

Interaction of spatial and temporal factors in psychophysical estimates of surround suppression

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Recent psychophysical work has shown that performance on a direction discrimination task decreases with increasing stimulus size, provided the stimulus is high in contrast. This psychophysical surround suppression has been linked to the inhibitory spatial surrounds that have been observed throughout the primate visual system. In this work we have examined a temporal factor that may also contribute to psychophysical surround suppression. Consistent with previous work, we found that psychophysical surround suppression is strongest when a high-contrast motion stimulus is presented very briefly so that the appearance of the stimulus coincided with its motion. However, when a brief delay was inserted between the stimulus onset and the onset of motion, the counterintuitive effects of stimulus size disappeared. The effect of the motion onset asynchrony (MOA) was strongest when the stationary stimulus immediately preceded the stimulus motion and when stimulus orientation during the MOA was very similar to that during the motion presentation. We conclude that psychophysical surround suppression is partially linked to the temporal structure of the stimulus, more precisely to a masking effect caused by sudden stimulus onsets (and to a smaller degree stimulus offsets).

Keywords: motion perception, surround suppression, masking

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Introduction

A common feature of visual neurons in the primate brain is the center-surround organization of spatial receptive fields (Hartline, 1940). The center of the receptive field is the area of space over which visual stimuli elicit a response, and the surround is a spatial region capable of modulating responses to stimuli placed in the center. Center-surround interactions are often inhibitory, and they are thought to be responsible for a number of psychophysical observations (Spillmann, 1994; Troncoso et al., 2007).

A striking perceptual analogue of center-surround neuronal interactions was recently demonstrated in the domain of motion processing. Tadin, Lappin, Gilroy, and Blake (2003) showed that increasing the size of a high-contrast moving stimulus decreased performance on a direction discrimination task. The effect reversed for low-contrast stimuli, so that the motion direction for larger stimuli was more easily discriminated. These findings on psychophysical surround suppression have subsequently been used to assess the strength of inhibitory influences in

clinical populations (Golomb et al., 2008; Tadin et al., 2006) and in subjects belonging to different age groups (Betts, Sekuler, & Bennett, 2009; Betts, Taylor, Sekuler, & Bennett, 2005).

Tadin et al. (2003) hypothesized that their results were due to center-surround interactions in visual cortical area MT. Neurons in MT are highly selective for motion direction, and roughly half of them exhibit inhibitory center-surround interactions (Born, 2000). Subsequent neurophysiological recordings showed that these inhibitory surrounds disappear at low contrasts (Pack, Hunter, & Born, 2005), which is consistent with Tadin et al.'s hypothesis.

The hypothesis that center-surround interactions are responsible for psychophysical surround suppression implies that perception in these studies is due entirely to the spatial structure of the stimuli. However, in the majority of the psychophysical experiments, discrimination performance is sampled using briefly presented, moving Gabor gratings. Indeed the psychophysical measure of discrimination performance is generally the duration of the stimulus required to obtain a criterion level of accuracy (Betts et al., 2005; Tadin et al., 2003) or the size of a brief

motion step between two stationary frames (Tadin et al., 2003). In these paradigms the onset of stimulus motion coincides with a change in contrast (and to a lesser extent, luminance) that corresponds to the appearance of the stimulus. The sudden onset and offset of a visual stimulus have been shown to exert various influences on neurons throughout the visual system (Maunsell & Van Essen, 1983; Movshon, Lisberger, & Krauzlis, 1990; Müller, Metha, Krauskopf, & Lennie, 2001), and these influences have a duration comparable to that of the motion stimuli used psychophysically. In particular the sudden appearance of a stimulus leads to a transient response that is by definition unselective for motion direction and can influence both the timing and the amplitude of the sustained portion of the response (Bair, Cavanaugh, Smith, & Movshon, 2002; Movshon et al., 1990). Moreover, responses to stimulus onsets and offsets might be expected to increase with stimulus size and contrast, and so they could account for some of the effects that have been previously attributed to space-domain mechanisms.

In this work we have attempted to isolate the influence of stimulus onsets and offsets on psychophysical surround suppression. We find that the diminished psychophysical performance for large stimulus sizes is eliminated when we introduce a stationary grating prior to the onset of stimulus motion. The stationary grating separates the appearance of the stimulus from its subsequent motion, and so our results suggest that psychophysical surround suppression depends strongly on the temporal, as well as the spatial, structure of the stimulus.

Apparatus and methods

Subjects

Four male subjects (mean age 27 years), including one of the authors (JC) and three naive paid subjects, participated in the experiments. All subjects had normal vision and some experience in psychophysical experiments. In the course of the experiments, the performance of one naive subject showed signs of over-training, resulting in a saturation of performance over all conditions. This subject's data were discarded from some of the later experiments (details provided below). Informed consent was obtained from the subjects before study participation, and all experimental protocols were approved by the Montreal Neurological Institute and Hospital Research Ethics Committee.

Visual stimuli

The stimuli were generated using a standard Pentium 3 PC computer with a spatial resolution of 1024×768

pixels and a presentation frame rate of 85 Hz. The stimuli were programmed in Matlab v7.0 using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and displayed by a CRT video projector (Electrohome 8000).

The Gabor stimuli used in our experiments consisted of a sinusoidal grating (spatial frequency of 0.5 cpd) windowed by a Gaussian envelope of varying widths. Stimulus diameter (defined as two standard deviations of the Gaussian envelope in each direction from the center (i.e. four standard deviations)) varied from trial to trial among 5.3, 7.9, 10.5, 13.2, 15.8, and 18.5 degrees. These values are similar to those used in previous work (Tadin et al., 2003). Stimuli were presented on a gray background with a luminance of 16 cd/m^2 . The Michelson-contrast of the gratings was always $\sim 98\%$ except in Experiment 1, in which we interleaved a condition in which the stimulus contrast was 1.5%.

General procedure

The experiments were conducted in a darkened room (luminance $< 0.2 \text{ cd/m}^2$). The subject was seated at a distance of 56 cm from a semi-transparent screen subtending a visual angle of 90×40 degrees. The subject's head was fixed using a forehead support to keep the distance between the eye and the screen constant. Each subject completed a training session of 1–2 hours before the start of each experiment to achieve reliable results.

The general form of the experiment is a modification of a paradigm that was previously used successfully to measure psychophysical surround suppression at different stimulus sizes (Tadin et al., 2003). Each trial began with a cue that was presented 20 degrees in the visual periphery to signal the start of the trial. The cue was used to reduce the temporal uncertainty about the appearance of the stimulus, which was otherwise difficult to detect in some conditions. This cue was followed 500 ms later by the appearance of a grating stimulus, which was always presented foveally, except where noted. The stimulus consisted of a horizontally oriented Gabor grating that subsequently underwent a phase advance corresponding to a single upward or downward motion step. For most experiments we manipulated the duration for which the stimulus was displayed before or after the motion step. We refer to the period between the appearance of the stimulus and the beginning of the motion step as the motion onset asynchrony (MOA), and to the time between the end of the motion step and the disappearance of the stimulus as the motion termination asynchrony (MTA). We interleaved conditions that involved various combinations of MOA and MTA durations, as well as stimuli of different sizes, orientations, and contrasts. Each stimulus variation is described in detail below (see also Figure 1).

