Correspondences

Monocular deprivation boosts long-term visual plasticity

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Monocular deprivation (MD) has been widely used to measure plasticity in the early visual system [1]. It is widely known that during an early critical period of an observer's life, the ocular dominance in the primary visual cortex is severely disrupted when measured immediately after the offset of MD. In contrast, hardly any change was observed when MD is conducted after the critical period [2]. Here we report that long-term plasticity occurred significantly more rapidly with the non-deprived eye than with the deprived eye of human adults when induced by training on a visual task conducted after three-day MD. Thus, the present results challenge the long-standing view that MD has no long-term influence on the visual function of normal adults.

The experiment consisted of pre-MD test, MD, post-MD test, and training stages (Figure 1A; see the Supplemental Information available on-line with this issue for details). In the pre-MD and post-MD test stages, subjects' (N = 4) performance was measured on a contrast detection task (Supplemental Figure S1A) separately for each eye. In the MD stage, one of the subjects' eyes was occluded with an eye-patch for three days during which the subjects performed no task. We found no significant effect of test (pre-MD versus post-MD tests), eye (deprived versus non-deprived), or their interaction (Supplemental Figure S1B), indicating no effect of MD or eyes on task performance *before* training.

Following the post-MD test stage, subjects underwent 12-day training on the same detection task in a separate trial for each eye. Despite some degree of variability, the same tendency was observed across the subjects (Figure 1B). While performance for the non-deprived eye was generally better than for the deprived eye in the early and middle periods of the training stage for all subjects, performance levels were similar between the eyes in the late period (Figure 1B). Significant differences were observed in the early (paired t-test, $P = 0.015$) and middle ($P = 0.001$) periods, but no significant difference in the late period ($P = 0.380$) (Figure 1C). These results suggest that MD selectively modulates the speed of performance improvement.

Did MD boost performance for the non-deprived eye, or impair performance for the deprived eye? To address this question, four new subjects participated in a control experiment, in which no MD was conducted during a three-day interval between the pre- and post-test stages. Mean performance for the non-deprived eye among the experimental subjects was significantly better than that of control subjects in the middle period (unpaired t-test, $P = 0.039$), but not in the early ($P = 0.124$) or late ($P = 0.480$) periods (Figure 1C). No significant performance differences were observed between the deprived eyes of experimental subjects and control subjects for any period ($P > 0.315$). That is, MD selectively boosted visual plasticity for the non-deprived eye without significantly influencing an initial level of visual performance before the onset of training. MD in adults can modulate *subsequent* plasticity.

Recent studies of adult vision have reported no or only slight visual function changes after MD [1,2]. Such changes, if any, lasted for a very short time (~3 h) [3,4]. In contrast, the boosting effect found here lasted for several days, which was longer than previously reported. While some studies suggest a plastic change after MD [5,6], it is unclear whether the change was caused by MD itself or by the training imposed during the MD stage. In contrast, our results clearly demonstrate that MD itself induced a greater degree of plasticity, as there was no training during the MD stage and that MD's subsequent boosting effect on perceptual learning lasted for several days. These findings are important, because MD has been used under the assumption that it does not change the long-term plasticity of adult vision.

What is the underlying mechanism for the boosting effect? In a normal adult, cross-inhibition occurs from each eye [7]. The boosting effect suggests that no cross-inhibition from the deprived to non-deprived eyes during MD reduces effectiveness of plasticity brake, which is usually effective after the offset of a critical
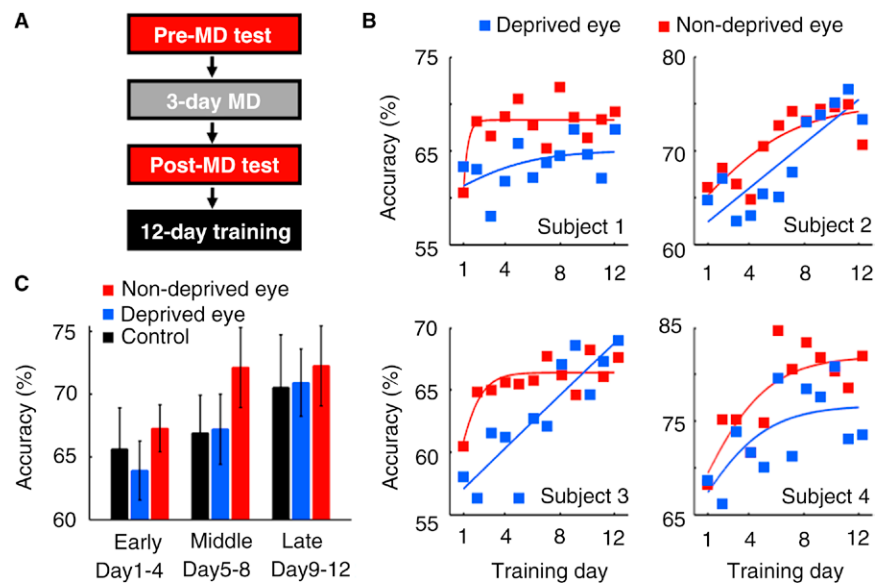

