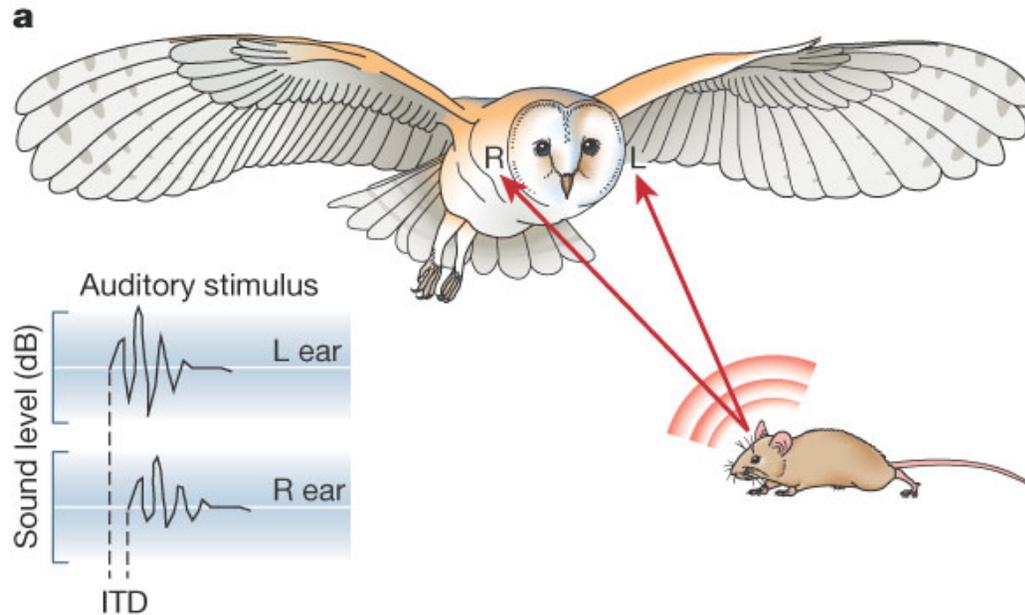




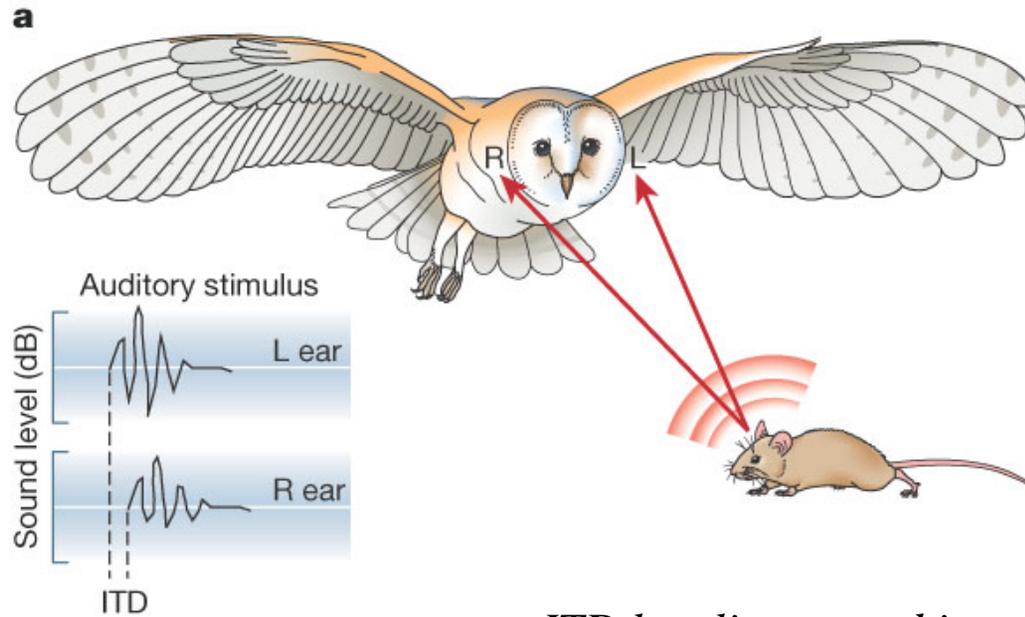
# Sound localization



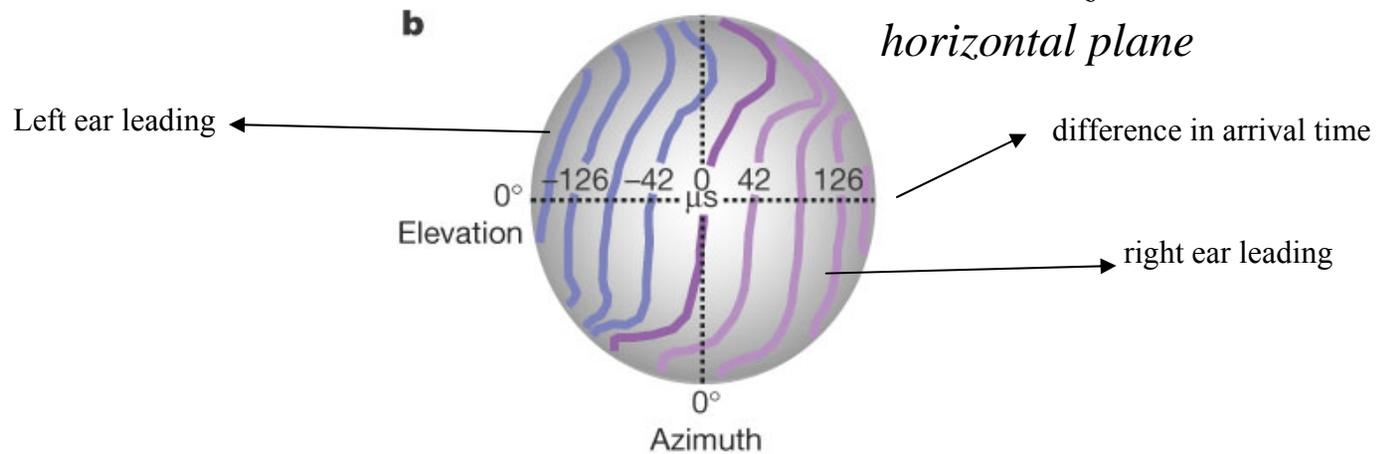
Interaural time difference : difference in arrival

Interaural level difference: difference in amplitude (intensity)

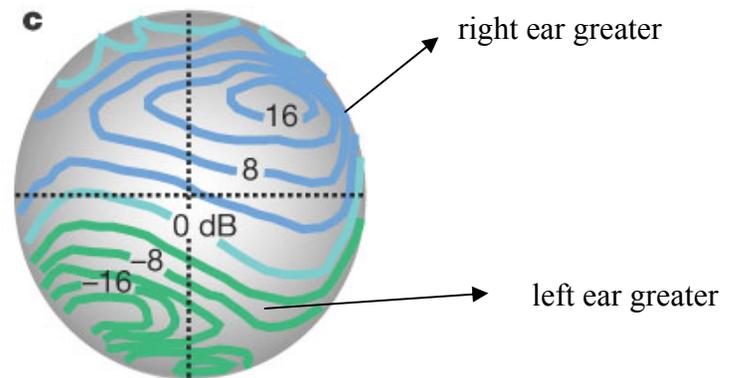
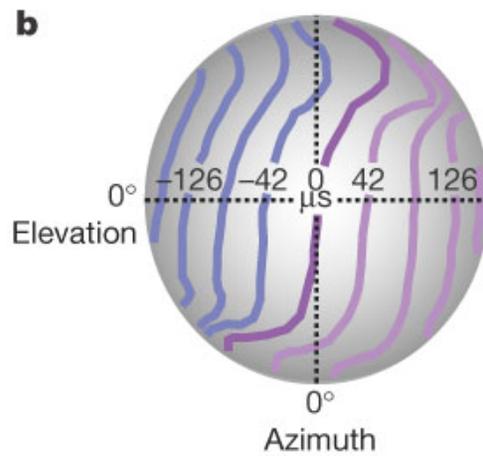
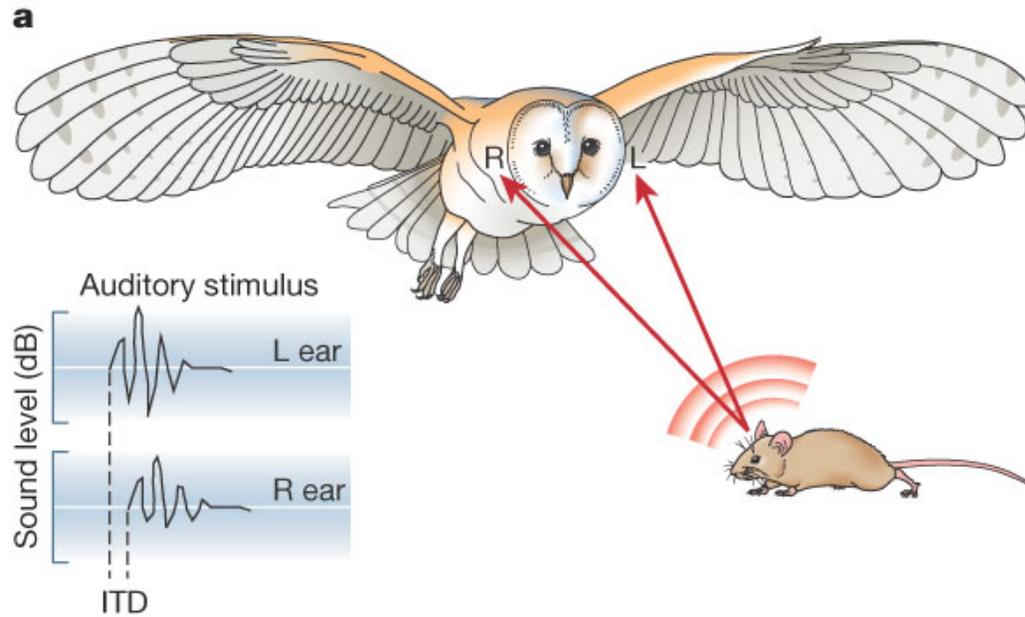
# Sound localization



