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We have studied neural circuitry involved in pattern recognition. In mammals, this is mainly mediated by a highly laminated cortical structure. We have studied alternate biological solutions to the same problem and found that comparable neuronal components can achieve similar, or even improved, performance using nonlaminated configurations of neurons. Our work has also highlighted the importance of an alternate parallel channel of visual information to the cortex. This alternate channel appears to be more "object oriented" in its information coding, rather than with individual line segments of complex patterns. In many vertebrates, the object oriented channel constitutes the major means of information transfer and analysis.

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Background:

The project originally proposed for support by the ONR centered on a re-evaluation of several widely accepted concepts regarding the role of retinotopy and lamination in the organization of visual pathways. Our findings suggested that the traditional concepts of visual information coding and of the neural networks involved in pattern recognition may constitute only one of several possible alternate mechanisms potentially operational in vertebrate (including human) brains.

a) Can alternate configurations of neural networks achieve similar levels of performance? Specifically, is lamination a requisite form of arrangement of components in the visual system, in order to achieve high levels of performance in acuity and discrimination?

b) Is maintenance of retinotopy at "cortical" levels essential to cognitive operations in a visual world?

c) What is the role of ascending retino-tectal projections upon the forebrain in visual discrimination?

These issues arose in relationship to the frequent observation that visual performance in many birds is equal or superior to that of primates, including man. In our initial analyses of the organization of the visual system extending to the forebrain in birds, we discovered that lamination and retinotopy at telencephalic levels were not essential to the high level of visual performance achieved by birds. These issues are highly relevant to our understanding of the organization of visual operations, from several points of view. 1) Study of the avian visual system has provided major new insights into the evolution of the mammalian cortex (see papers by Shimizu and Karten, 1990, Karten and Shimizu 1989). 2) Study of bird visual system has demonstrated the importance of a major visual input to the forebrain from the midbrain optic region. In mammals, this is designated as the superficial portion of the superior colliculus. In birds and other nonmammalian vertebrates it is designated as the optic tectum.

Progress:

In most general terms, the project has been highly productive in terms of the number of publications, and the initiation of a series of studies that have formalized several of the critical issues. Most significant amongst these issues have been the question of the role and importance of lamination in information processing, and the importance of nongeniculostriate pathways in visual processing.

This report consists of three parts:

I. Studies of the Wulst
II. Studies of the Tectofugal System
III. Conceptual Papers and Reviews

I. Studies of the Wulst:

The identity of the posterior (visual) Wulst of birds as structurally and histologically similar to the striate cortex of mammals was first recognized by Karten, et al., in 1968, 1973, and subsequently studied and characterized electrophysiologically by Pettigrew and co-workers. Despite extensive behavioral studies by Hodos, Shimizu, and others, little was known about the functional role of the visual wulst. Indeed, destruction of the wulst in pigeons and chickens produced little of the expected loss in visual performance. In order to attempt to better understand the nature of the wulst, we undertook a series of studies including:

1. Histochemical organization of the wulst (See Shimizu and Karten 1990)
2. Differential projections of individual components of the wulst.(See Shimizu and Karten 1992)
3. Interlaminar connections within the wulst (Shimizu and Karten, In Prep)

The results of the first two studies have been published and are included in the Appendix. Studies of interlaminar connections revealed that despite the apparent lamination of the several nuclei of the wulst, the interaction between HD and the overlying IHA/HA was restricted to axonal connections. There was little or no indication of interlaminar dendritic arborizations, one of the characteristic features of cortical types of structures.

An additional extremely important observation was the realization that the HD component appears to be of different developmental origin than the IHA/HA division. As outlined in Karten (1991), this may provide an important clue to understanding the early developmental embryogenetic events involved in the formation of the striate cortex of mammals and the wulst of birds.

II. Studies of the Tectofugal System: Tectal pathways to the telencephalon in birds and mammals.

The tecto-thalamo-telencephalic visual pathway is the major visual input system to the forebrain in the vast majority of vertebrates. However, it has received only minimal attention, particularly when compared to the more widely recognized geniculostriate system. Relatively little is known about the identity or response features of retinal ganglion cells that contribute to this system, or the throughput system of the tectum that conveys information upon the thalamus. We have concentrated upon the organization of this aspect of the tecto-thalamic pathway.

