related, yet distinct processes. All are complex, multi-step phenomena, likely to differ mechanistically, and therefore worthy of study individually.

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Brief periods of monocular deprivation disrupt ocular balance in human adult visual cortex

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Neuroplasticity is a fundamental property of the developing mammalian visual system, with residual potential in adult human cortex [1]. A short period of abnormal visual experience (such as occlusion of one eye) before closure of the *critical period* has dramatic and permanent neural consequences, reshaping visual cortical organization in favour of the non-deprived eye [2,3]. We used binocular rivalry [4] — a sensitive probe of neural competition — to demonstrate that adult human visual cortex retains a surprisingly high degree of neural plasticity, with important perceptual consequences. We report that 150 minutes of monocular deprivation strongly affects the dynamics of binocular rivalry, unexpectedly causing the deprived eye to prevail in conscious perception twice as much as the non-deprived eye, with significant effects for up to 90 minutes. Apparent contrast of stimuli presented to the deprived eye was also increased, suggesting that the deprivation acts by up-regulation of cortical gain-control mechanisms of the deprived eye. The results suggest that adult visual cortex retains a good deal of plasticity that could be important in reaction to sensory loss.

Seven observers each wore a translucent eye-patch on one eye for 150 minutes, then viewed a dichoptic binocular-rivalry display with horizontal grating patches presented to one eye and vertical to the other (Figure 1A), reporting by continuous key-press which pattern they perceived. Figure 1B shows the effect of monocular deprivation on the phase durations during rivalry, separately for the deprived (black symbols) and non-deprived (orange symbols) eyes. The bars show the mean phase durations (normalized to each subject's baseline condition, then averaged over subjects) for five contiguous three-minute sessions (see Figure S1 in the Supplemental Information for raw data). Immediately after eye-patch removal, phase durations of the deprived-eye pattern increased by 53%, while those of the non-deprived eye decreased by 24%, a two-fold difference between eyes (the effect was larger when patching the preferred than the non-preferred eye by factors of 2.6 versus 1.7). The difference in phase duration between the two eyes decayed steadily over time, but remained significant 15 minutes after eye-patch removal (paired t-test, $n = 11$, $\alpha = 0.025$, $p < 0.01$). Despite the strong bias towards the deprived eye, observers reported that the quality of binocular rivalry did not change after deprivation, with continued alternations between the two monocular images, with almost no periods of fused images.

Figure 1C shows the average instantaneous probability of seeing the deprived-eye stimulus, as a function of elapsed time, averaged over all subjects and sessions and smoothed with a Gaussian window of time constant of one second. Monocular deprivation biased the trace consistently towards the deprived eye. The initial percept of each testing session (a sensitive parameter of rivalry [5]) was most strongly biased: in the first session the deprived eye prevailed in 93% of first-phases, remaining at 78% after 15 minutes. Even after 90 minutes, the bias towards the deprived eye remained significant (64%: sign test, $n = 49$, $\alpha = 0.025$, $p < 0.001$). After deprivation, gratings viewed by the deprived eye appeared of higher contrast than those by the non-deprived eye, by a factor of 1.36 (on average), but detection thresholds were virtually unaffected. The increase in apparent contrast is qualitatively consistent with the relatively shorter binocular phase periods to the non-deprived eye (Levelt's second law), but the amount of increase is quantitatively insufficient to explain the imbalance in rivalry (see Figure S2 in the Supplemental Information).

Within a specific *critical period*, mammalian visual cortex is highly vulnerable to visual experience, but thought to show little plasticity after closure of this period [3]. However, a