Figure 1. Experimental design and training results after MD.
(A) Experimental procedure. (B) Training results for each subject (logistically fitted). (C) Mean (±SEM) performance in each period for the deprived eye, non-deprived eye, and control subjects during the training stage (see Figure S1C for performance for each eye).

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period [1]. If so, the facilitation of visual plasticity after binocular deprivation [8] may be due to the removal of mutual inhibitions between the two eyes. Moreover, the improvement in performance with an amblyopic eye as a result of occluding the fellow eye [5] might be at least partially accounted for by this boosting effect, although the combination of training with an amblyopic eye and deprivation of the fellow eye may be more effective [5,7].

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Could methane produced by sauropod dinosaurs have helped drive Mesozoic climate warmth?

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Mesozoic sauropods, like many modern herbivores, are likely to have hosted microbial methanogenic symbionts for the fermentative digestion of their plant food [1]. Today methane from livestock is a significant component of the global methane budget [2]. Sauropod methane emission would probably also have been considerable. Here, we use a simple quantitative approach to estimate the magnitude of such methane production and show that the production of the 'greenhouse' gas methane by sauropods could have been an important factor in warm Mesozoic climates.

Sauropod dinosaurs include the largest terrestrial animals known and exhibit a distinctive body shape, featuring a small head at the end of a very long neck. Their diversity and geographic range suggest that sauropods may have been keystone species in many ecosystems during the Jurassic and Cretaceous [1]. Based in part on data from the Late Jurassic Morrison Formation (Western USA), Farlow *et al.* [3] estimated population densities for sauropods ranging from a few large adult animals to a few tens of individuals per km². Specifically, they estimate that if dinosaurs had an endothermic, mammalian-style metabolism, then the total abundance of these megaherbivores would have been 11–15 animals/km² with a total biomass density of around 42,000 kg/km². It is, however, very unlikely that large-bodied sauropods had metabolisms as high as predicted by the assumption of mammalian metabolism [1]. If instead a reptilian metabolism in assumed, then Farlow *et al.* [3] calculate a predicted biomass density of 377,000 kg/km². The palaeoenvironment of the

Morrison Formation was, at least in part, semi-arid — probably not optimal megaherbivore habitat. For our calculation, we conservatively assume sauropod biomass density, averaged over the global vegetated land area, to be around 200,000 kg/km². Other recent estimates of the biomass density of herbivorous dinosaurs are 80,000–90,000 kg/km² [4] and 7–24 times the biomass of extant large-bodied herbivorous mammals [5], which taking a value of 28,000 kg/km² for mammals (Table 7 of [3]) gives a range between 186,000–672,000 kg/km². These studies all predict a higher herbivore biomass in the Mesozoic than seen in modern systems with large herbivorous mammals — such as African savannah. Three potential underlying mechanisms are conceivable: first, Mesozoic primary production per km² would reflect higher temperatures and CO_2 concentrations [6]. Second, large herbivorous dinosaurs would have had lower mass-specific metabolic rates than endothermic mammals of the same size [1]. Third, herbivorous dinosaurs featured a very large individual body size, and — as metabolism scales less than linearly — a larger individual body size allows a given primary production to support a greater herbivore biomass.

To estimate methane production we follow the relationship derived by Franz *et al.* [7] for modern non-ruminant herbivores, where Methane (litres per day) = 0.18 (body mass in kg)$^{0.97}$. The exponent (0.97) is not statistically different from one [8], indicating that to calculate total sauropod methane emissions, we need only estimate the total biomass density, since methane emissions will be insensitive to body size distribution of the constituent animals. As an illustrative example, we consider the sauropod biomass density of 200,000 kg/km² to consist of ten 20,000 kg sauropods; this is a conservative estimate of the adult mass of the medium sized sauropod *Apatosaurus louise*, colloquially known as 'Brontosaurus'. For this, the allometric relation gives methane emission of 2675 litres per day for one animal, equivalent to about 1.9 kg per day under the standard temperature and pressure conditions assumed in [7]. For a density of ten adults per km², assuming, for comparability,