Temporal frequency tuning of cross orientation inhibition in the striate cortex of cats.

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PURPOSE

A sinusoidal MASK grating oriented orthogonal to and superimposed on an optimally oriented BASE grating reduces a cortical neuron's spike response amplitude. The spatial parameters of this cross-orientation inhibition (XOR) have been previously measured (Morrone et al., 1982; Bonds, 1989; Bauman and Bonds, 1991). We describe here the temporal frequency response properties of XOR.

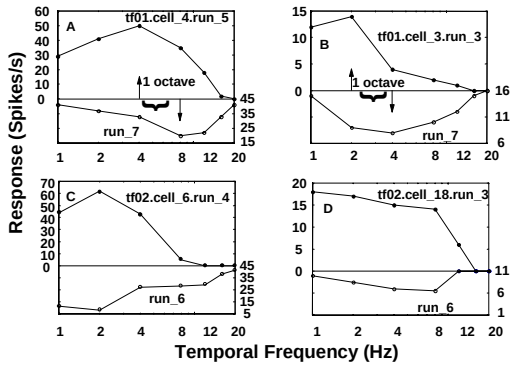
METHODS

We recorded from single striate cortical neurons (n = 65) in cats anesthetized with Propofol and paralyzed with Pavulon following established guidelines. We first quantified the structure (i.e., orientation and spatial frequency) of each cell's classical receptive field, then recorded the "excitatory" response of each neuron to variation of the temporal frequency of a spatially optimized sinusoidal BASE grating. Next, we measured the "inhibitory" temporal frequency response profile by systematically varying the temporal frequency of a second, spatially congruent MASK grating at one, then a second, "null" orientation positioned outside the cell's excitatory response domain. The orientation of the MASK is referred to "left" or "right" based on its tilt relative to the base (i.e., counterclockwise or clockwise, respectively).

RESULTS SUMMARIZED

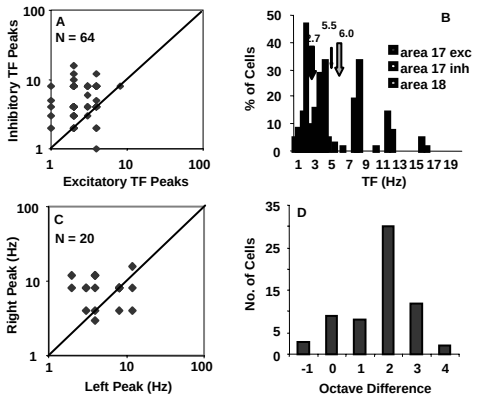
1) For most neurons, the "inhibitory" peak temporal frequency was higher than the excitatory peak temporal frequency (by an average of 1.1 ± 0.7 octaves).
2) The distribution of inhibitory peak temporal frequencies resembled the distribution of excitatory peak temporal frequencies recorded from a sample of area 18 cells.
3) Inhibitory peaks differed as a function of the MASK orientation.
4) The inhibitory cutoff frequency of most neurons was higher than the excitatory cutoff frequency (by an average of 0.6 ± 0.5 octaves).
5) The distribution of inhibitory cutoff frequencies resembled the distribution of excitatory cutoff frequencies recorded from a sample of area 18 neurons.
6) Inhibitory cutoff frequencies differed as a function of the MASK orientation.
7) Most excitatory response functions appeared to be low-pass, but this may be because we did not test below 1 Hz. Nevertheless, most inhibitory functions were band-pass.

EXAMPLES



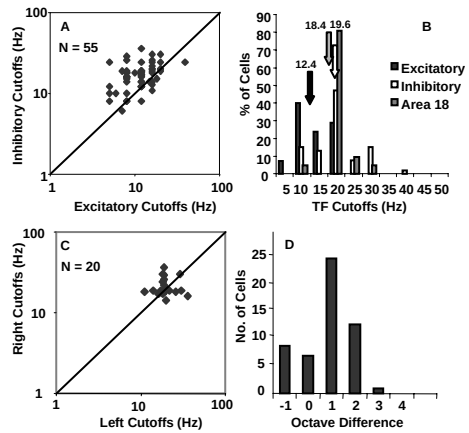
Four examples illustrate the excitatory response of striate cortical cells as a function of varying the temporal frequency of the BASE grating (solid circles, left axis). The "inhibitory" response (plotted on the right axis) as a function of varying the temporal frequency of the spatially congruent MASK grating is shown with open circles. The solid horizontal line is the response the spatiotemporally optimized BASE grating presented alone. Variation of the temporal frequency of the MASK grating produced a suppression of the response to the BASE at some temporal frequencies, but less or no suppression at others. Response profiles for both the excitatory and inhibitory responses were low- or band-pass. In most cases, e.g., A and B, the peak and cutoff frequencies of the inhibitory responses were higher.

