constitute a barrier for axon regeneration after ischemia or injury. These new results also suggest that this undesired VAB-1 activity functions in the guidepost cells and the tissues that growing axons traverse, which is quite reminiscent of the astrocytic expression of Eph receptors in the injured mammalian spinal cord. In theory, selective removal of this repulsive activity might help to restore axonal connection in nervous system injuries caused by hypoxic insults.

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Mapping the microcircuitry of attention

John H Reynolds

A study uses electrophysiological recordings from primary visual cortex of the monkey to demonstrate that the effects of attention are modulated by task difficulty and that two different neuronal populations mediate this effect.

A major goal of neuroscience is to understand cognitive functions in terms of their underlying neural circuitry—to link the mental level of description used in cognitive science with the physiological and anatomical levels that are the province of neurobiology. In this issue of *Nature Neuroscience*, Chen *et al.*[1] take a substantial step toward such mechanistic understanding of an important cognitive function, selective attention. Although spatial attention has been shown to modulate responses of cells in the primary visual cortex (V1), it is unclear how task difficulty affects this modulation. Moreover, are different cell populations affected uniformly by attention or not? Answers to these questions are important for building realistic models of how this information is coded in V1 and modulated by attentional state. On page 974, Chen *et al.*[1] take an important first step in this direction. By recording neuronal responses in the primary visual cortex of monkeys performing an attention-demanding task, the authors show distinct roles for two major types of neurons in selecting task-relevant stimuli from among task-irrelevant distracters.

In the experiment, monkeys had to attend to a stimulus to detect a change in its color. The color change could be easy or hard to detect, thus varying the attentional effort required to perform the task. Furthermore, attention was either directed to a stimulus appearing in the receptive field of the neuron under study or to one of several stimuli that appeared simultaneously around the receptive field. When attention was directed into the receptive field, neuronal responses typically grew stronger with increased attentional effort. However, when attention was directed to one of the stimuli outside of the receptive field, firing rates typically diminished with increased effort. That is, increasing attentional effort appeared to enhance neuronal responses at the focus of attention while suppressing responses outside of the focus of attention. This suggests that attention may modulate the neural circuitry that gives rise to the center-surround organization of the receptive field in V1. This study also found evidence that enhancement and suppression are, to some extent, mediated by distinct groups of neurons. Neurons that showed the strongest response suppression with attention outside of the receptive field tended to show the weakest response enhancement with attention to the center. Neurons that showed the strongest response enhancement showed no response suppression.

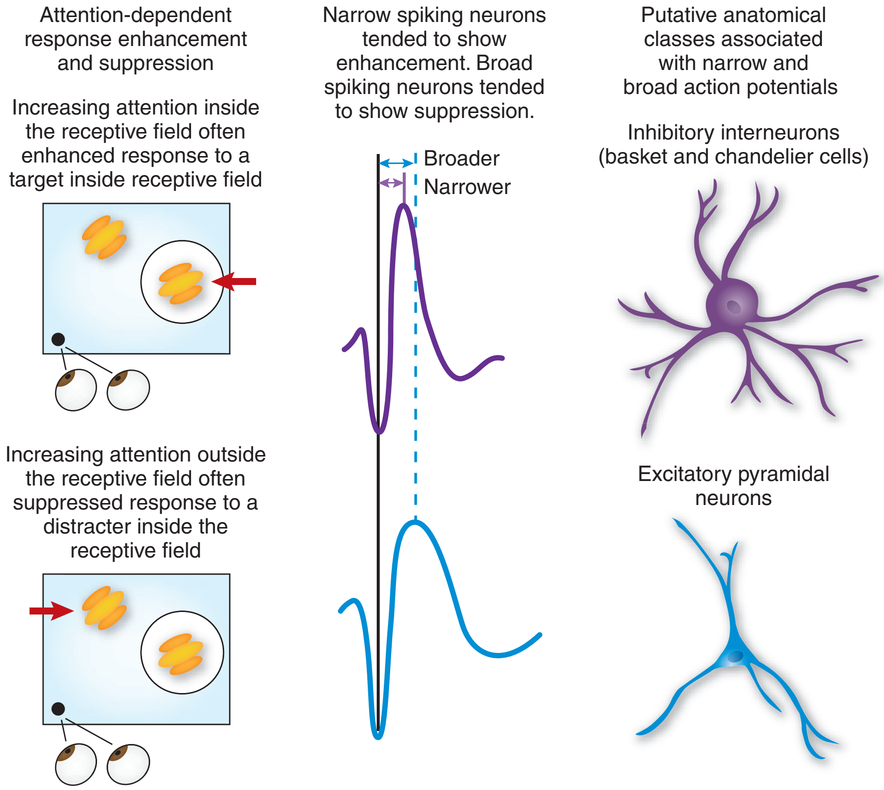

Figure 1 Attention enhanced responses at the attended location and suppressed responses to nearby distracters (red arrows indicate focus of attention). These two types of attentional modulation were associated with different classes of neurons.