After the stimulus presentation the subject indicated the perceived motion direction by pressing one of two mouse buttons. Following the response, the observer was given

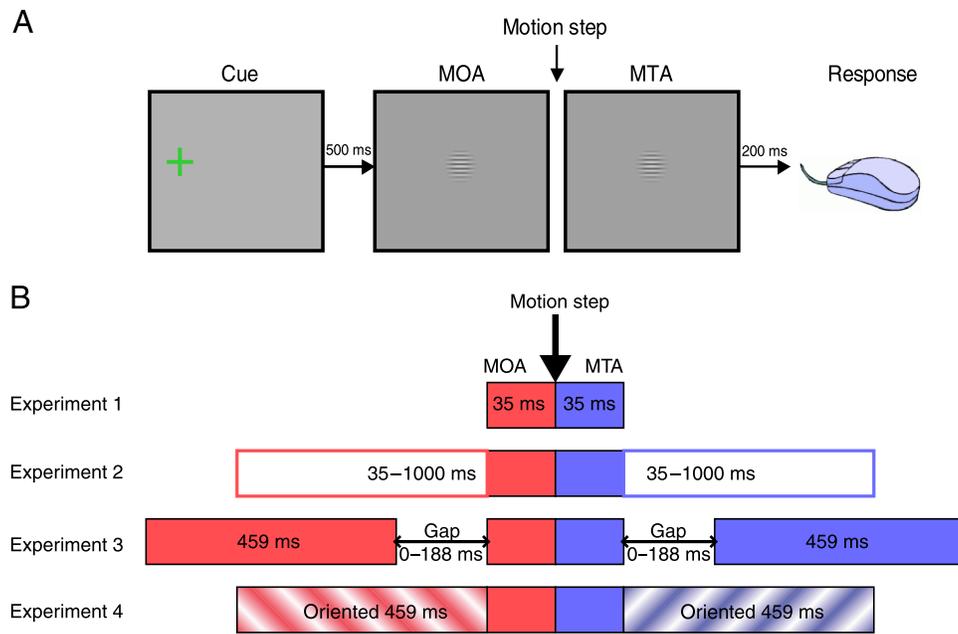


Figure 1. A: The time course of one trial. First a temporal cue was presented 20 degrees in the visual periphery to signal the start of the trial. 500 ms later the motion stimulus with a specific MOA/MTA was presented. The subject had to indicate the perceived motion direction by pressing one of two mouse buttons. B: The timing of stimulus presentation in the different experiments: The stimulus presentation in a time window from 35 ms before to 35 ms after the motion step was identical in all experiments. However, the context in which the motion step was presented varied between the experiments. In the first experiment, the MOA and MTA was 35 ms. In the second experiment we introduced MOAs and MTAs that varied in duration between 35 and 1000 ms. In the third experiment a gap of variable duration (0–188 ms) was introduced during the MOA and MTA periods, separating the motion step from presentation of the static grating. In Experiment 4 before and after the motion step the grating was presented at a different orientation than in the motion step.

feedback in the form of a red spot presented in case of a wrong response, and after a short delay (~ 300 ms) the next trial started. Performance in each discrimination task was quantified by the size of the phase step (0 to 90 degrees) necessary for the subject to discriminate reliably between the two motion directions. This motion discrimination threshold was obtained by a weighted up-down staircase procedure (Kaernbach, 1991), which adaptively applied different phase-step sizes between 0 and 90 degrees. The staircase procedure started at a phase step of 90 degrees and was terminated after 16 reversals. The step sizes were 10 degrees up and 5 degrees down for the first 5 reversals and 2 degrees up, 1 degree down for subsequent reversals. This staircase procedure converges on a performance of 66% correct responses on the psychometric function (Kaernbach, 1991). The threshold was then calculated as the mean of the last four reversals. Since the maximal phase step used was 90 degrees, thresholds close to this value show that the subject was unable to discriminate the direction of motion under the relevant task conditions. In most cases we randomly interleaved several staircase procedures corresponding to the different conditions tested in a given session. Each staircase procedure typically required 40–50 trials to complete.

Experiment 1: Contrast experiment

In this experiment the grating was displayed for 35 ms before and after the motion step at low (1.5%) or at high ($\sim 98\%$) contrast (Figure 1B, top row). We define the period before the motion step as the Motion Onset Asynchrony (MOA), and the period after as the Motion Termination Asynchrony (MTA). For one subject with relatively poor contrast sensitivity (JC), the lower contrast was increased to 3%. The two contrasts and six different stimulus sizes (5.3, 7.9, 10.5, 13.2, 15.8, and 18.5 deg.) resulted in 12 randomly interleaved staircase procedures during this experiment. The experiment required approximately 30 minutes to complete.

Experiment 2: Changes of MOA and MTA durations

This experiment addressed the influence of MOA and MTA durations on the discrimination thresholds for high-contrast gratings. On each trial the MOA or MTA was chosen from among 35, 71, 118, 494 and 1000 ms, with the duration that was not varied set to 35 ms (Figure 1B, second row). In separate versions of the experiment we tested the performance when only the MOA, only the MTA or both simultaneously were changed. Six stimulus

sizes were investigated, resulting in 30 interleaved staircases in each of the three versions of the experiment. Since this large number of trials could not be performed during one experimental session, the experiments were split into two blocks, one for the sizes of 5.3, 10.5 and 15.8 degrees and the other one for 7.9, 13.2 and 18.5 degrees. Each block required about 45 minutes, and the blocks were carried out in a randomized order.

Experiment 3: Gap in presentation

This experiment investigated the effect of a transient break in stimulus presentation on the discrimination thresholds (Figure 1B, third row). The MOA and MTA were both 494 ms. On each trial we introduced a gap of variable duration to separate the 35 ms before and after the motion step from the rest of the presentation. During the gap there was no stimulus, and the screen was blank. The duration of the gap varied among 0, 12, 24, 47, 94 and 188 ms. In the different versions of the experiment the gap was introduced either before or after the motion step, and in a third condition, the gap was applied in both periods. Six stimulus sizes were tested, resulting in 36 interleaved staircases for each of the three versions of the experiment. As described for Experiment 2, each measurement was split into two blocks. The execution of each block required approximately 60 minutes.

Experiment 4: Orientation of grating preceding motion

This experiment was designed to test the effect of changes in grating orientation on motion discrimination performance. The motion step was presented in the same way as in Experiment 1, with MOA and MTA set to 35 ms. However, before and after this period the grating was presented at a different orientation for another 459 ms (Figure 1B, fourth row). The difference in orientation between the moving grating and the static grating was 0, ± 2 , ± 5 , ± 10 , ± 20 , ± 45 or ± 90 degrees, resulting in 13 interleaved staircase procedures. Each of the six stimulus sizes was investigated separately in randomized order. The experiment required about 30 minutes for each size.

Data analysis

To make the trends in the data of different subjects independent of their individual performance in motion discrimination, we normalized the results of each subject in each experiment, according to:

$$T_{\text{norm}} = \frac{T - T_{\text{min}}}{T_{\text{max}} - T_{\text{min}}}, \quad (1)$$

where T_{min} and T_{max} give the minimal and maximal thresholds obtained from the subject on any condition in the particular version of the experiment.

The effects of stimulus size and contrast in experiment one were investigated by a two-factor ANOVA. For experiments two and three, the relationship between stimulus parameters and discrimination thresholds was investigated using a three-factor ANOVA model. The stimulus factors included in this model were:

1. The *version* of the experiment (i.e. whether the duration of the grating or the duration of the gap was changed during the onset or the offset periods).
2. The duration of the MOA or MTA (Experiment 2) or duration of the gap (Experiment 3).
3. The size of the stimulus.