*ITD localizes sound in horizontal plane*

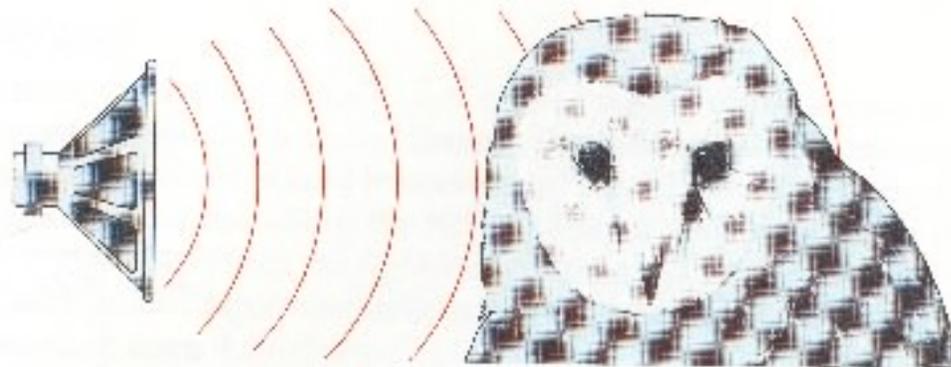


# Sound localization

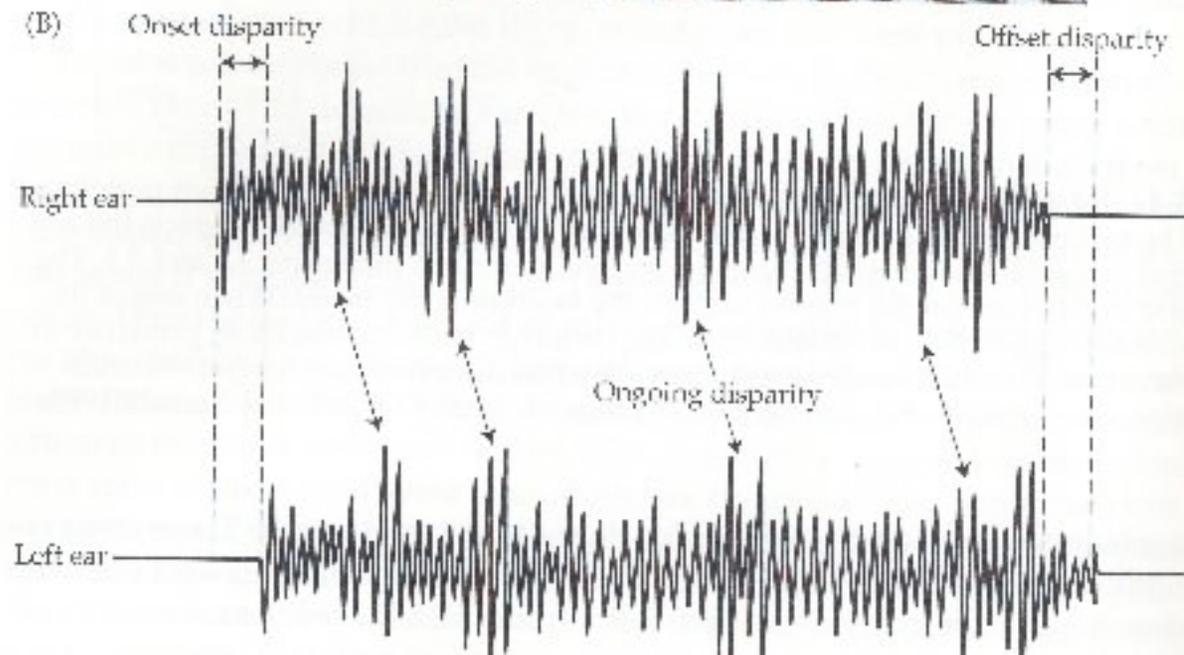


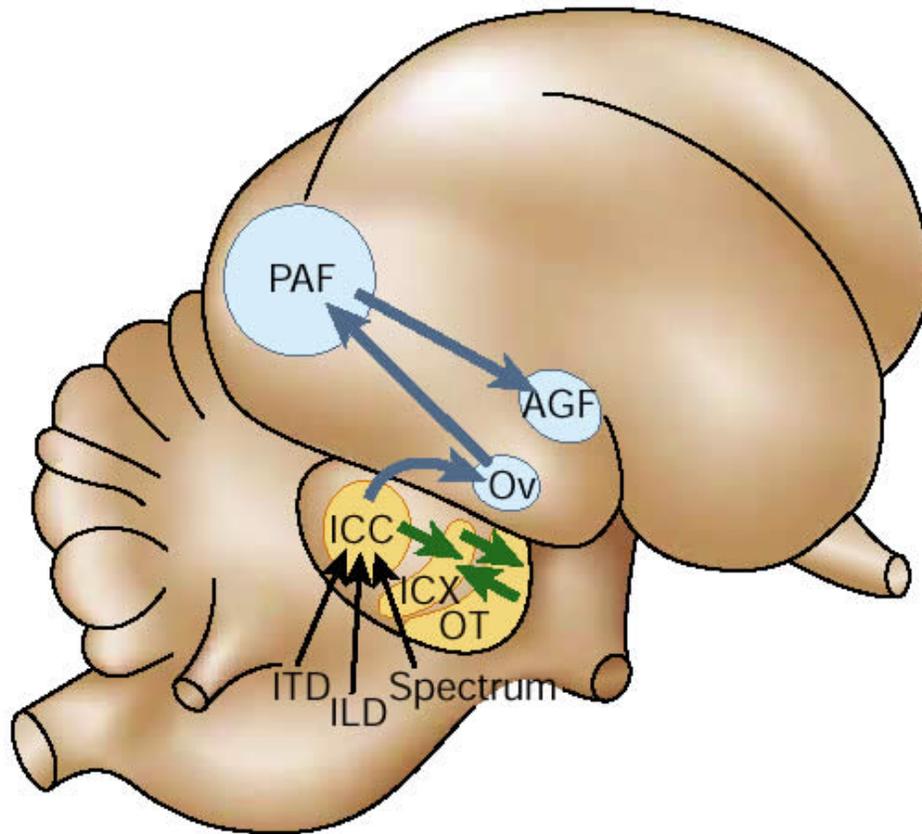
*ILD localizes sound  
in vertical plane*

(A)



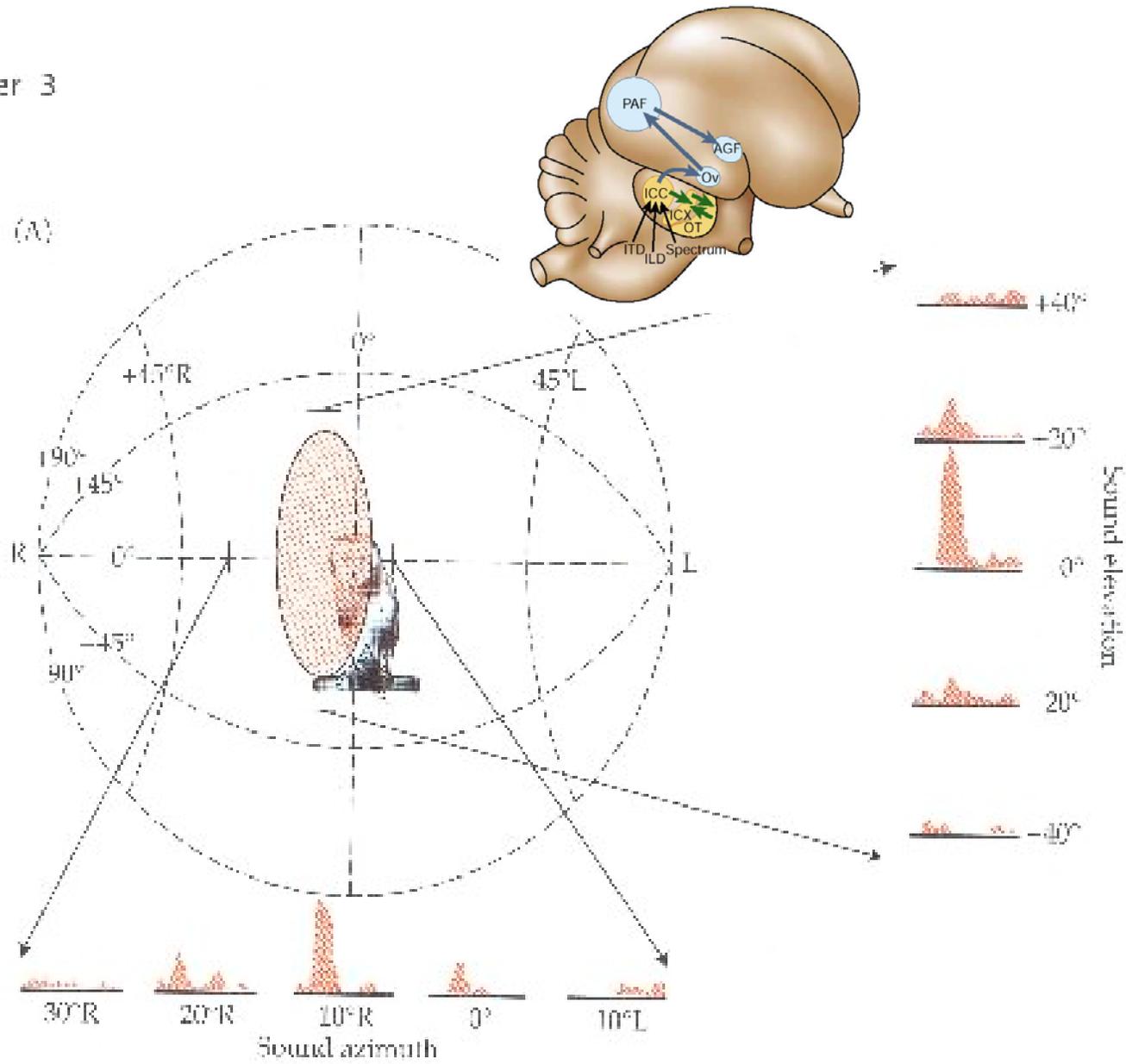
(B)



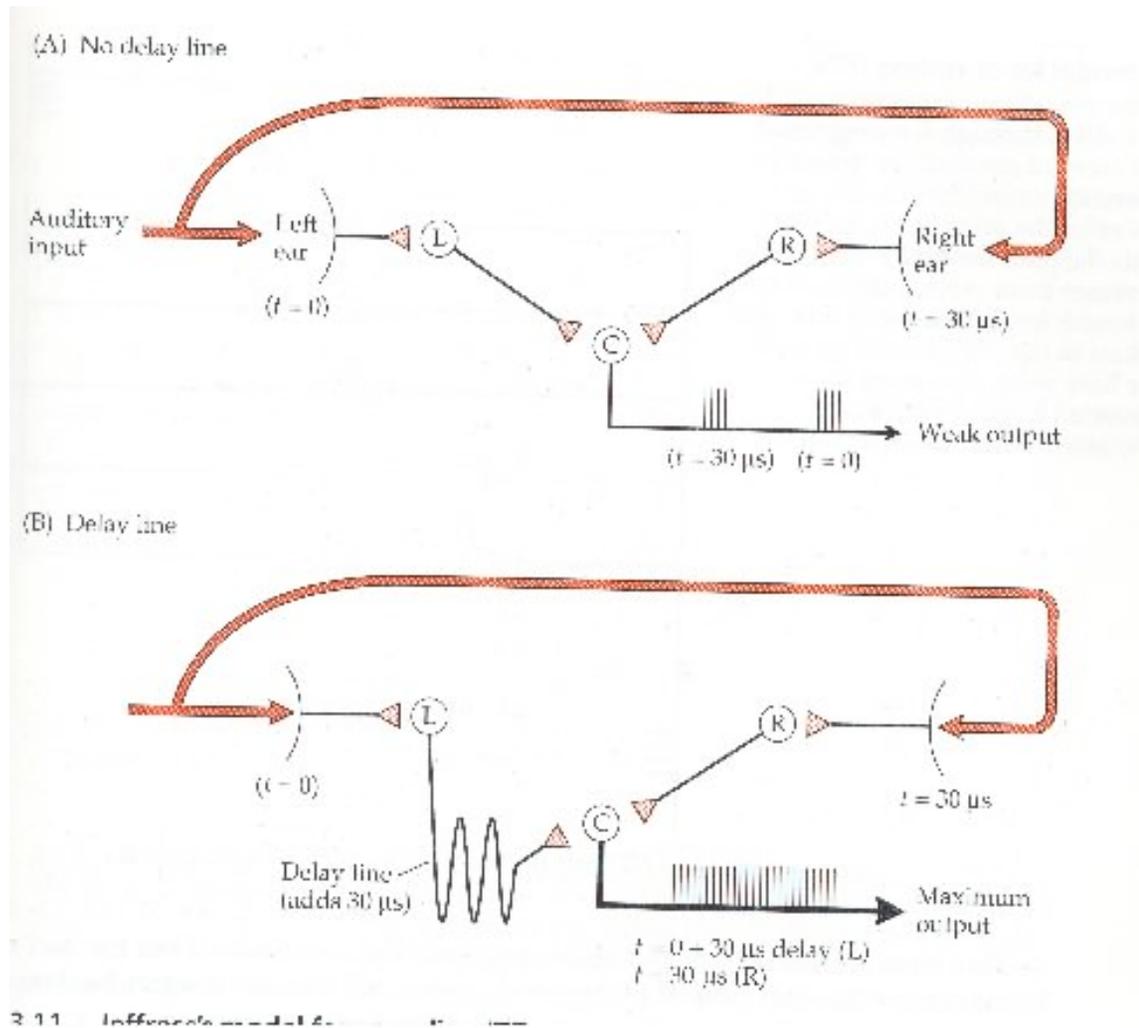


**ICX** (external nucleus of the inferior colliculus) contains neurons with "auditory spatial" receptive fields!

Chapter 3



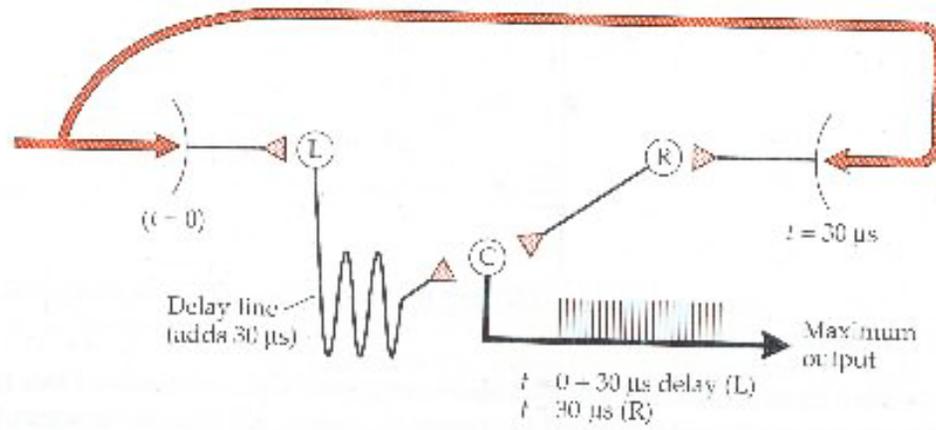
Interaural time differences can be calculated in the nucleus laminaris by comparing signals from left and right ears



Each location has specialized delay line

This model, first proposed by Jeffress in 1948, transforms a time code into a space code

