Brief motion stimuli preferentially activate surround-suppressed neurons in macaque visual area MT

Jan Churan, Farhan A. Khawaja, James M.G. Tsui and Christopher C. Pack

Intuitively one might think that larger objects should be easier to see, and indeed performance on visual tasks generally improves with increasing stimulus size [1,2]. Recently, a remarkable exception to this rule was reported [3]: when a high-contrast, moving stimulus is presented very briefly, motion perception deteriorates as stimulus size increases. This *psychophysical surround suppression* has been interpreted as a correlate of the neuronal surround suppression that is commonly found in the visual cortex [3–5]. However, many visual cortical neurons lack surround suppression, and so one might expect that the brain would simply use their outputs to discriminate the motion of large stimuli. Indeed previous work has generally found that observers rely on whichever neurons are most informative about the stimulus to perform similar psychophysical tasks [6]. Here we show that the responses of neurons in the middle temporal (MT) area of macaque monkeys provide a simple resolution to this paradox. We find that surround-suppressed MT neurons integrate motion signals relatively quickly, so that by comparison non-suppressed neurons respond poorly to brief stimuli. Thus, psychophysical surround suppression for brief stimuli can be viewed as a consequence of a strategy that weights neuronal responses according to how informative they are about a given stimulus. If this interpretation is correct, then it follows that any psychophysical experiment that uses brief motion stimuli will effectively probe the responses of MT neurons that have strong surround suppression.

We used Gabor stimuli similar to those used in the experiments on psychophysical surround suppression [3–5] to study the responses of 88 neurons in area MT of two alert macaque monkeys. MT neurons can be characterized as surround-suppressed or non-suppressed using standard statistical criteria [7,8], and these two types of neurons are clustered topographically [9] with separate projections [10] and different links to behavior [11]. In accordance with previous results [7,8], we found that suppressed (24/47, 51%) and non-suppressed (23/47, 49%) cells were roughly equally represented in MT. Figure 1 shows the mean responses of the suppressed (upper row) and non-suppressed (lower row) MT neurons to a motion stimulus that lasted 40 ms, a duration for which psychophysical surround suppression was shown to be quite strong [3–5]. The different panels of Figure 1 show the responses to preferred-direction (blue line) and null-direction (red line) stimuli ranging in size from 5° (left) to 14° (right). This range of stimulus sizes corresponded well to the range of excitatory receptive field sizes in our MT population (see Supplemental Experimental Procedures in the Supplemental Data available on-line with this issue).

From inspection of Figure 1, it is clear that the surround-suppressed cells (top row) are more strongly modulated by motion direction than are the non-suppressed (bottom row) cells, particularly for the two smallest sizes. Thus, for very brief stimuli, a simple strategy that involved counting the spikes fired by populations of MT neurons preferring opposite directions would presumably yield better performance

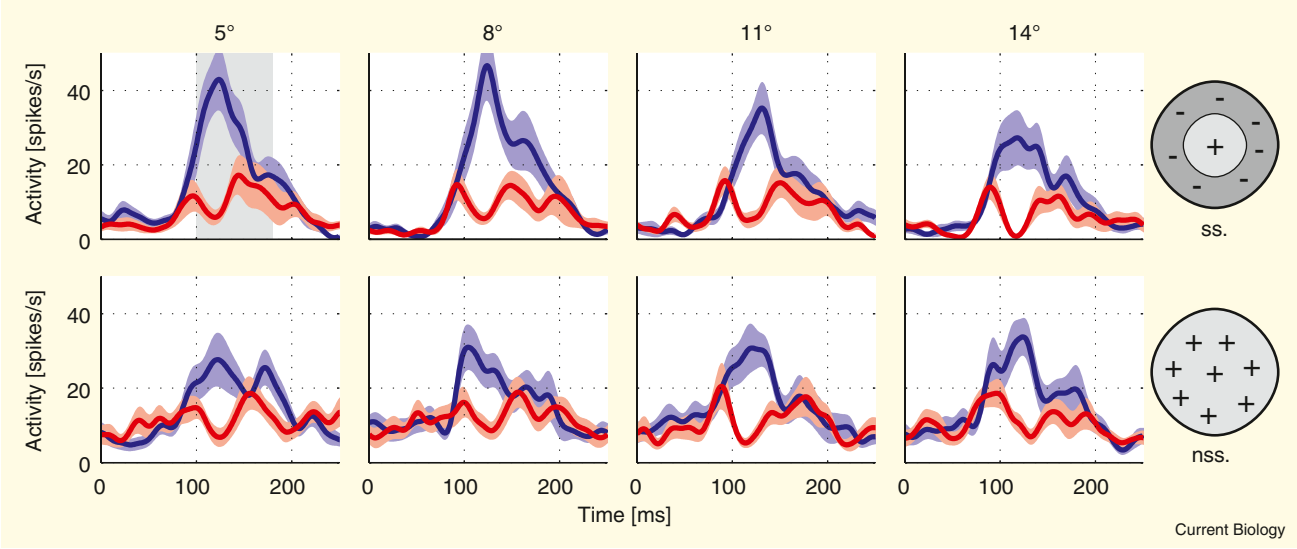

Figure 1. Responses of MT neurons to brief stimuli.