The dependence on stimulus size was quantified as the difference between the normalized thresholds of the two smallest and the two largest stimulus sizes for each condition and each subject. Spearman rank correlation coefficients were calculated to relate the discrimination thresholds to various parameters of the stimuli. ANOVA statistics were calculated using the statistics package SPSS (ver. 13, SPSS Inc.) In Experiment 4, Gaussian functions were fitted to the data using the least squares algorithm implemented in the MATLAB optimization toolbox (ver. 4.0).

Results

Experiment 1: Discrimination performance depends on stimulus size and contrast

The first experiment was designed to quantify the dependence of motion discrimination performance on stimulus size and contrast for a very brief stimulus presentation (35 ms). Figure 2A shows the performance of the four subjects for high-contrast (98%; black line) and low-contrast (1.5%; gray line) stimuli across the different grating sizes. For all subjects the relationship between stimulus size and discrimination threshold depends strongly on stimulus contrast. For the low-contrast condition performance improves (as indicated by a decreasing discrimination threshold) with increasing stimulus size, while for the high-contrast condition performance deteriorates. The average results are shown in Figure 2B.

A two-factor ANOVA using the factors ‘contrast’ and ‘stimulus size’ revealed a significant main effect of contrast ($p < 0.001$) and no significant effect of size ($p = 0.23$). Importantly the interaction between the two factors was highly significant ($p < 0.001$), indicating that the effect of size on the discrimination threshold is different for the two contrasts. This relationship can also be quantified by the Spearman correlation coefficient between the size of the grating and the normalized discrimination threshold. This value was -0.80 ($p < 0.001$) (correlations between -0.71

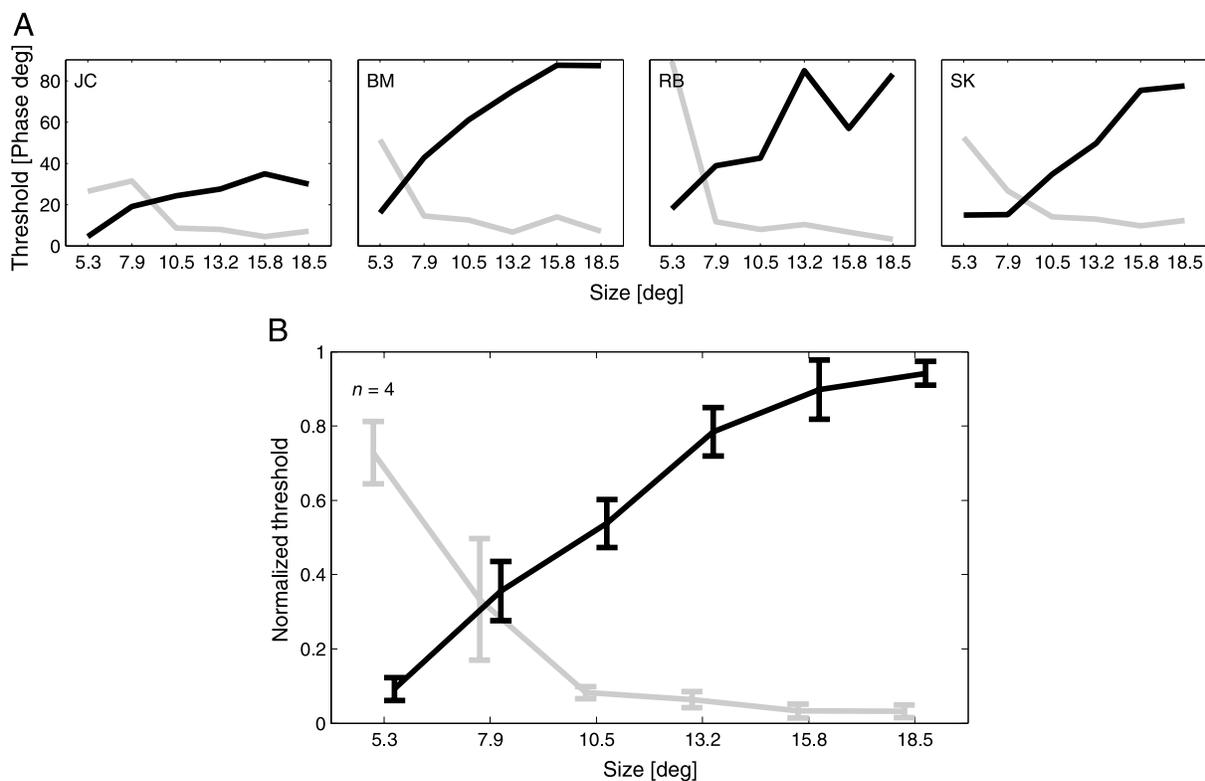


Figure 2. A: Performance of the four subjects in Experiment 1 for low contrast gratings (gray line) and high contrast gratings (black line) at different stimulus sizes. All subjects show increasing performance (decreasing threshold) for increasing stimulus sizes when low-contrast gratings are presented and decreasing performance with increasing size for high-contrast gratings. B: Mean values and standard errors of normalized thresholds across all subjects.

and -0.94 for individual subjects) for the low-contrast gratings and 0.88 ($p < 0.001$) (correlations between 0.83 and 1 for individual subjects) for the high-contrast gratings. The curves for high and low contrast intersect at a stimulus size of ~ 8 degrees (between 6 and 9 degrees for individual subjects). This result confirms earlier findings (Betts et al., 2005; Tadin & Lappin, 2005; Tadin et al., 2003) obtained under similar stimulus conditions.

Experiment 2: Effect of MOA and MTA durations

Psychophysical surround suppression of the kind observed in Experiment 1 can be attributed to a space-domain mechanism, namely the inhibitory surround mechanisms that are known to exist in the visual cortex (Tadin et al., 2003). The finding that surrounds are weak or absent during low-contrast stimulation in the motion-sensitive area MT (Pack et al., 2005) is generally consistent with this idea. In the next set of experiments we tested a potential time-domain explanation. Specifically, we hypothesized that the sudden appearance of the visual stimulus masks the responses to briefly presented motion stimuli. The masking effect might be expected to

increase with stimulus size and contrast, and so might lead to the psychophysical results seen in Figure 2. A similar argument could be made for a backward masking affect caused by a sudden offset of the stimulus. Indeed in our preliminary data, we have found that the transient responses to stimulus onsets in MT are less sensitive to contrast than are the sustained responses (Churan, Khawaja, Tsui, Richard, & Pack, 2008a). This may explain why psychophysical surround suppression disappears at low contrast, as neuronal responses to stimulus onset are largely absent in this case. Of course the space- and time-domain explanations are not mutually exclusive, and in fact we have recently provided further evidence that surround suppression is important in explaining diminished motion perception for large, briefly presented stimuli (Churan, Khawaja, Tsui, & Pack, 2008b).

If the sudden appearance of the stimulus is partly responsible for the above-mentioned effects of size and contrast, then increasing the MOA should abolish these effects. In this case the stationary stimulus would provide no information about the subsequent motion direction, but it would separate the transient stimulus onset from the motion step. Similarly, increasing the MTA should eliminate the effect of the sudden disappearance of the stimulus. Thus in the next set of experiments we varied

the duration of presentation of the stationary gratings both before and after the motion step. We refer to these periods as the MOA and MTA durations.