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To examine the possibility that these two effects were mediated by distinct classes of neurons, Chen *et al.*[1] divided the population into two groups: difficulty-enhanced neurons, which on average increased responses with increased task difficulty, and difficulty-suppressed neurons, which showed decreased responses with increased task difficulty. These two groups of neurons differed in their direction selectivity, contrast sensitivity and interspike interval distribution, supporting the idea that they correspond to distinct classes of neurons. To test this directly, the authors examined action potential waveform width, a parameter that has been found to vary across anatomically distinct classes of neurons. Difficulty-enhanced neurons tended to have narrow action potentials, whereas difficulty-suppressed neurons tended to have broad action potentials. Studies in anesthetized animals and cortical slices, where different types of neurons can be distinguished on the basis of morphology and protein expression, have found that parvalbumin-expressing GABAergic interneurons with basket or chandelier morphology have narrow action potentials. Pyramidal neurons, on the other hand, typically have broad action potentials. As the authors are careful to note, this separation of neurons into putative interneurons and pyramids on the basis of action potential width is not one-to-one; there are a few narrow-spiking pyramidal neurons[2] and a substantial fraction of interneurons that have broad action potentials. However, given that 70–80% of all cortical neurons are broad-spiking pyramidal neurons, it is probable that the large majority of broad-spiking neurons are indeed pyramidal neurons. Furthermore, as narrow-spiking pyramidal neurons are uncommon, it is probable that most narrow-spiking neurons recorded in this study are indeed inhibitory interneurons. Thus, the authors propose that the center-surround organization that they observed is mediated by two distinct classes of neurons: narrow-spiking inhibitory interneurons that tend to show elevations in activity when attention is directed to a stimulus in the receptive field and broad-spiking pyramidal neurons that tend to be suppressed when attention is directed outside of the receptive field (**Fig. 1**).

The present study advances our understanding of attention in several ways. First, it is one of the few studies to date that have examined differences in attentional modulation across distinct classes of neurons. This is an essential step forward for understanding the cortical circuits that mediate attention. Second, this study shows that, as in area V4, attention increases the responses of inhibitory interneurons[3]. Third, these findings strongly support models of attention in which reductions in the neuronal responses evoked by distracters result from attention-dependent increases in the activity of inhibitory interneurons[4–7]. This study provides particularly strong support for the proposal that attention modulates the circuits that give rise to center-surround interactions[8–10]. If so, the influence of a stimulus appearing in the surround should be diminished when attention is directed to the neuron's classical receptive field center and magnified with attention to the surround stimulus. Chen *et al.*[1] did not measure the influence of the extra-receptive field stimuli in their study in the absence of attention, but if the present findings do reflect attentional modulation of center-surround interactions, the neurons that were suppressed by attention would be predicted to be those that were suppressed by inhibitory interneurons whose responses were magnified by attentional feedback[10]. It will be interesting to see this prediction tested in future experiments.

The central importance of attention in perception and behavior has been recognized since the dawn of experimental psychology and its scientific investigation has been marked by a progressive improvement in our understanding of underlying mechanisms. Research from multiple laboratories has revealed that when attention is directed to a location in space, feedback signals are generated in attentional control centers of the brain[11–15]. These signals feed into the visual cortices, where they enhance the neural signals evoked by attended stimuli and diminish responses evoked by task-irrelevant distracters. In the present study, Chen *et al.*[1] have shed light on the neural circuits in the visual system that transform attentional feedback signals into these two forms of attentional modulation. They have thus made a substantial contribution to our understanding of the neural substrates of this essential cognitive function.

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Face to face with cortex

Chris I Baker

Two new studies in *Science* and *Nature Neuroscience* combine functional magnetic resonance imaging and electrical microstimulation to reveal face-selective temporal and frontal areas and their connectivity.

Faces are everywhere, and we are very good at extracting all sorts of information (such as identity, emotional state, direction of attention, etc.) from them. This effortlessness belies the difficulty of the tasks, as faces are complex stimuli, with a great deal of similarity between different faces. In both human and non-human primates, there is considerable neural architecture that is devoted to processing faces, and researchers have identified multiple 'face-selective' brain regions in the temporal lobe that respond more when observers view faces than when they view other objects. However, exactly how these regions connect to each other and whether they constitute part of a specialized 'face network' that extends throughout the brain is a matter of current debate[1–3].

In two studies in *Science* and *Nature Neuroscience*, Moeller *et al.*[4] and Tsao *et al.*[5] used a powerful and technically challenging combination of functional

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