The responses of V1 cortical neurons to flashed presentations of orthogonal single lines and edges

Timothy J. Gawne

Department of Vision Sciences, University of Alabama at Birmingham, Birmingham, Alabama

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Gawne TJ. The responses of V1 cortical neurons to flashed presentations of orthogonal single lines and edges. J Neurophysiol 113: 2676–2681, 2015. First published February 11, 2015; doi:10.1152/jn.00940.2014.—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 counterphase-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 gratings 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 gratings being due to non-orientation-specific contrast gain control (Koeling M, Shapley R, Shelley M. J Comp Neurosci 25: 390–400, 2008; Priebe NJ, Ferster D. Nat Neurosci 9: 552–561, 2006; Walker GA, Ohzawa I, Freeman RD. J Neurophysiol 79: 227–239, 1998). 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.

METHODS

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 (Bonds 1989; Carandini and Heeger 1994; Carandini et al. 1997; Creutzfeldt et al. 1974; Heeger 1992; Morrone et al. 1982; Petrov et al. 1980; Ramoa et al. 1986) This has variously been referred to as cross-orientation inhibition or, more generally, as cross-orientation suppression. However, a gratings can have effects due both to its orientation and to its coverage of a large area, and studies have demonstrated suppression by either nonoriented 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 orientation per se at all (Priebe and Ferster 2006; Walker et al. 1998). 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 (Gawne and Martin 2002a; Richmond et al. 1999). Therefore this study explores the responses of primate V1 neurons to flashed presentations of single crossed contours, and also of single contours and gratings stimuli.

The finding here is that while a high-contrast gratings 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 receptive fields, which could allow for multiple orientations to be represented at one location in a visual image.
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 (Gawne and Martin 2002a; Richmond et al. 1999). The stimuli consisted of oriented single lines, gratings, luminance edges defined by hemiplanes, and nonoriented random dot textures. Eight uniformly distributed orientations separated by 22.5° were used.

The stimuli were presented on a video monitor running at 67 Hz 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 ms), 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 ms 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 ms 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 METHODS. 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 (SD) spikes/s, range 0.00–5.71 spikes/s. The orientation tuning (ratio of spike count at optimal/null) was a mean of 13.89 ± 26.46 (SD), range 2.15–140.0, median 4.785.

Figure 1A illustrates the responses of an example neuron to a high-contrast oriented line (bottom row, dashed medium gray line), a low-contrast hemiedge (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 ms). 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 1, B and C, shows the spike count and the response latency for the example neuron, and Fig. 1, D and 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 Fig. 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) generates the shortest latency response (consistent with Gawne 2011).

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 hemiedge (left bar in the plot), the same optimally-oriented low-contrast hemiedge 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 Fig. 2A, the response to an optimal low-contrast hemiedge 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 nonoriented random dot textures (see also Priebe and Ferster 2006).

DISCUSSION

In accord with previous studies (Koeling et al. 2008; Priebe and Ferster 2006; Walker et al. 1998) 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 nonoriented 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.

Lampi 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 receptive field, multiple effective stimuli within the receptive field 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 (Kapadia et al. 2000; Levitt and Lund 1997; Sillito and Jones 1996). 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 (Luck et al. 1997; Moran and Desimone 1985; Reynolds et al. 1999; Reynolds and Desimone 2003; 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 (Finn and Ferster 2007; Gawne 2008; Gawne and Martin 2002b; Heuer and Britten 2002; Lampl et al. 2004; Oleksiak et al. 2011; Rolls et al. 2003; Sato 1989). How should we resolve this apparent contradiction?

Consider that when two stimuli are presented in the receptive field 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 nonspecific 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 receptive field (Gawne 2008; Gawne and Martin 2002b). However, because receptive fields 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 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 receptive field. In this case one might really be recording the response to a part of a line as it sweeps across the receptive field, 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 (Hubel and Wiesel 1968; Kjaer et al. 1997), 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, are 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 Fig. 1, orientation for high-contrast stimuli, but varies much more category of cells than another paradigm, are very small. However, because the same procedures for identifying and isolating single neurons were performed on different cells on different days. This study was supported by National Eye Institute (NEI) Grant EY-11552-01, National Science Foundation Grant IOS-0622318, and NEI Grant EY-003039 (CORE).

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DISCLOSURES
No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS
Author contributions: T.J.G. conception and design of research; T.J.G. performed experiments; T.J.G. analyzed data; T.J.G. interpreted results of experiments; T.J.G. prepared figures; T.J.G. drafted manuscript; T.J.G. edited and revised manuscript; T.J.G. approved final version of manuscript.

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