Figure 3A shows the effect of changing the duration of MOA and MTA on the performance of one example subject,

while Figure 3B shows the mean and standard errors of performance for the 4 subjects on all three tasks. In all cases the stimulus was a high-contrast Gabor patch, for which performance deteriorated with increasing size in the previous experiment. The top row of Figures 3A and 3B

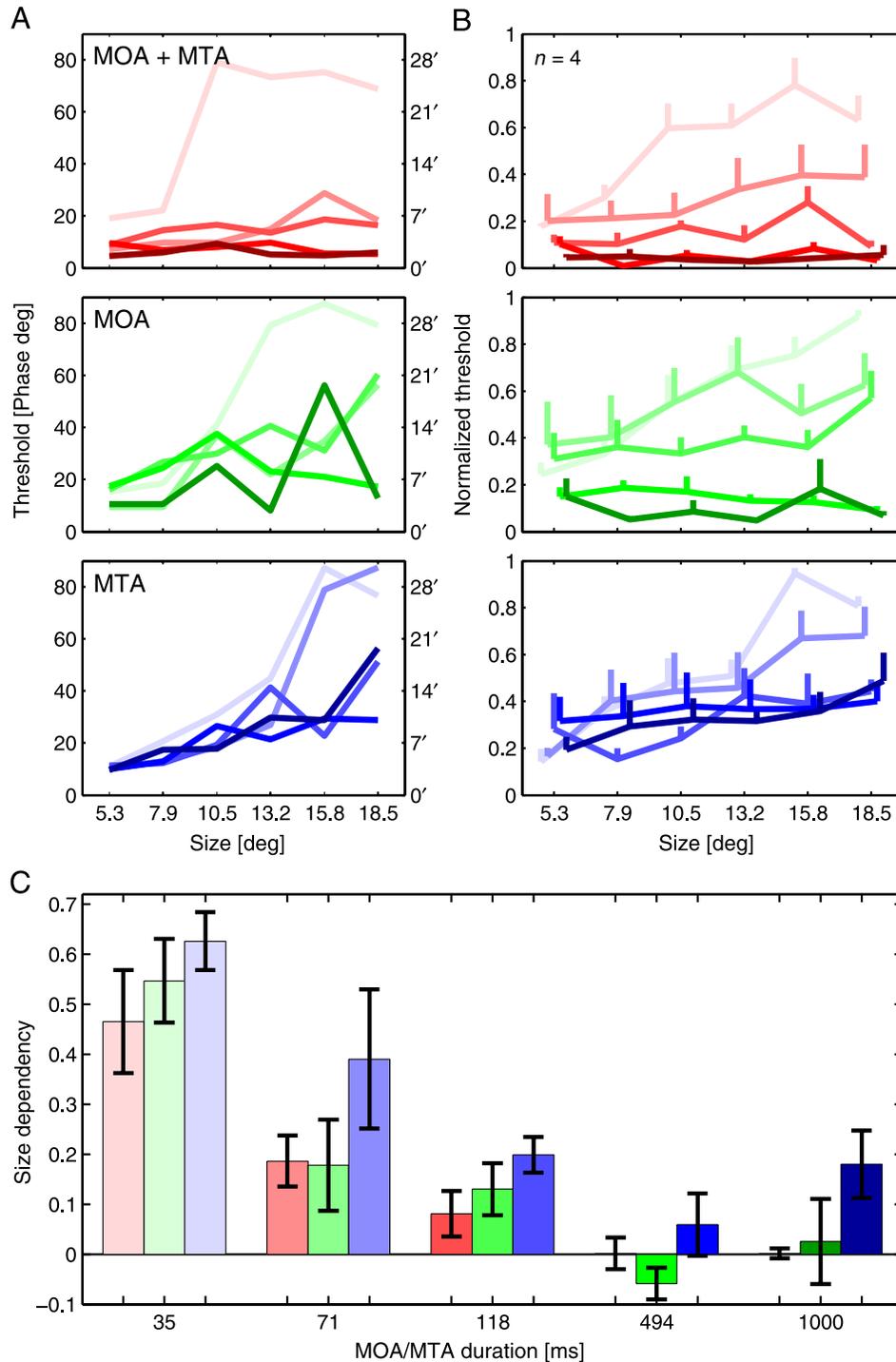


Figure 3. A, B: The performance of subject RB (A) and the average performance of four subjects (B) when a static grating was presented for different durations (light colors indicate short durations, dark colors long durations), as an MOA (green, middle panel), an MTA (blue, lower panel), or both (red, top panel). C: The differences in normalized thresholds between the average of the two largest and the two smallest stimulus sizes as a measure of the size-dependence of the thresholds. Error bars always show SEM.

shows the effect of manipulating both the MOA and the MTA for stimuli of different sizes. As in Figure 2, performance was quantified as the size of the step necessary for reliable direction discrimination, so that smaller values indicate superior performance. Each line indicates performance for a different MOA/MTA. The results clearly show that the effect of stimulus size decreases as the length of the stationary stimulus periods increases, even though the duration of the motion stimulus was constant across all conditions. Thus, for very brief motion stimuli, the introduction of a stationary stimulus before and after the motion step eliminates the dependence of performance on stimulus size.

These results are consistent with the idea that the sudden appearance and disappearance of the stimulus masks the subsequent motion percept. We next tested the effects of the MOA and MTA durations separately. In these experiments we varied either the MOA or the MTA, while keeping the other duration fixed at 35 ms (as in Experiment 1). These results are shown in the second and third rows of Figure 3.

Increasing the MOA or MTA durations beyond 35 ms had two main effects on direction discrimination performance, both of which can be seen in Figure 3B. First, the thresholds generally decreased, and second the dependence of stimulus size weakened or disappeared completely. To quantify the first result, we calculated the correlations between the discrimination threshold and the duration of the MOA or MTA for all stimulus sizes. The resulting Spearman correlation coefficients were -0.86 ($p < 0.001$) when both the MOA and MTA were changed, -0.81 ($p < 0.001$) when only the MOA was modified, and -0.44 ($p = 0.055$) when just the MTA was modified. Thus increasing the MOA improved performance, and a similar (though weaker) trend was observed for the MTA.

Our results in the long MOA condition are similar to displacement thresholds reported recently for low stimulus velocities under similar conditions (Lappin, Tadin, Nyquist, & Corn, 2009). Expressed in terms of spatial displacements (rather than phase-steps), thresholds for direction discrimination of a large (18.5 deg) patch changed from 17 arcmin for MOA and MTA durations of 35 ms to 2 arcmin for MOA and MTA durations of 494 and 1000 ms.

To obtain a measure of the size dependence of discrimination performance at different MOA and MTA durations, we calculated the difference between the discrimination thresholds for the two smallest and two largest stimulus sizes, and the results are summarized in Figure 3C. When only the MOA was increased (green bars), the size effect disappears completely at MOA durations above ~ 120 ms. In contrast, when only the duration of the MTA was increased (blue bars), the size effect weakened but remained present for all durations. This differential effect of MOA and MTA was confirmed by the Spearman correlations between stimulus size and discrimination threshold (Table 1). The correlation was significant for only the shortest MOA, indicating that the

	Duration [ms]				
	35	71	118	494	1000
MOA and MTA	.69**	.39	.15	-.01	-.07
MOA only	.77**	.29	.35	-.38	.02
MTA only	.82**	.60**	.52**	.32	.45*

Table 1. Spearman correlations between grating size and discrimination threshold for different MOA and MTA durations. Note: * $p < 0.05$, ** $p < 0.01$.

size dependence was sharply reduced as the MOA was increased to 70 ms. In contrast, the correlation remained for almost all MTA durations. Thus the size dependence of discrimination performance is more closely linked to the duration before the motion onset, while the presentation of the stimulus after the motion step can reduce but not completely extinguish the effect of stimulus size (as shown in the lower panel of Figure 3B).

