competition over who shall reproduce, but because it is apparently more efficient for the colony to cycle between phases of reproduction and foraging. Why cycling should be more efficient than continuous reproduction, as is seen in most eusocial insects, has not yet been addressed. Perhaps it is the only way these ants can control egg production. Interestingly, females of some solitary insects show similar cycling, and some aspects of the behaviour of eusocial species may be derived from these cycles [9].

The Teseo paper [2] is important because it brings into sharp focus the relative importance of colony conflict and colony efficiency in the evolution of worker policing. In all other study systems, conflict and efficiency are confounded. A honey bee colony is less efficient if the workers lay eggs [10,11], but did policing first evolve to reduce genetic conflict or increase colony-level efficiency? Teseo *et al.* [2] have demonstrated that efficiency alone seems to maintain policing in *C. biroi*, but it still seems that in most other cases it is kin conflict that has driven the evolution of worker policing. Predictions about policing behaviour from conflict theory are strongly supported empirically [1,12]. So, it seems that both conflict and efficiency can be important to the evolution of policing. It is interesting to speculate on whether the policing behaviour observed in *C. biroi* originally evolved to resolve genetic conflict, and was then co-opted to its present function, or if it arose when the species became clonal, abandoned queens and adopted its current practise of reproductive cycling. In any case, it is now timely to re-emphasise that the concept of worker policing encompasses behaviour that improves colony efficiency as well as resolving conflict [13].

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Cognitive Neuroscience: Targeting Neuroplasticity with Neural Decoding and Biofeedback

New research combining neural decoding and biofeedback to target neuroplasticity causally links early visual cortical plasticity with improved perception. This is an exciting new approach to understanding brain function, one which may lead to new ways of treating neurological disorders by targeted intervention.

Aaron R. Seitz

A central goal of cognitive neuroscience is to understand how brains give rise to behavior. The holy grail of many fields of cognitive neuroscience is to make causal links between the processing within, or between, various brain regions and people's perceptions, decisions or actions. Establishing such causality between brain and behavior is extremely difficult given that so many brain regions are normally active during task performance, that correlations between brain processing and behavior can be spurious or epiphenomenal, and that the directionality of such correlations is always ambiguous. Here we discuss two new studies [1,2] that have overcome these limitations by using a novel approach combining neural decoding of functional magnetic resonance imaging (fMRI) signals with biofeedback to target neuroplasticity within specific brain regions.

In the field of perceptual learning, there has been a long and heated debate regarding the role of early visual cortical plasticity in perceptual learning [3]. To date, the case for early visual cortex being important in behavioral learning effects has been based upon correlational arguments, and while there are numerous demonstrations of plasticity as early as primary visual cortex (V1), the effects are typically insufficient to explain the magnitude or pattern of behavioral results [4], and computational models show that most behavioral observations of perceptual learning can be accounted for without representational changes [5].

A fundamental difficulty in understanding the mechanisms of perceptual learning is that many different mechanisms can potentially give rise to the same behavioral outcome. For example, in a typical task of detecting a subtle orientation pattern (see pattern in Figure 1A), learning could in principle be achieved by many possible mechanisms; for example, reducing the system's noise [6], increasing the gain of the signal [7], improving an internal template of the target [8], better attending the location or features of the stimulus [9], improving decision rules regarding the stimulus [10], and so on. Learning in a typical task includes contributions from multiple factors, and each of these mechanisms can involve plasticity in a variety of brain regions that are involved in accomplishing that detection task. This makes it very difficult to understand the relationship between the processes of an individual brain area and the learning of a given task.

But what if, instead of training participants to conduct a task, they are trained to alter their brain activity through biofeedback? By targeting training to alter activity only in a specific region of the brain, we can learn about the function of that brain region and its contribution to behavior. Shibata *et al.* [1] and Scharnowski *et al.* [2] recently employed this approach by training participants to alter their brain activity in early visual cortex, as assessed using fMRI decoding techniques (Figure 1A), to match a desired activity pattern. Shibata *et al.* [1] instructed participants to alter their brain activity to maximize the size of a circle that was presented on screen (Figure 1B). Unbeknownst to the participants the size of the circle was determined by the similarity of the participants' brain activity in primary and secondary visual cortex (V1/V2) to that produced by viewing an oriented grating pattern (see example in Figure 1A). Similarly, Scharnowski *et al.* [2] asked participants to alter their brain activity to bring the level of a displayed thermometer to a high (up-regulated state) or low (down-regulated state) target position. However, instead of matching brain activity to a stimulus-induced pattern, the thermometer height was determined by the activity level of a targeted region of primary visual cortex (V1). Thus, in both studies, participants were required through trial and error to achieve a mental state that was read-out using fMRI decoding algorithms and compared to a target-pattern (Figure 1B), determined by the experimenter, and shown a feedback stimulus (circle or thermometer) that indicated their level of success at achieving the correct brain state.

Both studies show that training participants with biofeedback based upon decoded neural signals can result in perceptual learning. Shibata *et al.* [1] trained participants to repeatedly activate a particular activity pattern in V1/V2, finding that this results in enhanced perceptual sensitivity to the stimulus matching the trained pattern. Similarly, Scharnowski *et al.* [2] trained participants to up-regulate activity in a particular region of V1 and participants' sensitivity improved specifically at the trained location, but only when invoking the up-regulated state. Both studies report a number of control analyses which show that decoding signals from other brain regions could not account for the observed behavioral learning effects. Thus, both studies demonstrate a causal relationship between the altered activity in early visual cortex and the observed behavioral changes.

