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INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
34100 TRIESTE (ITALY) - P.O.B. 586 - MIRAMARE - STRADA COSTIERA 11 - TELEPHONE: 2240-1
CABLE: CENTRATOM - TELEX 460392 - I

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"Organization of the Auditory Cortex"

Michael MERZENICH
University of California
School of Medicine
San Francisco, CA
USA

Dr. Michael M. Merzenich
871 HSE
UCSF
San Francisco, CA 94143

College on the Neurophysics of the Brain

Lecture 1.

Organization of the Auditory Cortex

Lecture Outline

1. There are fundamental differences between auditory system organization and visual or somatosensory system organization. Among those differences are the following:

a) There is an extra representational dimension for the auditory sensory epithelium expressed by a point-to-line projection from the cochlear sensory epithelium to the cortex. That is, any given narrow sector of the organ of Corti is represented across a sheet of neurons of relatively constant width that extends across auditory cortical fields from edge to edge. This is in contradistinction to the point-to-point projection scheme described in other sensory systems.

b) There is a nearly all-to-all convergence and divergence of inputs across this isorepresentational dimension, recorded at every level of the auditory nervous system.

c) Cortical fields are on the 6th projection level above sensory epithelial cells in the auditory system; while visual and somatosensory cortical fields are on the fourth order.

d) There is a much more complex convergence of information from multiple afferent sources in the auditory system than is recorded at any level in the visual or somatosensory nervous systems.

e) Common spectral filtering/spectral integration is effected for inputs from manifold auditory brain stem sources at the level of the auditory midbrain. There is no known, equivalent processing effected in other sensory systems.

f) There is no simple cochlear representations of sound pitch or sound location. Even these most fundamental of perceptual continua must be constructed by cue-extraction and representation in the central auditory nervous system.

2. Initial studies of auditory cortex focussed on its tonotopic (or "cochleotopic") organization. More recent studies have described organization beyond tonotopicity. Those experiments have led to the following conclusions (among others):

a) Alternating bands of neurons orthogonal to the isofrequency axes of cortical fields respond in qualitatively different ways to binaural stimuli.

i. These "binaural bands" have been analogized to the ocular dominance columns of visual cortex. They receive inputs from segregated sheets of neurons ("lamina") in the principal auditory thalamic nucleus, the lateral part of the medial geniculate body.

ii. These bands are also distinguishable by their cytoarchitecture, and by band-class-specific corticocortical projection patterns.

b) In carnivores, behavioral-ablation studies indicate that primary auditory cortex is necessary and sufficient for binaural sound location behavior. However, no orderly representation of sound location has yet been identified within any auditory cortical field in carnivores or in primates.

c) On the other hand, numerous other input continua <u>have</u> been found to be represented <u>systematically</u> across auditory cortical fields in carnivores and primates. Examples include sharpness spectral filtering, sharpness of inhibitory sidebands, non-monotonicity, dynamic range, latency, aspects of AM and FM response selectivity, etc. In any given cortical field, some of these continua covary, while others are independent of one another.

d) The generation of representational continua beyond tonotopicity has been demonstrated in most dramatic fashion by the highly ordered cortical representations of echolocation cues in bats, defined in studies conducted by Nobuo Suga and colleagues. These cortical "maps" provide systematic two-dimensional representations of combinations of the fundamental and harmonics of constant frequency and frequency modulated components of a bat call and the returning echo. These emergent "maps" systematically represent prey or target distance, velocity, size, absolute location, surface disturbances, etc., relevant to the bat's echolocation behavior.

e) Representations of complex spectra (e.g., speech) have been little studied in auditory cortical fields, but there is some evidence for orderly representations of speech feature continua.

f) While orderly representations of sound location have not yet been recorded in any species except the mustache bat, highly ordered sound location constructs have been described in midbrain auditory representations in owls in studies led by Mark Konishi at Cal Tech and Eric Knudsen at Stanford; and sound location constructs of a similar (albeit somewhat cruder) nature have been described in midbrain auditory representations in cats and monkeys.

Suggested reading:

Knudsen, E.I. (1982) Auditory and visual maps of space in the optic tectum of the owl. J. Neuroscience 2:1177-1194

Knudsen, E.I. (1984) Synthesis of a neural map of auditory space in the owl. IN: Dynamic Aspects of Neocortical Function, G. Edelman, et al., eds., J. Wiley, New York. pp. 375-396.

Merzenich, M. M., W. M. Jenkins and J. C. Middlebrooks (1984) Observations and hypotheses on special organizational features of the central auditory nervous system. IN: Dynamic Aspects of Neocortical Function, G. Edelman, et al., eds., J. Wiley, New York, pp. 397-424.

Suga, N. (1984) The extent to which biosonar information is represented in the bat auditory cortex. IN: Dynamic Aspects of Neocortical Function, G. Edelman, et al., eds., J. Wiley, New York, pp. 315-373.

