The mechanisms studied here may well operate in the whole cortex, but for now we have only demonstrated that they do so in V1, and specifically in the processing of stimulus orientation. Future work could establish the degree to which our observations generalize to other stimulus variables beyond orientation and to other cortical areas beyond V1. Further work is also required to understand how the effects of adaptation in one sensory area cascade into subsequent ones, leading to compounding perceptual effects[44]. For instance, the effects of adaptation observed in primary visual cortex appear to be distinct from those observed in motion-processing area MT (refs. 34,45). The effects of adaptation in MT might be consistent with those that we propose. This could be established, for instance, by adapting MT neurons to aspects of the stimuli that do not elicit selective responses in V1.

Adaptation is thought to be a mechanism constantly at work throughout cortex. We tend to notice its perceptual effects only when it does not work properly, or rather when it is catching up with a marked change in stimulus statistics[1–4]. The simple arithmetical rules that we found to govern neural adaptation may help guide future work on perceptual adaptation. Moreover, they provide a framework for linking adaptation with other mechanisms of homeostasis, such as the ones at work during plasticity and development[46]. Meanwhile, the results we have observed in primary visual cortex offer a glimpse at how an entire cortical population can adapt to the statistics of its inputs.

METHODS

Methods and any associated references are available in the online version of the paper.

Note: Supplementary information is available in the online version of the paper.

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AUTHOR CONTRIBUTIONS

A.B. and M.C. conceived the experiments, A.B. acquired the data, A.B. did the analysis in **Figures 1–3**, M.C. did the analysis in **Figures 4** and **5**, and A.S. did the analysis in **Figure 6**. A.B. and M.C. wrote the paper.

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The authors declare no competing financial interests.

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