TF PEAKS



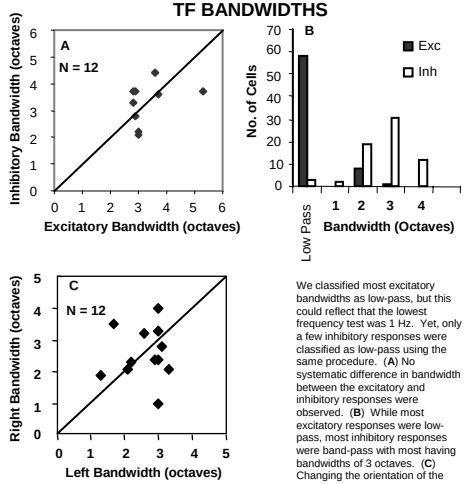
We found differences between the excitatory and inhibitory peaks recorded from most neurons. (**A**) The scatter plot shows that, for all but 3 neurons, the inhibitory peak is higher. (**B**) The distributions of excitatory responses (dark bars), inhibitory responses (open bars), and area 18 excitatory responses (gray bars) show that the excitatory responses found in area 18 more closely resemble the inhibitory responses observed in area 17. The peaks averaged 2.7 Hz, 5.5 Hz, and 6.0 Hz, respectively. (**C**) For most neurons tested, the inhibitory peak varied depending on the orientation (R vs. L) of the MASK. Different MASKS possibly stimulate different inhibitory cell populations with different peaks. (**D**) The distribution of the difference (in octaves) between the excitatory and inhibitory peaks illustrates that the inhibitory peak was, for most cells, 2 octaves higher than the excitatory peak. On average, the difference was 1.1 (± 0.7) octaves.

TF CUTOFFS



The temporal frequency cutoffs of the excitatory and inhibitory responses of most cells differed. (**A**) The inhibitory cutoff of most cells was higher than the excitatory cutoff. (**B**) The distribution of inhibitory cutoffs was higher than the excitatory distribution and more closely matched the excitatory distribution recorded from area 18. Cutoff frequencies averaged 12.4 Hz for area 17 excitatory responses, 19.6 Hz for area 17 inhibitory response, and 18.4 Hz for area 18 excitatory responses. (**C**)The inhibitory cutoff frequency for more neurons varied as a function of the MASK orientation. (**D**) Most neurons exhibited an inhibitory cutoff frequency that was 1 octave higher than their excitatory cutoff frequency. The difference, on average, was 0.6 (±)octaves.

TF BANDWIDTHS



We classified most excitatory bandwidths as low-pass, but this could reflect that the lowest frequency test was 1 Hz. Yet, only a few inhibitory responses were classified as low-pass using the same procedure. (**A**) No systematic difference in bandwidth between the excitatory and inhibitory responses were observed. (**B**) While most excitatory responses were low-pass, most inhibitory responses were band-pass with most having bandwidths of 3 octaves. (**C**) Changing the orientation of the MASK changes the bandwidth for most cells.

CONCLUSIONS

1) The temporal frequency response profile of most neurons in area 17 show that the cross-orientation inhibition mechanism has a higher temporal frequency peak than the excitatory response of most area 17 neurons.
2) Likewise, the inhibitory substrate of cross orientation inhibition has a higher temporal frequency cutoff.
3) In fact, the inhibitory temporal frequency response profile recorded from most neurons resembles the excitatory response profiles of many area 18 neurons, suggesting a role of feedback from area 18 (Alonso *et al*., 1993; Martinez-Conde *et al*., 1999).
4) No systematic differences were observed between the excitatory and inhibitory temporal frequency tuning bandwidths.

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