1. *Cholera Toxin (CTb) as a retrograde tracer:* Characterization of retinal ganglion cells projecting upon the optic tectum in birds. Although there have been a number of studies of the character of retinal ganglion cells projecting upon the tectum, little is known about their individual morphology, relative numbers in various regions of the retina, or differential cell types terminating within specific distinct sublayers of the tectum. Our recent application of Cholera Toxin B fragment (CTb) to this task has resulted in a dramatic improvement in sensitivity both in regards to our ability to label small ganglion cells, as well as demonstrating far more detail of the dendritic arbors of the individual ganglion cells. Though exact comparison of the relative efficiency of this methods compared to the use of e.g., HRP or HRP-WGA is difficult to assess, we

estimate that it may be 5-10x more sensitive, particularly in regard to the small retinal ganglion cells with somata less than 6-7 micrometers.

2. Tectal projections upon the nucleus rotundus: The sensitivity of CTb in identifying the inputs to the nucleus rotundus has been truly impressive. Two major findings not previously appreciated included a) Input to the anterior portions of rotundus are derived exclusively from the outer lamina of the stratum griseum centrale (layer 13a) of both the ipsilateral and contralateral optic tectum. The ratio of ipsi/contra was a surprisingly high 2:1, representing a far greater contralateral input than previously generally appreciated. (See previous papers of Karten, Hunt and Bischof), b) The amazing sensitivity of the CTb method demonstrated retrograde filling of dendrites of layer 13a neurons extending into layer 5 of the SGFS of the tectum. Layer 5 is the target of the small ganglion cells, and constitutes the lamina of highest density of terminations of retinal inputs. The prospect that layer 13a neurons may receive a direct retinal input, was suggested by Cajal (1911), and again by Hunt and Brecha (1984), but was denied by all other workers.

3. GABA-ergic inputs to the nucleus rotundus: Nucleus rotundus contains an extremely rich plexus of GABA and GAD immunoreactive axons. We have now shown that this is not of tectal origin, but rather derives from a nucleus that receives collateral input from tectal layer 13a, the nucleus subpretectalis (SP). We have demonstrated that SP somata are uniformly rich in GABA and GAD, and that these cells are retrogradely labelled after injections of retrograde tracer confined to the nucleus rotundus. The input to rotundus from SP is exclusively ipsilateral. Destruction of SP results is dramatic reduction in the density of GABA and GAD staining in rotundus. We were unable to completely eliminate GABA/GAD axons from rotundus after SP lesions. That may be due to incomplete lesions, or, more likely due to the presence of a second GABAergic input from the reticular nucleus of the thalamus (Benowitz and Karten, 1976).

Consequent to these observations, we developed a slice chamber preparation of nucleus rotundus, and have initiated a series intracellular and whole-cell patch clamp studies to characterize the inputs from the tectum versus those from the SP. Preliminary data at this point indicates that the input from the tectum may be glutamate, mediated by an atypical type of NMDA receptor.

III. Conceptual papers and reviews:

Karten, H.J. and Shimizu, T. (1989) The origins of neocortex: Connections and lamination as distinct events in evolution. J. Cog. Neurosci., Vol. 1, No. 4, pp. 291-301.

Shimizu, T. and Karten, H.J. (1991) Central visual pathways in reptiles and birds: Evolution of the visual system. Evolution of the Eye and Visual System, Vision and Visual Dysfunction, Vol. 2, Ch. 19, (R. L. Gregory and J.R. Cronly-Dillon, eds.) Macmillan Press, pp. 421-441.

Karten, H.J. and Shimizu, T. (1992) Are visual hierarchies in the brains of the beholders?: Constancy and variability in the visual system of birds and mammals. The changing visual system: Maturation and aging in the central nervous system (P. Bagnoli and W. Hodos, Eds.). Plenum Press. In press.

Future Directions of Research:

1) Characterization of retinal ganglion cells projecting upon the optic tectum.

2) Is there a covert topography in the tecto-rotundal organization.