Average activity for 24 surround-suppressed neurons (first row) and 23 non-suppressed neurons (second row) to a stimulus moving in the preferred (blue line) or anti-preferred (red line) directions. The moving stimulus appeared at time 0 and disappeared 40 ms later. The gray rectangle in the upper left panel indicates the time window used to calculate the values of d' shown in Figure 2A. Shaded regions represent standard error of the mean.

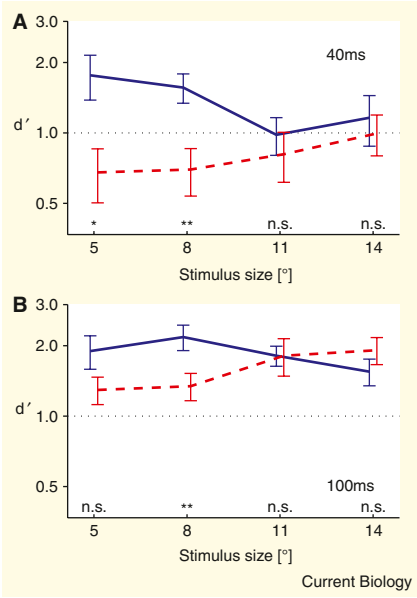

Figure 2. Motion discrimination analysis.

Mean *d′* values for the surround-suppressed neurons (solid line), and non-suppressed neurons (dashed line) for different stimulus sizes. (A) 40 ms stimulus duration. (B) 100 ms stimulus duration. The dotted horizontal line indicates the theoretical threshold for a single neuron to discriminate motion successfully 69% of the time. The significance markers at the bottom of each figure indicate significant differences between the surround-suppressed and non-suppressed neurons. Error bars represent standard error of the mean.

for small stimuli, and better overall performance if the readout gave greater weight to the surround-suppressed neurons. This disparity between the two subpopulations was largely eliminated when we extended the stimulus duration to 100 ms (see Figure S1 in the Supplemental Data), a duration for which psychophysical surround suppression was also found to be relatively weak [3–5].

To examine the MT data more quantitatively, we calculated each neuron's value of *d′*, a metric derived from signal detection theory [12] that can be used to describe the reliability with which visual motion information is transmitted. In particular *d′* = 1.0 can be thought of as the threshold for a single neuron to discriminate motion direction with ~69% accuracy. Figure 2A shows that, on average, the highest values of *d′* are found in the subpopulation of neurons that have significant surround suppression (solid line). Not surprisingly, this value decreases with increasing stimulus size, but in comparison the non-suppressed cells as a group (dashed line) are uninformative about motion direction for *any* stimulus size. This result was not a consequence of our method of dividing the MT population, because *d′* taken at the optimal size for each neuron was significantly correlated ($p < 0.01$; $r = 0.46$) with a continuous measure of surround suppression (defined in Supplemental Experimental Procedures). Thus, our results suggest that the phenomenon of psychophysical surround suppression is due to the fact that there is relatively little reliable information about large, briefly-presented stimuli in the output of most MT neurons.

Figure 2B shows the average discrimination ability of 59 MT neurons for the 100 ms duration condition. At this longer duration *d′* values improved substantially for the non-suppressed population ($p < 0.01$, ANOVA), while the effect of duration on the suppressed cells was only marginally significant ($p = 0.07$, ANOVA). We conclude that, in general, non-suppressed and suppressed MT neurons encode visual motion direction with roughly equal fidelity, but that the non-suppressed population requires a longer stimulus duration to respond reliably. One possible explanation for this finding is that the inhibition received by suppressed neurons is useful for eliminating noise in the input, and consistent with this idea we find that non-suppressed neurons have a significantly higher spontaneous firing rate than do suppressed neurons (t-test, $p < 0.01$).

The use of brief stimuli to probe psychophysical surround suppression has recently been extended in a number of interesting ways, with follow-up studies reporting reduced suppression in schizophrenic subjects [13], elderly subjects [4], young children [14], and subjects who suffer from depression [15]. However, there has been no functional explanation for why control subjects would rely so heavily on surround-suppressed neurons in these experiments. Our results on MT neurons provide a simple answer to this question, while suggesting that future psychophysical experiments can probe the properties of human surround suppression simply by using very brief motion stimuli.

