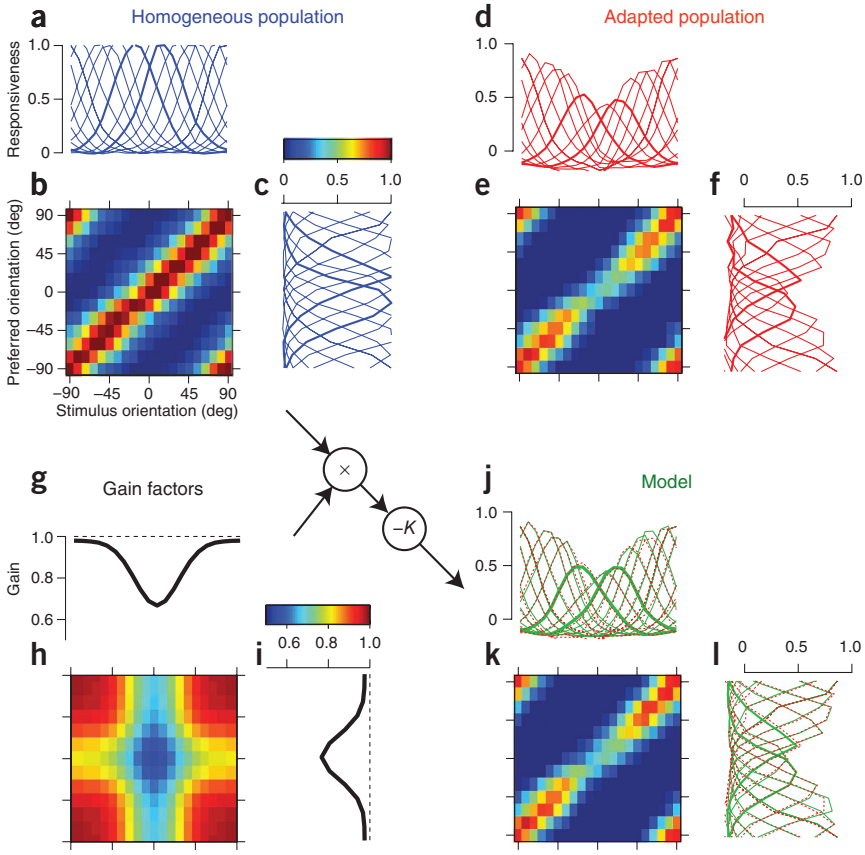

Figure 4 Neuron-specific and stimulus-specific components of adaptation. (**a**) Tuning curves measured with uniform stimulus ensembles, averaged over all 11 sessions in 4 cats. As elsewhere, 0 deg indicates the orientation of the adaptor. (**b**) Matrix of responses to individual gratings, as a function of preferred orientation and stimulus orientation. (**c**) Population response profiles for stimuli of different orientations. (**d**–**f**) Same as **a**–**c**, measured for stimuli with biased statistics. (**g**–**i**) A simple multiplicative model of adaptation, based on two gain factors, one dependent on stimulus orientation (**g**) and one dependent on neuronal preferred orientation (**i**). Their product is a gain matrix (**h**). (**j**–**l**) Model fits. Format is as in **d**–**f**. The predicted response matrix (**k**) is obtained by multiplying elementwise the gain matrix (**h**) by the response matrix (**b**) measured with the uniform ensemble. Predicted tuning curves (**j**, green curves) and population response profiles (**l**, green curves) closely resemble the measured ones (replotted in dotted red lines). Panels **b**, **e**, and **k** share the color map shown above **c**.

This effect amounted to creating a hole in the diagonal of the matrix (**Fig. 4e**).

There are two simple ways to create such a hole along the diagonal of the response matrix (**Fig. 4e**): across rows and across columns. The first possibility is intuitive and rests on neuron identity: adaptation would reduce mostly the responses of the neurons selective for the adaptor (**Fig. 4d**). The second possibility is less intuitive and rests on stimulus identity: adaptation would control the population responsiveness to different stimuli, reducing it most strongly for stimuli with the same orientation as the adaptor (**Fig. 4f**).

Both descriptions are rooted in studies of adaptation in single neurons. The neuron-specific description of adaptation evokes simple forms of neural fatigue and agrees with the view of adaptation as controlling a neuron's responsiveness or sensitivity[18–20]. The stimulus-specific description involves fatiguing stimuli (rather than neurons), reducing their effectiveness in driving the cortex. This description agrees with the stimulus-specific effects of adaptation that have been reported in single neurons[6,15–17,34].

To resolve the dichotomy in these descriptions, we designed a simple model that includes both neuron-specific and stimulus-specific factors (**Fig. 4g–i**). In the model, the response matrix is scaled by two multiplicative gain factors. One of these factors specifies how much to reduce the responsiveness of each neuron (**Fig. 4i**) and the other specifies how much to reduce the responses to each stimulus (**Fig. 4g**). We describe the gain factors as Gaussians peaking at zero (the orientation of the adaptor and the preferred orientation of neurons tuned for the adaptor). The two Gaussians are multiplied to obtain a matrix of gain factors (**Fig. 4h**). In practice, the model works as follows: take the response matrix measured with the uniform stimulus ensemble (**Fig. 4b**), multiply it pointwise by the matrix of gain factors (**Fig. 4h**) and subtract a constant offset. The model is defined by only five parameters: the two widths and two amplitudes of the Gaussians, and the constant offset.

This simple model described accurately the effects of adaptation (**Fig. 4j–l**). The fitted model predicted a response matrix (**Fig. 4k**) that was extremely similar to the actual one (**Fig. 4e**), explaining 89.3% of the variance in this matrix. This similarity is confirmed by plotting the tuning curves on top of the measured ones (**Fig. 4j**) or by plotting the

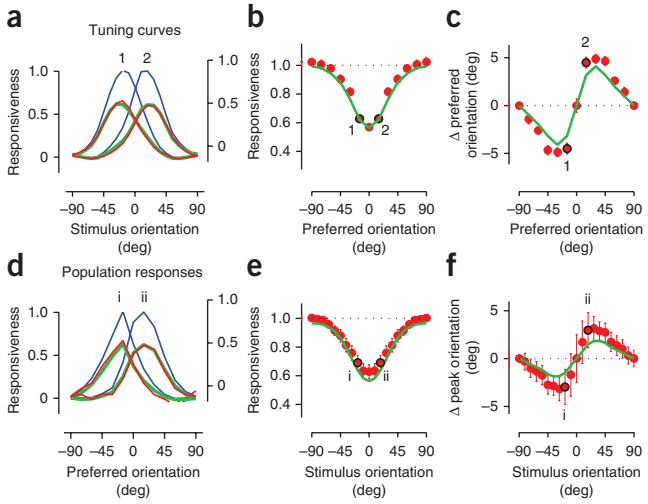

Figure 5 Effects of adaptation on tuning curves and population responses. (**a**) Tuning curves of neurons selective for +15 deg and –15 deg relative to the adaptor, measured with uniform stimuli (thin blue curves, left scale), with biased stimuli (thin red curves, right scale). Thick green curves show model fit. (**b**) Changes in tuning curve amplitude as a function of preferred orientation. Red dots are data, green curve is the model fit. Points marked 1 and 2 indicate the examples in **a**. (**c**) Same as **b**, but for changes in preferred orientation. (**d**–**f**) Same as **a**–**c**, but for population response profiles.