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CHAPTER 25

What do developmental mapping rules optimize?

Meijuan Xiong and Barbara L. Finlay*

Department of Psychology, Cornell University, Ithaca, NY 14853, USA

Convergence ratios between pre- and postsynaptic cells in the visual system vary widely between cell classes, areas of the visual field, between individuals and between species. Proper stabilization of the convergence and divergence of single visual neurons is critical for visual integration generally, and for specific functions such as those of rod and cone pathways, or the center and peripheral regions of the visual field. In early development, retinal ganglion cells, target cells and all their processes are produced in excess and stabilize at certain mature values. The intent of the investigations described here is to determine what features of cell connectivity are stabilized over normal variability by these developmental processes and how such stabilization is accomplished, using the developing mammalian retinotectal system as an example.

Orderly compression of the retinotopic map into a half tectum was induced by a partial tectal ablation at birth in hamsters, increasing the ratio of retinal ganglion cells to superior colliculus target cells. The convergence problem is solved in this case by undersampling the spatial array with respect to normal, preserving local spatial resolution, but potentially reducing sensitivity or introducing aliasing artifacts. Receptive field sizes of single neurons are indistinguishable from normal, and reduction of branching of presynaptic axon arbors is the mechanism of the remapping. Behaviorally, though the entire visual field is still represented in the remaining colliculus, the solution has a cost in decreased probability and increased latency to orient to visual stimuli, particularly in the peripheral visual field. The generality of this solution for retinal and other central convergence regulation problems is evaluated.

Introduction

During development, the visual system must solve functional problems that are defined at the level of visual information processing, using mechanisms that are defined at the level of interactions, growth, and trophic requirements of cells. These problems must often be solved in the absence of any immediate evaluation of visual function, leaving the tuning of developmental processes only under the control of natural selection. In most cases of early nervous system development, there is substantial variability in the initial deployment of neurons and their processes, but a reasonably stable adult solution is produced. What features of visual organization are optimized in early development, and how is that control expressed through the interactions of developing neurons?

The particular case we will discuss is the control of convergence between populations of neurons in the visual system. The total number of neurons projecting to a number of neurons in a target structure sets the boundaries of convergence, but within these limits, any solution is possible: an afferent neuron could establish a synaptic connection with every neuron in the target population, or with only one. Close to this range of variability is seen in the visual system, from the one-to-one convergence of retinal neurons in the primate fovea to the extended distribution of wide-field amacrine cells. Differences in convergence ratios are directly related to the different functions of the retina, within individuals and across species. The low convergence ratio from cones to ganglion cells in the central retina preserves high acuity in photopic conditions but

* Corresponding author. Tel.: +1 607 2556394; fax: +1 607 2558433; e-mail: blf2@cornell.edu

sacrifices sensitivity, whereas the high convergence ratio from rods to ganglion cells in the peripheral retina allows high sensitivity in scotopic conditions but loses spatial resolution. Different functional cell classes, such as the X/Y, color-opponent or motion sensitive classes require different organization of input convergence. Across species, highly developed central vision versus panoramic vision require variable convergence across the retina in the first case, and more consistent convergence in the second case.

What might happen if an array of target neurons is reduced by some fraction, with the requirement that the entire input array must be represented in the target structure? Two classes of solutions are possible. The number of neurons in the target population projecting to any one target neuron could increase: a cell usually receiving four inputs might accept eight, spread over a larger area of visual field. This solution lowers the spatial frequency represented by the targets, blurring spatial resolution, but preserves some measure of sensitivity by keeping the number of target neurons potentially reporting activity in some visual field location as high as possible. Alternatively, the number of neurons projecting to a target neuron could be held constant, but the number of neurons in the target structure representing any particular location in the visual field could be reduced. This preserves high frequency selectivity, but spatial localization may be compromised. To adequately sample a simple sine wave, a sampling array must at least give one sampling point for every peak and trough of the sine wave, and for a given sampling array with a regular sampling interval (d), the highest frequency sine wave (1/2 d) which can be unambiguously represented, is referred to as the Nyquist limit (Rowe, 1991). Spatial undersampling may occur when the frequency of the stimulus is above the Nyquist limit. For example, when spatial frequency of the sine wave is higher than the Nyquist limit of the sampling array, the output of the sampling array is ambiguous. A high frequency sine wave would appear to the system to come from a lower frequency, a phenomenon called aliasing. Additionally, since fewer target neurons can report the stimulus, sensitivity of the target neuron population to a visual stimulus of constant size is reduced.

Variation in population convergence ratios almost certainly occurs commonly in normal development, and certainly occurs over evolution. Which solution does the visual system favor, and how is it executed? Note that the 'best' solution might differ by cell class, e.g. photopic cells might choose blur, and scotopic cells spatial undersampling.

