

Figure 2 Adaptation equalizes population responses. (a) Time average of the population responses to uniform stimulus ensembles was normalized to 1. (b) Time averages of fits by homogeneous tuning curves, averaged across five experiments (blue curve; shaded area, ± 1 s.e.m.). (c) Time averages of predictions by adapted tuning curves, averaged across five experiments (red curve; shaded area, ± 1 s.e.m.). (d–f) Same as a–c in responses to stimuli in biased ensembles. Data and error bars (± 1 s.e.m., $n = 4$) illustrate equalization and are repeated in each panel. The homogeneous tuning curves incorrectly predict a large peak (e), whereas the fits by the adapted tuning curves correctly capture equalization (f).

could not be obtained with the adapted tuning curves, which predict a nonexistent hole in the population responses at the orientation of the adaptor (capturing $48\% \pm 11\%$ of the explainable variance; Fig. 2c).

This analysis, therefore, reveals that adaptation maintains equality in the time-averaged activity of different neurons in the face of biases in the stimulus ensemble. Achieving this equality requires appropriate calibration: if adaptation were stronger or weaker, there would be a valley or a peak in the population responses, and instead there is neither. Equality, however, can only be maintained for a range of stimulus biases. At the extreme, if a single orientation were shown 100% of the time (as has typically been the case in previous studies of adaptation), one would expect the neurons selective for that orientation to respond more than the rest. Indeed, whereas we saw complete equalization when the probability of the adaptor was 30–40% (Fig. 2e), equalization was less perfect when we increased this probability to 50% (Supplementary Fig. 4).

In addition to equalization, adaptation helped maintain decorrelation across the population (Fig. 3). Because of the width of the tuning curves, a biased stimulus sequence tends to engage not only the neurons selective for the adaptor orientation but also those selective for nearby orientations. In the absence of adaptation, the activity of these neurons would therefore become highly correlated (a ‘correlation catastrophe’). To look for these effects, we computed the correlation coefficients between pairs of bins, for each combination of orientation preference. These are known as signal correlations²⁸, and they reflect the similarity in tuning curves. As expected, the matrix of correlations in the uniform case was diagonal (Fig. 3a). The tuning curves obtained in this condition capture this diagonal aspect (Fig. 3b), but they also predict that in the responses to the biased stimulus ensemble there should be a strong central peak in the matrix (Fig. 3e): the correlation catastrophe. Instead, the population responses to the biased stimulus ensemble (Fig. 3d) showed a diagonal structure of correlations that was similar to the one seen with the uniform stimulus ensemble (Fig. 3a). Consistent with a longstanding theoretical proposal^{24,29–31}, therefore, adaptation prevented responses of cortical neurons from becoming more correlated.

This effect of decorrelation could be captured by the adapted tuning curves: running the biased stimulus ensemble through these adapted

curves resulted in a diagonal matrix of correlations without a central peak (Fig. 3f). The adapted tuning curves would not have been appropriate in response to the uniform stimulus ensemble, as they would have caused a central hole in the matrix of correlations (Fig. 3c).

Taken together, these results indicate that adaptation provides two homeostatic effects to the population, maintaining equality not only in the first-order statistics but also in the second-order statistics. These effects were achieved quickly, with an average time constant of 1.7 ± 0.4 s (s.d.; Supplementary Fig. 5). In this short interval the cortex was able to engage adaptation mechanisms that effectively counteracted the bias in the stimulus ensemble, in terms of both first- and second-order statistics. However, adaptation is known to operate on more than one timescale^{6,32,33}. Perhaps a relevant determinant of timescale is the number of stimuli that the adaptation mechanisms need to observe to be fully engaged. In our experiments, 1.7 s correspond to ~ 53 stimuli. It was sufficient for V1 to observe the same orientation in 16–26 of those stimuli to adapt its responsiveness and selectivity.

What does adaptation change in a population to allow it to discount these stimulus statistics? Because the effects of adaptation are captured by changes in tuning, the answer lies in the attributes of the tuning curves (Fig. 1c,d). To characterize these tuning curves and to reveal the precise effects of adaptation, we examined the full matrix of responses to individual flashing gratings, averaging the results of all our experiments (Fig. 4a–c). This response matrix (Fig. 4b) depends both on the preferred orientation of the neurons (rows) and on the orientation of the stimulus (columns). Taking sections across the rows yields the familiar tuning curves of each preference bin (Fig. 4a). Taking sections across columns instead yields population response profiles, one for each stimulus orientation (Fig. 4c).

The response matrix measured with the biased ensemble summarizes the effects of adaptation (Fig. 4d–f). A look at these tuning curves and population responses indicates that adaptation had two main effects. The first effect was an offset: a small reduction of all responses, regardless of orientation preference (Fig. 4d) and of stimulus orientation (Fig. 4f). We modeled this effect with a simple subtractive shift. The second effect was a marked reduction in amplitude, which was strongest for the tuning curves of neurons with orientation preference near zero, the nominal orientation of the adaptor (Fig. 4d).

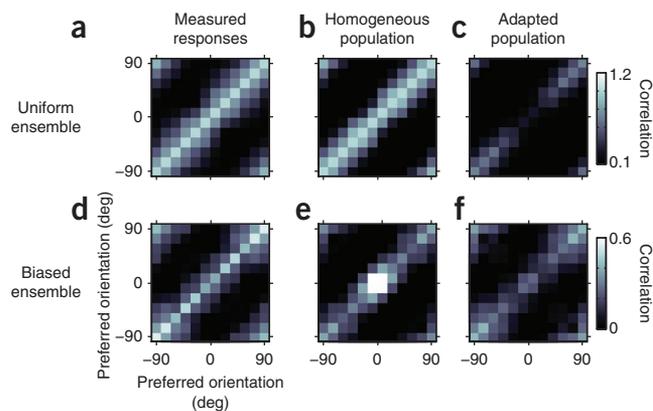


Figure 3 Adaptation decorrelates population responses. (a) Correlation coefficients between pairs of neuronal bins measured with the uniform stimulus ensemble ($n = 5$). The values on the diagonal are scaled to 1. The subsequent panels have the same scaling factors. (b,c) Correlation coefficients of responses fitted by uniform tuning curves (b) and predicted by adapted tuning curves (c). (d–f) Same as a–c for responses to stimuli in the biased ensemble. The homogeneous tuning curves incorrectly predict a central peak in correlation (b), whereas the fits by the adapted tuning curves correctly capture a diagonal matrix (c).