(B) Delay line

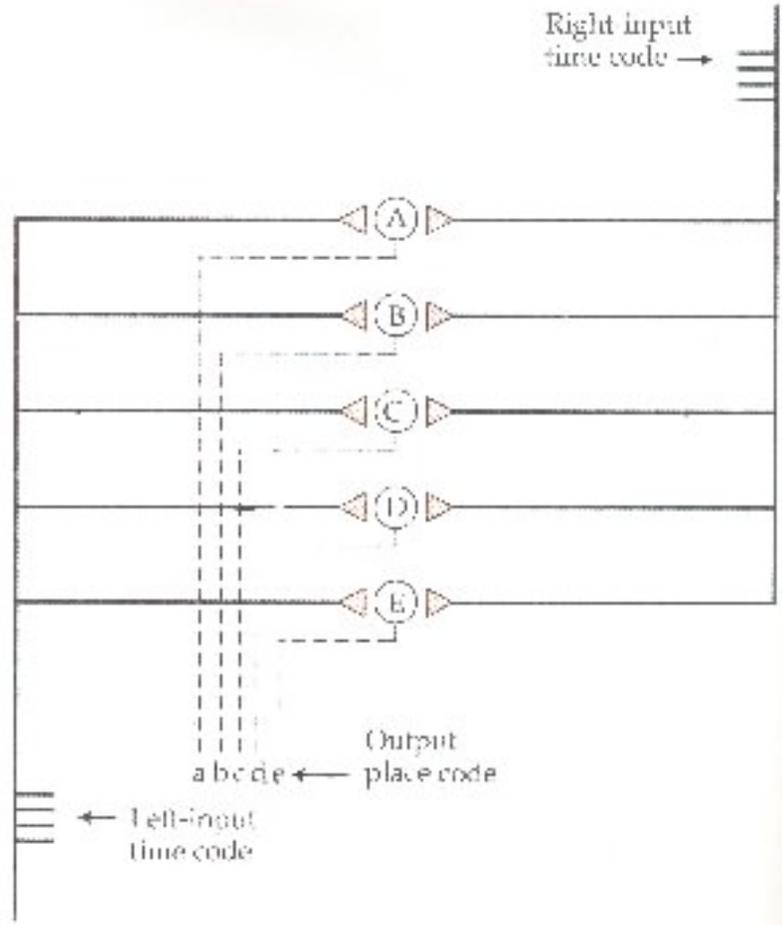


3.11 Inference...

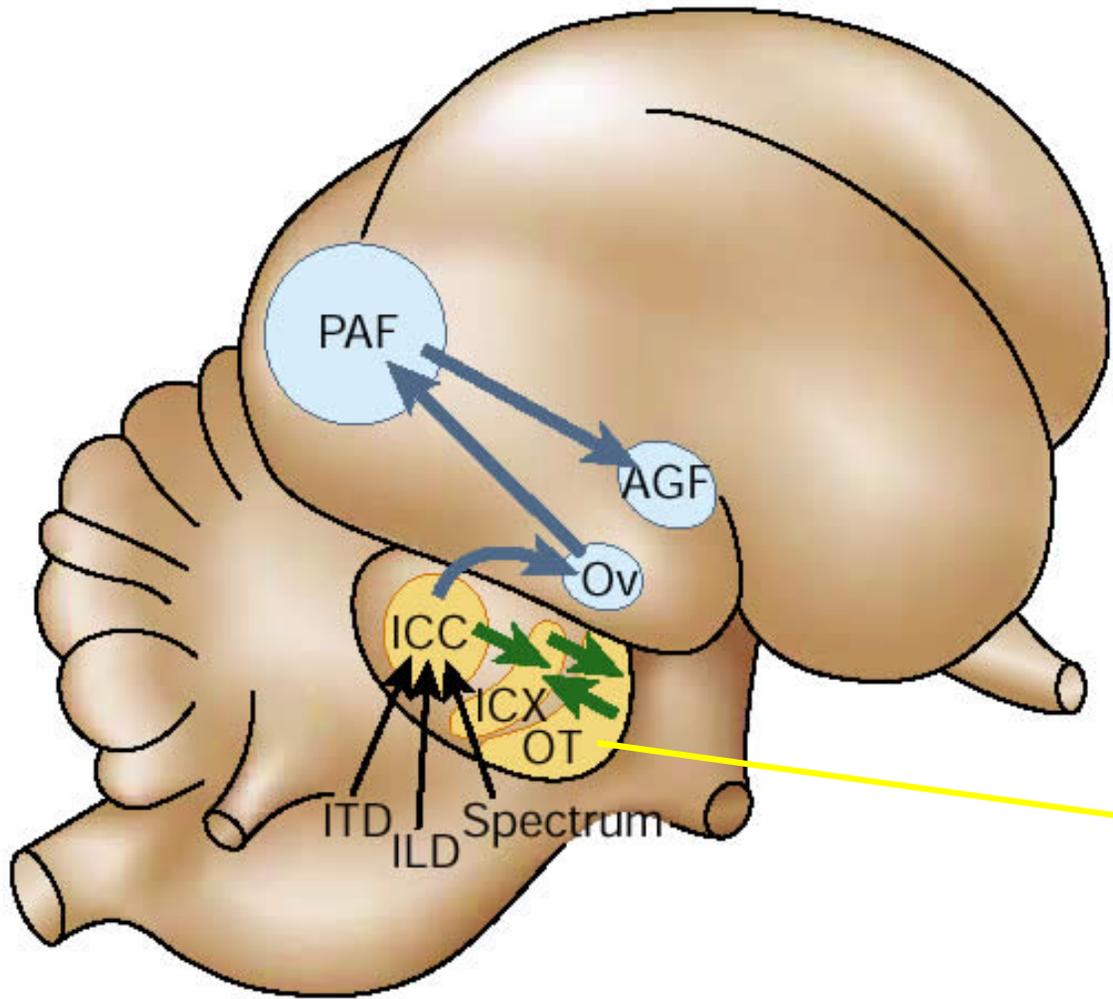


3.13 Anatomical evidence supporting the ITD...

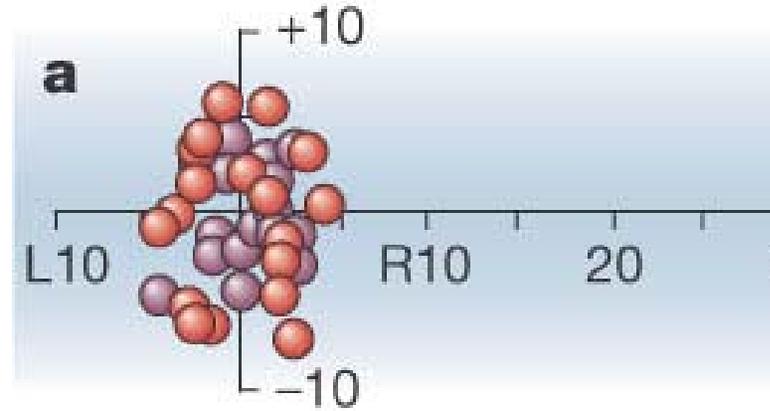
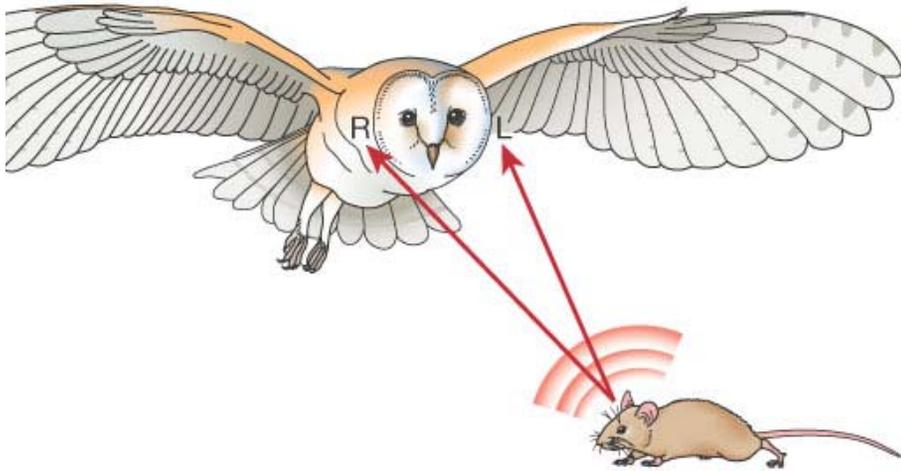
TDs  
 time dif-  
 ferent a  
 ctors,  
 fl and  
 opposite  
 right  
 n, while  
 ncreases  
 ovides  
 array  
 9)  
 6.



- 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

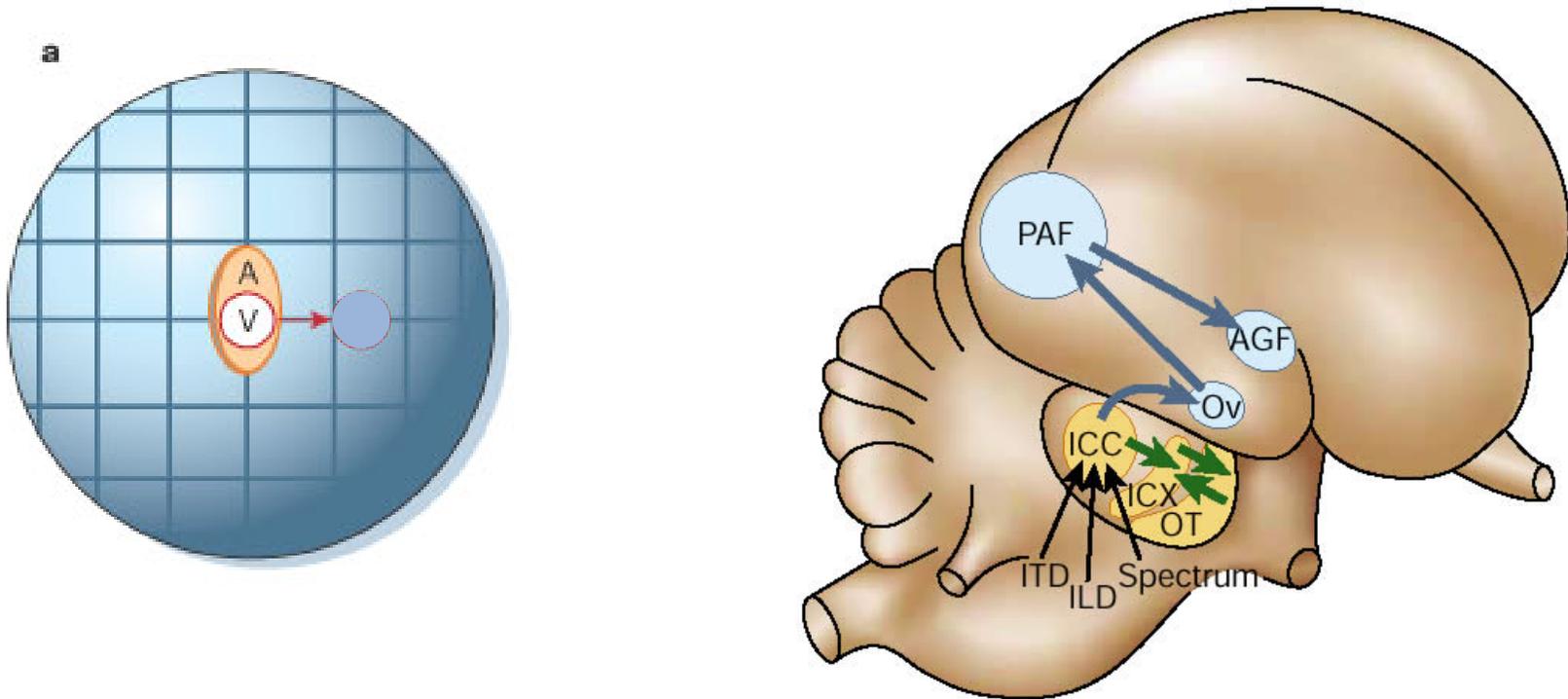


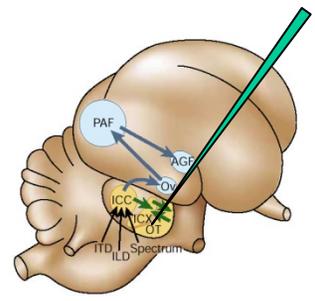
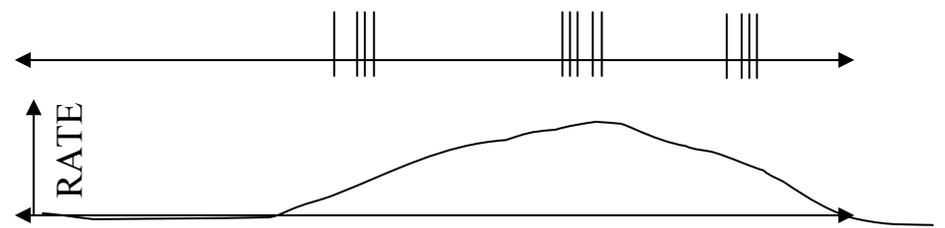
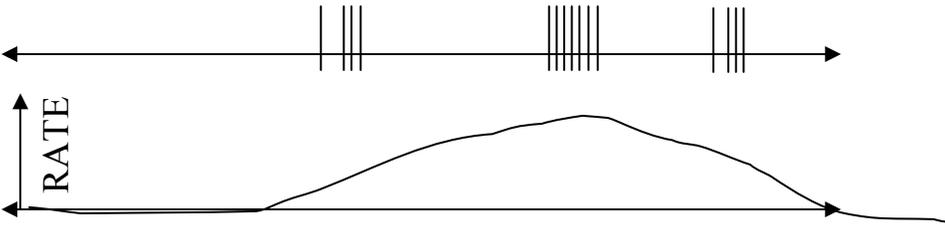
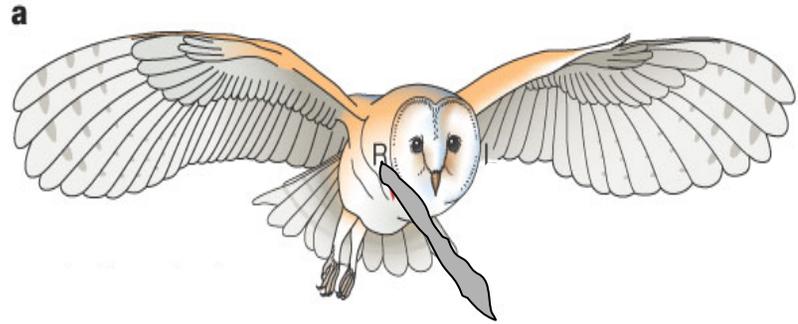
Optic tectum:  
integrates visual and  
auditory inputs