Some examples of convergence variation and their relation to measured acuity

Sterling et al. (1988) demonstrated that the convergence ratio between cones and ganglion cells set visual resolution close to the Nyquist limit. They determined the convergence of cones onto ganglion cells by tracing dendrites through serial ultrathin sections from electron micrographs in the cat. In the cat, 16 cones converge onto four cone bipolar cells which then converge onto one ON-beta ganglion cell. The Nyquist limit for the cone array is 18.7 cycles/degree, however, the 4:1 convergence of cones onto cone bipolars reduces the resolution of the cone signal by a factor of four to about 9.3 cycles/degree, which is very close to the Nyquist limit for the cone bipolar (CBb1) array alone (the Nyquist limit for the cone bipolar array alone is 9.2 cycles/degree). In contrast, the rod system appears to have a much higher convergence ratio: 1500 rods converge onto 100 rod bipolars which can innervate five AII amacrines, eventually innervating one on-beta ganglion cell. The Nyquist limit for rods in the cat is 64 cycles/degree, which would be reduced to about 14 cycles/degree by a 20:1 convergence onto rod bipolars. This higher convergence ratio compared to cone-bipolar convergence sacrifices resolution but gains higher sensitivity. Behavioral measurements of visual resolution are consistent with the anatomical data. The cat beta ganglion cells can resolve gratings as high as 9 cycles/degree (Cleland et al., 1979).

Convergence ratios have considerable variability from one region to another region in the retina within individuals and across species. In the rabbit, there is a potential convergence of seven rod bipolars onto one AII amacrine cell at the peak visual streak, 11–16 rod bipolars in the inferior retina, and as many as 40–75 rod bipolars may converge on each AII amacrine cell in the superior retina (Vaney et al., 1991). In the primate fovea, one cone connects to one ganglion cell (Wässle et al., 1990), and the ratio of cones to ganglion cells increases continuously toward the peripheral retina where at 10 mm eccentricity there are 16 cones for each ganglion cell (Wässle and Boycott, 1991).

In the visual pathway beyond the retina such as the projection from the retina to the visual cortex through the LGN or the SC, there are also various convergence solutions. An example of variation in convergence ratios has been reported in the macaque (Schein and de Monasterio, 1987; reviewed in Finlay and Pallas, 1989). In the geniculocortical projections, the convergence ratio between parvocellular cells and layer 4 visual cortical cells remains relatively constant from central to peripheral visual field. However, the convergence ratio of magnocellular cells upon layer 4 cells increases from center to periphery by about a factor of seven.

How are these different convergence ratios set during development and what is the structural basis for variations in the convergence ratio? A large, but fully definable set of developmental mechanisms could be responsible (Fig. 1).

Developmental processes underlying array matching

Fundamental developmental mechanisms that establish convergence ratios are cell generation, cell death, variation in axonal arbor, synaptic density and variation in dendritic arbor. Each of these could serve as an independent or dependent variable: for example, excess neurogenesis might upregulate synaptic density in a target population, or depression of the growth of synaptic arbor might increase afferent cell death. Cellular recognition and response to changing convergence conditions could take many forms, including trophic interactions, competitive interactions between afferent neurons or any number of types of activity-dependent stabilization.

Cell generation

At a population level, numerical matching may be set by neurogenesis alone. This has most often been described in invertebrates, in which individual cells are identifiable and in which cell death may play a limited role (see review by Williams and Herrup, 1988). In vertebrates, even though substantial cell death may reduce both afferent and target populations, in some cases, the initial afferent/target neuron ratios persist unchanged (Sperry, 1990).

Cell death

Overproduction of cells and subsequent cell death is a common feature of developing nervous systems. Cell death does appear to stabilize particular ratios of afferent-to-target neurons in some interconnecting populations. Perhaps the best example of this is the numerical relationship between Purkinje cells and their granule cell inputs. Herrup and Sunter (1987) have studied granule cell death in chimeric mutants of mouse and have shown that numerical imbalance of Purkinje cells and granule cells is corrected linearly by cell death in granule cells. It is unclear whether this is a general rule. Doubling the size of target tissue in a case where half of the afferent cells normally die does not prevent all cell death (reviewed in Oppenheim, 1991); similarly, large removals of target can result in no change in afferent neuron survival, due to axon remodeling (reviewed in Finlay, 1992).

Axonal remodeling and collateral elimination

Often in early vertebrate development, axonal terminal arbors are widespread, and later excess

branches are retracted and axonal arbors are refined. To cite a well-known example, the retinogeniculate axonal arborizations are initially diffuse and then later restrict their territory and segregate into eye-specific laminae (Shatz and Sretavan, 1986). Callosal projections from sensory cortex are very diffuse in neonates and later are pruned to the adult form (Innocenti et al., 1977). This developmental process does not function to regulate the number of afferents and target cells, but rather the types and spatial extent of input a postsynaptic neuron receives.

