Serial dependence in perception requires conscious awareness

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unknown, and questions remain as to the molecular details of the induced conformational changes that these proteins experience. Furthermore, the effects of cofactors and substrates during their functional cycle needs to be further investigated. In the coming years, one can expect that functional and structural studies will answer these and other questions arising along the way.

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Serial dependence in perception requires conscious awareness

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Perception depends not only on the currently viewed stimulus, but also on expectations built from previous perceptual history, often termed perceptual *priors*. Perhaps the clearest example is '*serial dependence*', where perceptual judgements — in orientation, numerosity, and so on — are robustly biased towards recent experience [1–3]. Here we ask whether stimuli need to be consciously perceived in order to influence perception, by measuring serial dependence for orientation following binocular rivalry between orthogonal gratings. We find that only the perceptually dominant rivalrous stimulus biased perceived orientation of subsequent stimuli, suggesting that the construction of perceptual priors requires conscious awareness of stimulus history.

Sixteen participants viewed trial sequences that alternated between a rivalrous display of orthogonal gratings presented separately to each eye, and a monocular test grating (Figure 1A). After each stimulus presentation, whether rivalrous or monocular, participants reproduced the orientation of the perceived stimulus by matching it with a rotatable line. On test trials, a grating was presented to the eye of the previous dominant or previous suppressed percept (randomly, with equal probability), rotated ±10° from that orientation (see Supplemental Information for full details). The orientation of the other eye's grating, whether suppressed or dominant, was always ±80° away from the test stimulus and thus outside the range of serial dependence [2,3]. The results (Figure 1B) show that when the test orientation was near that of the dominant rivalrous grating, estimates were strongly biased towards the previous dominant orientation, with a strong positive serial dependence of about 20%. But when the test orientation was near that of the suppressed rivalrous grating, there was no significant serial effect.

We measured significance in several ways. Figure 1C illustrates the permutation test where we shuffled the labels (±10°) across the trials, and calculated the average serial dependence for 10,000 independent shuffles. On not one reiteration did the perturbation of the dominant condition exceed a bias of 1° (while the effect size was 2°), implying that the probability of the observed effect arising by chance was far less than $p < 10^{-4}$. On the other hand, the probability that the negative effect for the suppressed condition arose by chance was $p = 0.44$, not significant ($\alpha = 0.025$ on two-tailed sign test). The complementary approach was the standard bootstrap, retaining the labels and sampling (with replacement) the aggregated data 10,000 times, measuring the average effect on each reiteration. Again, for the dominant condition, all reiterations produced positive serial dependence, yielding $p < 10^{-4}$ by bootstrap sign test. For the suppressed condition, however, 5215 reiterations were positive, giving $p = 0.48$, not significant. Finally, we considered the results separately for the individual participants and tested significance by paired two-tailed t-test and confirmed the same results: for the dominant condition, $t_{15} = 5.6$, $p < 0.001$; for the suppressed $t_{15} = -0.12$, $p = 0.91$, failing significance in either direction.

The results show that, for stimuli to act as a perceptual *prior*, they need to be consciously perceived. This is interesting in light of conflict in the literature over the role of attention, with one report [1] suggesting serial dependence requires attention (which squares with our finding) while another [4] that it occurs automatically, so that one object feature will yield a positive serial effect even when a different feature was attended to on the previous trial. With attentional manipulations there is always a query over how effective the manipulation was and whether observers followed instructions. Our use of binocular rivalry has the benefit that conscious awareness of the stimulus can be manipulated with a greater certainty.

