PERSPECTIVES: NEUROSCIENCE

Sensory Maps on the Move

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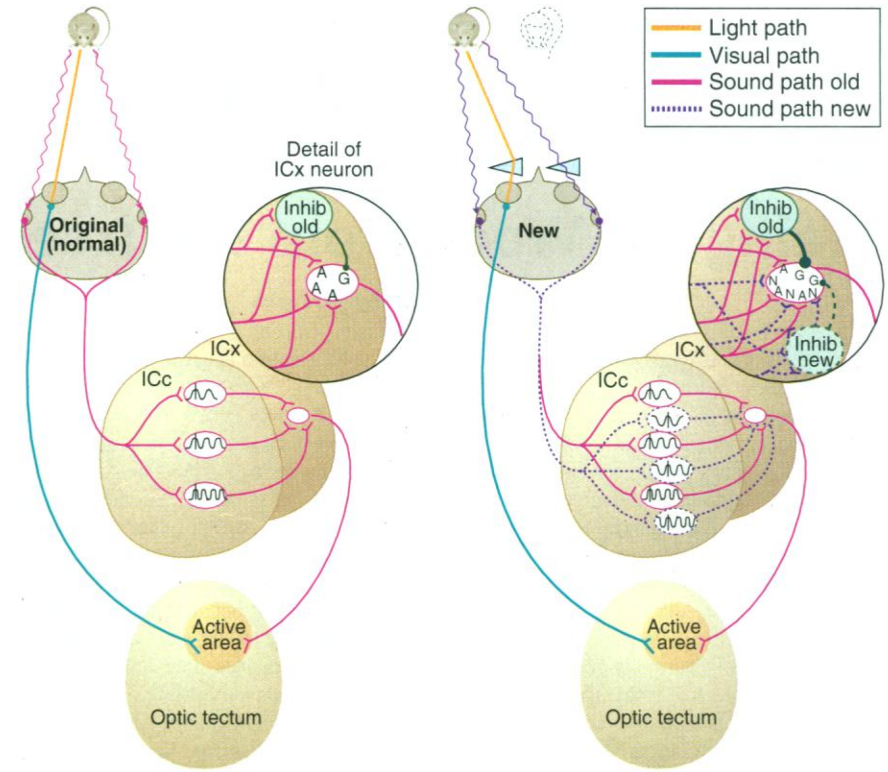
Many features of the world are represented in the brain as orderly maps. These maps can show remarkable plasticity, undergoing reorganization after brain damage or changes in sensory stimulation. In some cases, the maps may even shift so that stimuli activating one group of neurons now activate a completely different set of neurons. The report by Zheng and Knudsen on page 962 of this issue (*1*) offers new insight into how brain maps move. These investigators analyzed how the auditory space map of young barn owls changes in response to alterations in the visual space map. (The auditory and visual space maps of barn owls are closely connected so that the birds, which cannot rotate their eyes, are able to precisely locate their prey using either hearing or sight.) In previous work the authors demonstrated that a newly learned auditory map requires the formation of new excitatory connections. Now they show that the excitatory inputs for the old and new auditory maps coexist but that excitation from the old map is selectively overwhelmed by inhibition from GABA-containing neurons. These results raise new questions about the specification and control of inhibitory connections in the brain and the critical periods for neural plasticity during animal development.

The Knudsen and Konishi laboratories have spent many years describing the neural circuits that control auditory localization in the barn owl (*2*). Unlike visual or tactile space maps, the auditory space map must be constructed by the brain in the external nucleus of the inferior colliculus (ICx). Neurons in the ear respond in the same way to a sound of a particular frequency and intensity no matter where the sound comes from. The brain constructs the auditory space map by comparing the responses of neurons in the two ears to a sound that stimulates both. Left-right positioning of the sound source is computed from the different arrival times of the sound at each ear.

The computation is subtle because the actual time at which a sound begins is not known to the brain, and most auditory neurons are tuned to respond to tones of air pressure of a particular frequency. The sound waves from a source that is straight ahead arrive at the two ears at the same moment. But if the sound source of a particular frequency is displaced so that it is exactly one wavelength nearer to or farther from one ear than the other, the sounds reaching the ears are very similar to the sound arriving from straight ahead. Thus, there is an ambiguity about the localization of pure-tone stimuli. The brain resolves this ambiguity by combining information from neurons that are selective for different frequencies of sound. The signal in each neuron is ambiguous, but only one position of the sound source will be consistent with all of these ambiguities when examined in combination (*3*). This combination occurs through connections from neurons in the central nucleus of the inferior colliculus (ICc)—which is tonotopically organized according to sound frequency—to neurons in the ICx—which is organized according to left-right positioning encoded by differences in arrival times (see the figure). The inferior colliculus neurons send their main output to the optic tectum and activate neurons that are also driven by visual stimulation from the same point in space as the sound source. Thus, either the sight or the sound of the mouse can stimulate the owl to the same action, turning toward its prey.

Zheng and Knudsen (*1*) reared young owls in prism spectacles that displaced the visual image of the world to the left or right. If the owls wear these spectacles during a critical period in early life, they learn to compensate and regain the ability to accurately locate prey. The compensation takes place in the auditory space map of the ICx, which changes to become consistent with the visual map. Earlier work showed that the changes in the auditory space map are partly attributable to the growth of new



Maps of sound and light. The auditory and visual space maps of barn owls are connected, enabling the birds to precisely locate prey. The sight of the mouse stimulates retinal neurons to send signals to activate part of the optic tectum, which orients the owl toward its prey. The sound of the mouse stimulates the two ears with a particular interaural time difference, to which certain neurons in the ICx are sensitive. (These neurons receive input from the ICc at conventional AMPA receptors, A). The ICx neurons activate the same region of the optic tectum as visual stimuli. In juvenile owls reared in prism spectacles that alter the visual space map, the ICc makes new excitatory connections (through NMDA receptors, N) to the ICx. Excitatory signals from the old connections are overcome by a selective increase in inhibition from GABA-containing neurons, G). Thus, the sound and sight of the mouse again cause orientation to the same position.

