The Responses of V1 Cortical Neurons to Flashed Presentations of Orthogonal Single Lines and Edges

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ABSTRACT (250 words max)
How cortical neurons process multiple inputs is a fundamental issue in modern neuroscience. Neurons in visual cortical area V1 have been shown to exhibit cross-orientation suppression, where the response to an optimally oriented visual stimulus is reduced by the simultaneous presence of an orthogonally oriented stimulus. This is consistent with the view that cortical neurons respond to multiple inputs with a weighted average (or normalization) of the responses to the inputs presented separately. However, most of these studies have used drifting or counter-phase modulated grating stimuli, potentially confounding orientation effects with non-orientation specific gain control mechanisms. Additionally, primate vision depends to a great extent on transient stimulus presentations during fixations between saccades. Therefore this study examined the responses of primate V1 neurons to orthogonal flashed-onset single edges and lines, and to their combinations. Single edges or lines do not typically cause strong suppression of the responses to an orthogonal stimulus, even though a grating does. This appears to hold true regardless of the relative contrasts of the orthogonal single lines or edges. This is consistent with response suppression from an orthogonal grating being due to non-orientation specific contrast gain control (Walker et al., 1998, Priebe and Ferster 2006, Koeling et al., 2008). While normalization mechanisms are clearly important for the cerebral cortex, under many conditions the responses of V1 cortical neurons to an optimally oriented stimulus can be unaffected by the presence of orthogonal stimuli, which may be important to avoid confounding the interpretation of a neural response.

INTRODUCTION
It has been proposed that V1 cortical neurons selective for a particular orientation should inhibit neurons of similar receptive field location but of orthogonal orientation selectivity (Heeger, 1992; Carandini and Heeger, 1994; Carandini et al., 1997; Bonds 1989; Creutzfeldt et al, 1974; Morrone et al., 1982; Ramoa et al., 1986; Petrov et al 1980) This has variously been referred to as cross-orientation inhibition or, more generally, as cross-orientation suppression. However, a grating can have effects due both to its orientation and to its coverage of a large area, and studies have demonstrated suppression by either non-oriented or non-orthogonally oriented stimuli similar to that seen for crossed gratings (Bonds, 1989; DeAngelis et al., 1992; Walker et al., 1998). It has also been proposed that cross orientation suppression may not involve
A single line or edge might allow us to disentangle these effects, because it would have orientation but its smaller spatial extent would likely be less effective in activating non-orientation specific gain control mechanisms. Thus, determining how the presence of a single line or edge affects the response to another line or edge could be important in increasing our understanding of visual cortical function.

A great deal has been learned about the visual system by using stimuli that are either drifting or counter-phase flickering. However, much of primate vision is driven by the abrupt change in the retinal image caused by saccadic eye movements. For most visual cortical neurons the effects of flashing a stimulus on in the receptive field with the eyes fixed is comparable to having a saccade bring a constant stimulus into the receptive field (Richmond et al., 1999; Gawne and Martin 2002a). Therefore this study explores the responses of primate V1 neurons to flashed presentations of single crossed contours, and also of single contours and grating stimuli.

The finding here is that while a high-contrast grating will strongly suppress the response of a single orthogonal low-contrast edge, a single high-contrast line typically has little effect on the response to an orthogonally oriented low-contrast edge. Under many conditions V1 cortical neurons likely respond to a single line or edge independently of other orthogonally oriented stimuli in their RFs, which could allow for multiple orientations to be represented at one location in a visual image.

METHODS

The methods have been previously described in Gawne and Martin 2002b. In brief, Two rhesus monkeys (Macaca mulatta) were anesthetized with halothane and prepared for single-unit recording by implanting a recording chamber over striate cortex. A coil of stainless steel wire was placed under Tenon’s capsule of one eye to monitor eye position with the use of the magnetic field/search coil technique (Judge et al., 1980) (Riverbend Instruments, Birmingham AL).

