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PERSPECTIVE | NEUROSCIENCE

Sensory Maps on the Move

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Article

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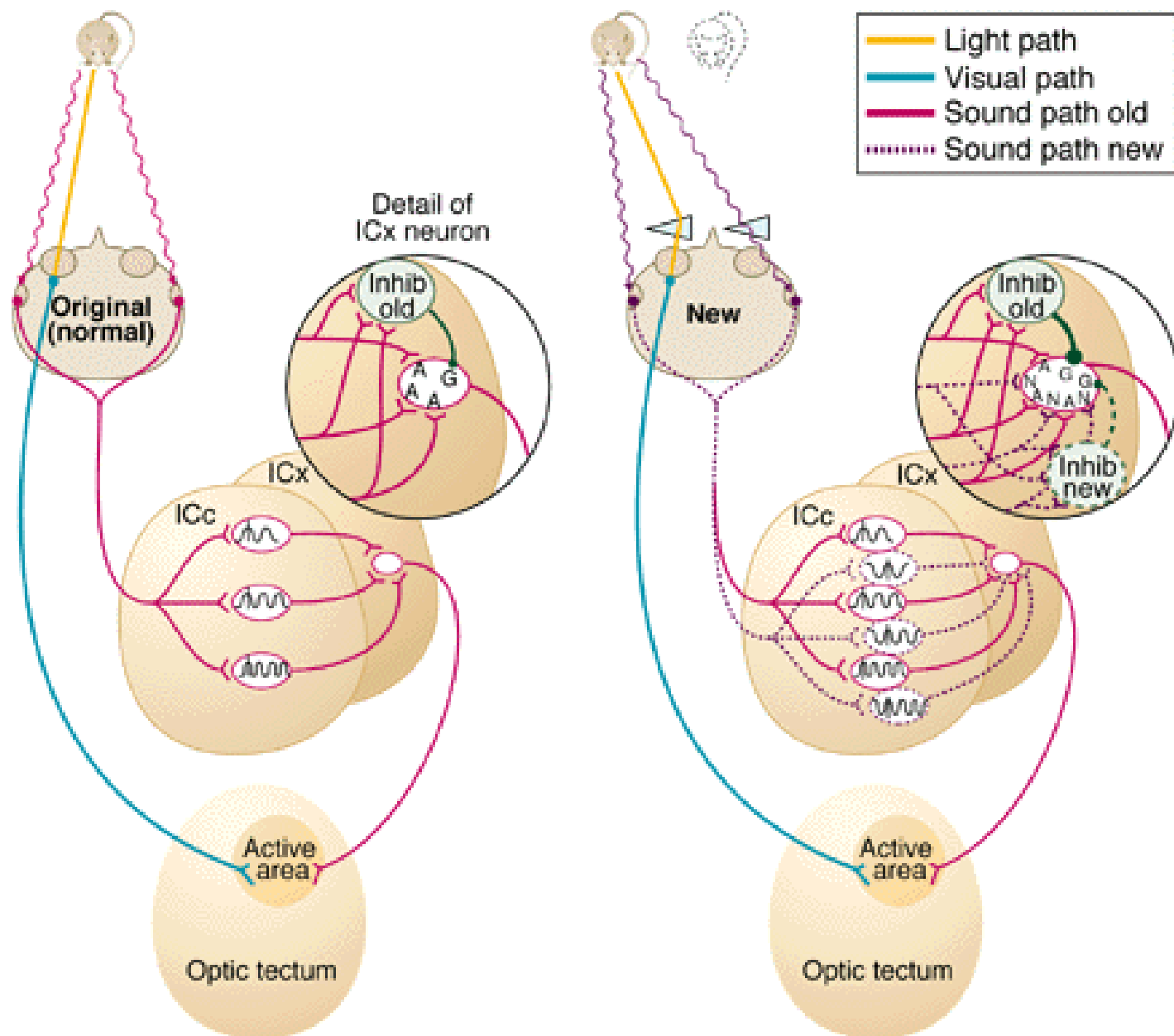
eLetters

Many features of the world are represented in the brain as orderly maps [HN1]. 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 [HN2] 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 [HN3] 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 [HN4] 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 [HN5]. 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 [HN6] laboratories have spent many years describing the neural circuits that control auditory localization in the barn owl [HN7] (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) [HN8]. 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 [HN9] 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.