Dendritic and synaptic remodeling

Dendritic arbor and synaptic density have been shown to be quite malleable in development, principally in cases where changes in total activity or learning have occurred (Greenough and Bailey, 1988). Developmental sculpting of functional systems by hormones often targets the dendritic arbor of target cells as a means of regulating the number of cells and connectivity of a multiple-neuron circuit (Sengelaub, 1986)

Experimental manipulation of afferent / target cell ratios: compression and expansion of the retinotectal projection

'Compression' of projections into experimentally reduced targets has been demonstrated in both regenerating and developing nervous systems. After removal of part of the tectum, the retina is able to compress its projection into a smaller than normal tectal volume while preserving topographic order in the goldfish (Gaze and Sharma, 1970) and frog (Udin, 1977). In the hamster, early partial tectum ablation results in compression of the retinotectal projections (Jhaveri and Schneider, 1974; Finlay et al., 1979a) (Fig. 2). Similarly, a hemi-retina can expand in an orderly way into a complete tectum in goldfish (Schmidt et al., 1978). In the hamster, neonatal enucleation of one eye results in the loss of the normal massive contralateral projection to the superior colliculus, and an expanded ipsilateral projection from the remaining eye (Finlay et al., 1979b) (Fig. 2).

Compression of the retinotectal projection of the hamster can be demonstrated both electrophysiologically and anatomically. Multi-unit recording in the tectal fragment reveals that the visual field is represented in an orderly way in the residual tectum and the size of multi-unit receptive fields is increased (Finlay et al., 1979) (Fig. 3, left). The area of retina projecting to a zone of defined size in the tectum is larger in 'compressed' animals (Pallas and Finlay, 1991) (Fig. 4). In contrast, the size of single unit receptive fields

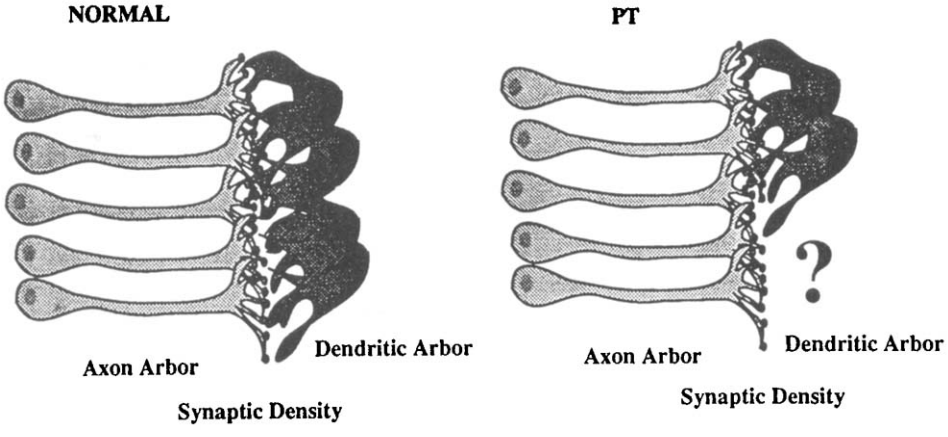

Fig. 1. Schematic of a size disparity experiment.

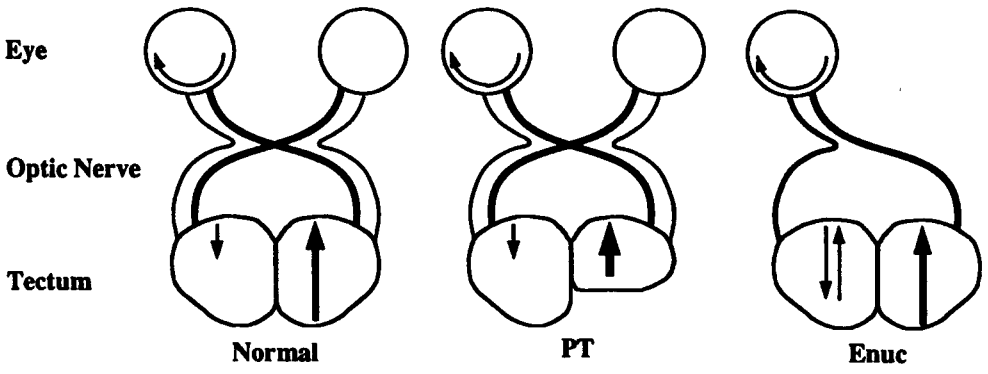

Fig. 2. Schematic of (left) the normal mapping of the two retinas on the normal colliculus of a hamster; (center) a hamster with a partial lesion of the superior colliculus on the day of birth and (right) a hamster with one eye enucleated at birth.

remains constant (Pallas and Finlay, 1989) (Fig. 3, right). Moreover, a number of properties of single neuron responses, such as selectivity for stimulus velocity and preferred stimulus size also remains normal. Therefore, the convergence from retinal ganglion cells to the tectal fragment is increased at the population level, but it remains the same at the single neuron level. This solution to compression of a projection thus retains the spatial resolution of single tectal neurons, but reduces the number of neurons representing any particular location in the visual field. Spatial resolution is