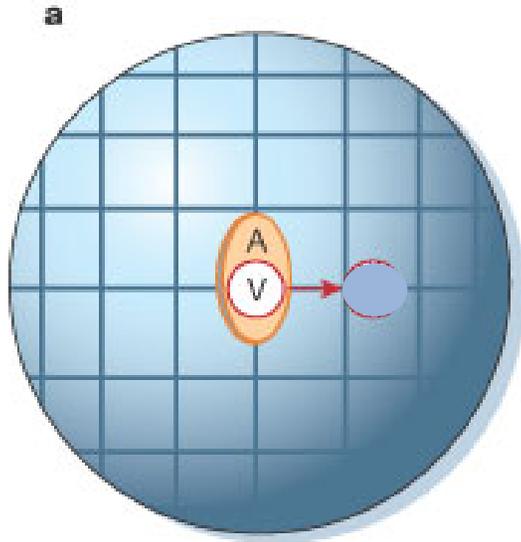
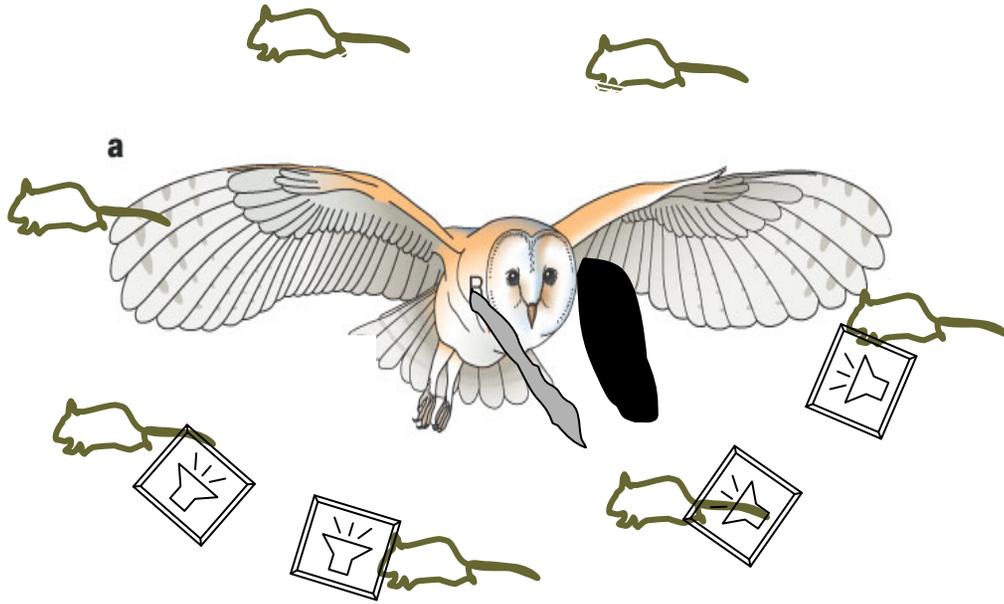


Head orientation to visual and auditory stimuli coincides in control animals

Neurons in the optic tectum have overlapping visual and auditory receptive fields

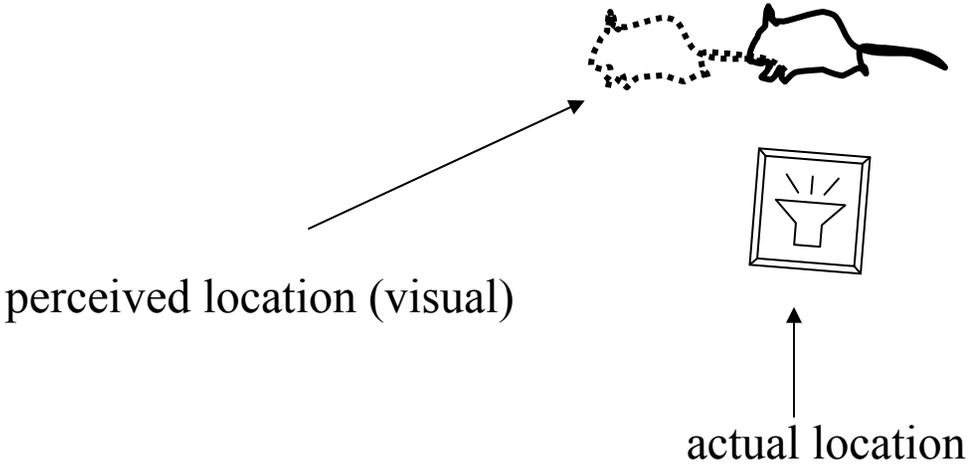


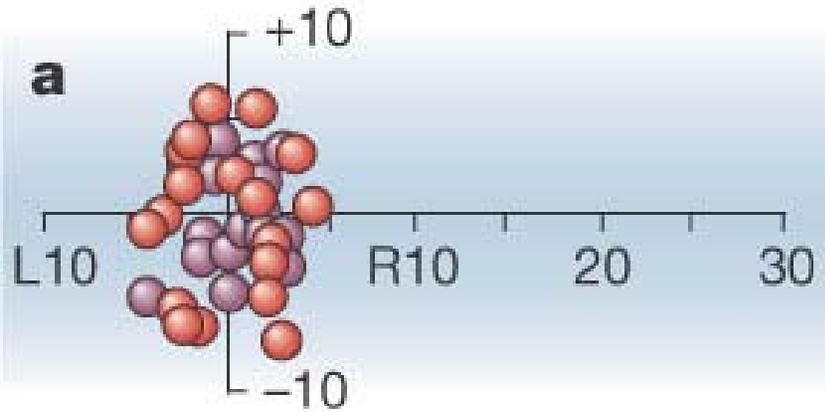
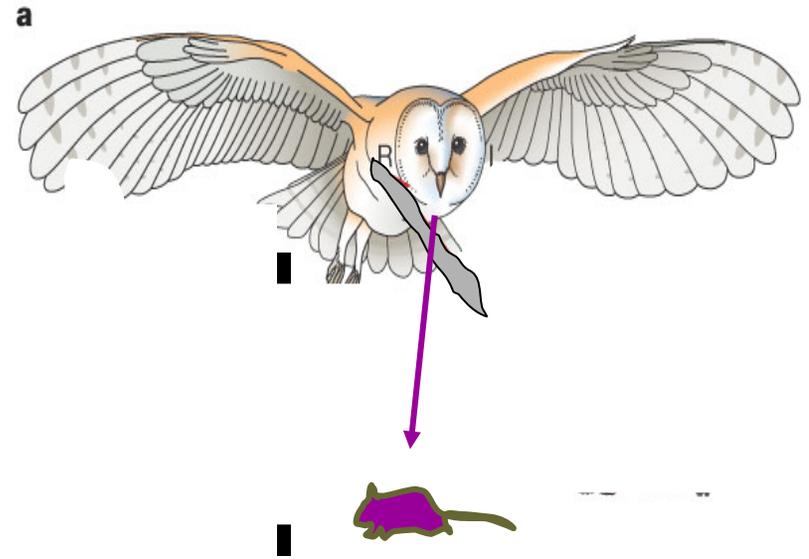
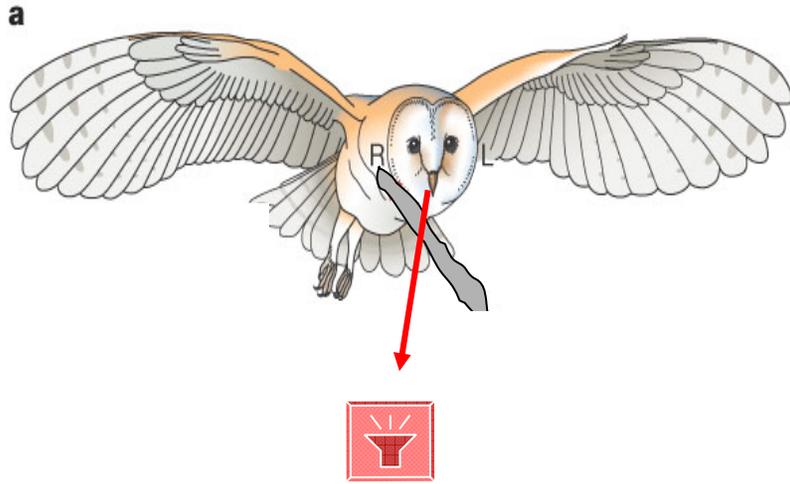




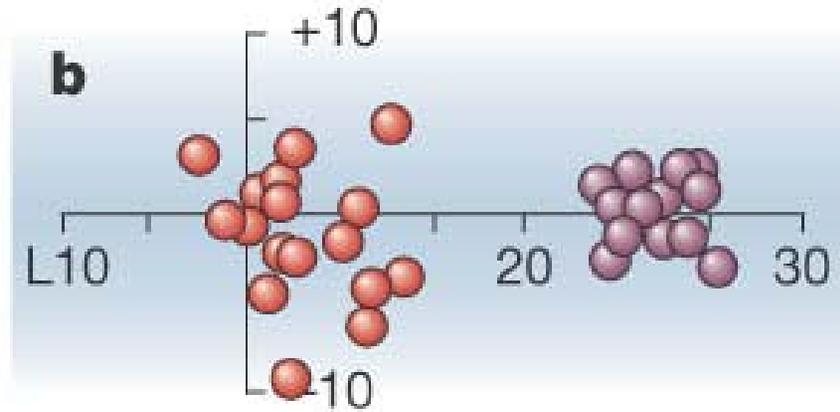
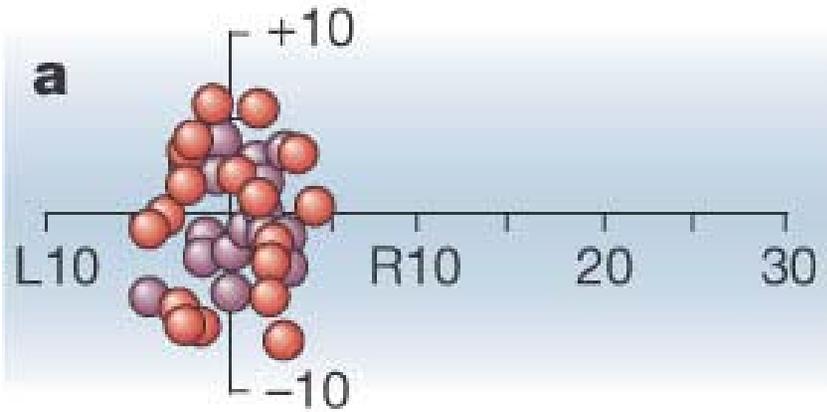
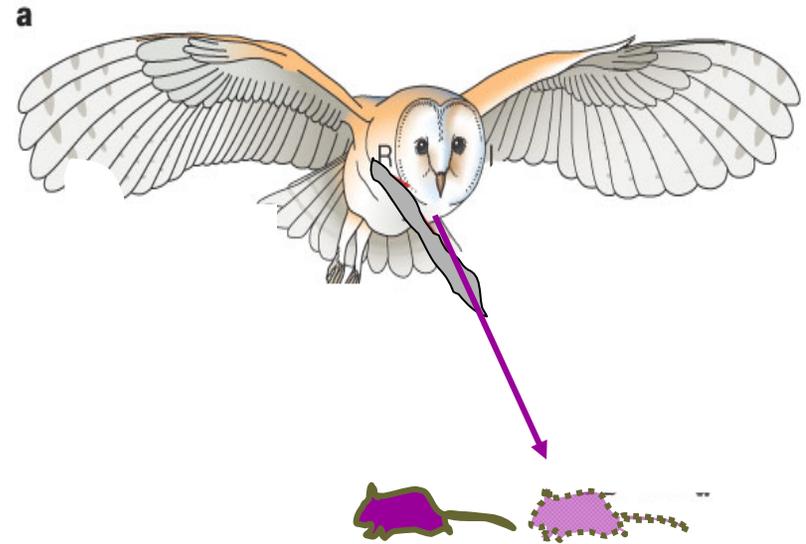
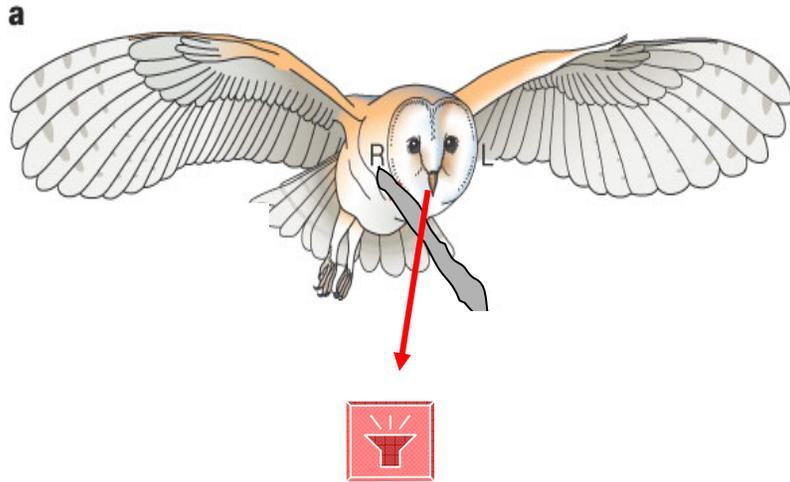


Prismatic spectacles displace optical field : animal sees object in a location that does not correspond to the actual physical location



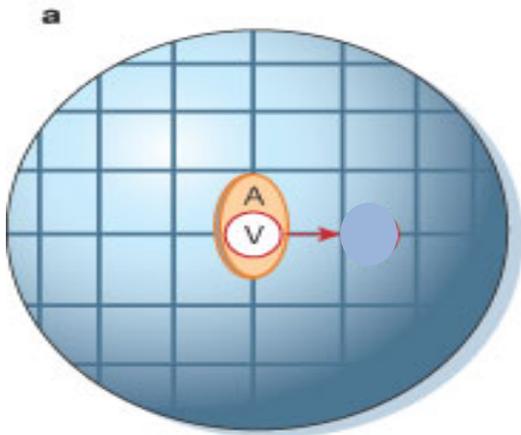
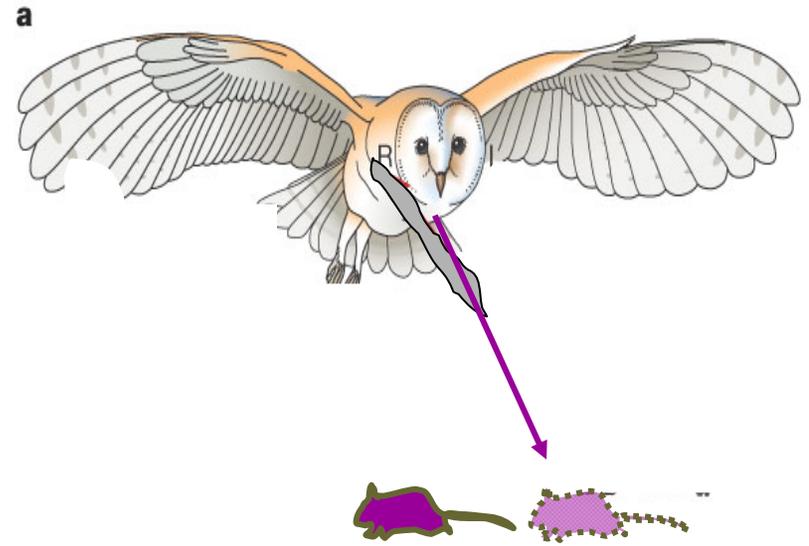
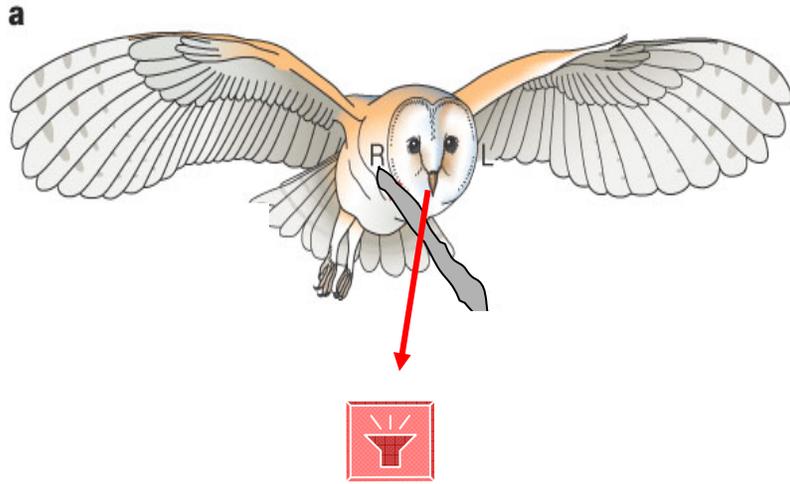


