Binocular Rivalry: Neurons Unwire When They Can't Simultaneously Fire

Binocular rivalry, where very different monocular images appear to alternate, changes its perceptual characteristics over time. New evidence suggests that this results from synaptic weakening or decoupling of neurons that are prevented from firing together.

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Binocular rivalry is an inherently fascinating phenomenon where viewing two very different monocular images (Figure 1) gives rise to a dynamic percept in which the two monocular images alternate approximately every one to three seconds in a competition to dominate conscious vision [1,2]. In recent years, rivalry has become a vehicle for the study of a wide range of neural phenomena, including effects of attention, brief perceptual memory [3], meditation [4], neural decisions [5] and consciousness [6].

In a study reported recently in *Current Biology* [7], rivalry invades a new domain: negative learning or reverse synaptic plasticity. In order to permit very long durations of rivalry viewing, subjects experienced rivalrous monocular stimuli for 100 seconds followed by 10 second rest periods viewing a gray screen. Early in rivalry, the perceptual alternations tended to be primarily between exclusive right eye or left eye views, as shown at the top of Figure 1. After several minutes of rivalry, however, these periods of exclusive dominance by monocular views became less frequent, and mixed percepts (Figure 1 bottom), either superposition or piecemeal, were seen with increasing regularity.

This decrease in exclusive monocular views is illustrated by the red curve in Figure 2, which was normalized for each subject to the exclusive monocular duration before the experiment began. Not surprisingly, some form of adaptation has occurred. Indeed, given that rivalry models typically explain exclusive monocular dominance as a product of strong, competitive inhibition between monocular representations [8,9], Klink *et al.* [7] predicted that a reduction in the strength of such inhibition would lead to the observed increase in mixed percepts. They went even further, however, and predicted that this was a consequence of inhibitory synaptic depression.

Following the pioneering work of Hebb [10], it is now well established that "neurons that fire together wire together". That is, when one neuron consistently fires concurrently with a neuron on which it makes synaptic connections, these synaptic connections become stronger. This is regarded as a consequence of long-term potentiation mediated by NMDA synapses [11]. The converse of this is that neurons which virtually never fire together should begin to unwire, a process the authors term 'anti-Hebbian inhibitory plasticity'.

Clearly, exclusive monocular rivalry precludes the simultaneous activation of left and right monocular neurons in the cortex, and it should therefore be conducive to anti-Hebbian plasticity. How could this be tested in binocular rivalry? The elegant answer was to study recovery from the rivalry adaptation, shown by the red curve in Figure 2 [7]. This was done by controlling non-rivalrous viewing during the recovery phase, while interspersing short rivalry test periods. When the subject was allowed to look around the laboratory during recovery,

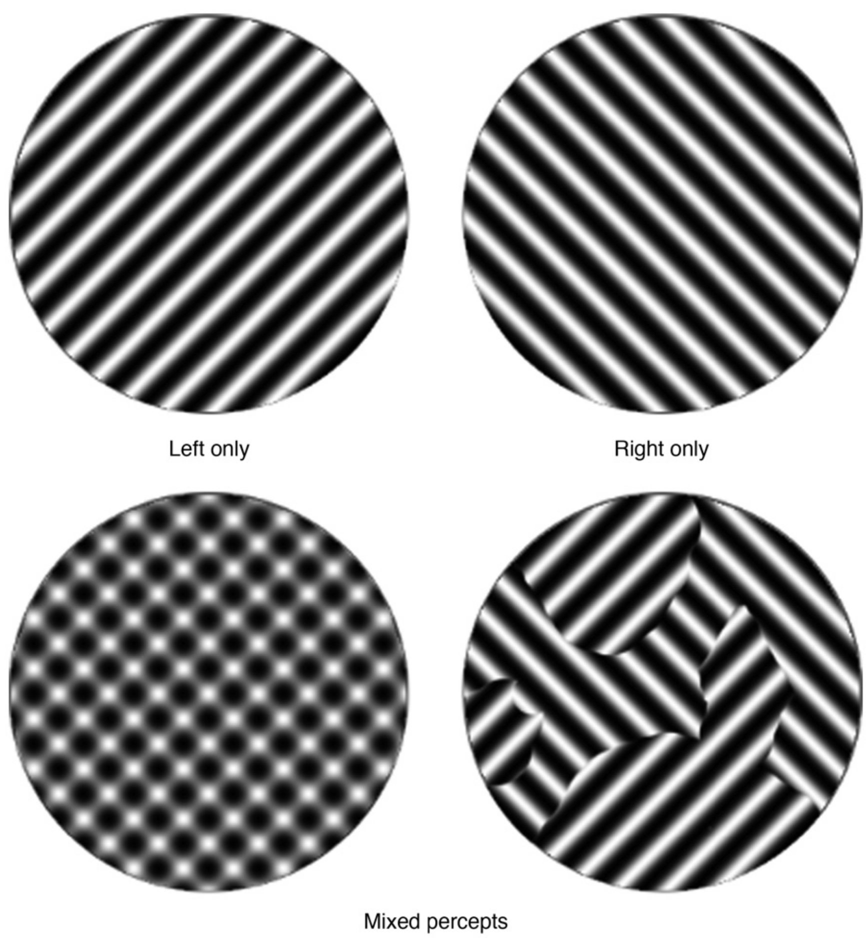

Figure 1. Stimuli presented to the left and right eyes (top) to produce binocular rivalry.
During the early stages of rivalry, exclusive perception of the left alternating with the right eye view dominates perception. The reader can experience this by either crossing or diverging their eyes. Later in rivalry the mixed percepts depicted at the bottom become more common.