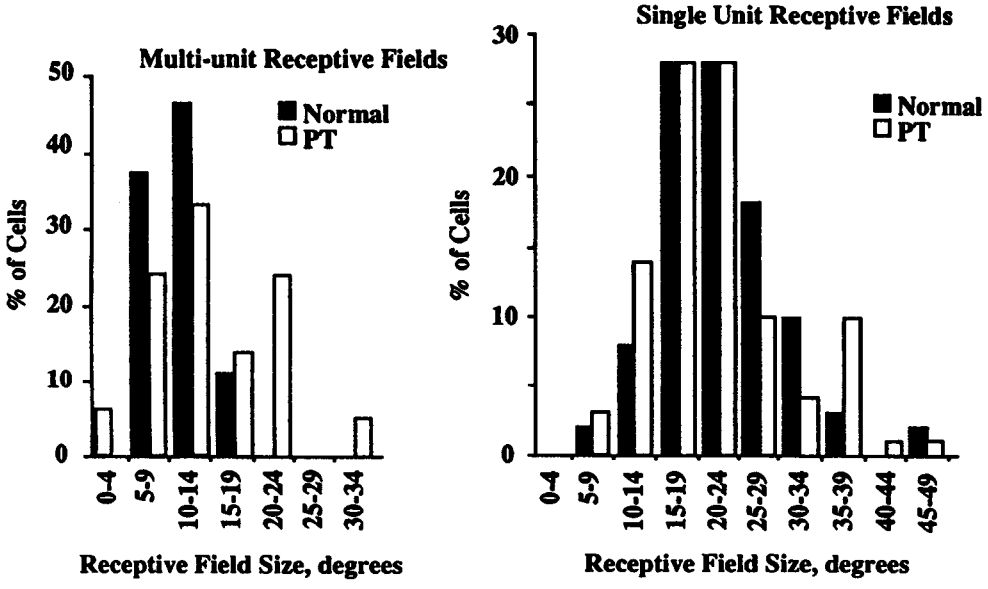

Fig. 3. Comparison of frequency histogram of the receptive field diameters of multi-unit evoked response in normal and partially-ablated superior colliculi (left) and the same for single-unit evoked responses (right).

maintained at the potential cost of spatial localization and sensitivity.

Developmental mechanisms producing this solution

Cell death

After partial unilateral ablations of 20–75% of the caudal tectum in neonatal hamsters resulting in a compression of the entire contralateral visual field on to the remaining tectal fragment, there was only a minor increase in cell death (8%) in the contralateral retina and no change in cell death rates within the tectum (Wikler et al., 1986). This means that a half-sized tectum would potentially face double the amount of retinal inputs (Fig. 4).

The 'population match' hypothesis for cell death (reviewed in Hamburger and Oppenheim, 1982; Oppenheim, 1991), that neuronal death serves to quantitatively match the numbers of the projecting neuronal populations to the numbers of their targets is thus not supported in this case. Violations of this hypothesis, however, are commonplace (reviewed in Finlay, 1992). The residual tectum accommodates an apparently larger than normal ratio of retinal inputs, indicating that mechanisms other than death of excess retinal ganglion cells are involved in the compression of visual field onto the tectum.

Synaptic and dendritic remodeling

One way to keep the convergence at the single neuron level stable would be to increase synaptic density without a reduction in ganglion cell axonal arbors. We tested this hypothesis by electron microscopy to compare the synaptic density between normal and partially ablated tectum. The synaptic density did not increase in the tectal fragment (Xiong and Finlay, 1993). Since the volume of neuropil to neurons is unaltered, we can also infer that the number of synaptic sites per postsynaptic neuron is constant. A similar result is found in the regenerating compressed retinotectal projection of goldfish (Murray et al., 1982; Hayes and Meyer, 1988). Thus, synaptic density is not up-regulated by excess input and is not responsible for the constant spatial convergence at the single neuron level.

Retinal ganglion cell axonal arbor size and complexity

Using in vitro HRP injection to reconstruct retinal ganglion cell axonal arbors in the partial

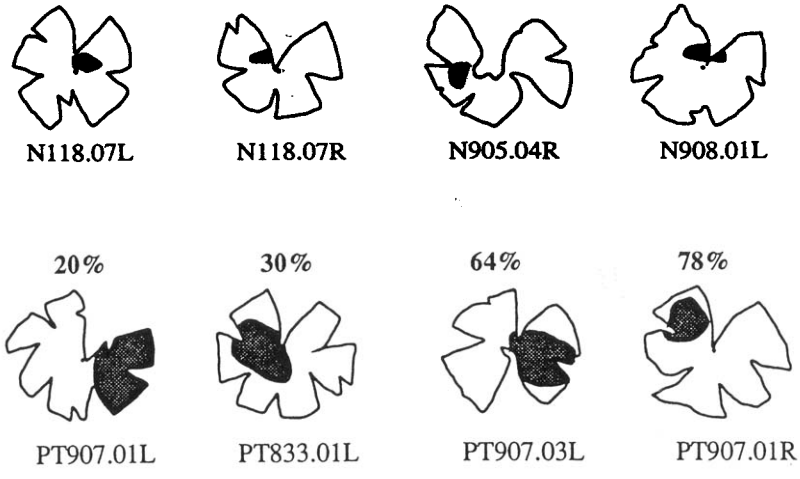

Fig. 4. Examples of the area labeled in the retina by injection of a constant amount of HRP in four normal superior colliculi (upper row) and four partially ablated colliculi (bottom row).