Before prisms: head orientation overlaps in response to visual or auditory stimuli

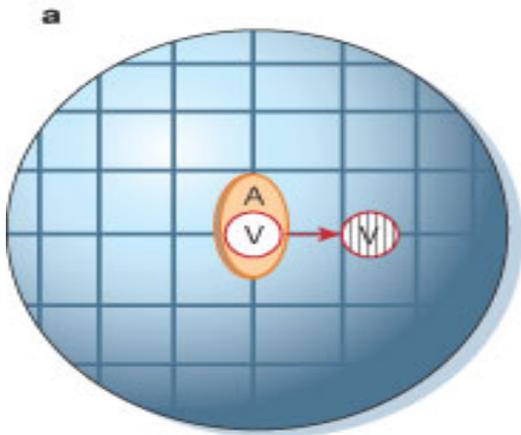
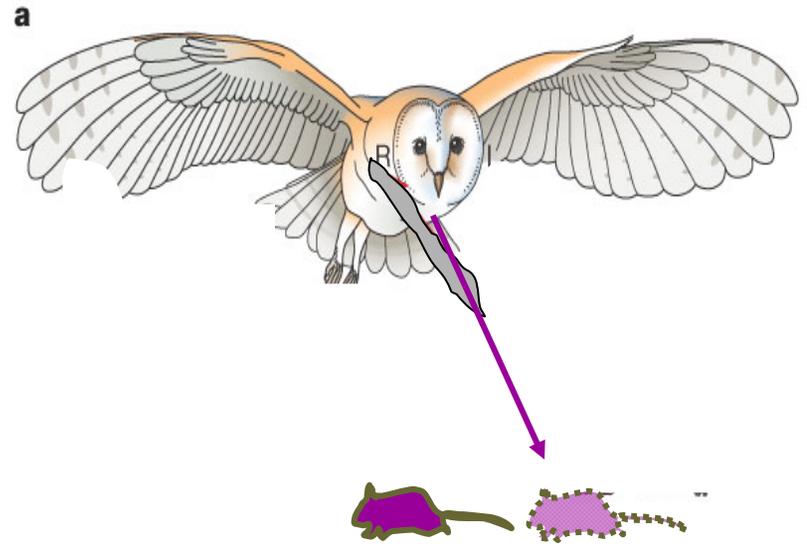
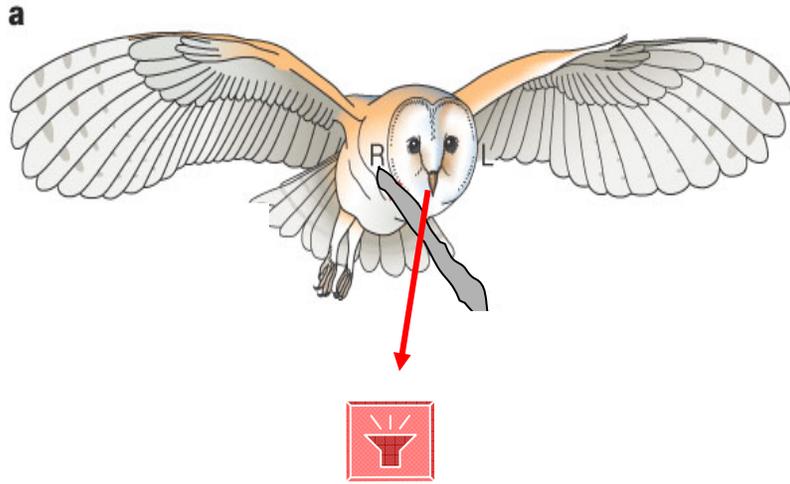


Before prisms: head orientation overlaps in response to visual or auditory stimuli

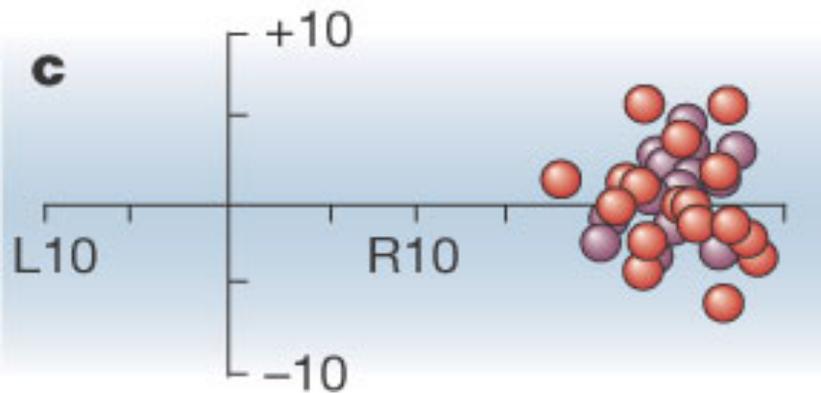
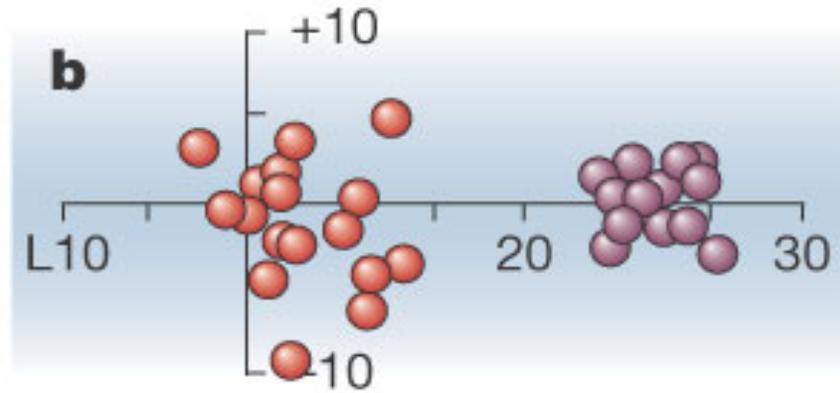
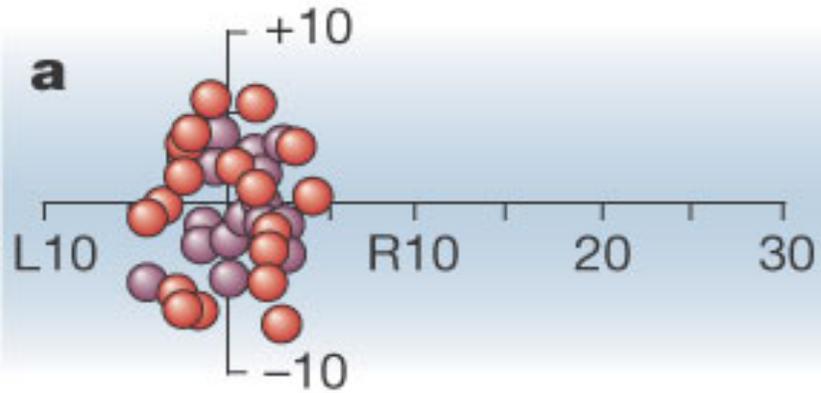
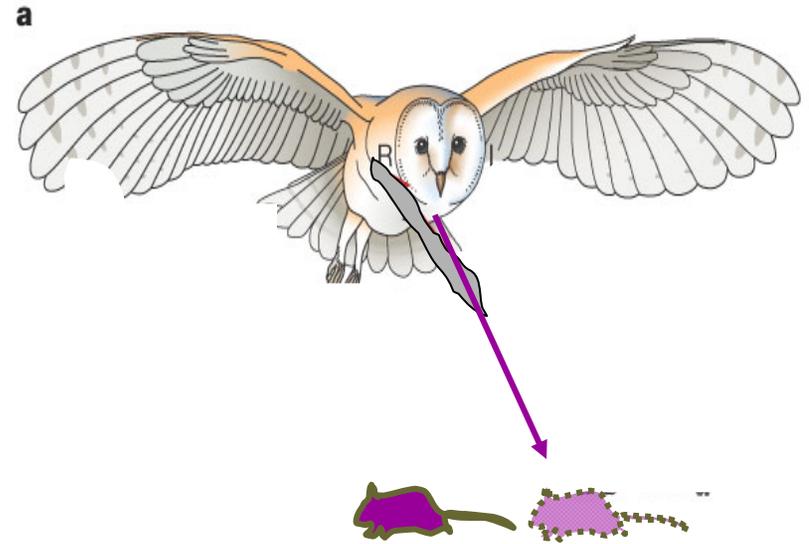
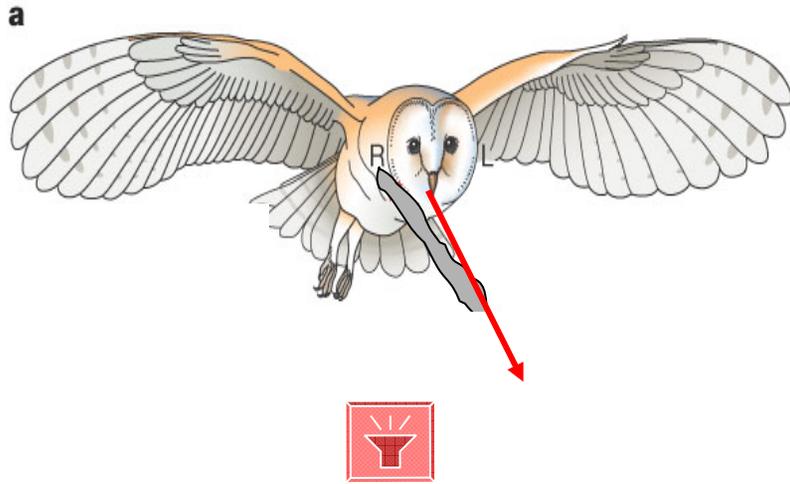
After prisms: head orientation non-overlapping in response to visual or auditory stimuli



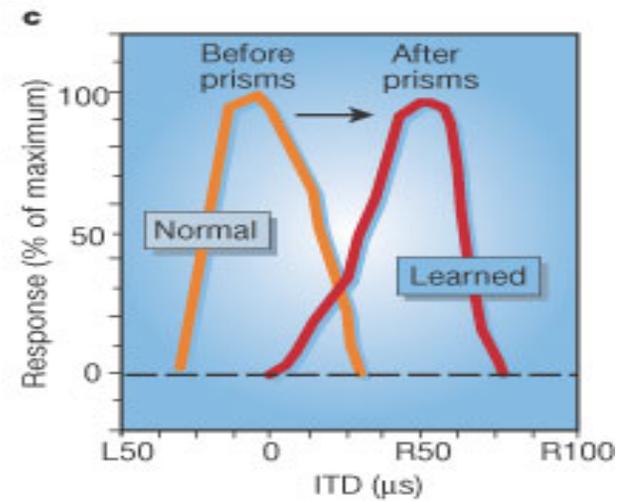
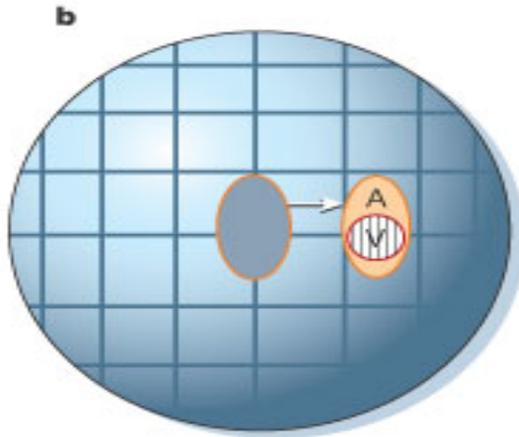
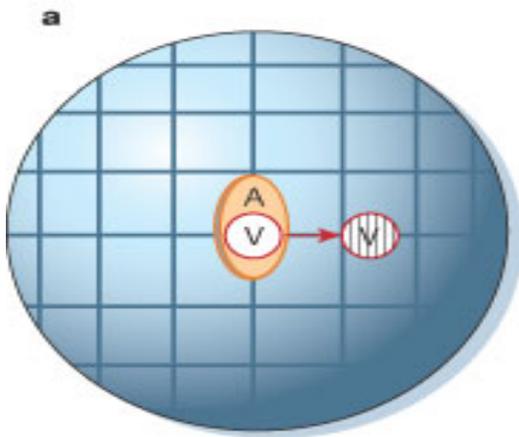
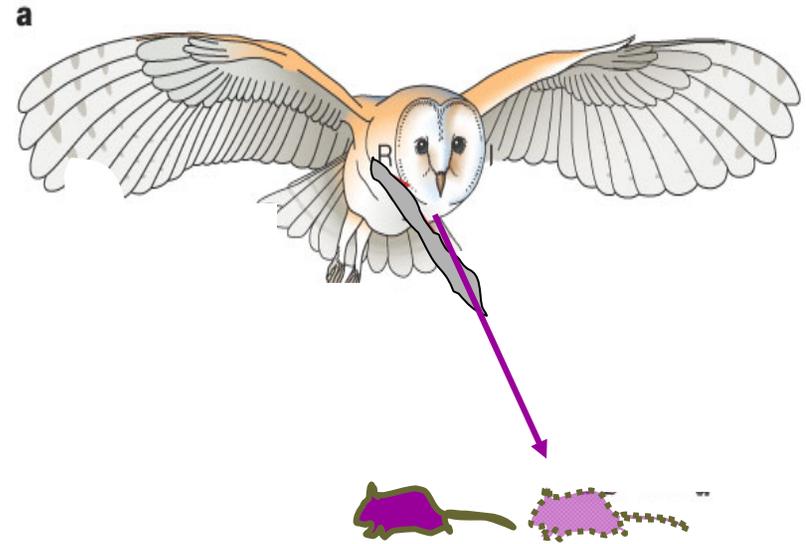
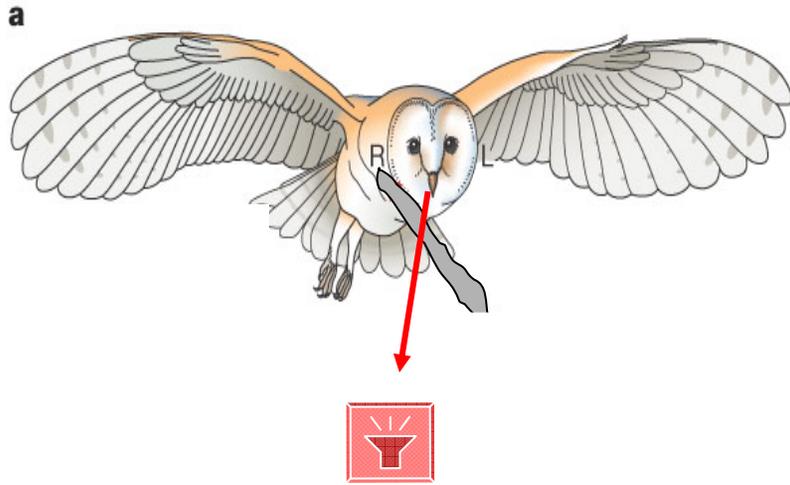
before prisms: auditory  
and visual tuning curves  
overlap