We confirmed this analysis further with a three-factor ANOVA performed on the normalized thresholds using the factors 'version', duration of MOA/MTA, and size of the stimulus. The results revealed a significant main effect for all three factors ($p = 0.031$ for version, $p < 0.001$ for MOA/MTA and size). The interactions of version with MOA/MTA ($p = 0.018$) and MOA/MTA with size ($p < 0.001$) also reached significance.

In the experiments described thus far, all of the stimuli were presented foveally. To examine the dependence of our results on retinal eccentricity, we collected data from one subject (author JC) using stimuli presented 30 degrees in the periphery. In this experiment the MOA and MTA durations were varied simultaneously. We also varied the spatial frequency between two values: 0.5 cpd (as in the foveal experiments) and 0.25 cpd. Figure 4 shows that the interaction between MOA and MTA durations and psychophysical surround suppression is largely independent of both eccentricity and spatial frequency. That is, the size dependence of motion discrimination performance decreases with increasing MOA/MTA for foveal stimulus presentation (red bars), as well as for peripheral presentation using the same (dark blue) or a lower (light blue) spatial frequency. For lower frequency gratings the size dependence may even reverse at grating durations higher than ~ 100 ms.

Experiment 3: Influence of a transient gap

Experiment 2 revealed a strong influence of the MOA on the subsequent perception of motion. Specifically, the presentation of static grating for approximately 100 ms before the onset of stimulus motion improved direction discrimination and abolished the effect of stimulus size. One possible explanation for these results is that the abrupt onset of the stimulus interfered with the perception of the

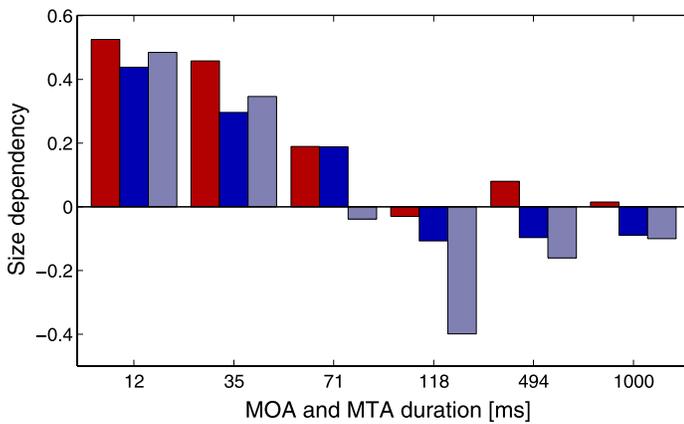


Figure 4. Comparison of size effects for foveal (red bars) and peripheral (blue bars) presentation of the stimulus for one subject. The spatial frequency of stimuli presented in the periphery was either the same as foveal presentation (0.5 cpd, dark blue) or decreased to 0.25 cpd (light blue).

brief motion step by means of a forward-masking process (Georgeson, 1988). Under this hypothesis, the increase of the MOA or MTA separates the transient change in contrast from the response to the motion, allowing for improved motion discrimination. If this idea is correct, then the MOA/MTA should be effective only insofar as it immediately precedes or follows the motion step.

To test this idea we used a long duration (494 ms) for both the MOA and MTA and introduced a gap of variable duration 35 ms before and after the motion step (Figure 1B). During the gap the screen was blank, allowing us to measure the extent to which the effects of the MOA/MTA depended on its temporal proximity to the motion step.

Figure 5 shows the effect of gaps of different durations on motion discrimination thresholds. In one version the gap was introduced before the motion step (green lines); a second version examined the effect of a gap inserted after the motion step (blue lines). We also tested the effect of introducing the gap both before and after the motion step (red lines). Figure 5A shows the performance for one example subject, and Figure 5B shows the average performance of 3 subjects. The data from the fourth subject were discarded due to an apparent effect of over-training, which resulted in very low thresholds for all conditions in these and some later experiments. Increasing the duration of the gap in general leads to an increase of discrimination thresholds independently of whether the gaps are presented before or after the motion step. The Spearman correlation between the mean normalized threshold and the duration of the gap was 0.86 ($p < 0.001$) when the gap preceded the motion step, 0.79 ($p < 0.001$) when it followed the motion step, and 0.87 ($p < 0.001$) when it was introduced both before and after the motion step.

As with the effects of the stationary gratings described above, the effect of the gap is stronger when it is presented before the motion step than when it is presented after.

This is shown clearly in Figure 5B, which indicates that the size dependence of direction discrimination performance increases more sharply when the gap is introduced before the motion step. We analyzed these effects further using the same method as in Experiment 2, by quantifying the size dependence of discrimination performance as the difference in thresholds obtained with the two smallest and the two largest stimulus diameters. The results for the different conditions are shown in Figure 5C. When no gap is introduced, the threshold is not influenced by the size of the stimulus, as shown in Experiment 2. However, the size dependence returns when the gap is introduced, and this is seen even for the shortest gap duration tested (12 ms). This size dependence increases with gap duration until about 50 ms, beyond which it remains constant. Spearman correlation coefficients between stimulus size and discrimination threshold (Table 2) support the differential effects of the gap presented before and after the motion step. Before the motion step the shortest gap duration induces a significant correlation between stimulus size and discrimination threshold, while a gap after the motion step does not show a significant correlation for any duration of the gap.

A three-factor ANOVA performed on normalized thresholds shows a significant main effect for each of the three factors ($p = 0.048$ for version, $p = 0.001$ for gap duration, $p = 0.007$ for stimulus size) as well as for the interactions of version with size ($p = 0.024$) and gap duration with size ($p = 0.006$). The significant interactions between version and size and between gap duration and size indicate that the effect of size on discrimination thresholds changes depending on the duration of the gap and its timing with respect to the motion step.

Experiment 4: Effect of changes in orientation

The previous experiments demonstrated that motion discrimination, particularly for large stimuli, is impaired by abrupt stimulus onsets, and that performance can be improved by introducing a stationary stimulus for a brief period prior to the onset of motion. This effect of the MOA depends critically on the temporal proximity of the static stimulus to the motion step. One possible explanation for these results is that the static grating allows the visual system to adjust contrast gain in a manner that is beneficial for motion discrimination. Another possibility is that improved performance with increasing MOA is specific to the structure of the stationary grating, rather than to its contrast. In the next experiment we examined these possibilities by varying the orientation (but not the contrast) of the static grating that preceded the stimulus motion. As in the previous experiment the MOA and MTA durations were 459 ms. During this time the stimulus did not move, but its orientation was tilted with respect to the subsequent horizontal grating that underwent the motion step (Figure 1B).

