

Adaptation maintains population homeostasis in primary visual cortex

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Sensory systems exhibit mechanisms of neural adaptation, which adjust neuronal activity on the basis of recent stimulus history. In primary visual cortex (V1) in particular, adaptation controls the responsiveness of individual neurons and shifts their visual selectivity. What benefits does adaptation confer on a neuronal population? We measured adaptation in the responses of populations of cat V1 neurons to stimulus ensembles with markedly different statistics of stimulus orientation. We found that adaptation served two homeostatic goals. First, it maintained equality in the time-averaged responses across the population. Second, it maintained independence in selectivity across the population. Adaptation scaled and distorted population activity according to a simple multiplicative rule that depended on neuronal orientation preference and on stimulus orientation. We conclude that adaptation in V1 acts as a mechanism of homeostasis, enforcing a tendency toward equality and independence in neural activity across the population.

Sensory systems constantly exhibit perceptual adaptation, which goes unnoticed in our daily experience but becomes apparent after prolonged exposure to a given stimulus. Visual perception, for instance, can be profoundly affected after viewing steady motion^{1,2} or constant orientation^{3,4}. Such perceptual phenomena are thought to arise from adaptation mechanisms that adjust neuronal activity on the basis of recent stimulus history.

Sensory systems indeed exhibit various forms of neural adaptation^{5–14}. In V1 in particular, adaptation controls the responsiveness of individual neurons^{6,15–20} and shifts their visual selectivity^{6,15,16,21,22}. Whereas the first effect is akin to general neural fatigue, the second suggests a more specific adjustment of stimulus representation. However, sensory processing is mediated by neuronal populations²³, and the overall effects of adaptation on population activity have been hypothesized^{2,24–26} but not measured. What benefits does adaptation confer on a neuronal population?

RESULTS

To characterize coding and adaptation in a large population of cortical neurons, we recorded spiking activity from V1 of anesthetized cats using 10×10 electrode arrays (Fig. 1). We characterized responses as a function of stimulus orientation²⁷ using sequences of static gratings with random orientation and phase, each presented for 32 ms (Fig. 1a). We considered stimulus ensembles with two statistical distributions^{5,7–10}: uniform and biased. In the uniform case, the probability of each orientation was equal²⁷. In the biased case, the probability of one orientation was markedly higher than the others.

As shown previously²⁷, population responses to stimuli with uniform statistics could be accurately fitted on the basis of the tuning curves of the neurons (Fig. 1c,e–g). The stimulus was a time series of orientations (Fig. 1e), and the population responses varied as a function of time and of the preferred orientation of the neurons (Fig. 1f).

We divided the axis of preferred orientation evenly into bins, each pooling the activity of neurons with similar orientation preferences. The population activity tracked the stimulus closely. By applying regression to these responses, we obtained tuning curves for each of the bins of preferred orientation (Fig. 1c). These tuning curves are homogeneous: they are similar to each other except for their preferred orientation. As expected²⁷, the tuning curves could be used to fit the population responses to the stimulus sequence through summation (Fig. 1g). This simple operation (followed by a mild nonlinearity²⁷) captured a high proportion (63%) of the explainable variance in the population responses in this experiment. We obtained a similar result in five more experiments (Supplementary Fig. 1a).

When we changed the statistics of the stimulus ensemble, the cortex displayed a notable ability to adapt (Fig. 1i–k). We biased the stimulus sequence markedly in favor of one orientation (the ‘adaptor’), presenting it three times more often than the rest (Fig. 1i). If the tuning curves were still those we had measured with the uniform stimulus ensemble (Fig. 1c), the neurons selective for the adaptor orientation would respond on average much more than the others (Fig. 1k). The actual response of the population instead showed no such bias: the average over time of the cortical response to the biased stimulus ensemble was equal across neurons, regardless of preferred orientation (Fig. 1j). From the cortical responses, it was not apparent that one orientation was shown three times more than the others. Evidently the neurons in visual cortex had adapted to the biased ensemble, and their adaptation had been strong enough to counteract the bias in the ensemble. Moreover, this adaptation was not so strong as to overcompensate; that is, as to create a ‘hole’ in the population responses.

The effects of adaptation were well described by a new set of tuning curves, one that was tailored for the biased ensemble (Fig. 1d,l). We obtained these adapted tuning curves (Fig. 1d) by applying

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