A Model of Spontaneous Activity and Neural Development

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Purpose

To develop a unified model of the activity-dependent refinement of retinotopy, eye-specific layers and on/off sub-layers in neural projection from the retina to the lateral geniculate nucleus (LGN) in cats and ferrets.

Biological Background The initial ingrowth of retinal afferents into the LGN is quite disordered. The afferents from both eyes and both functional classes arborize and synapse on cells throughout the depth of the LGN (Shatz, 1983). There is coarse retinotopy in the initial retinogeniculate projection, but there is no evidence for precise retinotopy until maturity.

Over development, the retinogeniculate projection sharpens extensively. Each mature LGN cell receives retinal input from only 1-8 ganglion cells from one functional class (on-/off-center) in one eye. LGN cells with similar inputs are clustered into eye-specific layers and on/off sub-layers. Further, the retinotopic map in the mature LGN is nearly perfect.

During the height of this refinement, retinal ganglion cells (RGC's) spontaneously fire bursts of action potentials which propagate across the retina in waves. These waves change around the onset of on/off layer segregation and disappear just before eye opening (Wong& Oakley, 1996). During the period of wave activity, LGN cell responsivity is heightened and inhibition is attenuated. Notably, there is no evidence for long-range intra-LGN connections at any stage in development.

Computational Background It is known that spatially correlated input activity and Hebbian processes can generate maps and segregation of afferents (Keesing, Stork & Shatz, 1991; Miller, 1989). This model concentrates on the character of the input activity and the specific physiological and anatomical characteristics of the LGN in order to develop a predictive and cohesive model of a well-described system.

Model System

The model simulates the projection from a small patch of each retina to a portion of the LGN. The model simulates the period from retinogeniculate fiber ingrowth, when layers are undifferentiated and retinotopy is probably coarse, to eye-opening, when layer segregation is nearly complete.

Intra-LGN Connectivity Each LGN cell connects with fixed positive weights to its 4 nearest intra-layer neighbors, and its nearest inter-layer neighbor, biasing the model toward layer formation. In addition, each LGN cell inhibits itself with increasing strength over development. There are no longer-range connections.

Initially, the model afferents arborize across all layers, but in a restricted random retinotopic location (that is slightly biased towards its retinotopically correct location). Snap-shots of waves are iteratively presented and the weights are updated using a modified Hebbian algorithm. The simulated waves change over training, matching the changes in the observed waves over development.

Weight Change Algorithm The algorithm consists of four steps. First, the input to LGN cells is computed as a (weighted) linear sum of the input and neighbor activities. The LGN activity is iterated until reaching steady state, effectively blurring the retinal input to the LGN. The amount of blurring is determined by the self-inhibition in LGN cells and the efficacy of the retinal synapses. The blurring decreases over time in correlation with physiological changes over development, it thus plays an analogous role to shrinking neighborhood functions in other models.

Second, the retina-to-LGN weights are updated proportionally to the product of the RGC and LGN cell activities and the previous weight. Third, the weights are blurred to mimic a branching factor. Fourth, the weights are normalized such that the total connection strength of each neuron stays constant.

Results

In the model, wave-like retinal activity was found to support the development of retinotopy, eye-specific and on/off layer segregation. The time-course of refinement in the model qualitatively matches the time-course of refinement observed in cats and ferrets. Specific model parameter requirements were explored.

References

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