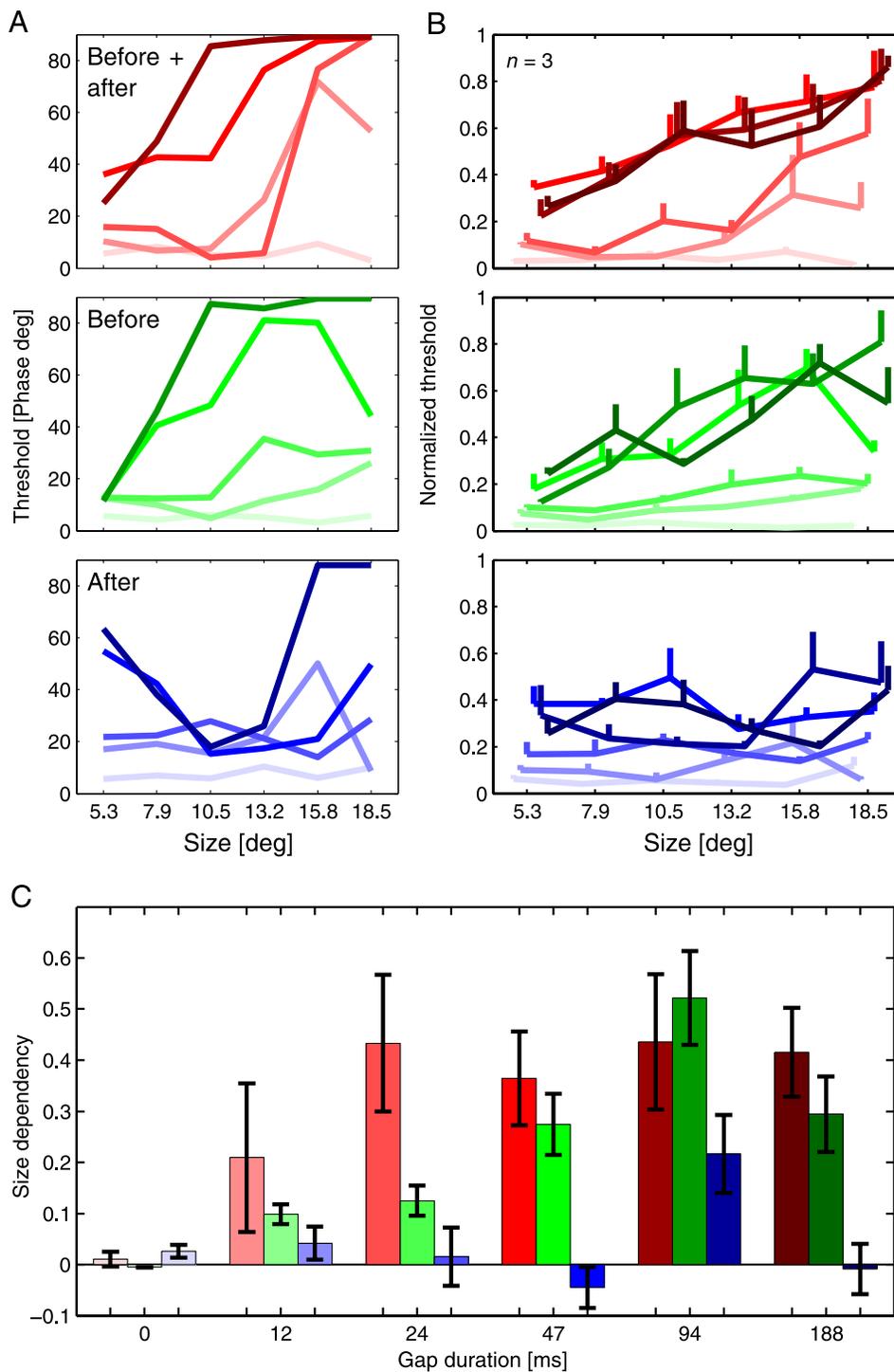


Figure 5. A, B: The performance of subject RB (A) and the average performance of three subjects (B) when a gap is introduced preceding the motion step (green lines, middle panel), following the motion step (blue, lower panel), or both (red, upper panel). Short gaps are coded as light colors and long gaps as dark colors. C: The differences in normalized thresholds between the average of the two largest and the two smallest stimulus sizes as a measure of size-dependence of the thresholds. Error bars always show *SEM*.

Overall we found that performance decreased as the orientation difference between the static and moving grating increased. Most notably, when the stationary grating was oriented orthogonal to the moving stimulus

the subjects were not able to discriminate the direction of stimulus motion for any step size. Discrimination performance for one example subject as a function of the orientation difference is shown in Figure 6A, with different

	Gap duration [ms]					
	0	12	24	47	94	188
Before and after	-.14	.27	.65**	.56*	.64**	.63**
Before	-.28	.67**	.58*	.48*	.71**	.55*
After	.13	-.02	-.02	-.09	.40	.05

Table 2. Spearman correlations between stimulus size and discrimination threshold for the different gap durations. Note: * $p < 0.05$, ** $p < 0.01$.

stimulus sizes coded by different shades of gray. We found that performance as a function of the tilt of the stationary grating for each subject at each stimulus size was well fit by a Gaussian function, and Figure 6B shows the average Gaussian for each orientation for the three subjects. The results show that the widths of the Gaussians decrease with increasing size of the stimulus. Figure 6C plots the standard deviations of each subject's best-fitting Gaussians against the stimulus size. For all subjects there is a significant negative correlation between the stimulus size and the standard deviation of the Gaussian curve, although the slopes differ from subject to subject.

To examine further the effect of orientation on performance, we compared the performance for different orientations of the static grating with the thresholds obtained from the same subjects in Experiment 1, which used MOA and MTA of 35 ms. Figure 6D shows the Gaussian fits for one subject along with his thresholds in Experiment 1 (dashed horizontal lines) for the same stimulus sizes. The intersections between each pair of lines show the orientations at which the performance with and without the presence of the static grating was identical. These points are found at an average orientation of 15.7 deg. (range 14 to 18 deg.) irrespective of stimulus size, indicating that even modest rotations of the static stimulus eliminated any benefit due to the long MOA.

Discussion

We have examined the dependence of psychophysical surround suppression on the temporal structure of the stimulus. Consistent with previous results (Tadin et al., 2003) we find that performance on a motion discrimination task changes with stimulus size, and that the direction of this change is dependent on the contrast of the stimulus. For high-contrast stimuli performance decreases with size, and the opposite trend is observed for low-contrast stimuli. In our second experiment we showed that the counterintuitive effect of stimulus size at high contrast disappears when the motion onset asynchrony (MOA; the duration between the onset of a stationary stimulus and the motion step) is increased. A smaller effect was observed for the motion termination asynchrony (MTA), which is

the duration between the motion step and the offset of the stationary stimulus. Experiment 3 revealed that this latter effect was not due to the duration of the stimulus *per se*, since the introduction of a brief gap between the static and moving gratings caused the size dependence of psychophysical performance to return. Furthermore, the effect of the MOA duration was not due to a general effect of contrast gain, since Experiment 4 showed that it was tightly tuned to the orientation of the static stimulus. In the following sections we relate these findings to previous work and consider the possible underlying mechanisms.

Comparison with previous results

The results of Experiment 1 confirmed previous findings (Tadin et al., 2003) obtained in a very similar discrimination paradigm. Performance in the direction discrimination task increased with increasing stimulus size for low-contrast stimuli and decreased with increasing stimulus size for high-contrast stimuli. Tadin et al. (2003) interpreted their results as an effect of the inhibitory center-surround influences that are observed in about 50% of the neurons in area MT (e.g. Born, 2000). This interpretation was supported by the finding that the inhibitory surrounds of MT neurons are far weaker when low-contrast stimuli are used (Pack et al., 2005).

