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"Experimentally Induced Visual Projections Into Auditory Thalamus and Cortex"

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EXPERIMENTALLY INDUCED VISUAL PROJECTIONS INTO AUDITORY THALAMUS AND CORTEX

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ABSTRACT

Retinal cells have been induced to project into the medial geniculate nucleus, the principal auditory thalamic nucleus, in newborn ferrets by reducing targets of retinal axons in one hemisphere and creating alternative terminal space for these fibers in the auditory thalamus. Many cells in the medial geniculate nucleus are then visually driven, have large receptive fields, and receive input from retinal ganglion cells with small somata and slow conduction velocities. Visual cells with long conduction latencies and large contralateral receptive fields can also be recorded in primary auditory cortex. Some visual cells in auditory cortex are direction selective or have oriented receptive fields that resemble those of complex cells in primary visual cortex. Thus, functional visual projections can be routed into nonvisual structures in higher mammals, suggesting that the modality of a sensory thalamic nucleus or cortical area may be specified by its inputs during development.

What is intrinsically "visual" about visual thalamus and cortex? Can visual projections be induced into nonvisual targets and are these projections functional? The organization of the visual pathway in ferrets is similar to that in cats (1); the visual system of cats has been studied extensively both anatomically and physiologically. However, unlike cats, retinofugal projections in ferrets are very immature at birth (2), and we reasoned that it might be possible to induce extensive plasticity in the retinothalamic pathway by surgery in neonatal ferrets.

Retinal targets were reduced in newborn ferret pups by ablating the superior colliculus and visual cortical areas 17 and 18 of one hemisphere (3) (Fig. 1). Ablating visual cortex causes the lateral geniculate nucleus (LGN) in the ipsilateral hemisphere to atrophy severely by retrograde degeneration. Concurrently, alternative target space for retinal afferents was created in the medial geniculate nucleus (MGN) by ablating either the inferior colliculus or sectioning fibers ascending to the MGN in the brachium of the inferior colliculus (4,5).

Experiments were done on 10 normal adult ferrets and 16 operated ferrets that were reared to adulthood. In five operated animals, intravitreal injections of anterograde tracers (6) revealed retinal projections to normal thalamic targets, including the surviving, shrunken LGN, as well as aberrant projections to auditory thalamic nuclei (Fig. 2). The new retinal projection zones included patches of label in the dorsal, medial, and ventral (or principal) divisions of the MGN, along with the lateral part of the posterior nuclear complex adjacent to the MGN and the lateral posterior nucleus. The retinal projections to the MGN complex occupied up to a third of the volume of the MGN. We confirmed that the MGN in operated animals projected normally to auditory cortex (Fig. 1), both by the transneuronal label in auditory cortex after intraocular injections (6) and by the extensive retrograde labeling of cells in the MGN after restricted injections of horseradish peroxidase (HRP) or fluorescent retrograde tracers into primary auditory cortex (Fig. 2).

These experiments also indicated that the ipsilateral MGN is the major route for visual inputs to reach primary auditory cortex. Along with receiving major thalamic projections from the various divisions of the MGN (7), the primary auditory cortex in operated animals retained its connections with other auditory cortical areas. These included ipsilateral and contralateral connections with the second auditory area located lateral to primary auditory cortex, and with areas on the ectosylvian gyrus located anterior, posterior, and ventral posterior to primary auditory cortex (8).

We next recorded electrophysiologically from the MGN in operated animals (9) and compared visual responses there with responses from the surviving LGN in the same animals as well as from the LGN in normal animals. We studied the visual responses of single cells to a battery of tests (10). We also tested the auditory responses of cells in the auditory thalamus with click or tone stimuli delivered through earphones.

In the LGN of normal animals, we recorded X, Y and W cells (Fig. 3A); X and Y cells were found in the A laminae, and Y and W cells were found in the C laminae (11). In the LGN of operated animals, we recorded almost exclusively Y cells in the A laminae (Fig. 3B). We ascribe the loss of X cells in the LGN to the retrograde degeneration of geniculate X cells after ablation of visual cortex. A similar result has been shown in cats (12); in cats, neonatal visual cortical ablation also leads to transneuronal retrograde loss of X cells in the retina (13), and we have confirmed a reduction in medium-sized retinal ganglion cells in our operated ferrets (14).