Upon recovery the monkeys were trained to fixate a spot of light to within ±0.5° for juice reward, although their actual fixation was more accurate than this (typical standard deviation of
mis-fixation of ±0.17°, a precision commonly attained with maintained fixation, see Snodderly and Kurtz 1985).

Extracellular recordings of neurons were made using glass-coated platinum iridium microelectrodes, impedance approx. 1.3 megohms (Frederick Haer). The receptive fields were mapped by hand using black and white oriented bars, and the receptive field location and extent, as well as the optimal orientation, were determined. Only neurons that were clearly orientation-selective (at least a 2-1 ratio of response strength optimal vs non-optimal orientations) and had identical preferred orientations for both single lines, single edges, gratings, and hand-mapping with single bars, were used in this study.

Stationary visual stimuli were flashed on one at a time in shuffled random order centered in the receptive fields of the neurons. This paradigm was chosen to approximate the ecologically normal presentation of stimuli by saccadic eye movements, and previous work has determined that for most neurons there are only small differences between stimuli that are presented by flashing the stimuli or by making a saccadic eye movement (Richmond et al., 1999; Gawne and Martin 2002a). The stimuli consisted of oriented single lines, gratings, luminance edges defined by hemiplanes, and non-oriented random dot textures. Eight uniformly distributed orientations separated by 22.5 degrees were used.

The stimuli were presented on a video monitor running at 67Hz using a custom display program on a Macintosh PowerPC computer. Only data where there were at least 10 repetitions per stimulus were kept for analysis. The stimuli were flashed on for 10 video frames (150 msec), and responses were quantified by counting spikes in an epoch starting 30 ms after stimulus onset (shorter than the shortest latency we found here) and lasting 150 ms (thus avoiding the off-response, if any). Stimulus timings were verified accurate to 1 msec by recording the responses of a photocell taped to the video monitor. The background was a uniform gray of luminance 6.96 cd/m². The luminances of all crossed stimuli were adjusted to be consistent with the case of transparency/shadows: for example, the luminance of a thin white line was increased as it crossed a boundary from the dark to a light region of a hemiplane-defined edge, precisely as if the thin white line had been projected onto two surfaces of different reflectance. It may be that when the conditions of transparency/shadows are not adhered to, the interpretation could be of the corner of a new object rather than two independent overlapping contours. Certainly changing the contrast of stimuli to be consistent or inconsistent with transparency can have large effects on
the responses of visual cortical neurons (Snowden et al. 1991; Yazdanbakhsh and Livingstone, 2006). The high-contrast stimuli ranged from 65 to 82% contrast, and the low contrast stimuli ranged from 8 to 18% contrast, depending on the cell. The stimuli were located 4-6° from the fixation point, and were 2° in width, wider than that of the largest receptive field studied.

Spike latencies were calculated as in Sundberg et al. 2012. Spike counts were taken from the interval from 30 to 180 msec after stimulus onset: shorter than the shortest latency, and before any detectable off-response.

All experimental procedures and care of the animals were carried out in compliance with guidelines established by the National Institutes of Health and were approved by the UAB Animal Care and Use Committee.

Results

Data were recorded from a total of 42 neurons in the different paradigms. An additional 25 neurons were recorded but their data were not used because they did not meet the criteria detailed in the methods section. Each paradigm was run on different cells on different days interleaved with a series of other experiments. The spontaneous firing rate of the cells before stimulus onset was 1.33 +/- 1.12 (std) spikes/sec, range 0.00 to 5.71 spikes/sec. The orientation tuning (ratio of spike count at optimal/null) was a mean of 13.89 +/- 26.46 (std), range 2.15 to 140.0, median 4.785.