1 day after prisms: visual tuning curve is displaced

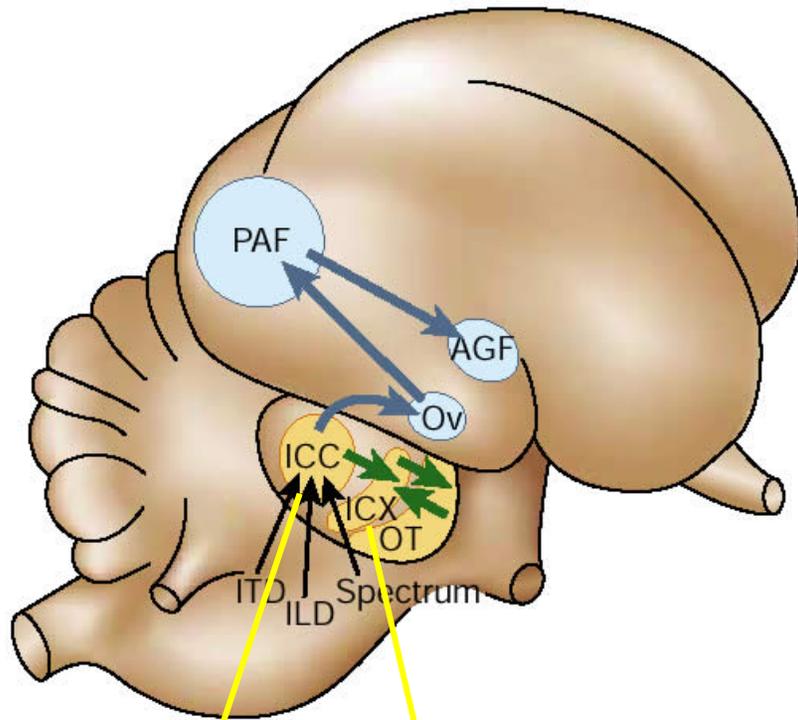


42 days with prisms: head orientation to auditory stimuli becomes aligned with that to visual stimuli



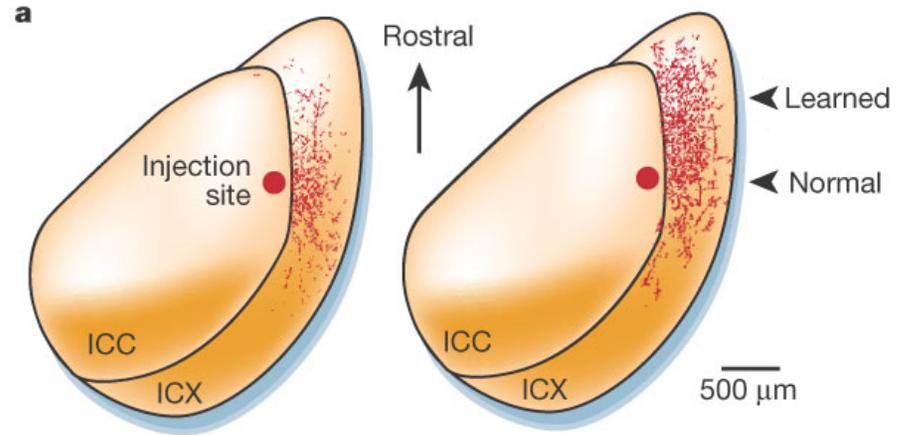
1 day after prisms: visual tuning curve is displaced

after 8 weeks, the auditory tuning curves are aligned with the visual tuning curves

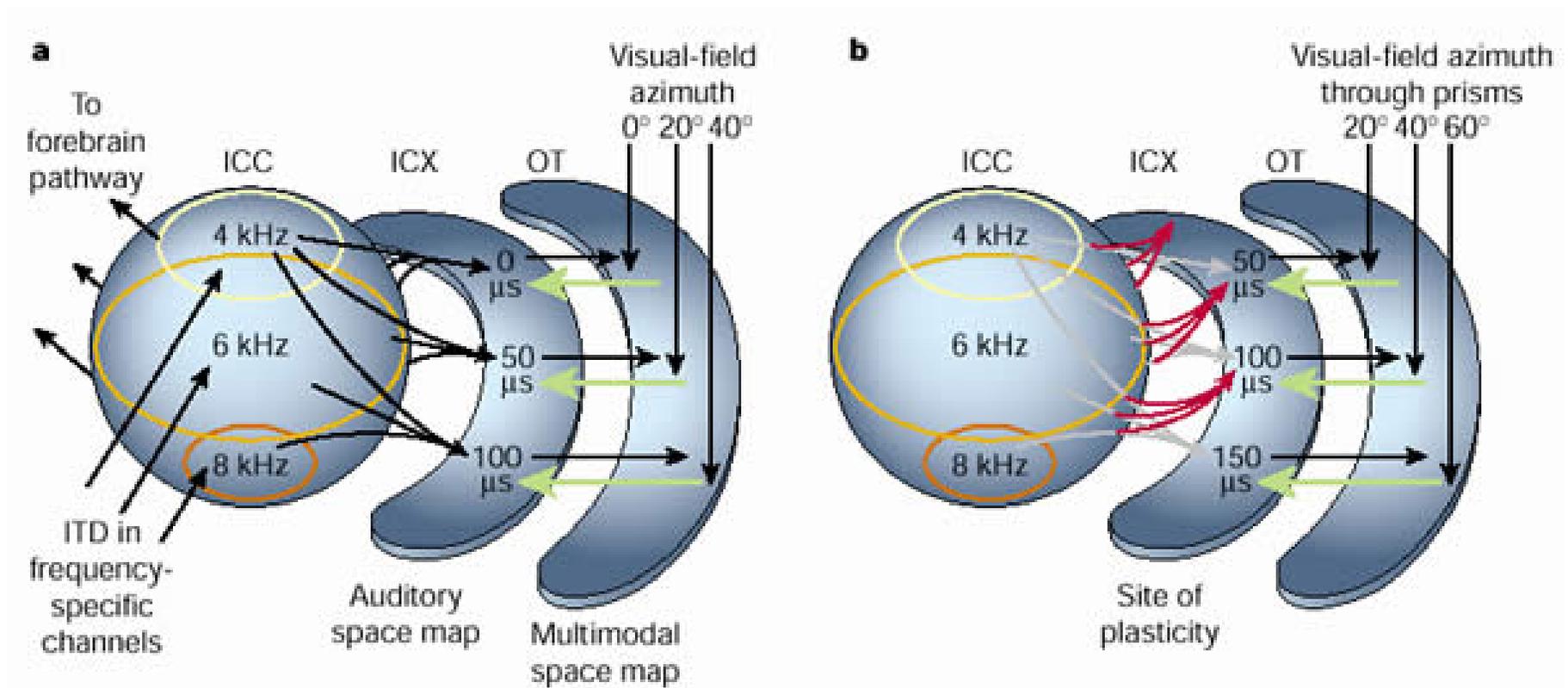


*spatial tuning curves - change*

*ITD tuning curves - do not change*

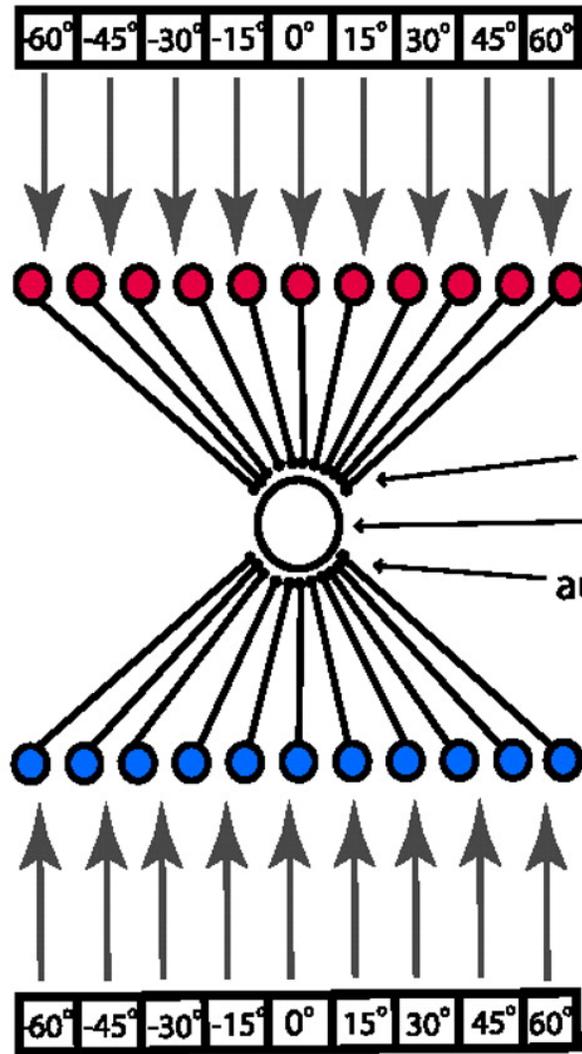


**projections from ITD-tuned neurons to spatially tuned neurons change**

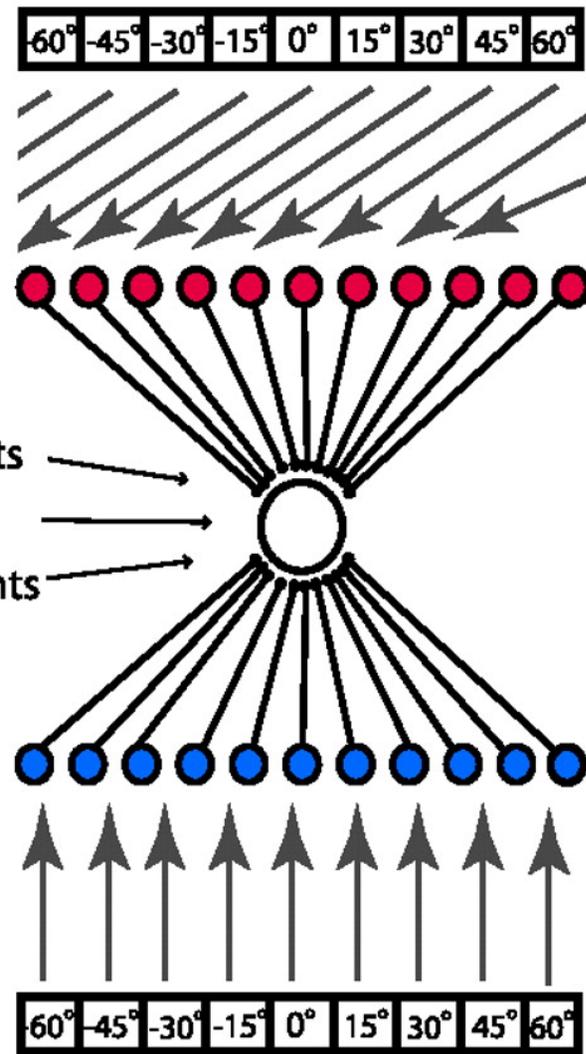


**a**, The pathway in a normal owl; and **b**, in a prism-reared adult with a shifted map of ITD<sup>40</sup>. ITD is measured and mapped in frequency-specific channels in the brainstem. This information ascends to the ICC, and converges across frequency channels in the projection from the ICC to the 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<sup>53</sup>.

