

Visual dominance of visual/auditory map adjustment in the barn owl

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Summary

The barn owl optic tectum (OT) contains aligned visual and auditory maps. Following prism-shifted visual experience, the OT auditory map shifts to re-establish alignment with vision. Surprisingly, this shift occurs in the external nucleus of the inferior colliculus (IC_x), a purely auditory structure that projects to OT. We constructed a neural network in which the shift is driven by gain control through a neurobiologically identified OT- IC_x feedback projection. Although the model contained several plastic projections, the shift occurred at the IC_x , as in the barn owl, but only if the feedback projection was sufficiently strong, and the dimension of the visual input exceeded that of the auditory input.

Introduction

Multisensory processing requires the registration of sensory maps of various modalities during development. This process has been studied in the optic tectum (OT) of the barn owl, which contains aligned visual and auditory maps [1-3]. The OT auditory map adjusts to realign with the visual input [4], if the owl is exposed to prism-shifted visual experience during a sensitive period extending from 60-200 days of age [5]. The shift occurs at the external nucleus of the inferior colliculus (IC_x), the structure that relays topographically organized auditory input to the OT [6,7]. It involves reorganization of the projection from the central nucleus of the inferior colliculus (IC_c) to IC_x [8,9].

Since IC_x neurons exhibit no overt responses to visual stimuli, it was proposed that map realignment is driven by a foveation error signal rather than a topographic visual signal [10-12]. Hyde and Knudsen [13] demonstrated that the observed shift must involve a topographic visual signal. A topographic projection from the OT back to the IC_x capable of mediating this putative signal has also been identified [14]. Here, we develop a model of prism adaptation in which map organization occurs via a Kohonen process, and the OT- IC_x projection exerts a modulating influence.

Materials and methods

Our model is an artificial neural network containing an OT layer and an IC_x layer. The IC_x layer receives topographic input from an auditory (A) input layer and projects to the OT. The OT also receives topographic input from a visual (V) layer. We model

stimulus variation in azimuth only. The response y_i^m of a sensory node to a stimulus at location L_s is defined as:

$$y_i^m = \mathbf{j}^m \exp \left[-\frac{1}{2} \left(\frac{L_s - L_i^m}{\mathbf{s}^m} \right)^2 \right], \quad (1)$$

where \mathbf{j}^m is a scaling constant, and \mathbf{s}^m is the receptive field width for modality m (v or a) centered at L_i^m for each unit i . The summated input $u_j^{IC_x}$ to node j in the IC_x layer is:

$$u_j^{IC_x} = b + \sum_{i=1}^{N^a} w_{ji}^a y_i^a, \quad (2)$$

where y_i^a is the activity of auditory node i , w_{ji}^a is the synaptic weight of the connection to IC_x node j from auditory node i , N^a is the number of auditory nodes, and b is the bias.

The output of an IC_x neuron, $y_j^{IC_x}$, is:

$$y_j^{IC_x} = \frac{1}{1 + e^{-\mathbf{b}_j^{IC_x} u_j^{IC_x}}}. \quad (3)$$

$\mathbf{b}_j^{IC_x}$ is a scaling factor defined below. Each node k in the OT layer gets input from the V layer and the IC_x layer:

$$u_k^{OT} = b + \sum_{j=1}^{N^{IC_x}} w_{kj}^{IC_x} y_j^{IC_x} + \sum_{i=1}^{N^v} w_{ki}^v y_i^v. \quad (4)$$

OT unit output y_k^{OT} is again computed using a sigmoid, with \mathbf{b}^{OT} as a fixed scalar :

$$y_k^{OT} = \frac{1}{1 + e^{-\mathbf{b}^{OT} u_k^{OT}}}. \quad (5)$$

We postulate that OT uses back-projections to modulate IC_x through a form of multiplicative gain control. Each OT node projects to its counterpart in IC_x and affects $\beta_j^{IC_x}$ as:

$$\mathbf{b}_j^{IC_x} = \mathbf{q} y_k^{OT} + 1. \quad (6)$$

We assume $N^{OT} = N^{IC_x}$, and therefore $j = k$. \mathbf{q} specifies modulating influence strength. Multiplicative gain control of this sort could arise in various ways [15,16].