In the MGN of operated animals, we recorded cells with long latencies to optic chiasm stimulation (Fig. 3C). The conduction latencies of cells in the MGN of operated animals (range of latencies 2.8 to 11.0 ms, mean latency 4.8 ms, for 94 cells in 5 animals) were significantly longer than the latencies of X and Y cells in the LGN of normal animals (range of latencies 1.5 to 3.0 ms, mean latency 2.0

ms, for 101 cells in 5 animals; P<0.005, Mann-Whitney U-test, for a comparison of mean latencies in individual normal and operated animals). The visual responses of cells in the MGN were often variable or "sluggish" (15); cells responded best to large, flashing or moving spots of light. Receptive fields were large, with diameters that were two to five times the diameters of normal LGN X cell receptive fields and up to twice the diameter of LGN Y cell receptive fields at similar eccentricities. Neurons dorsal in the MGN represented the upper visual field, neurons located ventrally represented lower visual field, neurons located medially represented central visual field and those located laterally represented peripheral field. Receptive fields were on, off, or on-off center and circular. Visually driven cells were not orientation selective though 2 of 32 visual units were direction selective (16). We filled retrogradely with HRP retinal ganglion cells that projected to the LGN or superior colliculus in normal animals and to the LGN or MGN in operated animals (17). In normal adult ferrets, retinal ganglion cells include large-sized α (Y-like) cells that project to the LGN and superior colliculus, medium-sized β (X-like) cells that project mainly to the LGN, and a heterogeneous population of small and medium-sized (W-like) cells that project to the LGN and to the superior colliculus (18). In operated ferrets, the projection to the MGN arose mainly from the small retinal ganglion cells with heterogeneous morphologies (Fig. 3D). Our physiological and anatomical results thus suggest that the retinal ganglion cells that project to the MGN in operated animals belong to the W class. However, we cannot rule out the possibility that at least some cells that give rise to the aberrant projection are X or Y cells that fail to develop normally.

We also recorded from single units in primary auditory cortex of operated animals to determine their visual response features. Visual responses were strongest in the middle layers, at depths of 600 to 900 μm. In primary auditory cortex, as in the MGN, cells had long latencies to optic chiasm stimulation; the

latencies ranged from 5.5 to 17.0 ms, with a mean latency of 9.0 ms (57 cells recorded in 6 operated animals). For comparison, latencies to optic chiasm stimulation in primary visual cortex of normal animals, which is dominated by the moderate- and fast-conducting X and Y pathways through the LGN (1), ranged from 2.0 to 6.5 ms, with a mean latency of 4.2 ms (63 cells recorded in 4 normal animals). The latencies in normal animals were significantly shorter than those in operated animals (P<0.005, Mann-Whitney U-test, for a comparison of mean latencies in individual animals). Cells in primary auditory cortex that were driven by visual stimulation formed a subset of the cells that were driven by electrical stimulation of the optic chiasm (Table 1). Visual cells in auditory cortex had large receptive fields and preferred slowly flashing or moving large spots or bars. As in the MGN, receptive fields were confined to the contralateral hemifield (19). About 25% of the cells that we could drive visually (10 of 38 units) showed direction selectivity. About 20% of cells showed orientation selectivity (Table 1) (Fig. 4) (20). All the oriented cells had coextensive on and off zones and responded to light onset and offset or to light and dark edges, and we classified them as complex (21).

We could drive few neurons in the MGN or primary auditory cortex of the operated hemisphere with acoustic stimuli. This was not an unexpected result since we had deafferented the MGN, but it confirmed that severed axons did not regenerate from the inferior colliculus to the MGN, at least in large numbers. We could reliably elicit auditory responses from the MGN and primary auditory cortex in the unoperated hemisphere. We could not elicit responses to either electrical stimulation of the optic tract or visual field stimulation from cells in primary auditory cortex in normal animals (n=48 single and multiple units) (22).

