Figure 6 Adaptation to biased ensembles does not affect pairwise noise correlations. (**a**) Noise correlations between pairs of units in response to uniform and biased ensembles. Colors distinguish data sets ($n = 11$). For graphical purposes, only a randomly selected 5% of the 69,596 pairs are displayed. (**b**) The same data, averaged within each data set ($n = 11$, each with 1,892–9,120 pairs). The error bars indicate ± 1 s.d. of the difference in noise correlations in responses to the uniform and biased ensembles.

population response profiles on top of the measured ones (**Fig. 4l**). Similar results were obtained when working with matrices obtained separately from the experiments with adaptor probabilities of 30–40% ($n = 6$, 80.0% of the variance) and with an adaptor probability of 50% ($n = 5$, 86.7% of the variance).

In particular, the model correctly predicted that adaptation would reduce the tuning curves and repel them away from the adaptor orientation (**Fig. 5a–c**). Because one of the gain factors depends on stimulus orientation (**Fig. 4g**), it scales the tuning curves more on the flank toward the adaptor than on the other flank, pushing them away from the adaptor orientation (**Fig. 5a**). The result for tuning curves is a reduction in amplitude[6,18–20] (**Fig. 5b**) and a shift in preferred orientation[15,16,21,22] (**Fig. 5c**). Our simple model captures these effects accurately (**Fig. 5a–c**).

In addition, the model makes a prediction: that adaptation should not only reduce population response profiles but also repel them from the adaptor (**Fig. 5d–f**). The second gain factor depends on preferred orientation (**Fig. 4i**), so it scales the population profiles more on the flank where neurons are selective for the adaptor than on the opposite flank, pushing them away from the adaptor orientation. We verified these predictions in the data: population responsiveness was reduced (**Fig. 5e**) and the peak of the population response profile was pushed away from the adaptor orientation (**Fig. 5f**). The model predicts these effects (**Fig. 5d–f**).

Because it accounts for responses simultaneously recorded from a population, the model allows us to measure the relative importance of stimulus-specific adaptation and neuron-specific adaptation. Notably, the less intuitive component of the model, the one that is stimulus specific (**Fig. 4g**) was stronger than the neuron-specific one (**Fig. 4i**). The reduction in stimulus-specific gain was consistently larger than the reduction in neuron-specific gain, both in individual experimental sessions and in averages across sessions (**Supplementary Fig. 6**). The most important effect of adaptation was therefore the one that is stimulus specific, as if adaptation had reduced the effective strength of stimuli with orientations near the adaptor.

Our analysis of the effects of adaptation on populations has concerned the average responses to repeated stimulus presentations ('signal') and not the trial-by-trial deviations from these average responses ('noise'). Measurements in awake primates following prolonged exposure to single stimuli suggest that adaptation reduces the

correlation among these deviations ('noise correlations'; ref. 28) in neuronal pairs[35]. Our experiments, however, gave little support for this conclusion: adaptation reduced noise correlations in some pairs but increased it in others (**Fig. 6a**). The overall effect varied across data sets (**Fig. 6b**): in some, adaptation slightly reduced noise correlations (6 of 11 with $P < 0.05$: Wilcoxon rank-sum test), but in others it slightly increased them (4 of 11), or had no significant effect (1 of 11). On average, the change in noise correlations was a negligible $0.02 ± 0.06$ (s.d., $N = 69,596$ pairs). We obtained similar results when we shifted the spike bins relative to the stimulus refresh times (data not shown), when we used longer bins (**Supplementary Fig. 7**), and when we distinguished among pairs on the basis of preferred orientation (**Supplementary Fig. 8**). In summary, under our experimental conditions, the main effects of adaptation on the population code concerned the signals and their correlations, not the trial-by-trial deviations from these signals.

DISCUSSION

We discovered that primary visual cortex displays a remarkable ability to counteract biases in the stimulus ensemble, by rapidly introducing the appropriate opposing biases in the responsiveness and selectivity of neurons. These adaptation phenomena are due to homeostatic mechanisms that work toward two simple goals: to maintain equality in the time-averaged responses across the population and to enforce independence in selectivity across the population.

These results provide experimental evidence for previous proposals. The first goal, equalization, is consistent with proposals made by psychophysicists of adaptation being a 'graphic equalizer' counteracting changes in the statistics of the environment[1]. It also echoes proposals that adaptation may act to 'center' a population response by subtracting the responses to the prevailing stimulus distribution[25], or to scale responses so that the average of a measured signal is kept constant[26]. The second goal, independence, matches a longstanding proposal that the function of cortical adaptation is to maintain decorrelation[24,25,29,30].

We were able to characterize these homeostatic mechanisms because we measured responses in a whole population and because we measured activity concurrently with changes in stimulus statistics[5,7–10]. Recording from a whole population is a promising technique for studying adaptation[36]. The key to our results, however, was our choice of stimuli. These stimuli allowed us to observe the homeostatic mechanisms achieve their stable (and arguably intended) effects rather than their fleeting (and unintended) aftereffects. By contrast, previous studies of adaptation in V1 used the traditional adapt-test design[6] developed in psychophysics[1,3,37–41], in which the phases of adaptation and response measurement are distinct. This design can only reveal adaptation's aftereffects, those that persist after a change in stimulus properties even though they are no longer needed.

We further discovered that adaptation in primary visual cortex follows a simple arithmetical rule to shape the population responses. At the heart of this rule is multiplication by two gain factors, one that depends on stimulus attributes and one that depends on neuronal preference. This rule provides a unified framework that encompasses the known effects of adaptation on responsiveness and orientation selectivity of individual V1 neurons. Having this arithmetical rule, in turn, may guide and constrain research into the underlying circuits and mechanisms. These could involve synaptic depression[42,43] and fatigue at an earlier cortical stage[34]. For instance, as our recordings mostly targeted layer 2/3, the adaptation we measured there could be at least partially inherited from inputs from layer 4.