Supplemental Data

Supplemental data are available at http://www.current-biology.com/supplemental/S0960-9822(08)01290-6.

Acknowledgments

We thank Julie Coursol for technical assistance and Aaron Seitz for helpful comments on the manuscript. This work was supported by grants from the CIHR (MOP-79352) and NSERC (341534-07) to C.C.P, as well as an award from the Fonds de la recherche en santé du Québec to F.A.K.

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Supplemental Data: Brief motion stimuli preferentially activate surround-suppressed neurons in macaque visual area MT

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Supplemental Experimental Procedures

Electrophysiological recordings. Two rhesus macaque monkeys took part in the experiments. Both underwent a sterile surgical procedure to implant a headpost and recording cylinder, and following recovery were seated comfortably in a primate chair (Crist Instruments) and trained to fixate a small red spot on a computer monitor in return for a liquid reward. Eye position was monitored at 200 Hz with an infrared camera (SR Research), and required to be within 2º of the fixation point in order for the reward to be dispensed. All aspects of the experiments were approved by the Animal Care Committee of the Montreal Neurological Institute, and were in compliance with regulations established by the Canadian Council on Animal Care

We recorded from well-isolated single neurons in area MT. Single waveforms were sorted online and then re-sorted offline, using spike-sorting software (Plexon, Inc). Area MT was identified based on anatomical MRI scans, the prevalence of direction-selective neurons, and on the correlation between receptive field size and eccentricity. We recorded from neurons with receptive fields centered at a mean eccentricity of 12.1º (s.d. 4.1º). The eccentricities for the surround-suppressed neurons were 11.7º (s.d. 4.5º), while those for the non-suppressed neurons were 12.4º (s.d. 3.8º). This difference was not significant (t-test, $p = 0.6$).

Once a neuron was isolated, we determined its optimal spatial frequency and stimulus position manually. We then obtained a direction tuning measurement with a Gabor stimulus of optimal spatial frequency, centered on the receptive field, and with a duration of 500 ms. Measurements of preferred speed and size were then obtained using stimuli moving in the cell's preferred direction. For the main experiment we interleaved Gabor stimuli of different sizes, directions, and durations at the optimal spatial frequency.

Visual stimuli. Stimuli were displayed at 85 Hz at a resolution of 1920x1200 pixels. The viewing area subtended 70° x 42° degrees of visual angle at a distance of 42 cm. Stimuli consisted of Gabor patches displayed on a gray background (luminance of 70.3 cd/m^2). For the initial characterization of the cell we drifted the Gabor in 8 directions to obtain the preferred direction, and then performed speed tuning (values: 1, 2, 4, 8, 16, 32, 64 º/s) and size tuning (values: 5, 10, 15, 20, 25, 30, 35º) measurements, with the size of the stimulus being defined as 2 standard deviations of the Gaussian envelope of the Gabor.

For the main experiment, sizes were drawn randomly on each trial from values of 5, 8, 11, and 14º. This range of sizes was chosen because it approximated the range of excitatory receptive field sizes in our population (see size tuning methods below). We also varied the motion direction, contrast (10% or 100%), and motion onset delay (0, 35, 100, 200 ms) from trial to trial [S1], although here we report results only for the conditions corresponding to 100% contrast and 0 ms motion onset delay. Stimulus duration was either 40 ms or 100 ms, with both durations being tested on 37/88 neurons. Limiting our analysis to only this latter group of neurons did not change any of the results reported here.

Analysis of neuronal data. We characterized the ability of each neuron to discriminate motion direction by calculating the quantity [S2]:

$$d' = \frac{(\mu_p - \mu_n)}{\sqrt{\frac{\sigma_p^2 + \sigma_n^2}{2}}},$$

where μ_p and μ_n represent the mean responses to the preferred- and null-direction stimuli, and σ_p and σ_n represent the standard deviation of these responses across multiple trials. The d' values for each neuron were calculated using neuronal response integrated over a time window between 100 ms and 180 ms after the onset of the motion stimulus for 40 ms stimulus duration (visible as the gray bar in Figure 1) and between 100 ms and 240 ms after stimulus onset for the 100 ms stimulus duration. The main results did not change when a variety of other time windows (between 60 and 340 ms) was used.