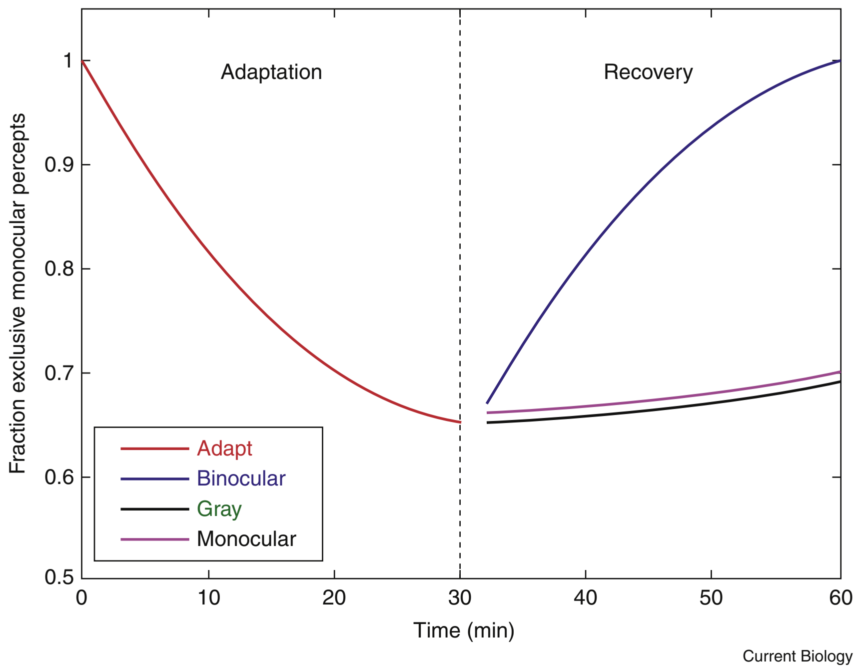

Figure 2. Schematic plot of key data.

Prolonged rivalry produces adaptation in which the fraction of exclusive monocular percepts declines significantly (red line). Following this, binocular stimulation (blue line) produces recovery to the original level. However, absence of any visual stimulation (black line) or monocular pattern viewing (magenta line) failed to produce any recovery from adaptation. This pattern of data is predicted by anti-Hebbian inhibitory synaptic plasticity.

thereby guaranteeing normal, non-rivalrous binocular input, recovery followed the course of the blue curve. Strikingly, however, absence of any visual stimulation during recovery generated the black curve: essentially no recovery was possible. Even more strikingly, monocular viewing of the room while the other eye was covered, a condition that produces neither rivalry nor binocular depth perception, also prevented recovery from rivalry adaptation, as shown by the magenta curve. Furthermore, monocular viewing for 24 hours also produced essentially no recovery from rivalry adaptation.

These recovery phase measurements clearly demonstrate that normal binocular viewing is a necessary condition for recovery from rivalry adaption. Neither absence of visual stimulation nor purely monocular activation sufficed to produce recovery. Furthermore, by using binocular stimulation with superimposed left and right gratings during the recovery period, it was shown that recovery required the spatial frequency and orientation to be the same as for the rivaling gratings. In other words, it was necessary to binocularly activate exactly the same neurons that had been rivaling for recovery to occur. From this the authors concluded that normal Hebbian facilitation, requiring concurrent pre- and post-synaptic activation, was necessary for recovery from rivalry adaptation [7]. That being so, rivalry adaptation apparently represents the converse: anti-Hebbian inhibitory plasticity between monocular neurons.

Long-term adaptation has been demonstrated in several other visual phenomena, including negative afterimages [12] and the McCollough effect [13]. The unique feature of the current study [7] is the detailed evidence for anti-Hebbian inhibitory synaptic plasticity. The evidence is, of course, indirect, as no pre- or post-synaptic neurons were actually investigated. Thus, this study should lead to future neurophysiology experiments in which multi-electrode arrays actually sample from competing neural populations in macaque primary visual cortex (V1). Furthermore, ocular dominance columns in human V1 have been imaged using fMRI [14], and differing orientation columns in V1 can also be shown by fMRI imaging [15]. Therefore, there is also a natural extension of the current experiments to human brain imaging.

Another natural extension is in psychophysics. This novel technique for revealing anti-Hebbian inhibitory plasticity should prove extremely valuable in exploring a vast range of adaptation techniques. For example, techniques have been developed that appear to by-pass the earlier stages of binocular rivalry [16], thereby revealing subsequent stages in a rivalry hierarchy [17]. It would be very interesting to study adaptation of these hierarchical stages using the present technique. The technique also holds promise of elucidating the link between rivalry and normal binocular vision.

In recent years, it has become clear that the adult visual system remains plastic at many levels, not just at the highest levels of visual memory storage. Indeed, the fascinating case of 'Stereo Sue' [18] indicates that plasticity of cortical binocular interactions is present throughout adulthood. Susan Barry is a neuroscientist who was born with misaligned eyes (strabismus) so that, for decades, she could not perceive stereoscopic depth, despite eye realignment surgery. Through extensive orthoptic training, however, she suddenly developed stereoscopic vision for the first time at age 50 [19]. As inhibition clearly seems to be involved in suppression of one monocular image in favor of the other in strabismus, it is conceivable that the present demonstration of anti-Hebbian inhibitory synaptic plasticity may lead to a deeper understanding of the development of binocular vision and to new forms of strabismus therapy.

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