# NON-DISPLACED VISUAL FIELD



# DISPLACED VISUAL



visual space

-60° -45° -30° -15° 0° 15° 30° 45° 60°

visual presynaptic layer

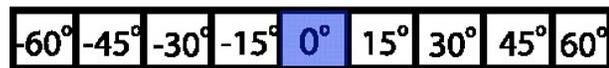
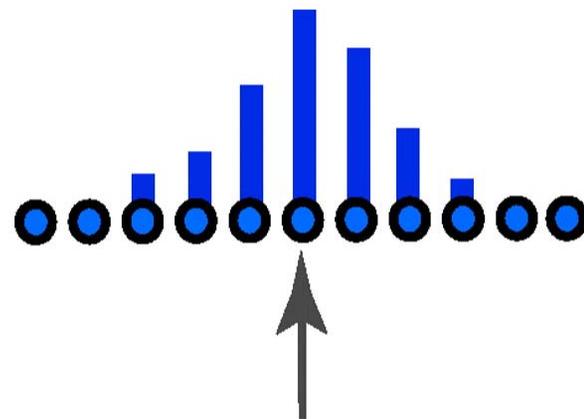
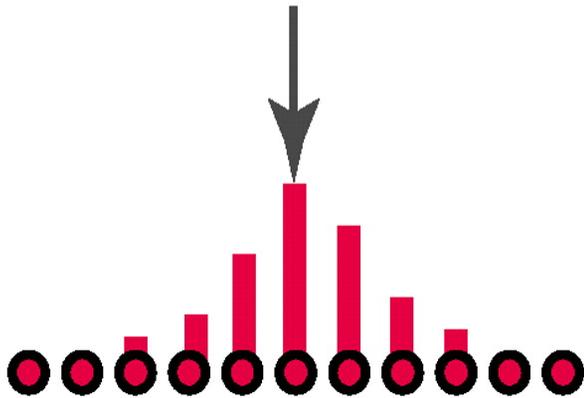
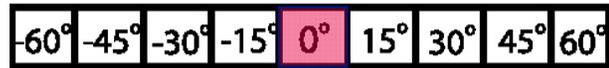
visual synaptic weights  
postsynaptic neuron  
auditory synaptic weights

auditory presynaptic layer

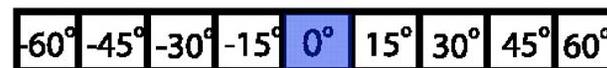
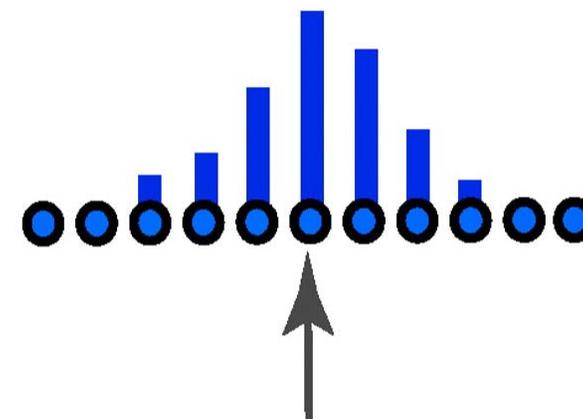
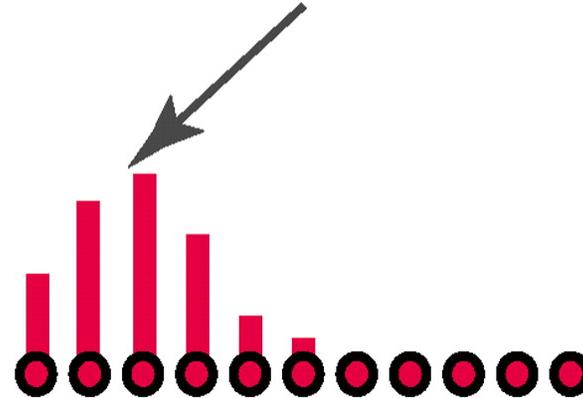
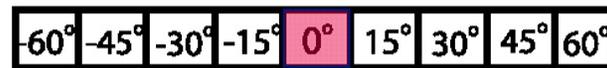
auditory space

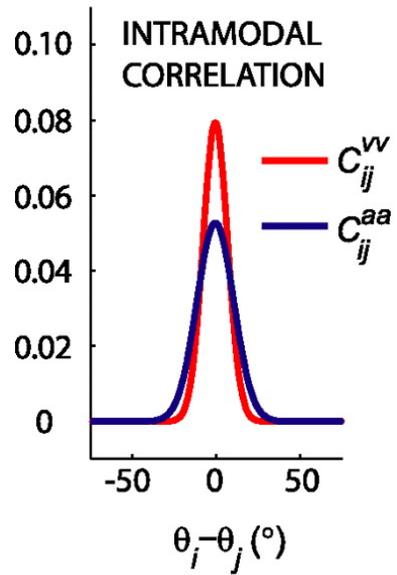
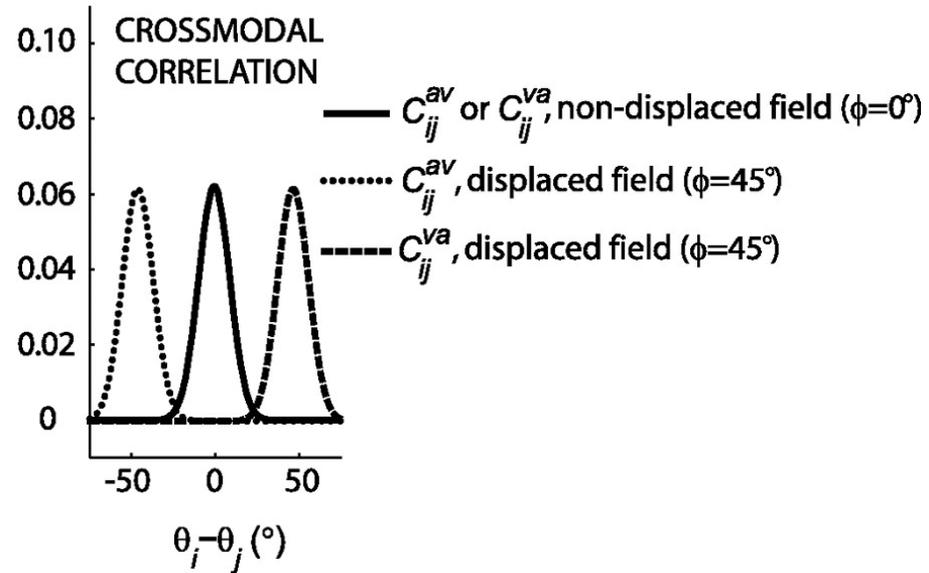
-60° -45° -30° -15° 0° 15° 30° 45° 60°

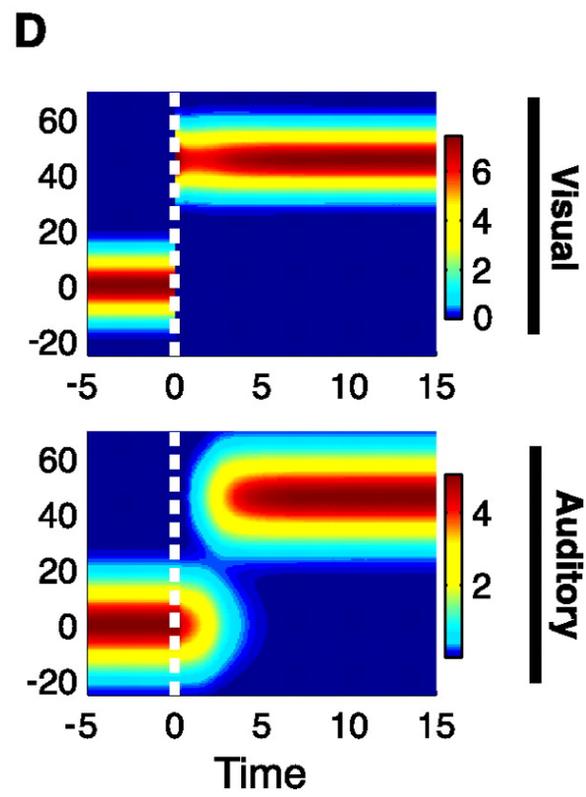
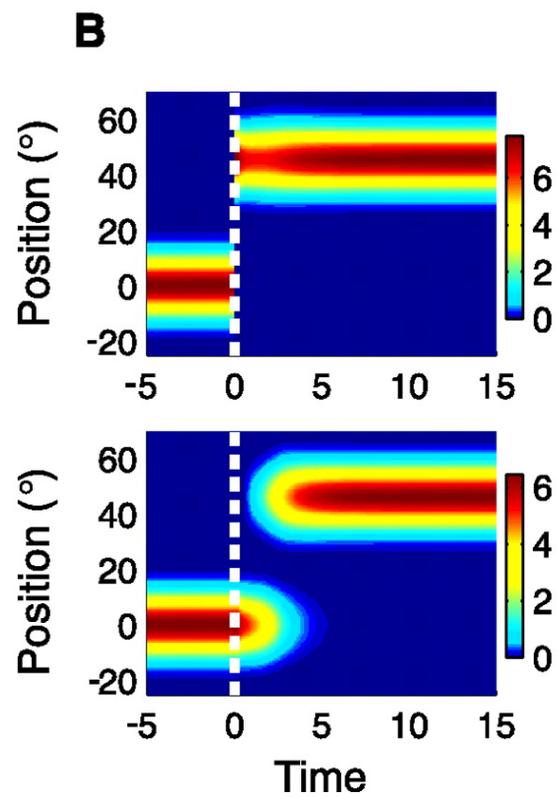
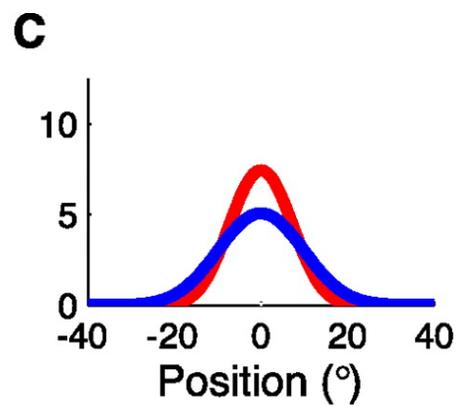
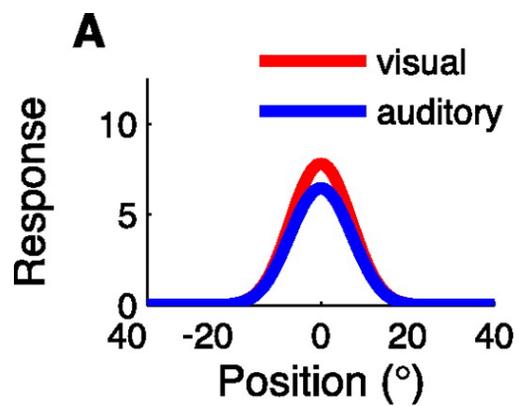
### NON-DISPLACED VISUAL FIELD

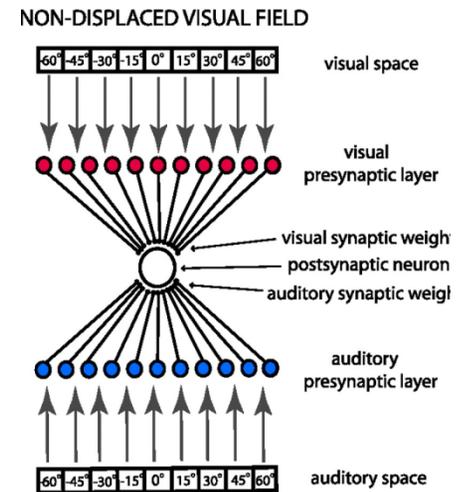
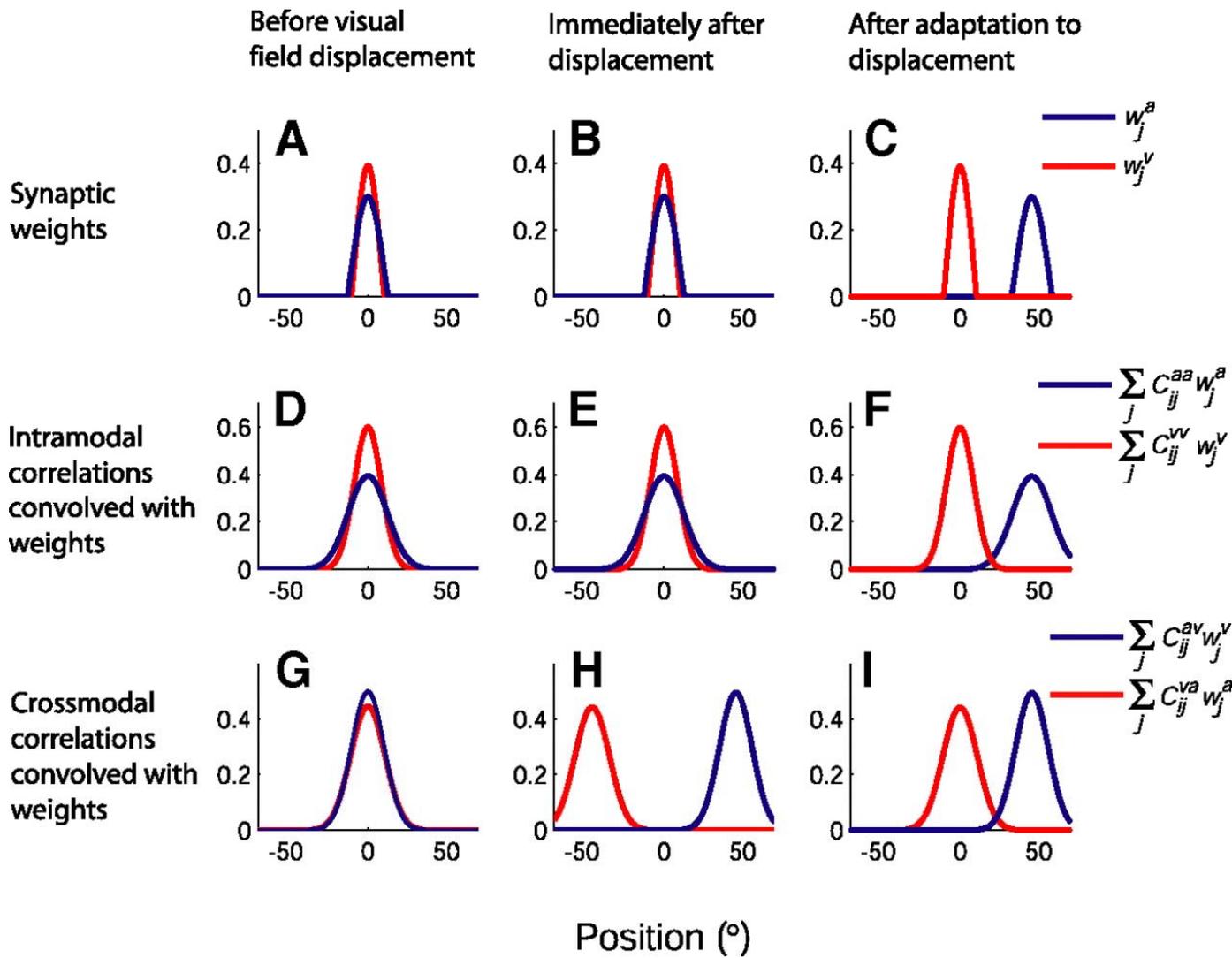