These results demonstrate that retinal projections can be induced to grow into nonvisual thalamus in ferrets, and that these projections can impart visual function (that is, visual driving and discernible receptive field properties) to

cells in nonvisual thalamus and cortex. We suggest that, at least early in development, the modality of sensory thalamus or cortex can be specified by its inputs. Unlike rodents which have transient retinal projections to nonvisual thalamus that can be made permanent (23), the retina does not project to auditory thalamus in newborn ferrets (24). The novel retinal projections to the auditory thalamus thus represent sprouting from retinofugal fibers. If temporal factors play a role in the plasticity we describe, those retinal ganglion cells that have yet to establish stable thalamic or midbrain connections at the time of our lesions - including the smaller retinal ganglion cells that are generated last in the retina (25) - would be the most likely to innervate novel targets. Thus, surgery performed even earlier in development might induce more ganglion cells and perhaps other ganglion cell classes to reroute their axons as well. Alternatively, only certain retinal axons, intrinsically different from others, may be able to recognize cues in the denervated MGN and sprout into the nucleus.

Apart from the retinal cell classes that are involved in novel projections to the auditory system, our experiments provide a direct comparison of visual responses of neurons in the normal visual pathway vs. those induced into a pathway through nonvisual thalamus to cortex. Ideally, an evaluation of visual response features in primary auditory cortex and in normal striate cortex, for example, should involve cells that receive input from the same class of retinal ganglion cell in both structures (26). Still, our experiments suggest that some of the transformations on visual input performed in visual structures such as primary visual cortex in normal animals are possible as well in the primary auditory cortex in operated animals. One possibility consistent with our results is that visual inputs induce the development of specific intrinsic connections in primary auditory cortex. An alternative possibility is that intrinsic processing in primary auditory cortex is similar in certain respects to that in primary visual cortex. This might allow auditory cortex to process visual information; indeed, a parsimonious

explanation of our results is that primary areas of sensory neocortex perform certain similar, stereotypical, operations on input regardless of modality (27).

Table 1. Visual cells recorded in primary auditory cortex of operated animals. Cells in primary auditory cortex were considered to receive retinal input if they were driven by electrical stimulation through electrodes implanted at the optic chiasm. They were then characterized by their responsiveness to visual stimuli. See text for details.

Cell characteristic	No. of cells
Driven electrically from optic chiasm	57
Driven visually	38
Oriented receptive fields	6
Non-oriented receptive fields	23
Full field flashes	9

References and Notes

1. Major features of organization of the retinogeniculate and geniculocortical pathways in mustelids (ferrets, mink), which are carnivores like cats, have been described [R.W. Guillery and M.D. Oberdorfer, J. Comp. Neurol. 176, 515 (1977); M.P. Stryker and K.R. Zahs, J. Neurosci. 3, 1943 (1983); S.K. McConnell and S.LeVay, J. Comp. Neurol. 250, 109 (1986); S. LeVay, S.K. McConnell, M.B. Luskin, J. Comp. Neurol. 257, 422 (1987)]. For a review of the visual pathway in cats, see S.M. Sherman and P.D. Spear, Physiol. Rev. 62, 738 (1982).

2. Ferrets are born after 41 days of gestation compared to 64 days for cats. At birth, the development of the retinogeniculate pathway in ferrets [D.C. Linden, R.W. Guillery, J.Cucchiaro, J. Comp. Neurol. 203, 189 (1981)] resembles that in cats at about embryonic day 41 [C.J. Shatz, J. Neurosci. 3, 482 (1983); D.W. Sretavan and C.J. Shatz, J. Neurosci. 6, 234 (1986)], and subsequent retinofugal development in ferrets matches that in cats almost on a day-by-day basis.

3. Our basic surgical procedure is modified from that described for hamsters by G.E. Schneider [Brain Behav. Evol. 8, 73 (1973)]; see also D.O. Frost, J. Comp. Neurol. 203, 227 (1981).