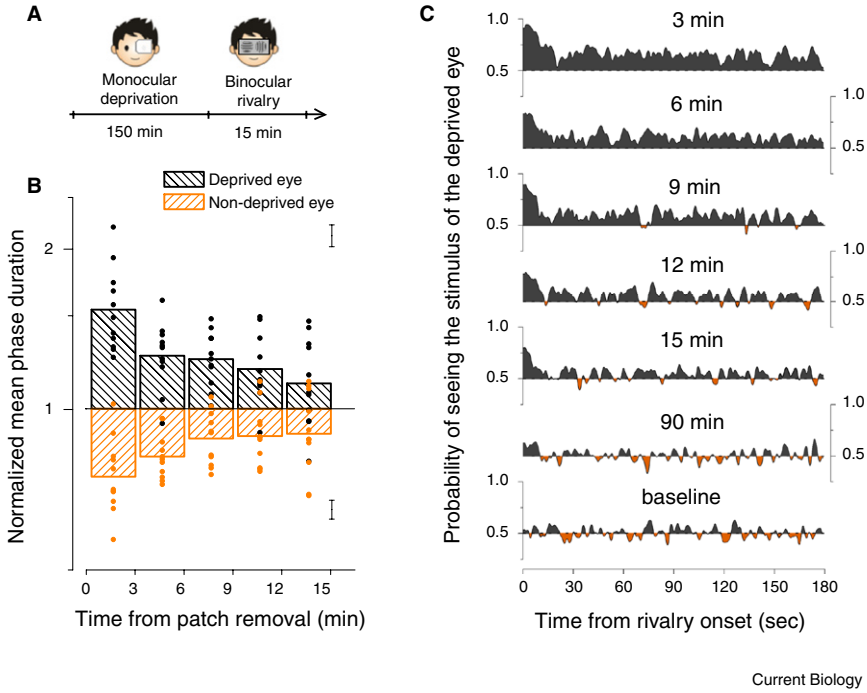

Figure 1. Effect of monocular deprivation on mean phase durations.
(A) After 150 minutes of patching, five consecutive sessions of binocular rivalry were recorded, where observers viewed orthogonally oriented Gabor Patches, vertical to one eye and horizontal to the other. (B) Relative phase durations (expressed as a fraction of the mean baseline phase duration for each observer) of the two visual stimuli, as a function of time elapsed from the removal of the eyepatch, for the stimulus presented to the deprived (black) and non-deprived (orange) eyes. The points show individual data, the bars group averages: bar symbols at right show average s.e.m.). (C) The average proportion of times observers reported seeing the stimulus presented to the deprived eye, expressed as a function of time elapsed from the onset of each experimental session, smoothed within a Gaussian window of time constant one second. For at least six minutes after deprivation, the probability stays above chance, indicating that it was always more probable to see the stimulus presented to the deprived eye.

growing bulk of literature suggests that the adult human visual system retains some plasticity [1,6–8], and some of these alterations, such as perceptual learning, may have long lasting effects. A recent study [6] has shown that prolonged periods of binocular rivalry (>35 minutes) increase the frequency of mixed binocular rivalry, suggesting that exposure to incongruent signals between the two eyes may decrease the reciprocal interocular inhibition that causes rivalry, promoting fusion rather than competition between the two incompatible images. Our study reveals a further form of deprivation-induced plasticity in adult human cortex, one which boosts signal strength of the deprived eye.

That deprivation causes an increase in apparent contrast suggests that the deprivation-induced changes to the dynamics of binocular rivalry may be mediated by up-regulating contrast gain-control mechanisms in the deprived eye in response to the period of reduced signal-strength. The increase in gain-control probably occurs at the cortical level, given that the patch was translucent (causing no dark-adaption), and the long timecourse of the effects (while retinal and LGN adaptation time-courses are short [9]). However, the changes were not by themselves sufficient to explain the prevalence of the deprived eye, implicating additional mechanisms specific to binocular rivalry. Gain-control mechanisms are ubiquitous in mammalian brains, and in several neurological dysfunctions, subtle changes of contrast gain have been observed [10], indicating that the excitatory/inhibitory balance that modulates gain control mechanisms could be particularly susceptible to abnormal developmental events. Increasing cortical contrast gain of the deprived eye may reflect neuroplastic mechanisms attempting to optimize weak or absent information.

Overall, the present results demonstrate that abnormal visual experience can drastically affect adult vision. The effects probably reflect transient changes, not long-lasting as for perceptual learning, in neuronal circuitry in primary visual cortex, possibly related to calibration of the system. That binocular rivalry can reveal significant neural plasticity in adult visual cortex suggests that it could become an important non-invasive tool to assess reorganization of the visual cortex in visual pathologies like amblyopia and to monitor excitation/inhibition balance during plastic changes in human.

Supplemental Information

Supplemental Information includes two figures and Supplemental Experimental Procedures, and can be found with this article online at doi:10.1016/j.cub.2011.06.004.

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