Equally important is that different mechanisms account for the observed learning effects in the two studies. Shibata *et al.* [1] found that repeated activation of the target activity pattern in V1/V2 resulted in improved sensitivity, even without the participants activating this state during the post-training test, implicating local mechanisms of plasticity. Scharnowski *et al.* [2] taught participants to up-regulate overall activity in the region of interest and found that the improvement of sensitivity was dependent upon participants being in the up-regulated state. Furthermore, these authors used functional connectivity analysis to show that this up-regulated state involved a network between V1 and superior parietal lobe, a brain structure known to be involved in the regulation of spatial attention.

Thus, while the two studies tested improved discrimination of the same

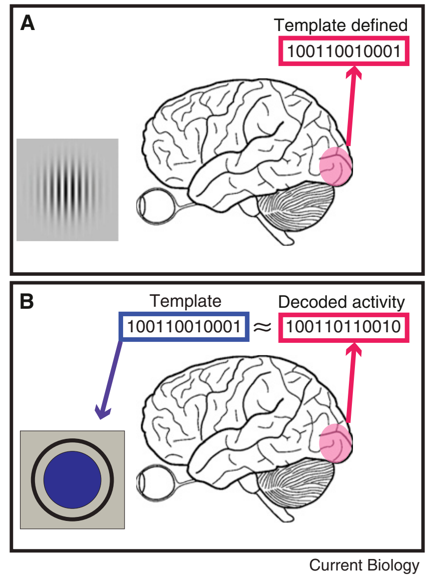

Figure 1. Procedure for neuroplasticity experiments based on neural decoding and biofeedback.

(A) The first stage is to define template by decoding stimulus inducted activity pattern in the region of interest. (B) Participants attempt to fill (blue disk) the entire circular region (black circle) by inducing an activity pattern in the region of interest that matches (as determined by the decoder) the template.

type of stimuli (orientation patterns), the Shibata *et al.* [1] result is consistent with a representation change in V1, whereas the Scharnowski *et al.* [2] result is consistent with improved attentional focus to the trained region of interest. These results suggest that these new imaging techniques can be used not only to target the role of specific brain regions in learning but also to distinguish between different mechanisms of plasticity involving these brain areas.

Interestingly, in both studies [1,2], unlike most studies of perceptual learning, participants learned without viewing a specific stimulus during training. Scharnowski *et al.* [2] informed participants of target location and instructed them to engage in visual imagery at that location. Shibata *et al.* [1] provided no specific instructions to their participants, though many participants in that study also engaged in forms of mental imagery. Notably, in neither study did the participants' subjective report of their mental activity match up with the stimuli that the investigators used for testing. Still, using visual imagery to induce perceptual learning is an interesting approach that has also shown success in other studies. For example, perceptual learning can be evoked through mental imagery of hyperacuity patterns [11] or motion patterns [12] and results in similar training benefits as those achieved through training on the same tasks with visually presented stimuli. Interestingly, training with imagined stimuli showed a similar degree of specificity to the characteristics of the imagined stimuli as found through traditional training with real stimuli. While it is unlikely that the task-related mental imagery resulted in the same type of focused activity pattern as manipulated through biofeedback, it is likely that there are some common mechanisms of plasticity in these cases and suggests an important role for mental imagery in perceptual learning.

Together, the two studies [1,2] show that this new approach of using decoded neural signals as biofeedback to induce targeted neural plasticity is a powerful way of identifying the function of individual brain regions as well as neural networks involving multiple brain regions. These approaches are particularly useful in that they can support causal relationships between brain activity patterns and behavior. However, participants use unstructured approaches, such as mental imagery [11,12], to induce the target brain states. This can give rise to significant individual differences in outcomes [2], it is likely that there are changes in brain state that are epiphenomenal to those targeted by the investigators, and there are certainly differences in the learning induced through biofeedback compared to that achieved through task performance. Thus, to gain a complete understanding of the human learning process biofeedback will need to be used in conjunction with standard approaches.

These studies are not just scientifically interesting; they are exciting in their potential applications to develop behavioral therapies for neurological disorders. Biofeedback [13] has had a long and mixed history as a medical intervention, but has always held the promise that an individual's function can be improved by learning to emulate the processes of a healthier counterpart. New methodologies using decoded neural signals as biofeedback to induce neural plasticity [14] are advantageous in that they can be targeted to highly specific activity patterns within and across brain regions. Initial studies suggest promise of these techniques in the treatment of pain [15], emotional regulation [16], social learning [17], tinnitus [18], and Parkinson disease [19]. While more research will be required to determine the most optimal training conditions — for example, only half of Scharnowski *et al*'s. [2] participants learned the task — the appropriate target activity patterns to help individuals suffering from different conditions, and costs and accessibility of the high-end fMRI facilities used are currently prohibitive to standard treatment, these studies demonstrate a very exciting future for fMRI-based biofeedback as targeted neuroplasticity-based therapy for treating individuals with neurological conditions.

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