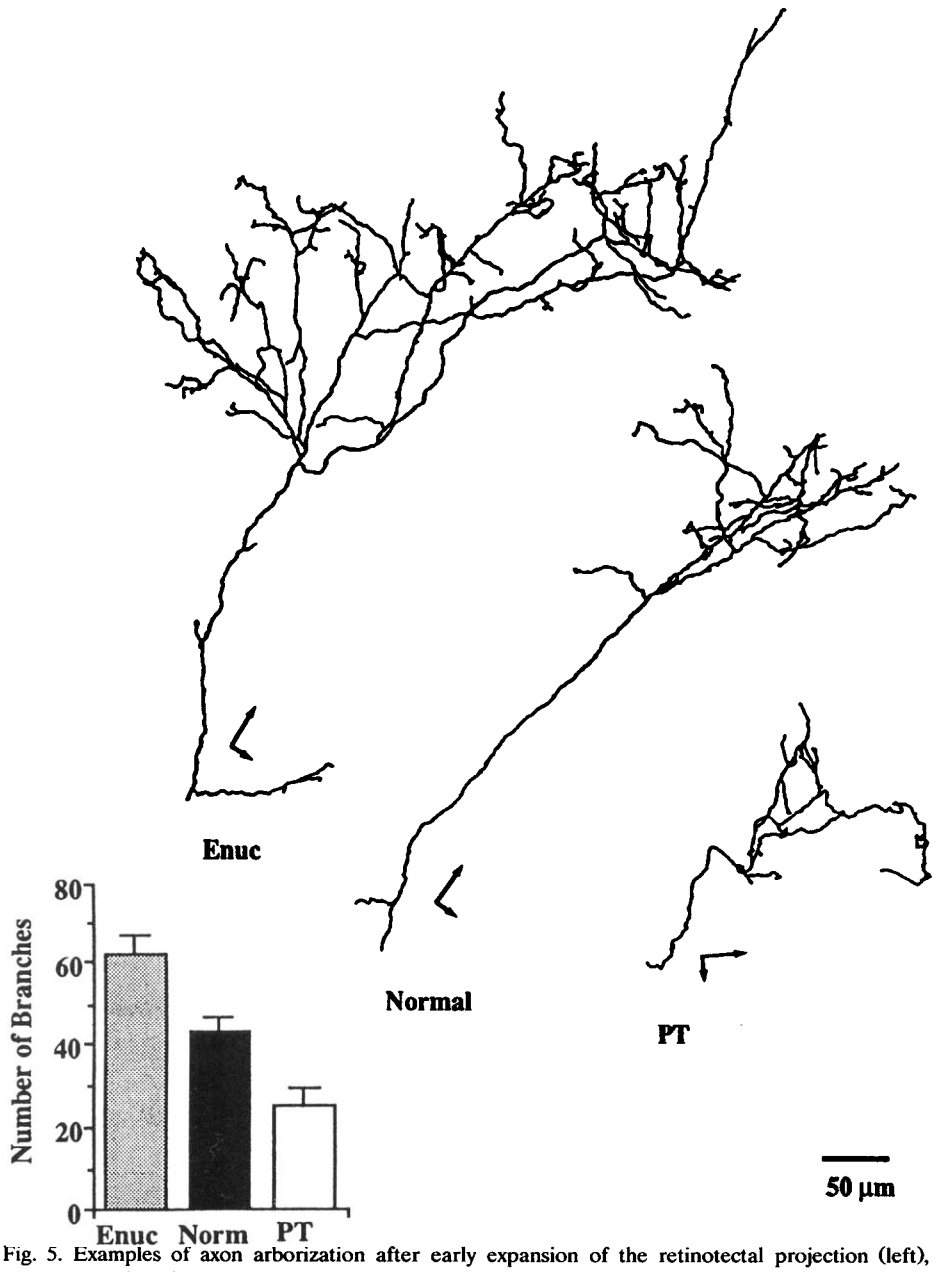

Fig. 5. Examples of axon arborization after early expansion of the retinotectal projection (left), the normal case (middle), or compression (right).

tectum, we saw that the retinal ganglion cell axonal arbor area was markedly reduced from normal (Fig. 5). The basic geometry of the arbor is unchanged: branch density within the area covered by the arbor is normal, but the number of branches and the area over which the arbor spreads are reduced (Xiong et al., 1994) (Fig. 6).

Many studies have shown extensive axonal arbor remodeling during initial growth and regeneration of axons in the central nervous system

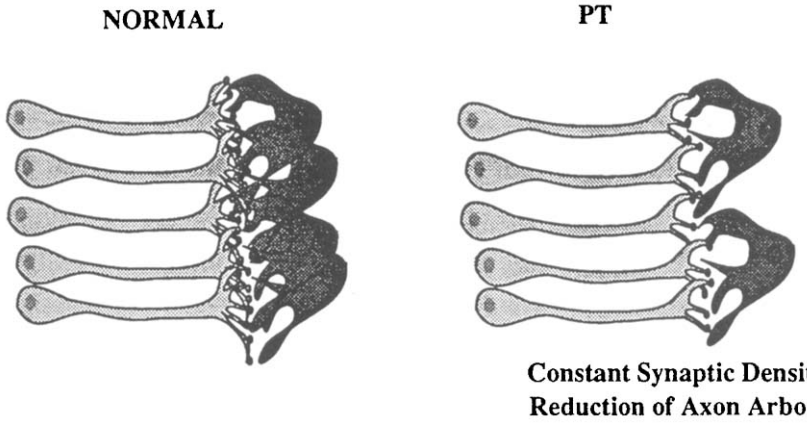

Fig. 6. Schematic drawing of the hamster's solution to a reduction in postsynaptic terminal sites in the retinotectal position.