4. On the day of birth, ferret pups were anesthetized by hypothermia. An incision was made to expose the skull, and a flap of bone was removed over visual cortex and superior colliculus of one hemisphere. Visual cortex corresponding to areas 17 and 18 and superior colliculus were then ablated unilaterally by cautery. Ascending auditory fibers in the brachium of the inferior colliculus were sectioned at the level of the mid-superior colliculus by inserting a blade coronally in the lateral portion of the midbrain. The scalp incision was sutured, pups were revived, and returned to

the litter for rearing to adulthood.

5. In control experiments, we have examined the necessary and sufficient conditions for inducing retinal projections to auditory thalamus. Retinal fibers do not enter the MGN unless it is deafferented. Ablating the superior colliculus alone, along with deafferenting the MGN, causes a weak projection to the MGN. The projections are much heavier if visual cortex is ablated as well. We have been unable to induce retinal projections into nonvisual thalamic structures in cats by neonatal surgery, perhaps because by birth, in cats, retinal axons have already grown into their target visual structures.

6. Adult ferrets were anesthetized with 2 to 3% halothane or with a mixture of ketamine (30 mg/kg) and xylazine (2 mg/kg). Intraocular injections were made with 15 to 25 ul of either wheat-germ agglutinin conjugated to HRP (2%) or ^{35}S-Methionine (500 uCi) dissolved in saline. Survival times ranged from one to several days. Animals were then deeply anesthetized and perfused intracardially with saline followed by a mixture of 1% paraformaldehyde and 2% gluteraldehyde. Frozen sections (50 μm) were cut in the parasagittal or coronal plane, and processed for visualization of HRP [M.-M. Mesulam, J. Histochem. Cytochem. 26, 106 (1978); J.C. Adams, Neurosci. 2, 141 (1977)] or for autoradiography.

7. R.A. Andersen, P.L. Knight, M.M. Merzenich, J. Comp. Neurol. 194, 663 (1980); J.C. Middlebrooks and J.M. Zook, J. Neurosci. 3, 203 (1983).

8. S.L. Pallas, A.W. Roe, M. Sur, Neurosci. Abstr. 14, 460 (1988).

9. Physiological experiments were done on 12 operated ferrets and 8 normal ferrets. Animals were anesthetized, paralyzed, and artificially respired. The eyes were refracted and focused on a tangent screen 114 cm in front of the animal. Stimulating electrodes were placed across the optic chiasm. Cells in the LGN and MGN, or in visual and auditory cortex, of normal and

operated animals were recorded using glass micropipettes or parylene insulated tungsten microelectrodes. Electrolytic lesions were made during recording with metal electrodes, and these lesions as well as electrode tracks were reconstructed and compared with architectonic regions to locate recording sites within the LGN and MGN, or within primary visual and primary auditory cortex, of normal and operated animals.

10. Parameters we studied included receptive field size, latency to optic chiasm stimulation, linearity of spatial summation within the receptive field, time course of response to a stationary stimulus and response to a fast moving disk of contrast appropriate for the surround. See C. Enroth-Cugell and J.G. Robson, J. Physiol. (London) 187, 516 (1966); S. Hochstein and R.M. Shapley, J. Physiol. (London) 262, 237-264 (1976); and M. Sur and S.M. Sherman, J. Neurophysiol. 47, 869 (1982) for application of these tests to classification of W, X, and Y cells in cat LGN. We also studied the responses of cells to stationary flashed bars at different orientations and spots moving in different directions at different velocities. For 19 visually responsive MGN cells, peri-stimulus time histograms were generated in response to a drifting or counterphasing sine-wave grating, or a bar moving at different orientations and velocities.

11. M. Esguerra, P.E. Garraghty, G.S. Russo, M. Sur, Neurosci. Abstr. 12, 10 (1986).

12. M.A. McCall, N. Tumosa, W. Guido, P.D. Spear, Neurosci. Abstr. 12,591 (1986).

13. L. Tong, P.D. Spear, R.E. Kalil, E.C. Callahan, Science 217, 72 (1982).

14. M. Sur, A.W. Roe, P.E. Garraghty, Neurosci. Abstr. 13, 590 (1987).

15. B.G. Cleland and W.R. Levick, J. Physiol. (London) 240, 421 (1974).

16. None of 12 X and 16 Y cells in the LGN of normal animals, and 19 Y cells studied in the LGN of operated animals showed orientation or direction selectivity.