Surround suppression and size tuning

Methods for determining surround suppression and receptive field size were identical to those described previously [S3, S4]. Briefly, we categorized neurons as suppressed or non-suppressed by fitting data from size tuning curves to two models. One model was a scaled error function of the form:

$$R(w)=R_0 + A_e erf(w/\alpha),$$

where w is the stimulus size, R_0 is the baseline response, A_e is the excitatory amplitude and α is the size of the excitatory receptive field. The error function represents the integral of a Gaussian function, which was the underlying model of the excitatory receptive field. Similarly the contribution of an inhibitory surround was modeled by adding a second error function:

$$R(w)=R_0 + A_e erf(w/\alpha) - A_i erf(w/\beta),$$

where A_i is the inhibitory amplitude and β the size of the inhibitory receptive field. Neurons were considered surround-suppressed if the addition of the second error function provided a significantly better fit (sequential F-test, $p<0.05$) to the data than one error function alone. Surround suppression was quantified in a continuous manner as the ratio of the areas under the inhibitory and excitatory Gaussians defined above.

The size tuning data were also used to determine the extent of each neuron's excitatory receptive field [S3, S4]. Average receptive field sizes were 5.2º (s.d. = 2.3º) for the surround-suppressed cells and 7.2º (s.d. = 4.4º) for the non-suppressed cells. All but one of the neurons in our MT population had receptive fields that were smaller than the largest stimulus size used in the experiments (14º).

Statistical methods. Statistics were calculated using the statistics toolbox of MATLAB (The MathWorks) except for multivariate methods where SPSS v.13 (SPSS Inc.) was used. Parametric tests (t-test, ANOVA) were applied, since a Kolmogorov-Smirnov test performed on the d' values for different stimuli and sub-populations of neurons did not reveal a significant difference from normal distributions ($p>0.1$ for 15 out of 16 samples tested). We verified that the same results were obtained using non-parametric methods.

Supplemental Results

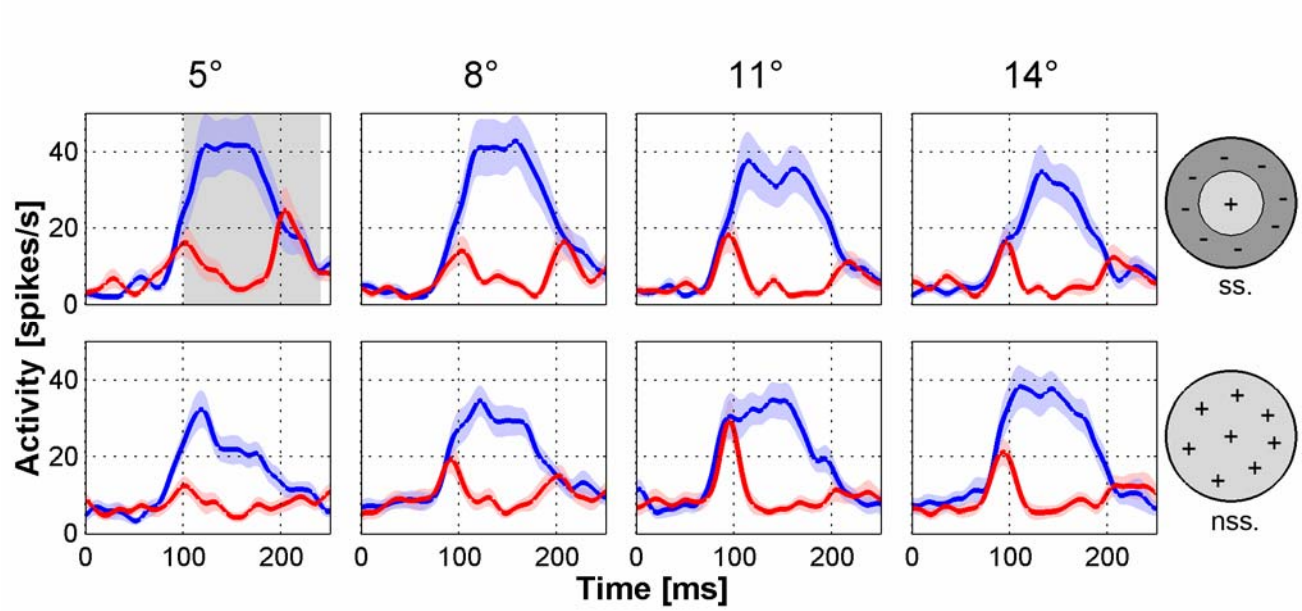

Figure S1. Average responses for 26 surround-suppressed neurons (first row) and 33 non-suppressed neurons (second row) to a 100 ms stimulus moving in the preferred (blue line) or anti-preferred (red line) directions. The gray rectangle in the upper left panel shows the time window used to calculate the d' values shown in Figure 2b. Shaded regions represent standard error of the mean.

Supplemental References

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