Suga, N., H. Niwa, I. Taniguchi and D. Margoliash (1987) The personalized auditory cortex of the mustached bat: Adaptation for echolocation. J. Neurophysiol. 58:643-654.

Lectures 2, 3.

Role of Neuronal Activity in Maintenance of Organization in the Mature Brain

Lecture Outline

1. Our basic objectives:
a) To discuss neural mechanisms underlying ideosyncratic development of different perceptual and motoric abilities;
b) To consider the nature of the general operation(s) of the neocortex in adult mammals.

2. Historically, it was widely believed that responses of cortical neurons were modified by experience throughout life. Among early exponents of this view were Sherrington, Lashley, and Hebb.

3. In more recent neuroscience history, it has been widely asserted that the responses of cortical neurons are determined very early in life and are subsequently static and predictable.

4. Recent evidence has challenged that view. Among those challenges:

a) Cortical fields have been found to reorganize following peripheral nerve transection or amputation, and following dorsal root section.

b) Cortical representations have been found to reorganize following restricted cortical lesions destroying substantial parts of them. By that reorganization, skin surfaces or movements represented within the zone of lesion come to be represented in the cortical zone surrounding it.

c) Cortical representations reorganize following restricted lesions involving primary cortical input sources.

d) Cortical representations are remodeled in adults wearing digital casts; in animals given arthritic-inducing drugs; in animals trained behaviorally using strategies that result in heavy differential excitation of limited skin surfaces; in animals in which there is heavy differential use of limited movements; and in animals in which vibrissae are cut or surgically extirpated.

e) Movement representations, auditory cortex and vibrissal representations are remodeled in classically conditioned animals, with the specific conditioning stimuli or conditioned responses gaining extended representations in the trained animal that are again reduced when training is extinguished.

5. We can conclude from these studies that:

a) Cortical representations are remodeled by experience throughout life.
b) There are many possible forms of cortical representations. In animals with more intensive and/or varied use of the hands, for example, cutaneous and motor cortical representations of the hands are larger and/or more complex.
b) Experience-induced changes likely underlie the acquisition of motoric skill and improvement of perceptual abilities with practice.

6. What can we say about mechanisms underlying this "representational plasticity"?

a) First, these alterations of effective cortical inputs at given cortical locations, by use, manifest lifelong operation of mechanisms of afferent input <u>selection</u> in the neocortex.
b) Second, representational alterations likely involve changes in the effectivenesses of in-place cortical inputs. There is an impressive body of evidence that suggests that an extensive afferent input repertoire projects to any given cortical location; while at any one time neurons at each location normally respond to only a small subset of those anatomically-delivered inputs.
c) Third, effectivenesses of inputs for altering cortical representations are modulated as a function of behavioral state.
d) Fourth, considered in detail, cortical representations map the probabilities of coincident or nearly-coincident afferent inputs by operation of Hebb-like synaptic mechanisms. Several experiments demonstrating that cortical representations can be greatly distorted by distorting input time structures argue strongly for this conclusion.
e) Fifth, input selection is an accomplishment of a positively-coupled neuronal group, normally several tens of microns in diameter.

7. These findings bear a number of practical implications, which shall be a subject of discussion.

Suggested reading:

Clark, S.A., Allard, T., Jenkins, W.M., Merzenich, M.M. (1988) Receptive fields in the body-surface map in adult cortex defined by temporally correlated inputs. Nature 332:444-445, 1988.

Edelman, G. M., and L. H. Finkel (1984) Neuronal group selection in the cerebral cortex. IN: Dynamic Aspects of Neocortical Function, Edelman, et al., eds., J. Wiley, New York, pp. 653-695.

Jenkins, M.W., and Merzenich, M.M. (1987) Reorganization of Neocortical Representations After Brain Injury: A Neurophysiological Model of the Bases of Recovery From Stroke. In: Progress in Brain Research, Vol. 71 (F.J. Seill, E. Herbert, and B. Carlson, eds) Elsevier Science Publishers, Amsterdam, 249-266.

Merzenich, M.M., Nelson, R.J., Stryker, M.P., Cynader, M.S., Schoppmann, A., and Zook, J.M. (1984) Somatosensory Cortical Map Changes Following Digit Amputation in Adult Monkeys. J. Comp. Neurol. 224:591-605.

Merzenich, M.M. (1986) Sources of Intraspecies and Interspecies Cortical Map Variability in Mammals:Conclusions and Hypothesis. In: Comparative Neurobiology: Modes of Communication in the Nervous System (M.J. Cohen and F. Strumwasser, eds) John Wiley and Sons, New York, 105-116.

Merzenich, M.M., Recanzone, G., Jenkins, W.M., Allard, T.T. and Nudo, R.J. (1988) Cortical Representational Plasticity. In: Neurobiology of Neocortex. (P. Rakic and W. Singer, eds) John Wiley & Sons Limited, Chichester, pp. 41-68.