***** FIGURE 1 AROUND HERE *****

Figure 1 A illustrates the responses of an example neuron to a high-contrast oriented line (bottom row, dashed medium gray line), a low-contrast hemi-edge (middle row, light gray line), and the orthogonal intersection of the two (top row, response to combined stimuli represented as the solid black line). Responses are the spike density functions (smoothed with a Gaussian kernel sigma = 8 msec). Stimulus onset and offset times are represented by the vertical dotted lines. When the crossing stimuli have the high-contrast line near the optimal orientation (top row, middle panels), the orthogonal low-contrast edge has essentially no effect. When the low-contrast edge is near the optimal orientation (top row, panels at far left and far right), the responses are still quite robust. Figure 1B,C show the spike count and the response latency for the example neuron, and Figure 1 D,E the mean of the mean of 16 neurons. The response magnitude tends to follow whatever is the maximum of the response to either stimulus when
presented separately at those orientations. For some stimulus conditions with few spikes the 95% bootstrapped confidence intervals for latency can be quite large (see Figure 1C), but nevertheless, it is clear that in general the response latency is locked to the response to whichever stimulus (high-contrast line or low-contrast edge) that generates the shortest latency response (consistent with Gawne 2011).

***** FIGURE 2 AROUND HERE *****

Figure 2A shows the responses of an example neuron to an optimally oriented low-contrast edge (far left, light gray line), a non-optimally oriented high-contrast grating (second from left, dashed medium gray line), and the superposition of the two (middle panel, solid black line). The non-optimally oriented high contrast grating almost completely suppresses the response to the optimally oriented low-contrast edge. However, a non-optimally oriented low-contrast grating has essentially no effect on an optimally oriented low-contrast edge (rightmost two panels). Figure 2B illustrates that a non-optimally oriented low-contrast edge has no effect on the response to either a low or a high contrast, optimally oriented grating. Figure 2C shows summary data from 14 cells for the response to an optimally oriented low-contrast hemi-edge (left bar in the plot), the same optimally-oriented low-contrast hemi-edge with an orthogonal high-contrast grating superimposed (middle bar in plot), and also with an orthogonal low-contrast grating superimposed (rightmost bar in plot). As with Figure 2A, the response to an optimal low-contrast hemi-edge is suppressed by an orthogonal high-contrast grating but not a low-contrast grating. Figure 2D shows summary data from a different set of neurons, and illustrates that the same pattern of contrast-dependent suppression is found with non-oriented random dot textures (see also Priebe and Ferster 2006).

DISCUSSION

In accord with previous studies (Walker et al., 1998, Priebe and Ferster 2006, Koeling et al., 2008) the interactions between orthogonal contours seen here in the responses of V1 cortical neurons can be most simply explained by a non-orientation-specific contrast gain control that requires only a large amount of high-contrast ‘energy’ (oriented or not) across the receptive field. Certainly a single orthogonal line has less orientation ‘energy’ than an orthogonal grating made up of many oriented lines, but because non-oriented textures show the same pattern of
suppressive effects as gratings, the simplest explanation is that suppression by an orthogonal 
grating depends primarily upon the amount of contrast energy and not the large numbers of 
oriented lines per se (although see Koeling et al. 2008, for a discussion of this issue). In the 
ecologically common case of single contours rapidly presented in the receptive field of a V1 
neuron, suppression by single orthogonal oriented lines or edges does not appear to be either 
common or robust.

Lampl et al. (2004) found that, for parallel optimally oriented lines in the receptive field 
of a V1 cortical neuron, the response to two lines was most often similar to the largest response 
of a single line presented separately. Their results are commentary to those shown here for 
orthogonal stimuli, and support the idea that, for stimuli that do not ‘cover’ large parts of the RF, 
multiple effective stimuli within the RF of a single neuron do not routinely engage normalization 
mechanisms.