17. HRP (30% in saline) was iontophoresed into physiologically identified sites in the LGN, superior colliculus or MGN. After 24 to 48 hours of survival, animals were perfused with 1% paraformaldehyde and 2% gluteraldehyde. The retinas were dissected, reacted with O-dianisidine [J.S. De Olmos, Exp. Brain Res. 29, 541 (1977)], and flat mounted on slides. Retrogradely filled retinal ganglion cells were examined under a 50X objective and their soma areas measured.

18. D.J. Vitek, J.D. Schall, A.G. Leventhal, J. Comp. Neurol. 241, 1 (1985); A.W. Roe, P.E. Garraghty, M. Sur, Neurosci. Abstr. 13, 1023 (1987). See also, for central projections of cat retinal ganglion cells, A.G. Leventhal, R.W. Rodieck, B. Dreher, J. Comp. Neurol. 237, 216 (1985); L.R. Stanford, J. Neurophysiol. 57, 218 (1987).

19. This is consistent with the fact that there are no visual inputs into primary auditory cortex through the corpus callosum from visual areas in the contralateral hemisphere.

20. For each neuron showing orientation or direction selectivity, we defined the width of orientation or direction tuning as the range of orientations or movement directions to which the cell responded. Six visual units in primary auditory cortex that were orientation selective (Table 1) had orientation tuning widths of 60° to 120° (mean, 94°), and 10 units that were direction selective had direction tuning widths of 60° to 180° (mean, 125°). In comparison, cells in striate cortex of 3 normal animals had orientation tuning widths of 30° to 90° (mean, 59°; n=27) and direction tuning widths of 30° to 120° (mean, 85°; n=19). No orientation selective neuron in primary auditory cortex showed end-inhibition while 7 of 27 units in normal striate cortex were end-inhibited (see also Fig. 4).

21. D.H. Hubel and T.N. Wiesel, J. Physiol. (London) 160, 106 (1962); C.D. Gilbert, ibid 268, 391 (1977).

22. This confirms experiments on localization in the cat cortex, including early experiments in which visual and auditory evoked potentials were recorded from the cortical surface [W.H. Marshall, S.A. Talbot, H.W. Ades, J. Neurophysiol. 6, 1 (1943); R.F. Thompson, R.H. Johnson, J.J. Hoopes, ibid 26, 343 (1963)], that have distinguished primary auditory cortex as a region where only auditory and no visual responses can be recorded.

23. D.O. Frost, J. Comp. Neurol. 252, 95 (1986); D.O. Frost and C. Metin, Nature 317, 162 (1985).

24. D.C. Linden, R.W. Guillery, J. Cucchiaro (ref. 2); J. Hahm and M. Sur, Neurosci. Abstr. 14, 460 (1988).

25. C. Walsh, E.H. Polley, T.L. Hickey, R.W. Guillery, Nature 302, 611 (1983); C. Walsh and R.W. Guillery, J. Neurosci. 5, 3061 (1985).

26. While the visual projections through the MGN to primary auditory cortex in operated animals appear to arise chiefly from retinal W cells, visual inputs to striate cortex in normal animals arise from retinal X and Y as well as W cells. Although the literature on response properties of cells in normal visual cortex is extensive, little of it derives from cells with pure W cell input [see, however, B. Dreher, A.G. Leventhal, P.T. Hale, J. Neurophysiol. 44, 804 (1980)].

