Xiao et al., 1995, 1997). Our results are consistent with the physiological finding that, in macaque MT, the axis of maximum inhibition for bilaterally symmetric surrounds is usually orthogonal to the axis of the elongated excitatory receptive field, which tends to be orthogonal to the preferred direction (Xiao et al., 1995, 1997, see their neuron 7805, Figure 5; see also Born & Bradley, 2005 (their Figure 6c)). However, we note that Tanaka et al. (1986) did not find a differential effect of the surround when comparing two wedge-shaped surround stimuli, one aligned with the axis of preferred motion and the other orthogonal to it. Our results do not, of course, rule out alternative explanations. For example, the central excitatory receptive fields of center–surround mechanisms might change their shape depending on stimulus contrast, or the responses of motion sensors to different directions of motion (preferred vs. null) might be asymmetric and depend on contrast. Additionally, because we did not measure eye movements, we cannot be sure that the different stimuli did not evoke different eye movements. However, because the stimulus durations were so short ($2\sigma_t$ almost always <100 ms), whereas the latency for ocular following or pursuit eye movements is >50 ms, we believe that significant tracking movements are unlikely to have occurred.

In summary, this paper presents the first psychophysical evidence for anisotropic surround summation/suppression

in motion detection. It is consistent with known MT physiology and suggests new interpretations of existing psychophysical data.

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