Although our results confirmed the results of Tadin et al. in a similar paradigm, the relationship between stimulus size and discrimination performance changed dramatically when we manipulated the duration between the appearance of the stimulus and the motion step. Increasing this MOA beyond 35 ms decreased the size dependence of direction discrimination, and for MOA beyond ~100 ms the size dependence completely disappeared. Tadin et al. (2003) reported size effects using a MOA of 50 ms, and so their results are not inconsistent with ours. Thus we suggest that masking caused by the onset (and to a smaller degree by the offset) of the stimulus influences the subsequent percept of motion, and that this phenomenon contributes to the effects of size and contrast on motion perception.

At the same time we do not wish to imply that all effects of psychophysical surround suppression are due to abrupt stimulus onsets since similar psychophysical effects were obtained with long-duration stimuli by measuring motion after-effects (Tadin, Paffen, Blake, & Lappin, 2008), perception of counterphasing gratings (Aaen-Stockdale, Thompson, Huang, & Hess, 2008), and binocular rivalry (Paffen, Tadin, te Pas, Blake, & Verstraten, 2006), and there is little reason to believe that any of these measures would be affected by stimulus onsets. It is not clear to what extent these latter approaches engage the same mechanisms as the earlier experiments involving brief motion stimuli (Betts et al., 2009; Tadin et al., 2003), as neurophysiological data with comparable stimuli are not (to our knowledge) available. Moreover, we recently found that

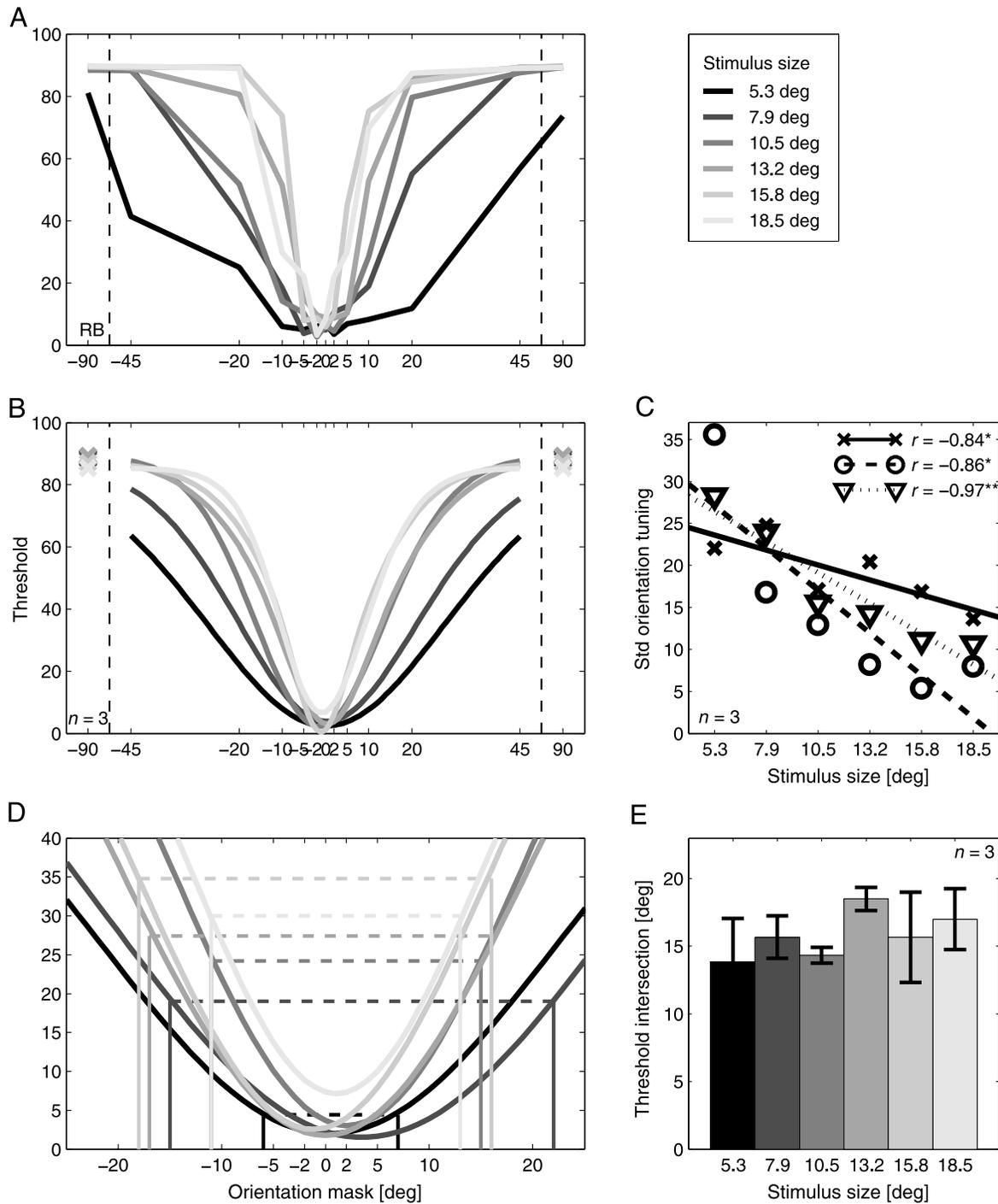


Figure 6. A: Thresholds for different orientations of the static grating and different stimulus sizes for one subject. Stimulus sizes are coded as different levels of gray, with dark representing small sizes and light representing large sizes. B: Average Gaussian fits to the orientation data for three subjects. C: Linear regression between size of the stimulus and the standard deviation of the fitted Gaussian function for each subject. D: Gaussian fits for one subject compared to his thresholds using MOA and MTA of 35 ms (obtained from the results of Experiment 1) (dashed horizontal lines). The intersections between the lines for each size give the orientations at which the perceptual benefit caused by long MOA and MTA durations is abolished by the orientation of the grating. E: The average orientation difference required to eliminate the benefit of long MOA and MTA for three subjects for different stimulus sizes (error bars show the SEM) show no systematic size-related changes. The average value for all sizes is 15.7 degrees.

brief motion stimuli similar to those used in our experiments and those of Tadin et al. (2003) preferentially activate MT neurons that have strong surround suppression (Churan et al., 2008b). This is consistent with a role for inhibitory surrounds in the phenomenon of psychophysical surround suppression. Thus temporal factors such as abrupt onsets appear to interact with spatial factors such as stimulus size in a rather complex way, and we are currently exploring this issue with additional MT recordings (Churan et al., 2008a).

Our results in Experiments 2 suggest that psychophysical surround suppression, as measured with brief stimuli, may share a common mechanism with forward masking. In studies on masking the presentation of one stimulus reduces sensitivity to another stimulus (Breitmeyer & Ögmen, 2006), even when the second stimulus differs in phase from the first (Georgeson, 1988). However, in most masking experiments increasing the duration of the mask stimulus does not restore sensitivity for the test stimulus (Georgeson, 1987), as it did in our experiment. Moreover, these experiments have generally used a fixed stimulus size and detection rather than discrimination as a measure of performance. Nevertheless our results on stimulus timing are generally consistent with the idea that forward (and to a lesser extent backward) masking is important to psychophysical surround suppression of motion stimuli.