27. Several lines of evidence support such a conclusion. (i) Intrinsic interlaminar connections described for cat striate cortex [C.D. Gilbert and T.N. Wiesel, Nature 280, 120 (1979); D. Ferster and S. Lindstrom, J. Physiol. (London) 342, 181 (1983)] share fundamental similarities with those described for cat primary auditory cortex [A. Mitani, M. Shimokouchi, K. Itoh, S. Nomura, M. Kudo, N. Mizuno, J. Comp. Neurol. 235, 430 (1985)]. (ii) Direction selective neurons (responding to the direction and rate of sound frequency modulation) have been noted in primary auditory cortex [I.C. Whitfield and E.F. Evans, J.Neurophysiol. 28, 655 (1965); J.R. Mendelson and M.S. Cynader, Brain Res. 327, 331 (1985)]. In the somatosensory cortex, direction and orientation selective neurons analogous to those in striate cortex have been described [J. Hyvarinen and A. Poranen, J. Physiol. (London) 283, 523 (1978); S. Warren, A. Hamalainen, E.P. Gardner, J. Neurophysiol. 56, 598 (1986)]. For a more general discussion of common aspects of processing in sensory cortex, see V.B. Mountcastle in The Mindful Brain (MIT Press, Cambridge, 1978). (iii) In our experiments, lesions are used to route retinal projections into the auditory thalamus, and the extrinsic and intrinsic connections of auditory cortex are not altered, at least directly (see text). Other experiments provide evidence for target-controlled differentiation of synaptic structure during development [G. Campbell and D.O. Frost, Proc. Natl. Acad. Sci. U.S.A. 84, 6929 (1987); P. Rakic, Science 241, 170 (1988)], suggesting that the neuropil of primary auditory cortex in operated animals would resemble that in normal animals. Thus the fact that auditory cortex in operated animals can process visual information in a fashion similar to normal visual cortex implies that at least some aspects of intrinsic processing are quite similar in visual and auditory cortex.

28. L.M. Aitkin, D.R.F. Irvine, W.R. Webster, in Handbook of Physiology: The Nervous System III (Amer. Physiol. Soc., Bethesda, 1984)].

29. M.I. Law and M.P. Stryker, Invest. Opthal. Vis. Sci. Supp. 24, 227 (1985).

30. We thank A. Graybiel, P. Schiller and G. Schneider for their comments on the manuscript, D. Frost and P. Rakic for invaluable help and advice, and M. MacAvoy and T. Sullivan for excellent technical assistance. Supported by NIH grants EY 07023 and EY 07719, March of Dimes grant 1-1083, and the McKnight Foundation.

Figure Legends

Fig. 1. The experimental design for induction of visual projections to the auditory system in ferrets. (Top) Projections in normal animals. The retina projects to the lateral geniculate nucleus (LGN) and superior colliculus (SC). The LGN projects to cortical areas 17 (primary visual cortex or striate cortex) and 18 as well as to other extrastriate areas including area 19 and the lateral suprasylvian (LS) cortex. In the auditory system, the inferior colliculus (IC) projects to the medial geniculate nucleus (MGN). The ventral and the dorsal divisions of the MGN project heavily to primary auditory cortex (AI), as well as to other cortical areas including the anterior auditory field (AAF) and the posterior auditory field (PAF) in cortex (28). (Bottom) If cortical areas 17 and 18 are ablated in neonatal ferrets, the LGN atrophies severely by retrograde degeneration. Ablating the superior colliculus as well, and deafferenting the MGN by ablating the inferior colliculus or sectioning fibers ascending from it, causes the retina to project to the MGN and hence to auditory cortex.

Fig. 2. Experimentally induced retinal projections to the auditory thalamus, and the connections of auditory thalamus with auditory cortex. The eye contralateral to the operated hemisphere projects to the surviving dorsal LGN (LGd) and ventral LGN (LGv) as well as to patches within the dorsal and ventral divisions of the MGN (MGd and MGv, respectively). The figure shows numbered parasagittal sections of the thalamus. In the same animal, an injection of HRP in primary auditory cortex (A1) (the injection site is shown at top left) fills cells retrogradely in MGv, MGd, and the lateral division of the posterior complex (POl). Many cells in MGd and MGv overlie the retinal projection zone.