It is certainly true that stimuli of different orientations can interact in their effects on V1 
cortical neurons (Sillito and Jones, 1996; Levitt and Lund, 1997; Kapadia et al. 2000). However, 
the results here suggest that there is no obligate competition in visual cortex between orientations 
for a specific region of visual space. This is in agreement with theoretical work proposing that at 
the early stages of visual processing all orientations should be capable of being represented at all 
locations in space (Elder and Zucker, 1998), and with human psychophysical work 
demonstrating that the orientation cues characteristic of lines and edges are processed 
independently at the same location (Victor et al. 2013). In contrast, the results here are not 
consistent with some other theoretical work, where it has been proposed that a combination of 
competition between neurons responding to different orientations at the same location and 
cooperation between neurons responding to the same orientation at different locations would 
help the visual system ‘lock in’ to a single unambiguous percept (Grossberg and Mingolla, 
1985).

More generally, there have been many studies exploring the interactions of multiple 
stimuli of all kinds – not just oriented gratings - in the receptive fields of visual cortical neurons. 
This approach has been used as a proxy to probe how cortical neurons perform computations on 
multiple inputs. Most such studies have supported the idea of a biased competition, where 
different stimuli compete to control the response of a neuron (Reynolds et al 1999; Reynolds and 
Desimone 2003; Moran and Desimone 1985; Luck et al 1997; Zoccolan et al 2005). In this
view, the response to multiple stimuli is a weighted average of the responses to the stimuli presented separately. Thus, when a neuron is stimulated with both an effective and an ineffective stimulus, its response should be midway between the two. On the other hand, a significant minority of studies have yielded evidence for a winner-take-all or “max” operation, where the response to two simultaneously presented stimuli is the same as the response to the single most effective stimulus (Heuer and Britten, 2002; Lampl et al. 2004; Sato 1989; Rolls et al 2003; Oleksiak et al. 2011; Finn and Ferster 2007; Gawne and Martin, 2002b; Gawne 2008).

How should we resolve this apparent contradiction?

Consider that when two stimuli are presented in the RF of a visual cortical neuron, we are not controlling the direct inputs to that neuron or even to the local microcircuit, but the visual stimuli are processed and filtered in many stages beforehand, which may result in additional interactions. Also, whenever visual stimuli are presented there will be non-specific gain control mechanisms (see Carandini and Heeger 2012), which will tend to lower the level of response to multiple stimuli (relative to single stimuli) no matter the computation actually performed by a single neuron (or local microcircuit) on its direct input. Finally, when multiple stimuli become closely apposed in space, nonlinear mechanisms may increasingly treat this configuration as a single stimulus of a different type, instead of as two independent stimuli.

In previous studies in V4 this issue was addressed by presenting two stimuli as far apart as possible while still remaining within the RF (Gawne and Martin 2002b; Gawne 2008). However, because RFs are smaller in V1, the approach of spatially separating different stimuli is more problematic in this earlier visual cortical area. Single thin lines and edges offer a different approach: the parts of these stimuli exhibiting contrast are spatially limited, which should reduce the recruitment of non-specific gain control mechanisms. Also, as long as the condition of transparency is maintained, these stimuli could remain functionally distinct even when they overlap (Snowden, Treue et al., 1991).

An issue when using single lines or edges is that, unlike gratings, one could possibly position the center of rotation away from the center of the RF. In this case one might really be recording the response to a part of a line as it sweeps across the RF, in such a way that even a non-orientation selective cell might appear to be orientation selective. Requiring the orientation tuning curves for single lines and edges to match those for extended gratings is a control for this possibility. In addition, the orientation tuning obtained by hand mapping matched the orientation
tuning when the stimuli were flashed on during the experiment. Given the high degree of actual
precision of maintained fixation (see methods), the size and offset of the receptive fields of the
neurons under study, and the long-observed insensitivity of V1 complex cells to small shifts in
position of a visual stimulus (Kjaer, Gawne et al., 1997; Hubel and Wiesel, 1968), it seems
unlikely that variability in eye position would have been a significant source of variance in the
results.

A limitation of this study is that the different experimental paradigms were performed on
different cells on different days. However, because the same procedures for identifying and
isolating single neurons were performed on all cells, the odds that one paradigm was performed
on a completely different category of cells than another paradigm, is very small.