(Shatz, 1990). The most studied system is the retinotectal projections in fish and frogs, in which the structure of retinal axonal arbors is extremely dynamic (Reh and Constantine-Paton, 1984; O'Rourke et al., 1990, 1994). Remodeling of retinal axon terminal arbors contributes both to the refinement of the topographical map and also helps maintain retinotopography as the entire retinal projection shifts in the tectum to compensate for differences in growth patterns in the retina and tectum (Gaze et al., 1979; Reh and Constantine-Paton, 1984; Easter and Stuermer, 1984; O'Rourke et al., 1990, 1994).

Behavioral consequences of compression of the retinotectal projection

In general, the most dramatic deficits after colliculus ablation are related to attending, localizing, and orienting to sensory stimuli (Stein and Meredith, 1993). Evidence from physiological studies also suggests that neurons in the superior colliculus have sacrificed the capacity for accurate spatial resolution and detailed analysis of objects, but serve optimally for the detection of direction and velocity of a moving stimulus. Common response properties for all visual neurons in the superficial layers of the mammalian superior colliculus have been described (Vanegas, 1984).

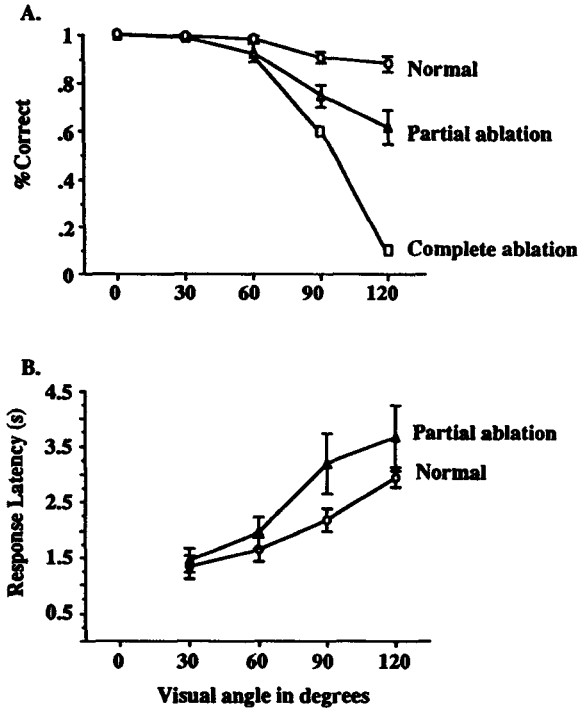

Fig. 7. (A) Comparisons of percentage of correct responses in a sunflower seed orientation task among normal, partial tectum-ablated and complete tectum-ablated hamsters. X-axis: visual angle in degrees. Y-axis: percentage of correct responses. (B) Comparison of response latency of sunflower seed orientation between partial tectum-ablated and normal hamsters. Y-axis, response latency; open circles, normal; open triangles, partial ablations; open square, complete ablation.

Neurons have receptive fields larger than those found in the geniculo-cortical system without separate on and off regions. Most neurons respond to both binocular and monocular stimuli, moving stimuli at relatively low velocities are preferred and some cells exhibit orientation specificity. Neurons in the tectum also respond optimally to stimuli far smaller than their receptive fields.

In the hamster, one behavior dependent on the superior colliculus is orientation to the head and body toward small objects, particularly in the peripheral visual field. In the central visual field, hamsters without a superior colliculus can still notice and approach food items (Schneider, 1969; Mort et al., 1980; Finlay et al., 1980). We used orientation to sunflower seeds to assess orientation behavior of the hamster. The hamster was first trained to face straight ahead on a small platform, and the sunflower seed was presented 2 cm away from several directions, both in the horizontal planes, and 45° above the hamster's head.

All 'compressed' animals perform as well as normal hamsters in their central visual field, the part of the field not dependent on the colliculus, but the response degrades towards the visual periphery (Fig 7a). Their performance level, however, is higher than that in animals with a complete tectal ablation (data replotted from Mort et al., 1980; Figs. 7a,b). In the peripheral visual field, both normal and ablated animals show greater latency to turn their heads in order to pursue sunflower seeds. Colliculus-ablated animals have even greater latency in organizing an orientation response to sunflower seeds than normal animals (Fig. 7b). Therefore, while hamsters with compressed projections show spared orienting behavior throughout their visual field, consistent with the representation of the full visual field in their colliculus, they fail to detect the stimulus a greater proportion of the time and take longer to respond when they do respond.