Fig. 3. Electrophysiological results from the thalamus of operated and normal

animals, and anatomical labeling of retinal ganglion cells that provide input to the thalamus in these animals. A. The distribution of the latencies of firing, after electrical stimulation of the optic chiasm, of X, Y and W cells in the LGN of normal animals. The histogram includes 107 cells pooled from 5 animals. X and Y cells are found in the A laminae while the C laminae contain Y and W cells (11). B. The LGN of operated animals contains Y cells (found in the A and C laminae), along with W cells (found in the C laminae), but very few X cells. Data from 81 cells pooled from 5 animals. C. Cells in the MGN of operated animals (94 cells in 5 animals) have long latencies to optic chiasm stimulation compared to cells in the LGN of normal animals (same data as in A). D. Histogram of soma sizes of retinal ganglion cells filled retrogradely from a HRP injection in the thalamus of a normal animal and an operated animal. The injection in the normal animal was centered on the LGN and the injection in the operated animal was centered on the MGN. Each bar in the histogram represents the ganglion cells in a given size range as a percentage of the total population of backfilled cells. Retinal input to the thalamus in normal ferrets (18) arises from α or Y-like cells [these are, in general, large (L) cells with soma sizes of 400 μm2 and larger), β or X-like cells [generally medium (M) sized cells with soma sizes between 300 and 400 μm2), and a heterogeneous population of W-like cells [generally small (S) cells with soma sizes smaller than 300 μm2, though this class can include medium sized cells as well]. In operated ferrets, the cells that project to the MGN lie mainly in the small size range.

Fig. 4. Receptive fields of visual cells in primary auditory cortex of an operated animal with visual projections induced into the auditory system, and comparison with receptive fields in primary visual cortex of a normal animal. Cells were classified as nonoriented or oriented simple or complex according to the criteria of Hubel and Wiesel (21): simple cells have oriented fields with

separate on (+) and off (-) zones, whereas complex cells have oriented fields usually with coextensive on and off zones.

(Left): Cells recorded in area 17 of a normal animal. Receptive field locations shifted progressively higher in the visual field as recording locations moved from medial to lateral in area 17, consistent with the map of visual space in area 17 in ferrets (29). The cross denotes the location of the area centralis. Small arrows within the receptive field denote the direction of stimulus movement yielding maximal response. Oriented line within each receptive field extending beyond receptive field edges denotes lack of end-stopping; lines that terminate at receptive field edges indicate end-stopped fields. (Right): In primary auditory cortex of an operated ferret, visual cells had either nonoriented (circular) or oriented (rectangular) receptive fields. The oriented fields were complex-like. Receptive fields moved from dorsal to ventral in the visual field as recording locations moved from posteromedial to anterolateral in auditory cortex. (Inset) (bottom left): Peri-stimulus time histogram of a visual cell in primary auditory cortex responding to a bar sweeping across the receptive field at the orientation indicated above the histogram, and for the directions of movement shown by arrows. Bar width 1°, bar length 20°, velocity 5°/s, 50 stimulus sweeps.