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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.

Zheng and Knudsen (1) reared young owls in prism spectacles [HN10] 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 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 [HN11] (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 [HN12] 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.

HyperNotes Related Resources on the World Wide Web

General Hypernotes

Neuroscience on the Internet is a searchable and browsable index of neuroscience resources available on the Internet.

The **WWW Virtual Library of Neuroscience** is maintained by the **Department of Neurology and Neuroscience**, Cornell University Medical College.

The **Center for the Neural Basis of Cognition** provides links to **Cognitive-Neurosciences Resources** on the Web.

A **neuroscience glossary** is provided for a course on **computational neuroscience** at the University of Wisconsin.

An **exploration of the nervous system** is offered by E. Chudler of the University of Washington on his **Neuroscience for Kids** Web site. His home page features an extensive list of **links** to neuroscience Web resources.

The **Howard Hughes Medical Institute** (HHMI) offers an illustrated **research report** for the general reader titled "Seeing, hearing, and smelling the world."

R. M. Robertson, Department of Biology, Queen's University, Kingston, Canada, provides extensive **lecture notes** for a **course** on integrative neurobiology and neuroethology.

P. Lennie, Center for Visual Science, University of Rochester, provides lecture notes for a **course on sensory systems**.

The **Neuroscience Tutorial** from the Washington University School of Medicine has sections on the **central visual pathways** and the **auditory system**.

The **summary report** of a **workshop**, held in December 1997 in Breckenridge, CO, on the neurophysiology of central auditory processing is presented by **C. deCharms**, Keck Center for Integrative Neuroscience, University of California, San Francisco.

Neuroethology of Barn Owl Sound Localization is a Web site prepared by J. Wen as a class project for a **course** on neural systems and animal behavior at Cornell University.

Numbered Hypernotes

1. An **overview** of brain organization and neural connections is provided in the **Brief Tour of the Brain** from Syracuse University's **Mind and Machine Module** project. A **neurobiology laboratory course** from the Division of Life Sciences, University of Texas, San Antonio, includes a presentation on **sensory processing** that includes a discussion of sensory maps in the brain. The **HHMI presentation** on the senses includes a discussion of **sensory processing** in the brain. R. M. Robertson provides **lecture notes** titled "Maps, columns, blobs, stripes and barrels."

2. W. Zheng and **E. Knudsen** are in the **Department of Neurobiology**, Stanford University School of Medicine; the faculty research directory also provides an **entry** for Knudsen. The Stanford University Medical Center Office of Communications issued press releases about Knudsen's research with barn owls on **2 October 1996** about research published in the 3 October 1996 issue of *Nature* and on **5 March 1998** about research published in the 6 March 1998 issue of *Science* (6).

3. **Peterson Online Birds** has an entry for the **barn owl**. The **Natural Histories of Raptors** Web site from the Southeastern Raptor Rehabilitation Center, Auburn University College of Veterinary Medicine, provides information about the **barn owl**. The **Owl Pages** presents photos and basic information about the **barn owl**. In his **Web**

presentation on sound localization in the barn owl, J. Wen provides information on the **phylogeny** and the **zoology** of the barn owl.

4. An **introduction** to auditory and visual localization in the barn owl is included in a **paper** by A. Haessly, J. Sirosh, and R. Miikkulainen titled "A model of visually guided plasticity of the auditory spatial map in the barn owl," which was presented at the 1995 annual conference of the Cognitive Science Society. G. Jacobs, Center for Computational Biology, Montana State University, Bozeman, provides **lecture notes** on visual calibration of sound localization in barn owls for a **course** in neuroethology.

5. **GABA** and **inhibitory synapse** are defined in the **On-line Medical Dictionary**. The **THCME Medical Biochemistry Page** provides information about **GABA** in the section on **biochemistry of nerve transmission**.