Latency tends to be relatively constant with changes in orientation for high contrast
stimuli, but varies much more strongly with orientation for lower-contrast stimuli (See Figure
IC,E), consistent with Gawne et al. 1996. It is hypothesized that for high-contrast stimuli, there
is a fairly synchronous volley of short-latency afferent inputs and the cells are driven above
threshold quite rapidly, similarly for both strong and weak responses. In this case there is a
relatively low correlation between response strength and response latency. However, for low-
contrast stimuli, the afferent inputs dribble in over time and the cell (or the local network) must
integrate the activity over time to generate a response, and you start to get a stronger correlation
between response magnitude and response latency. It should also be noted that, when two single
bars are present at the same time, that the response latency is generally locked to the shortest of
the two latencies (it is not clear how to perform this analysis when using high-contrast gratings,
because these stimuli tend to dominate the response of the neuron at all orientations). It is
hypothesized that for a stimulus that elicits short-latency afferent input, then even if this input is
too weak to generate a response on its own, it may nevertheless ‘prime’ the neuron (or local
circuit) and allow the slower but more numerous inputs from the longer-latency afferents to
generate a strong, short-latency response (at least for some stimulus configurations, see Gawne
2011).

Of course, this study was not a full survey of all cell classes in primate V1. It may well
be the case that there are other categories of neurons where orthogonal orientations do interact
strongly. Nevertheless, the results of this study do show that cross-orientation suppression for
single flashed stimuli is not obligate, and that neurons which do not show cross-orientation suppression to flashed stimuli must be extremely common.

The results of this study suggest that, under at least some conditions, many V1 cortical neurons respond to a single optimally oriented line or edge independently of orthogonal lines and edges. This lack of normalization may be important to avoid confounding the interpretation of a neuronal response, and allow for the accurate representation of multiple orientations at a single location in visual space.

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Figure Captions
Figure 1 A. Responses as a function of time to high-contrast single lines (bottom row, medium dashed gray lines), low-contrast hemi-edges (middle row, light gray lines), and orthogonal intersections of the two (top row, solid black lines), of eight equally spaced orientations. Thin lines are +/- the standard error of the mean (omitted from multi-line plots for clarity). The responses to the cross stimuli are typically locked to the response to the stimulus that is closest to the optimal, and relatively unaffected by the presence of an orthogonal stimulus. B,C. Spike count and response latency from the example neuron in panel A. Error bars are bootstrapped 95% confidence intervals. The spike count tends to follow what the strongest response of each single stimulus would be, while the latency follows the shortest latency of the two. D,E. Same presentation as in B,C, but the mean of the means across the population of 16 neurons, after the responses have all been aligned about the optimal orientation for the high-contrast line by itself (vertical black arrows).
Figure 2. A. The responses of an example V1 neuron to an optimally-oriented low contrast edge by itself (leftmost panel, light gray line), to a non-optimally oriented high-contrast grating (second to the left panel, dashed medium gray line), and the two combined (middle panel, solid black line). Thin lines are +/- the standard error of the mean (omitted from multi-line plots for clarity). Also shown are the responses to a non-optimally oriented low-contrast grating (second panel from the right) and an optimally-oriented low-contrast grating combined with an orthogonal low-contrast grating (rightmost panel). The high-contrast grating suppresses the response to a single low-contrast edge, but a low-contrast grating has basically no effect. B. Similar to A, but in this case the gratings are optimally oriented. A single low-contrast edge has no effect on optimally-oriented gratings of either contrast. C. Mean normalized spike counts (n=14) in response to an optimally oriented low contrast edge by itself, to an orthogonal high-contrast grating, and to an orthogonal low-contrast grating. Error bars are 95% bootstrapped confidence intervals. D. Similar to C but with non-oriented random dot textures. The response to an optimally oriented low-contrast edge is suppressed by large-area high contrast stimuli, be they gratings or random dots, but not by low-contrast large-area stimuli.

References