Activity dependence and convergence ratios

Summarizing these results, when retinal ganglion cells confront a smaller-than-normal tectum in development, preservation of spatial resolution at the level of the single neuron is the result, reducing the number of cells representing any particular receptive field location. This remapping is achieved primarily by reduction of retinal ganglion cell axonal arbors (Fig. 6). Behaviorally, while orientation is preserved over the entire visual periphery, it is slower and less accurate. We hypothesize that the compression of the retinotectal pathway has impaired the recruitment of the motor response of orienting. When a sensorimotor transformation is performed, the collicular output signal which is coded spatially has to be transformed to a drive for motoneurons which are coded temporally. Recruitment of this driving force may be impaired due to fewer cells in the superior colliculus representing each retinal location. Alternatively, spatial sampling may be distorted. Such neuronal scrambling could come from irregularity of distances in the sampling array, size of sampling elements, or spatial dislocation of connections. Hess and Field (1993) have argued that the loss of resolution in the human peripheral visual field comes from uncalibrated disarray rather than from spatial undersampling. Topographical order is somewhat subnormal in the representation of the visual periphery, which could also lead to slow and irregular responses.

Activity-dependent mechanisms, based on the highly correlated patterns of activity in neighboring retinal ganglion cells, are responsible for much of axonal remodeling and refinement of the topographical maps in the developing visual system (Udin, 1988). It seems likely that activity dependent stabilization can account for these results directly. A decreased number of target neurons does not change the pattern of correlation in its input array, and if a single postsynaptic cell is designed to select a certain level of correlation, the size of the input array will be irrelevant to the number of cells detected. A different setting for spatially-based correlation can produce receptive fields of different sizes for different functional classes of cells. The goal of sensory coding is to

represent the external world, not the features of the nervous system sensing it, and a mechanism that maintains spatial selectivity independent of numbers of cells in the nervous system has this useful feature.

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References

Cleland, B.G., Harding, T.H. and Tulunay-Keesey, U. (1979) Visual resolution and receptive field size: examination of two kinds of retinal ganglion cells. *Science*, 205: 1015–1017.

Easter, S.S. and Steurmer, C.A.O. (1984) An evaluation of the hypothesis of shifting terminals in the goldfish optic tectum. *J. Neurosci.*, 4: 1052–1063.

Finlay, B.L. (1992) Cell death and the creation of regional differences in neuronal numbers. *J. Neurobiol.*, 23: 1159–1171.

Finlay, B.L. and Pallas, S.L. (1989) Control of cell number in the developing visual system. *Prog. Neurobiol.*, 32: 207–234.

Finlay, B.L., Schneps, S.E. and Schneider, G.E. (1979) Orderly compression of the retinotectal projection following partial tectal ablation in the newborn hamster. *Nature*, 280: 153–154.

Finlay, B.L., Wilson, K.G. and Schneider, G.E. (1979) Anomalous ipsilateral retinal projections in Syrian hamsters with neonatal lesions: topography and functional capacity. *J. Comp. Neurol.*, 183: 721–740.

Finlay, B.L., Sengelaub, D.R., Berg, A.T. and Cairns, S.J. (1980) A neuroethological approach to hamster vision. *Behav. Brain Res.*, 1: 479–496.

Gaze, R.M. and Sharma, S.C. (1970) Axial differences in the reinnervation of the goldfish tectum by regenerating optic fibers. *Exp. Brain Res.*, 10: 71–180.

Gaze, R.M., Keating, M.J., Ostberg, A. and Chung, S.H. (1979) The relationship between retinal and tectal growth in larval *Xenopus*: implications for the development of the retinotectal projection. *J. Embryol. Exp. Morphol.*, 53: 103–143.

Greenough, W.T. and Bailey, C.H. (1988) The anatomy of a memory: convergence of results across a diversity of tests. *Trends Neurosci.*, 11: 142–147.

Hamburger, V. and Oppenheim, R.W. (1982) Naturally occurring neuronal death in vertebrates. *Neurosci. Comment.*, 1: 39–55.

Hayes, W.P. and Meyer, R.L. (1988) Optic synapse number but not density is constrained during regeneration onto a surgically halved tectum in goldfish: HRP-EM evidence that optic fibers compete for fixed numbers of postsynaptic sites on the tectum. *J. Comp. Neurol.*, 274: 539–559.

Herrup, K. and Sunter, K. (1987) Numerical matching during cerebellar development. *J. Neurosci.*, 7: 829–837.

Hess, R.F. and Field, D.J. (1994) Is the spatial deficit in strabismic amblyopia due to loss of cells or an uncalibrated disarray of cells? *Vision Res.*, 34: 3397–3406.

Innocenti, G.M. Fiore, L. and Caminiti, R. (1977) Exuberant projection into the corpus callosum from the visual cortex of newborn cats. *Neurosci. Lett.*, 4: 237–242.

Jhaveri, S.R. and Schneider, G.E. (1974) Neuroanatomical correlates of spared or altered function after brain lesions in the newborn hamster. In: *Plasticity and Recovery of Function in the Central Nervous System*, Academic Press, New York, pp. 65–109.