### DISPLACED VISUAL FIELD

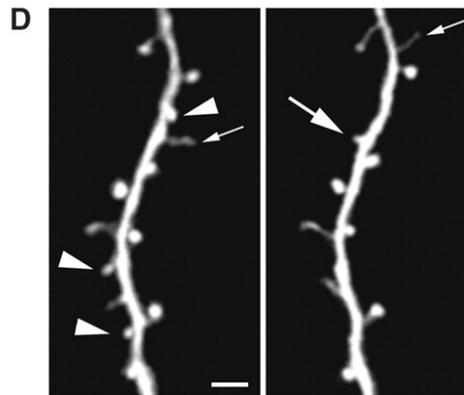
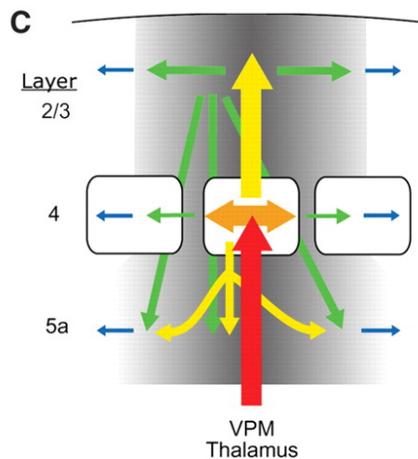
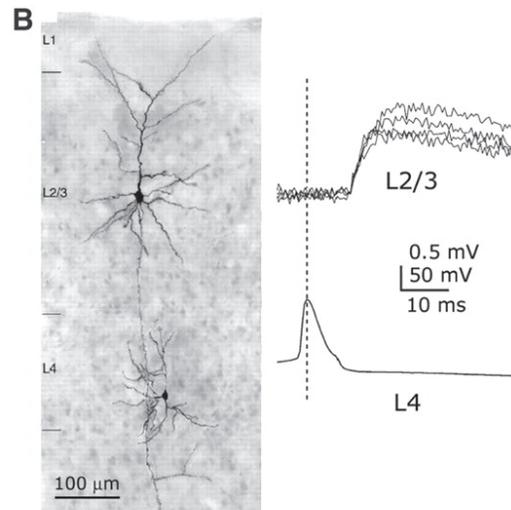
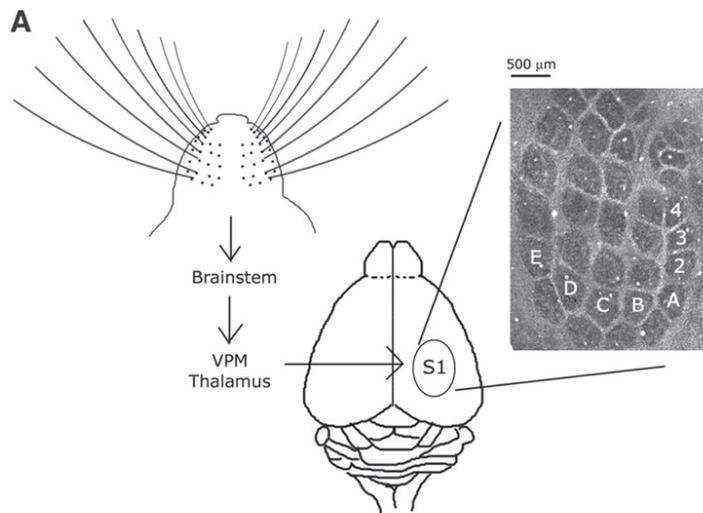


**A****B**

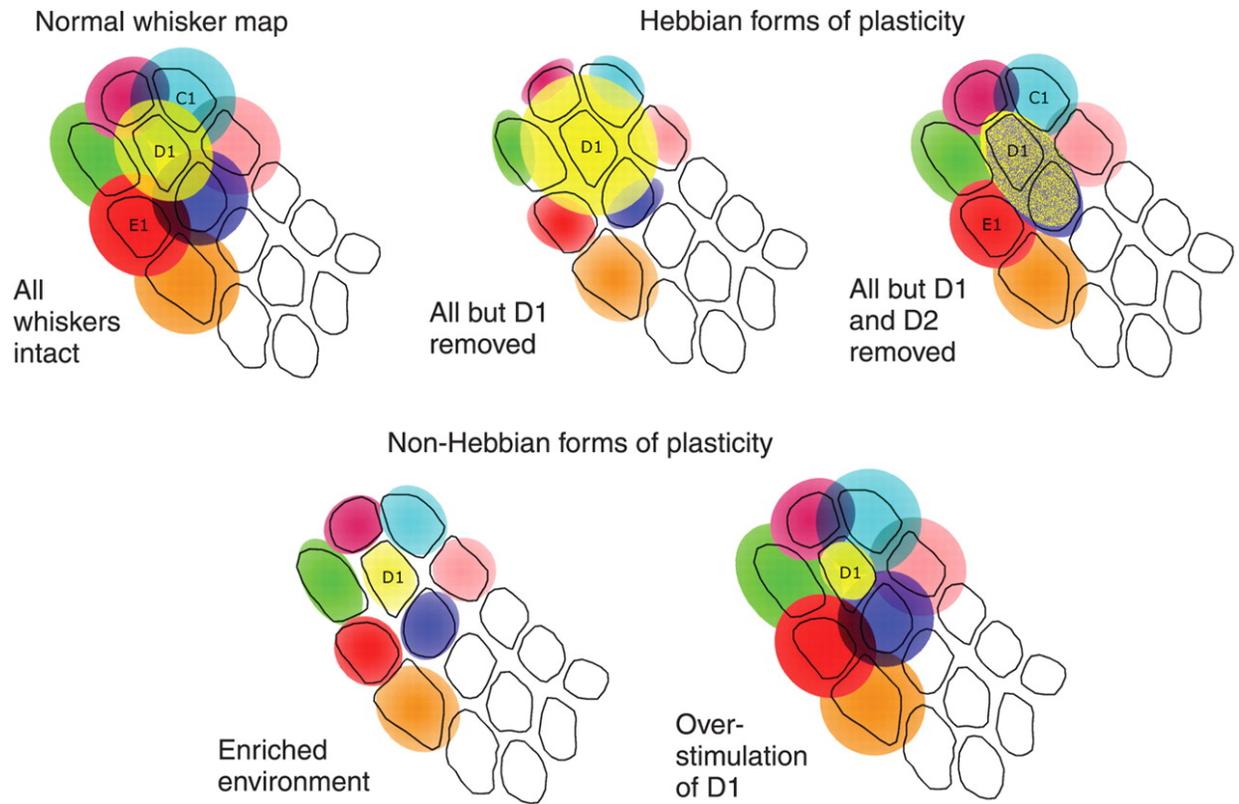




**Map Plasticity in Somatosensory Cortex**  
*Science 4 November 2005:*



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  $\mu\text{m}$ .



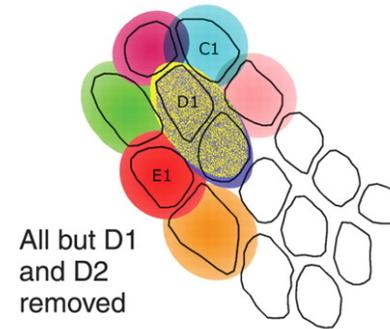
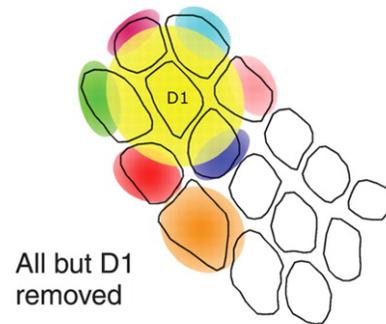
**Fig. 2.**

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 whisker responses (18), and overstimulation of a single whisker causes that whisker to shrink within the map.

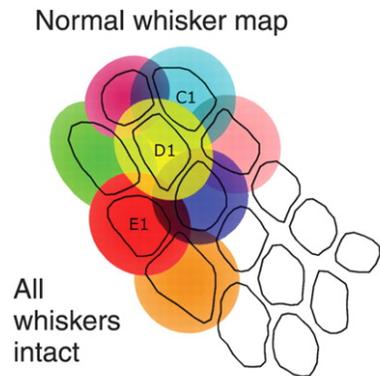
Normal whisker map



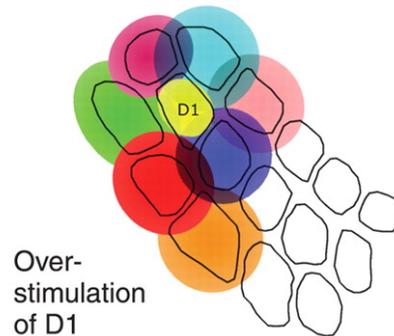
Hebbian forms of plasticity



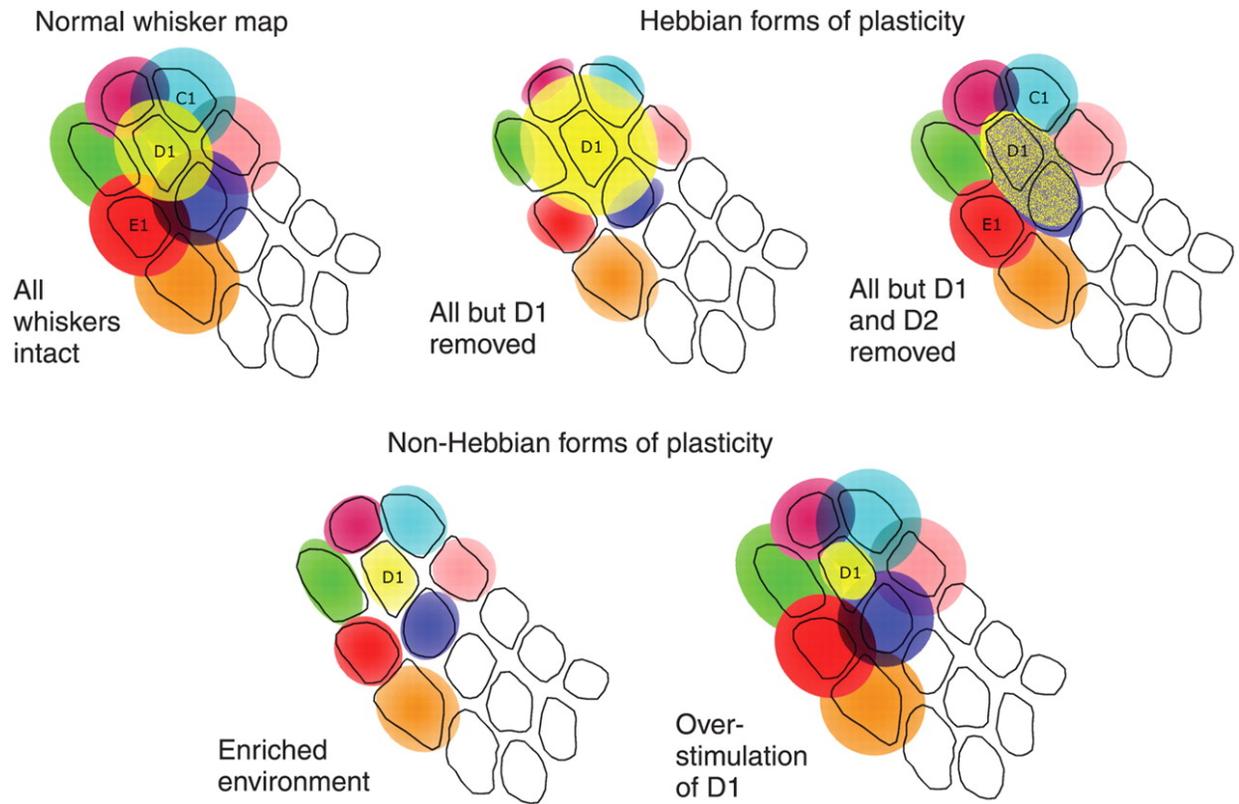
In a second, developmentally and genetically independent (6, 26) component of Hebbian plasticity, responses to spared whiskers become enhanced (15, 21, 27, 28). When isolated whiskers are spared, enhancement of spared whisker responses occurs in surrounding deprived columns, causing the spared whisker representation to expand in the S1 map (15, 21, 27). 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).



Non-Hebbian forms of plasticity



*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.



**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 whisker responses (18), and overstimulation of a single whisker causes that whisker to shrink within the map.