In the space domain, there are divergent reports about the link between stimulus size and masking. In particular several studies have found that increasing the size of a mask can lead to a decrease of masking (Herzog & Koch, 2001; Wehrhahn, Li, & Westheimer, 1996; Yu & Levi, 2000) which is not consistent with a role for surround suppression in these masking processes. However, other studies have found that increasing the size of the mask increases the strength of masking effects (e.g. Bonneh & Sagi, 1999). These divergent results are likely related to the different stimuli used in the different experiments, which suggests that the spatial layout of the mask and target are more important than the overall size of the mask.

One interpretation that may provide a unified account of our results and previous work on masking involves mechanisms of short-term adaptation. Adaptation following the sudden onset of a stimulus has been observed psychophysically (e.g. Crawford, 1947; Pokorny, Sun, & Smith, 2003; Yeh, Lee, & Kremers, 1996), and it is thought to have effects similar to masking for a wide range of stimuli (Georgeson, 1987). In our experiments, short-term adaptation would be induced by the presence of the stationary grating during the MOA (Müller, Metha, Krauskopf, & Lennie, 1999). This would be particularly useful in the discrimination task if the sudden onset of the stimulus saturated the nonlinear responses of direction-selective mechanisms. In this case the difference between preferred and null-direction responses would be relatively small, and the MOA would permit the visual system to lower contrast gain, thereby becoming more sensitive to

motion direction. This hypothesis requires (compressive) nonlinear processing of contrast, which is consistent with observations in the magnocellular processing stream (Maunsell, Nealey, & DePriest, 1990). However, it is not clear how it relates to the significant (though weaker) effects of the MTA.

Although our results may be interpreted in the context of contrast adaptation, any such adaptation effect must be specific to the orientation of the masking stimulus. In Experiment 4 we showed that improved performance for large stimuli depended strongly on the orientation of the stationary grating that preceded the motion step. Relative to performance with a short MOA, an orientation difference smaller than approximately 15 degrees improved discrimination performance, while a larger tilt worsened it. This effect is consistent with observations on cross-orientation contrast masking (Saarela & Herzog, 2008), although in our experiments the influence of the mask on motion perception was substantially stronger, with orthogonal masks rendering observers completely insensitive to motion direction.

In general we have interpreted our results under the assumption that observers were attempting to detect the motion of the stimulus. However, another possibility is that observers used a strategy that involved tracking the displacement of the grating, rather than measuring the motion *per se* (Lee, Wehrhahn, Westheimer, & Kremers, 1993; Westheimer, 1978). Indeed recent work has shown that the perception of very brief motion stimuli is limited by spatial acuity, and that psychophysical surround suppression disappears at very low speeds (Lappin et al., 2009). Visual mechanisms that track stimulus displacement are likely to differ from those that detect first-order motion (Seiffert & Cavanagh, 1998), and so it is possible that observers switched from a motion detection strategy at short MOA to a displacement detection strategy at MOA longer than ~ 100 ms. Our results in Figure 4 showing higher displacement thresholds for peripheral stimulation are consistent with this idea. This explanation is also compatible with a role for onset transients in psychophysical surround suppression, but it makes the additional prediction that brain regions involved in measuring displacement will exhibit weaker surround inhibition than those that detect motion.

Possible underlying mechanisms

One obvious neuronal correlate of our psychophysical findings could be the transient burst of activity associated with onset of a stationary stimulus (Maunsell et al., 1990). Such onset transients are particularly powerful in the magnocellular processing stream, where they are often found to be higher in amplitude than the response to a prolonged stimulus for which the neuron is selective (Maunsell et al., 1990). Functionally, onset transients may serve as a means of alerting the visual system to the

presence of particularly salient features in the visual scene. They are also a rich source of information about orientation and contrast that can be used to facilitate rapid detection and discrimination of static stimuli (Müller et al., 2001). However, when the motion step is presented close to the onset of the stimulus, the onset transient (which is by definition unselective for motion direction) may interact with the motion signal and decrease the direction selectivity of the response. A correlate of this type of masking for stationary stimuli was found in macaque V1 (Macknik & Livingstone, 1998).

On the other hand a pure feedforward effect of stimulus onset may not be sufficient to explain the differential effects of stimulus size on the perception of high- and low-contrast gratings. Indeed it has been suggested that the visibility of a stimulus is more closely correlated with the later portion of neuronal responses (Supèr, Spekreijse, & Lamme, 2001), which may represent a re-entrant activation from higher visual areas (for review see Breitmeyer, 2007). It remains unclear to what extent the various forms of masking are due to purely feedforward mechanisms (Macknik & Martinez-Conde, 2007) or a combination of feedforward and feedback mechanisms (Breitmeyer, 2007; Fahrenfort, Scholte, & Lamme, 2007; Thompson & Schall, 1999). We are currently examining the interaction of the MOA duration and the motion response in MT using stimuli similar to those used in our psychophysical experiments (Churan et al., 2008a).

Another potential neuronal correlate of our psychophysical results is a short-term modulation of contrast gain. As mentioned above, such an adaptation effect might be expected to reduce responses to individual visual stimuli (Müller et al., 1999), but for our task what matters most is the differential effects on response to the two directions of motion. As far as we know this latter quantity has not been measured neurophysiologically. However, we have recently shown (Churan et al., 2008b) that at very short MOA the results on psychophysical surround suppression for brief stimuli can be qualitatively accounted for by center-surround interactions in area MT, as suggested by Tadin et al. (2003). Thus it will be interesting to examine how MOA and surround suppression interact in MT.

Functional considerations

Perceptually, the abrupt appearance of a stimulus is the basis for a number of psychophysical effects, including forward masking (Breitmeyer & Öğmen, 2006), the Fröhlich Effect (Fröhlich, 1923), the flash-lag illusion (MacKay, 1958), and the capturing of bottom-up attention (Remington, Johnston, & Yantis, 1992). In all cases the perception of a particular stimulus feature is influenced by a sudden change in the visual input, and these effects

depend heavily on the relative timing of the abrupt change and the feature to be discriminated.

These effects, as well as the ones reported here, may be of relevance to visual perception under naturalistic conditions. Outside of a laboratory setting, humans and other primates execute several eye movements per second, and each eye movement causes a rapid shift of the visual scene across the retina. Small eye movements are particularly common, and they induce changes in the stimulus that may be important for neurons throughout the visual system (Huang & Paradiso, 2005). In particular, small saccadic eye movements elicit retinal velocities that influence the responses of neurons in motion-sensitive areas such as MT (Bair & O'Keefe, 1998). From these considerations it follows that brief pulses of wide-field motion are processed by neurons in the visual system tens of thousands of times per day. Previous work has provided support for the existence of specialized mechanisms that suppress the perceptual effects of such motion stimuli (Murakami & Cavanagh, 1998), and we have recently begun investigating these mechanisms with stimuli similar to those used in the current experiments (Richard, Churan, Guitton, & Pack, 2007).

Conclusion

Previous work has shown that performance on a motion discrimination task deteriorates with increasing stimulus size for brief, high-contrast stimuli. We have extended this finding by showing that the decrease in discrimination performance depends on the temporal context in which the motion stimulus is presented. Inserting a stationary grating for roughly 100 ms prior to the onset of stimulus motion abolishes the counterintuitive effects of stimulus size, suggesting that what was previously thought to be a purely spatial phenomenon (psychophysical surround suppression) may depend critically on the temporal structure of the stimulus.

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