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Stimulus contrast modulates functional connectivity in visual cortex

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Neurons in visual cortex are linked by an extensive network of lateral connections. To study the effect of these connections on neural responses, we recorded spikes and local field potentials (LFPs) from multi-electrode arrays that were implanted in monkey and cat primary visual cortex. Spikes at each location generated outward traveling LFP waves. When the visual stimulus was absent or had low contrast, these LFP waves had large amplitudes and traveled over long distances. Their effect was strong: LFP traces at any site could be predicted by the superposition of waves that were evoked by spiking in a ~1.5-mm radius. As stimulus contrast increased, both the magnitude and the distance traveled by the waves progressively decreased. We conclude that the relative weight of feedforward and lateral inputs in visual cortex is not fixed, but rather depends on stimulus contrast. Lateral connections dominate at low contrast, when spatial integration of signals is perhaps most beneficial.

Neurons in primary visual cortex (area V1) receive input from the thalamus and from an extensive network of lateral connections. The relative strength of these two signals remains controversial. One view holds that the responses of V1 neurons are largely determined by local processing of thalamic inputs[1–5], whereas another view states that V1 responses are substantially shaped by long-range lateral connections[6–13]. An implicit assumption in this debate has been that the relative weight of feedforward and lateral connectivity signals is fixed and is independent of the stimulus. We hypothesized that experimental findings supporting one or the other view could be reconciled if this relative weight was dependent on stimulus conditions.

To test this idea, we simultaneously recorded spiking activity and LFPs from multi-electrode arrays that were implanted in primary visual cortex in monkeys and cats. The LFP reflects the membrane potential of a local population of neurons. By computing spike-triggered LFP averages[14], we assessed the strength of postsynaptic activity at one cortical site that was caused by spiking at another location. Hence, this postsynaptic activity is a measure of functional connectivity between the site where the spikes are recorded and the site where the LFP is measured.

The LFP, especially in the absence of a sensory stimulus, is a highly variable signal characteristic of ongoing activity. We found that this activity was the result of the superposition of a myriad of traveling waves, each originating from spikes in a region spanning millimeters of cortex. Spikes at any given site generated a radial traveling wave of LFP activation representing net depolarizing synaptic input, whose amplitude decreased with distance. When the stimulus was absent, these lateral contributions extended over a large area and strongly influenced cortical activity, allowing us to predict the waveform of the spontaneous LFP traces with reasonable accuracy.

As the contrast of the visual stimulus increased, both the spatial footprint of lateral connectivity and its effect on visual responses were progressively reduced. These findings indicate that the relative weight of feedforward and lateral inputs is not fixed, but is contrast dependent. Our results offer a new conceptual framework that could help reconcile two views of cortical processing that have previously been believed to be incompatible.

RESULTS

We recorded spike activity and LFPs across 10 × 10 arrays of electrodes that were implanted in primary visual cortex of anesthetized monkeys (area 17) and cats (area 18). Previously, we established that the LFP represents a measure of local postsynaptic activity in a ~250-μm radius of the recording site[15]. Thus, sampling 400-μm intervals allows for estimates of postsynaptic activity in neuronal populations that are largely nonoverlapping.

To investigate how the spiking activity at one cortical site evoked synaptic input at another site, we calculated spike-triggered LFPs[14] (**Fig. 1a**). First, we selected an electrode as the reference site for the spiking activity (**Fig. 1a**). Then, we computed spike-triggered averages of the LFP signals across the entire electrode array (**Fig. 1a**). The spike-triggered LFP average was analyzed to estimate its peak (negative) amplitude and the time to peak relative to the generating spike (**Fig. 1b**). This procedure was repeated by selecting all possible reference electrodes in the array.

Cortical spikes trigger traveling waves of LFP activity

We first characterized spike-triggered LFPs during spontaneous activity and found that spikes at any given electrode site created outward

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