6. **M. Konishi** is in the Division of Biology, California Institute of Technology. The **HHMI presentation on the senses** includes a description of **Konishi's research** on the auditory system of barn owls. **J. Wen's Web site** provides an overview of **Konishi's early research** on sound localization in barn owls. The **Topics In Neuroethology: Model Systems** page that was developed for a graduate seminar at the Beckman Institute, University of Illinois, presents a **citation analysis** of the 19 May 1978 article in *Science* by Knudsen and Konishi titled "A neural map of auditory space in the owl."

7. **G. Jacobs**, Center for Computational Biology, Montana State, University, Bozeman, provides **lecture notes** (in Adobe Acrobat format) on sound localization in barn owls for a **course** in animal physiology. In his **Neuroethology of Barn Owl Sound Localization** Web site, J. Wen includes a **presentation** on the neural mechanism underlying the barn owl's sound localization. P. Lennie offers lecture notes on **sound localization** for a **course** on sensory systems.

8. **C. Carr**, Department of Biology, University of Maryland, discusses the **midbrain and the inferior colliculus** in lecture notes on hearing. D. Atkins, Department of Biological Sciences, George Washington University, Washington, DC, provides an introduction to the **midbrain** in **lecture notes** for a neurobiology course. An **illustration** from an **introduction to neuroanatomy**, presented by the **Institute for Neurology and Neurosurgery**, Beth Israel Hospital, NY, shows the location of the inferior colliculi in the human brain. **NeuroNames** has an **entry** for the central nucleus of the inferior colliculus with a link to an **illustration** of its location in the macaque brain.

9. The **On-line Medical Dictionary** defines **optic tectum**.

10. A photo of an **owl in prism spectacles** is displayed in the **HHNI presentation** titled "The value of having two ears."

11. **Neurotransmitter**, **glutamate**, and **NMDA receptor** are defined in the **neuroscience glossary** from the University of Wisconsin. The On-line Medical Dictionary defines **excitatory amino acid**. The **HotMolecBase** from the Bioinformatics Unit, Weizmann Institute of Science, Israel, has an entry for the **NMDA receptor**. E. Chudler's **Exploring the Nervous System** includes an **introduction to neurotransmitters and neuroactive peptides**. L. Clothier, Department of Psychiatry, University of Arkansas for Medical Sciences, presents overviews of **synaptic biology** and **neurotransmitter systems** in **lecture notes** for a **course** on behavioral sciences. For a **course** on the biopsychology of learning and memory, S. Grossman, Department of Psychology, University of Chicago, offers a **Web lecture** titled "Transfer of information between neurons," which includes a discussion of inhibitory and excitatory neurotransmitters. A **news article** in the Spring 1996 issue of *Stanford Medicine* describes D. Feldman and E. Knudsen's research on NMDA receptors and owl neurons.

12. The online **Dictionary of Cell Biology** defines **neuronal plasticity**. The **Web edition** of the forthcoming **MIT Encyclopedia of the Cognitive Sciences** includes articles on **neural plasticity** and **auditory plasticity**. **G. Wallis** discusses **neural plasticity** in his **D.Phil thesis** titled "Neural mechanisms underlying processing in the visual areas

of the occipital and temporal lobes.” The **Winter 1995 newsletter** of the Neuroscience Research Center, University of Texas, Houston, had an **article** by P. Kelly titled “Mechanisms regulating synaptic plasticity in brain.” The **Society for Neuroscience** includes an article on **brain reorganization** in its **Brain Briefings** collection. R. M. Robertson discusses synaptic plasticity in **lecture notes** on learning and memory for a course in integrative neurobiology.

13. M. P. Stryker is in the **Department of Physiology**, University of California, San Francisco.

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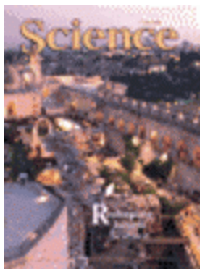
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