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excitatory inputs from the ICc to the ICx (*4*). These new neural connections respond to the excitatory neurotransmitter glutamate through synaptic membrane NMDA (*N*-methyl-D-aspartate) receptors (*5*).

New excitatory connections explain how neurons in the ICx respond to the appropriate position in space dictated by the altered visual map. But why do the ICx neurons stop responding to the old position? It turns out that the old excitatory inputs remain, but the ICx neurons now receive strong inhibitory input that is activated by the same auditory stimuli that activated the original excitatory connections. The inhibition sums with the excitation so that the ICx neurons no longer respond to the old stimuli. For the cells of the optic tectum that "listen" to the ICx neurons, the new auditory field appears similar in kind to the old one, but is just located in a different place. The neural circuitry that maintains the relocated receptive field is, however, quite different.

These findings explain why the normal auditory space map is restored in owls when the prism spectacles are removed, even at an age when normal owls have lost the ability to adapt to a rearranged visual map (*4*). The original neural circuitry is still there, and all that is needed for it to assume control is removal of inhibitory input. Inhibitory connections also explain why the capacity for plasticity in adult owls is greater if they have adapted to rearranged maps as juveniles (*6*).

What rule of neural plasticity regulates the strength of these inhibitory connections? Inhibition is selectively increased for those positions in space that receive strong excitatory input but do not match the position at which ICx neurons target cells in the optic tectum. Such a rule requires that a retrograde signal travels from the tectal cells to the axonal terminals of the ICx cells and thence to their cell bodies and dendrites, where it enhances responses to inhibitory inputs at GABA receptors. These dual contingencies show that inhibitory connections are weakened under circumstances in which excitatory connections are strengthened and vice versa (*7*). Such a reciprocal relationship between the excitatory and inhibitory inputs makes sense, although as yet has not been rigorously demonstrated.

How applicable are the new findings to the plasticity of other types of sensory maps? There is little evidence for selective inhibition as the mechanism of plasticity in the adult cortex—most long-range connections are excitatory not inhibitory. However, a combination of excitatory and inhibitory pathways may explain cases in which receptive fields move, for example, after denervation of a digit or of two adjacent digits (*8*). In contrast, experiments in the visual cortex show that the loss of response to the occluded eye after brief monocular deprivation is not the consequence of selective inhibition from deprived-eye pathways (*9*). Nonetheless, appropriate inhibition is essential for normal plasticity in the visual cortex (*10*).

In the brain, as in life, it is not just what you do that matters, it's also what you don't do. The plasticity of auditory spatial representation in the owl brain depends not only on new excitatory connections but also on overwhelming the persistent old connections through inhibition. By combining and overlaying different plasticity mechanisms in the auditory pathway, the owl is able to adjust its various sensory maps so that they are in harmony.

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PERSPECTIVES: CLIMATE WARMING

Seeing the Wood from the Trees

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In recent years, several studies (*1–5*) have attempted to reconstruct the history of hemispheric or global average surface air temperatures for much, or all, of the current millennium. The motivation for these studies is our need to establish the degree to which the 20th century is unusually warm when viewed against a background of preindustrial climate variability. Some papers describe simple averages of selected long temperature proxies (indirect recorders of temperature conditions), mostly annually resolved time series derived from tree rings, ice cores, and some corals. Others also incorporate the longest instrumental series stretching back into the 17th and 18th centuries. This direct averaging approach gives equal weight to each series and relies on sufficient regional coverage to provide a true representation of hemispheric or global conditions.

The alternative approach is multiple regression, where greater weight is placed on specific proxy series that exhibit greatest affinity with the modern large-scale instrumental record (*5*). The latest such study by Mann *et al.* (*6*) extends their previous reconstruction of Northern Hemisphere (NH) mean annual temperatures from A.D. 1400 back a further 400 years. This is important because much of the period from 1300 to the start of widespread instrumental records may have been relatively cool, thus potentially exaggerating the long-term significance of the observed 20th century warming. It has long been suggested, mostly on the basis of European information, that the medieval period may have been relatively warm, but the evidence from further afield is equivocal. A reliable, early NH temperature reconstruction is, therefore, a more appropriate benchmark against which to gauge the significance of 20th century warmth. In attempting to provide this, Mann *et al.* confront a number of problems currently limiting our ability to view such reconstructions as realistic indications of the full amplitude of past temperature changes.

An uninformed reader would be forgiven for interpreting the similarity between the 1000-year temperature curve of Mann *et al.* and a variety of others also representing either temperature change over the NH as a whole or a large part of it (see the figure) as strong corroboration of their general validity, and, to some extent, this may well be so. Unfortunately, very few of the series are truly independent: There is a degree of common input to virtually every one, because there are still only a small number of long, well-dated, high-resolution proxy records.

Mann *et al.* base their early (pre-1400) reconstruction on 12 series, of which nine are derived from tree rings and three from ice cores. Commendably, they present two standard error confidence limits on this reconstruction and show how these are considerably wider before 1600 than in later centuries. The upper bounds of the early limits are high enough to encompass even the upper limit of uncertainty associated with their 20th century temperature estimates (which run up to 1980). The warmth shown in the instrumental records during the past two

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