Sound localization

Interaural time difference: difference in arrival
Interaural level difference: difference in amplitude (intensity)
Sound localization

ITD localizes sound in horizontal plane

Auditory stimulus

Sound level (dB)

Left ear leading

Right ear leading

Difference in arrival time

Azimuth

Elevation

ITD localizes sound in horizontal plane
Sound localization

Sound localization in the horizontal plane is achieved through ITD (interaural time difference), where the sound arrives at one ear before the other. Sound localization in the vertical plane is achieved through ILD (interaural level difference), where the sound is louder in one ear than the other.

*a*

**Auditory stimulus**

- **L ear**
- **R ear**

**Sound level (dB)**

- ITD

**b**

- **Elevation**
  - **Azimuth**
  - **0°**
  - **126°**
  - **-126°**
  - **0 dB**
  - **-16 dB**
  - **16 dB**

**ILD localizes sound in vertical plane**

- **right ear greater**
- **left ear greater**
ICX (external nucleus of the inferior colliculus) contains neurons with "auditory spatial" receptive fields!
Interaural time differences can be calculated in the nucleus laminaris by comparing signals from left and right ears.

This model, first proposed by Jeffress in 1948, transforms a time code into a space code.
(B) Delay line

3.11 Leffner's model for ITD encoding

3.13 Anatomical evidence supporting the ITD encoding
A: spikes if right >>> left
B: spikes if right >> left
C: spikes if right = left
D: spikes if right << left
E: spikes if right <<< left
Optic tectum: integrates visual and auditory inputs
Head orientation to visual and auditory stimuli coincides in control animals
Neurons in the optic tectum have overlapping visual and auditory receptive fields.
Prismatic spectacles displace optical field: animal sees object in a location that does not correspond to the actual physical location.
Before prisms: head orientation overlaps in response to visual or auditory stimuli
Before prisms: head orientation overlaps in response to visual or auditory stimuli

After prisms: head orientation non-overlapping in response to visual or auditory stimuli
before prisms: auditory and visual tuning curves overlap
1 day after prisms: visual tuning curve is displaced
42 days with prisms: head orientation to auditory stimuli becomes aligned with that to visual stimuli.
1 day after prisms: visual tuning curve is displaced
after 8 weeks, the auditory tuning curves are aligned with the visual tuning curves
spatial tuning curves - change

ITD tuning curves - do not change

projections from ITD-tuned neurons to spatially tuned neurons change
a, The pathway in a normal owl; and b, in a prism-reared adult with a shifted map of ITD. ITD is measured and mapped in frequency-specific channels in the brainstem. This information ascends to the ICC, and converges across frequency channels in the projection from the ICC to the ICX, where a map of space is created. The map is conveyed to the optic tectum (OT), where it merges with a visual map of space. Green arrows represent the instructive pathway from the OT to the ICX.
Map Plasticity in Somatosensory Cortex

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Functional circuits in S1 cortex. (A) Pathway from whiskers to S1. (Inset) Cytochrome oxidase–stained barrels in layer 4 of S1. Letters and numbers indicate whisker rows and arcs. (B) Schematic flow of excitation evoked by single whisker deflection. Only the VPM input to cortex is considered. Order of events progresses from red to yellow to green to purple. Response strength is denoted by arrow thickness (6). Gray, cortical area with strong or moderate spiking responses to the whisker. (C) Example of characterization of synaptic physiology in S1, for a unitary connection from an L4 spiny stellate cell to a simultaneously recorded L2/3 pyramidal cell (11). Traces show excitatory postsynaptic potentials (EPSPs) (top right) evoked by single action potentials the L4 cell (bottom right). (D) Dynamic dendritic spines revealed by long-term in vivo two-photon imaging in S1 of an adolescent (1-month-old) rat [from (82)]. (Left) Apical dendritic segment from a layer 5 pyramidal cell. (Right) The same dendritic segment 2 weeks later. Arrowheads and arrows show spine elimination and formation. Thin arrows mark dynamic filopodia. Scale bar, 2 μm.
Fig. 2.
Forms of whisker map plasticity in S1 cortex. In these schematized functional whisker maps in L2/3 of S1, colored regions represent cortical areas responding to different whiskers, with color saturation coding response strength.

In normal rats, each whisker activates a cortical area slightly larger than the cortical column defined by its L4 barrel (barrels outlines are shown in black) (8). Removing all but the D1 whisker in adolescent rats causes Hebbian expansion of the spared, D1 whisker and weakening of deprived, surrounding whiskers within the map (6). Removing all but D1 and D2 whiskers causes D1 and D2 to merge within the map but not to expand into deprived columns (16).

In two non-Hebbian forms of map plasticity, exposure to a novel, naturalistic environment sharpens the whisker map and weakens the whisker responses (18), and overstimulation of a single whisker causes that whisker to shrink within the map.
In a second, developmentally and genetically independent (6, 26) component of Hebbian plasticity, responses to spared whiskers become enhanced (15, 21, 27, 28). When isolated whiskers are spared, enhancement of spared whisker responses occurs in surrounding deprived columns, causing the spared whisker representation to expand in the S1 map (15, 21, 25). When multiple neighboring whiskers are spared, enhancement occurs instead in neighboring spared columns, which causes the representations of individual spared whiskers to merge or overlap (16) (Fig. 2). The latter case exemplifies classical Hebbian strengthening of coactive inputs onto common targets (“Neurons that fire together wire together”), which is a robust feature of map plasticity (29). Both cases may reflect enhanced transmission on excitatory, cross-columnar pathways into deprived or spared columns (6, 30).
Regulation of map precision and signs of plasticity by sensory enrichment. Transferring adult rats from familiar home cages into complex natural environments causes another non-Hebbian form of plasticity in which whisker representations contract in L2/3, thus sharpening the whisker map (Fig. 2). L4 receptive fields are unaffected (18). Similar map sharpening occurs rapidly during acute arousal and exploration (33).

One possible mechanism is that environmental novelty upregulates arousal-related modulators, which are known to act in cortex to shrink whisker representations (33). Exposure to a novel environment for only a few minutes per week, which is not enough to sharpen the whisker map, also has the profound and unexplained effect of reversing the sign of Hebbian plasticity:

When all but one whisker are removed, the representation of the spared whisker shrinks, rather than expands (34). The existence of these functionally distinct forms of plasticity indicates that multiple cellular plasticity mechanisms and learning rules act in S1, beyond canonical Hebbian plasticity mechanisms.
Forms of whisker map plasticity in S1 cortex. In these schematized functional whisker maps in L2/3 of S1, colored regions represent cortical areas responding to different whiskers, with color saturation coding response strength. In normal rats, each whisker activates a cortical area slightly larger than the cortical column defined by its L4 barrel (barrels outlines are shown in black) (8). Removing all but the D1 whisker in adolescent rats causes Hebbian expansion of the spared, D1 whisker and weakening of deprived, surrounding whiskers within the map (6). Removing all but D1 and D2 whiskers causes D1 and D2 to merge within the map but not to expand into deprived columns (16). In two non-Hebbian forms of map plasticity, exposure to a novel, naturalistic environment sharpens the whisker map and weakens whisker responses (18), and overstimulation of a single whisker causes that whisker to shrink within the map.