Mort, E., Finlay, B.L. and Cairns, S. (1980)The role of the superior colliculus in visually-guided locomotion and visual orienting in the hamster. *Physiol. Psychol.*, 8: 20–28.

Murray, M., Sharma, S. and Edwards, M.A. (1982) Target regulation of synaptic number in the compressed retinotectal projection of goldfish. *J. Comp. Neurol.*, 209: 374–385.

Oppenheim, R.W. (1991) Cell death during development of the nervous system. *Annu. Rev. Neurosci.*, 14: 453–502.

O'Rourke, N.A. and Fraser, S.E. (1990) Dynamic changes in optic fiber terminal arbors lead to retinotopic map formation: an in vivo confocal microscope study. *Neuron*, 51: 159–171.

O'Rourke, N.A., Cline, H.T. and Fraser, S.E. (1994) Rapid remodeling of retinal arbors in the tectum with and without blockade of synaptic transmission. *Neuron*, 12: 921–934.

Pallas, S.L. and Finlay, B.L. (1989) Conservation of receptive field properties of superior colliculus cells after developmental rearrangements of retinal input. *Vis. Neurosci.*, 2: 121–135.

Pallas, S.L. and Finlay, B.L. (1991) Compensation for population size mismatches in the hamster retinotectal system: alterations in the organization of retinal projections. *Vis. Neurosci.*, 6: 271–281.

Reh, T.A. and Constantine-Paton, M. (1984) Retinal ganglion cell terminals change their projection sites during larval development of *Rana pipiens*. *J. Neurosci.*, 4: 422–457.

Rowe, M. H. (1991) Functional organization of the retina. In: B. Dreher and S.R. Robinson (Eds.), *Neuroanatomy of Visual Pathways and Their Development*, Vol. 3, CRC Press, Boca Raton, FL.

Schein, S.J. and de Monasterio, F.M. (1987) Mapping of retinal and geniculate neurons onto striate cortex of macaque. *J. Neurosci.*, 7: 996–1009.

Schmidt, J.T., Cicerone, C.M. and Easter, S.S. (1978) Expansion of the half retinal projection to the tectum in goldfish: an electrophysiological and anatomical study. *J. Comp Neurol.*, 177: 257–278.

Schneider, G.E. (1969) Two visual systems. *Science*, 163: 895–902.

Sengelaub, D.R., Dolan, R.P. and Finlay, B.L. (1986) Cell generation, death and retinal growth in the development of the hamster retinal ganglion cell layer. *J. Comp Neurol.*, 246, 527–543.

Shatz, C.J. and Sretavan, D.W. (1986) Interactions between ganglion cells during the development of the mammalian visual system. *Annu. Rev. Neurosci.*, 9: 171–207.

Shatz, C. (1990) Impulse activity and the patterning of connections during CNS development. *Neuron*, 5: 745–756.

Sperry, D.G. (1990) Variation and symmetry in the lumbar and thoracic dorsal root ganglion cell populations of newly metamorphosed *Xenopus laevis*. *J. Comp. Neurol.*, 292: 54–64.

Stein, B.E. and Meredith, M.A. (1993) *The Merging of the Senses*, MIT Press, Cambridge.

Sterling, P., Freed, M.A. and Smith, R.G. (1988) Architecture of rod and cone circuits to the on-beta ganglion cell. *J. Neurosci.*, 8: 623–642.

Udin, S.B. (1977) Rearrangements of the retinotectal projection in *Rana pipiens* after unilateral caudal half-tectum ablation. *J. Comp. Neurol.*, 173: 561–582.

Udin, S.B. and Fawcett, J.W. (1988) The formation of topographic maps. *Annu. Rev. Neurosci.*, 11, 289–328.

Vanegas, H. (1984) *Comparative Neurology of the Optic Tectum*, Plenum, New York.

Vaney, D.I., Gynther, I.C. and Young, H.M. (1991) Rod-signal interneurons in the rabbit retina 2. AII amacrine cells. *J. Comp. Neurol.*, 310: 154–169.

Wässle, H. and Boycott, B.B. (1991) Functional architecture of the mammalian retina. *Physiol. Rev.*, 71: 447–480.

Wässle H., Grunert, U., Rohrenbeck, J. and Boycott, B.B. (1990) Retinal ganglion cell density and cortical magnification factor in the primate. *Vis. Res.*, 30: 1897–1912.

Wikler, K.C., Kirn, J., Windrem, M.S. and Finlay, B.L. (1986) Control of cell number in the developing visual system: III. Partial tectal ablation. *Dev. Brain Res.*, 28,: 23–32.

Williams, R.W. and Herrup, K. (1988) The control of neuron number. *Annu. Rev. Neurosci.*, 11: 423–454.

Xiong, M.J. and Finlay, B.L. (1993) Changes in synaptic density after developmental compression or expansion of retinal input to the superior colliculus. *J. Comp Neurol.*, 330: 455–463.

Xiong, M.J., Pallas, S.L., Lim, S. and Finlay, B.L. (1994) Regulation of retinal ganglion cell axon arbor size by target availability: mechanisms of compression and expansion of the retinotectal projection. *J. Comp. Neurol.*, 344: 581–597.