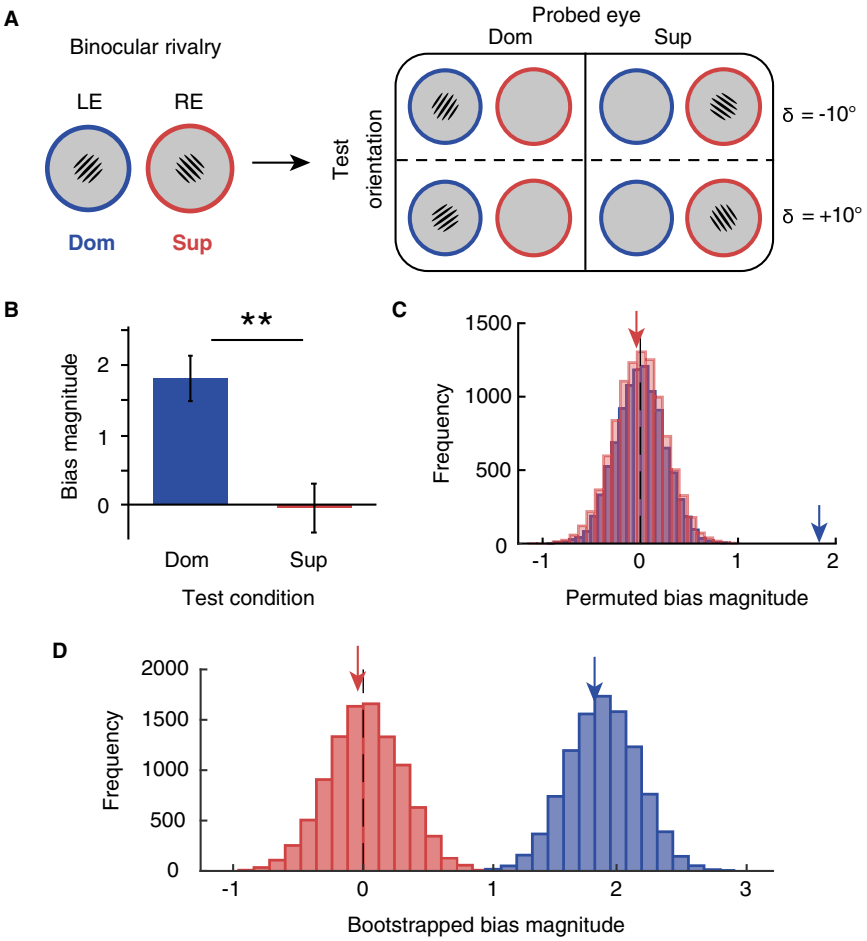

Figure 1. Trial sequence, results and statistical tests.
(A) Illustration of the trial sequence. Stimuli alternated between a brief (750 ms) binocular rivalry stimuli comprising orthogonal monocular gratings (oriented between ±25 and ±65°), and a monocular test grating (750 ms) presented to the previously dominant or suppressed eye and oriented ±10° from that eye's stimulus. (B) Average bias towards the orientation of the previous dominant (blue) or suppressed (red) stimulus. Error bars show standard error between participants. (C) Permutation test described in text. The colour-coded arrows show the mean serial dependence effects for dominant and suppressed stimuli. (D) Results of bootstrapping the aggregate data (described in text).

There has been considerable discussion on whether perceptual priors act within sensory circuits to bias perception, or at the decision level. While this has been controversial [5], much evidence shows that serial dependence acts directly on sensory circuits [1–3,6], probably at low levels of processing [7]. But while perceptual expectancies may act at low levels of sensory processing, this does not mean that the *priors* are themselves constructed at a low level. Indeed, many models of predictive coding assume that priors are generated at higher levels and back propagated by feedback (for example [8]). Our new results show that simply presenting a stimulus is not sufficient to bias subsequent perception: it needs to be perceived to exert a serial influence. If suppressed during binocular rivalry, a grating has no effect at all, either positive or negative, on subsequent perception. As rivalry suppression occurs early in visual processing in primary visual cortex, and suppression-related activity is not seen outside areas V1 or V2 [9], it seems unlikely that the prior is generated at an early stage. This is interesting, as visual adaptation, a form of negative serial dependence, does occur for suppressed stimuli [10], showing that stimuli that are suppressed from consciousness can in principle affect subsequent perception. Our finding that serial dependence occurs only for consciously perceived stimuli suggests that construction of priors is an active process occurring later in perceptual processing. Once constructed, however, the priors may act at early sensory levels [1–3,6,7], consistent with a back-propagation framework.

SUPPLEMENTAL INFORMATION

Supplemental information includes methods, analysis, results and two figures and can be found with this article online at https://doi.org/10.1016/j.cub.2020.02.008.

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