The network is trained using the Kohonen algorithm. Training stimuli are presented at random locations. Since there are recurrent connections between the IC_x and OT layer the network is allowed to settle following each stimulus. The index of the winner q is picked in each layer using:

$$q = \operatorname{argmax}_j (y_j) \quad (7)$$

The weights of the winner and its neighbors are updated using:

$$\Delta w_{ji} = \mathbf{h} \exp\left(-\frac{(q-j)^2}{2\mathbf{s}_r^2}\right) y_i, \quad (8)$$

where \mathbf{s}_r specifies the neighborhood of the winner, and \mathbf{h} is the learning rate. The weights are normalized using:

$$w_{ji}^a{}' = \frac{w_{ji}^a}{\sqrt{\sum_{i=1}^{N^a} w_{ji}^{a^2}}}, \quad (9)$$

for the IC_x layer, and:

$$\mathbf{w} = \sqrt{\left[\sum_{i=1}^{N^v} w_{ik}^v{}^2 + \sum_{j=1}^{N^{IC_x}} w_{jk}^{IC_x}{}^2 \right]}, \quad w_{ik}^v{}' = \frac{w_{ik}^v}{\mathbf{w}}, \quad w_{jk}^{IC_x}{}' = \frac{w_{jk}^{IC_x}}{\mathbf{w}} \quad (10)$$

for the OT layer.

Training proceeds in two stages. Stage 1 simulates initial development of topographic maps. Stage 2 simulates sensory experience with prism-deviated visual inputs during the sensitive period. The prism-deviated visual stimulus is presented 23° to the right of the auditory stimulus, as in experimental studies [4].

Results

The model contains three sets of equally plastic connections: A- IC_x, IC_x -OT, and V-OT, any of which may participate in producing the shift. We first investigate the effect of varying the strength of the back-projection (\mathbf{q}) on the role of each projection in producing the shift. The other parameters are fixed as follows: $N^v = 80$, $N^a = 20$, $N^{OT} = N^{IC_x} = 40$, $\mathbf{h} = 0.005$, $\mathbf{S}^v = 8.1$ and $\mathbf{S}^a = 32.1$. \mathbf{q} is varied from 0 to 10. When $\mathbf{q} = 0$, the A- IC_x projection is uninfluenced by the mismatch between auditory and visual input, and the IC_x -OT projection contributes about 80% of the shift. This result runs counter to neurobiological observation. As we increase \mathbf{q} , the shift moves to the A- IC_x projection. For $\mathbf{q}=1$, the A- IC_x projection contributes about 80% of the shift. Further increasing \mathbf{q} does not increase the shift. This result agrees nicely with the neurobiological observation that the shift occurs at the IC_x auditory map.

Next, holding $\mathbf{q} = 5$ and auditory input dimension $N^a = 20$, visual dimension N^v was varied from 5 to 80, with \mathbf{S}^v being reduced proportionally. When $N^v = 5$, about 80% of the shift occurred in the V-OT projection. Thus, in the model, when the dimension of the visual input is reduced below that of the auditory input, the auditory input actually causes the visual map to shift, in sharp contrast to neurobiological observation. As N^v increases, the contribution of the A-IC_x projection increases. When N^v reaches 20, the A-IC_x projection accounts for 80% of the shift, and this value remains

constant as N^v increases. Thus, increasing the dimension of the visual input to that of the auditory input restores the dominance of vision over audition for map shifting, given the q value chosen.

Discussion

Auditory/visual misalignment produces a shift in the IC_x auditory map despite the absence of overt visual responses in that structure. The discovery of back-projections from the OT to IC_x does not by itself explain this observation. Here we show, with a simple Kohonen map algorithm, that using back-projections to modulate the sensitivity of IC_x neuron responses to auditory input can produce shifts in the IC_x map, without producing overt visual responses in model IC_x neurons. The shift occurs predominantly in the A- IC_x projection, despite the fact that the IC_x -OT and V-OT projections are equally plastic. Concentrating the shift at the IC_x level, which is consistent with neurobiological observation, requires back-projections of sufficient strength, and visual input of dimension at least equal to that of the auditory input. While the functional properties of actual back-projections remain to be determined, greater visual than auditory input dimension is apparent in most vertebrate species. Even in the nocturnal barn owl, visual receptive fields are considerably smaller than their auditory counterparts. Our results suggest that OT to IC_x back-projections, combined with high visual input dimension, cause the auditory map shift to occur predominantly at the level of the IC_x . The model predicts that reducing visual input dimension, perhaps through optical means such as frosted lenses, should compromise the dominance of vision over audition in multisensory map alignment in the barn owl.

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