3) Morphology of tectal neurons projecting upon rotundus.

4) Further analysis of transmitter employed in the tecto-rotundal system.

5) Microcircuitry and transmitters in the telencephalic component of the tectofugal pathway.

6) Development of connections and transmitters in the tectofugal pathway.

Publications:

Karten, H.J. and Shimizu, T. (1989) The origins of neocortex: Connections and lamination as distinct events in evolution. J. Cog. Neurosci., Vol. 1, No. 4, pp. 291-301.

Britto, L.R.G., Keyser, K.T., Hamassaki, D.E., Shimizu, T. and Karten, H.J. (1989) Chemically-specific retinal ganglion cells collateralize to the pars ventralis of the lateral geniculate nucleus and optic tectum in the pigeon (*Columba livia*). Vis. Neuroscience 3:477-482.

Shimizu, T. and Karten, H.J. (1990) Immunohistochemical analysis of the visual wulst of the pigeon (*Columba livia*). J. of Comp. Neurol. 300:346-369.

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Shimizu, T. and Karten, H.J. (1991) Computational significance of lamination of the telencephalon. Visual Structures and Integrated Functions, Research Notes in Neural Computing (Michael Arbib and Jörg-Peter Ewert, eds.), Springer-Verlag, Vol. 3, pp. 325-327.

Shimizu, T. and Karten, H.J. (1991) Central visual pathways in reptiles and birds: Evolution of the visual system. Evolution of the Eye and Visual System, Vision and Visual Dysfunction, Vol. 2, Ch. 19, (R. L. Gregory and J.R. Cronly-Dillon, eds.) Macmillan Press, pp. 421-441.

Karten, H.J. (1991) Homology and evolutionary origins of the `Neocortex'. Brain, Behav. & Evolution, 38:264-272.

Karten, H.J. and Shimizu, T. (1992) Are visual hierarchies in the brains of the beholders?: Constancy and variability in the visual system of birds and mammals. The changing visual system: Maturation and aging in the central nervous system (P. Bagnoli and W. Hodos, Eds.). Plenum Press. In press.

Abstracts:

Shimizu, T., Karten, H.J., and Woodson, W. (1988) GABA-ergic inputs to the nucleus rotundus in pigeons (*Columba livia*). Soc. Neurosci. Abstract, 14: 991.

Shimizu, T., Woodson, W., Karten, H.J. and Schimke, J.B. (1989) Intratelencephalic connections between the visual areas in birds (*Columba livia*). Soc. for Neurosci. Abstract, 15:1398.

Woodson, W., Shimizu, T. and Karten, H.J. (1989) Transmitter and peptide content of the isthmo-optic nucleus in the pigeon (*Columba livia*): A study of non-tectal afferents. Soc. for Neurosci. Abstract, 15:459.

Shimizu, T., Karten, H.J. and Cox, K. (1990) Intratelencephalic projections of the visual wulst in birds (*Columba livia*): A phaseolus vulgaris leucoagglutinin study. Soc. for Neurosci. Abstract, 16:246.

Karten, H.J. and Shimizu, T. (1990) Functional significance of neural circuits and lamination of the neocortex: an evolutionary view. Workshop on Visual Structures and Integrated Functions, Univ. of Southern California. Accepted.

Shimizu, T., Britto, L.R.G., Karten, H.J. and Cox, K. (1991) Cholera toxin mapping of retinal projections in birds. Society for Neurosci. Abstract, 17:651.

Karten, H.J. (1991) Constancy and variability in the visual system of birds and mammals: A model for evolution, development and function. NATO ASI Course, Viterbo, Italy, May 1991.

Other Work, Still In Progress, Supported In Part by ONR:

Finally: retinal projections upon the rostromedial hypothalamus. A re-evaluation. (Shimizu, Britto, Hamassaki-Britto and Karten)

Bilateral tectorotundal projections arise from the Stratum Griseum Centrale-layer 13 of the optic tectum. (Karten, Bischof and Shimizu)

Telencephalic projections upon the optic tectum in pigeons: Archistriatal projections. In Prep. (Karten, Shimizu, Brecha and Cox)