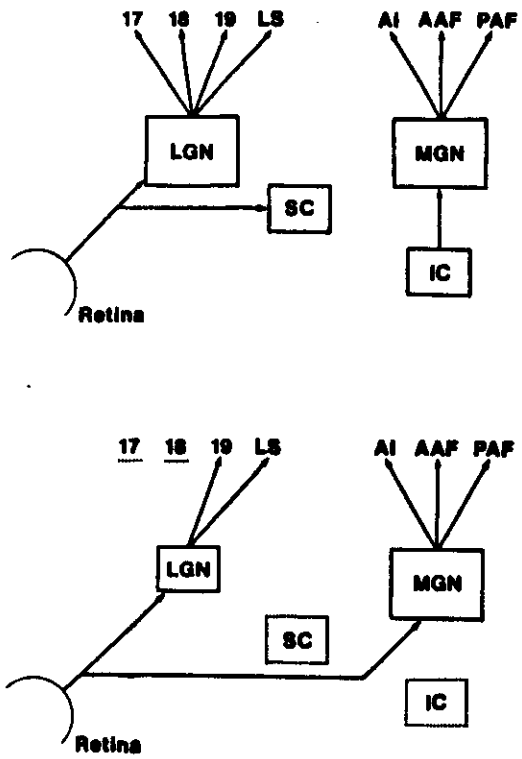
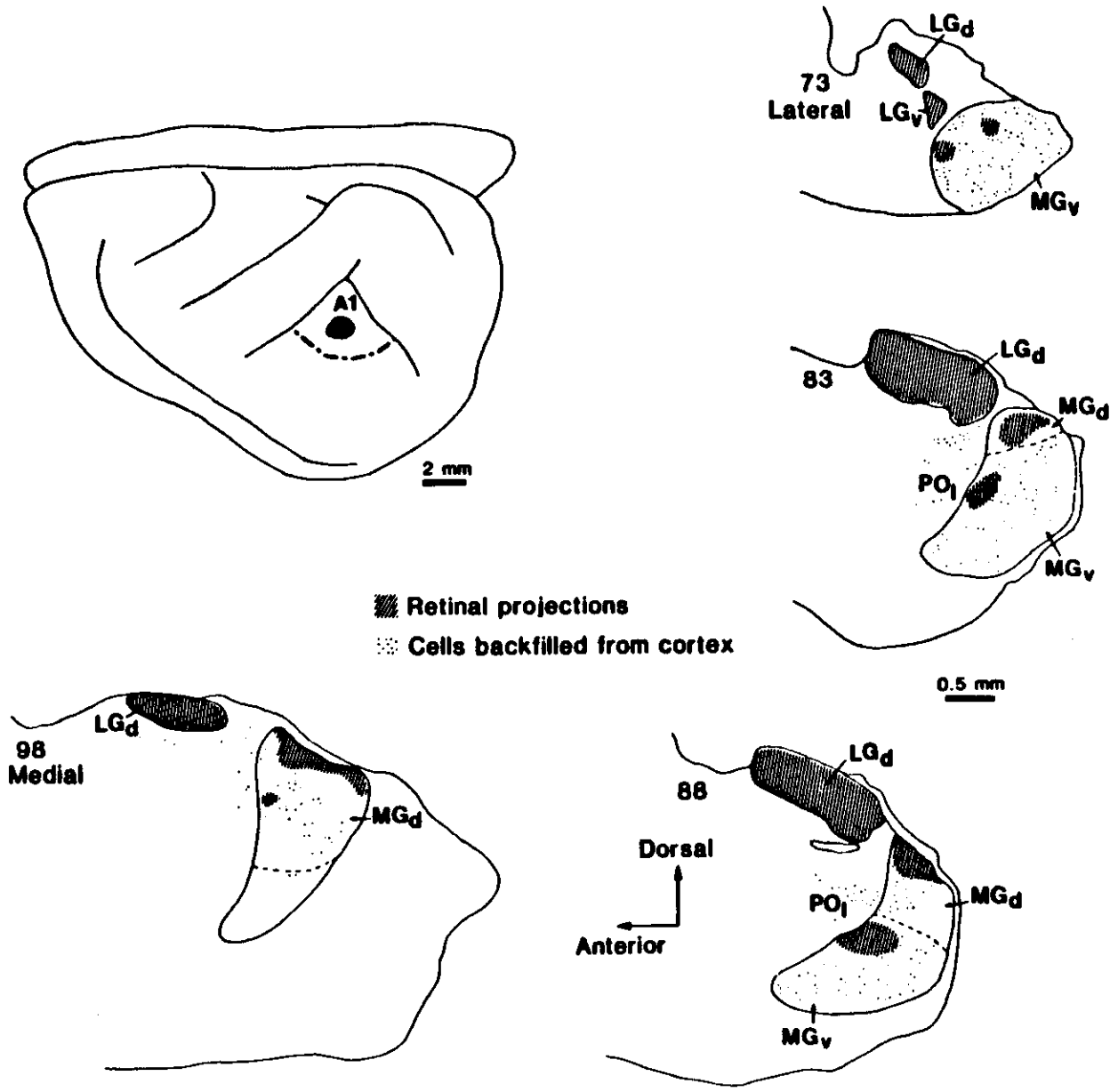


Figure 2


A1
2 mm
73
Lateral
LGd
LGv
MGv
83
LGd
MGd
POl
MGv
Retinal projections
Cells backfilled from cortex
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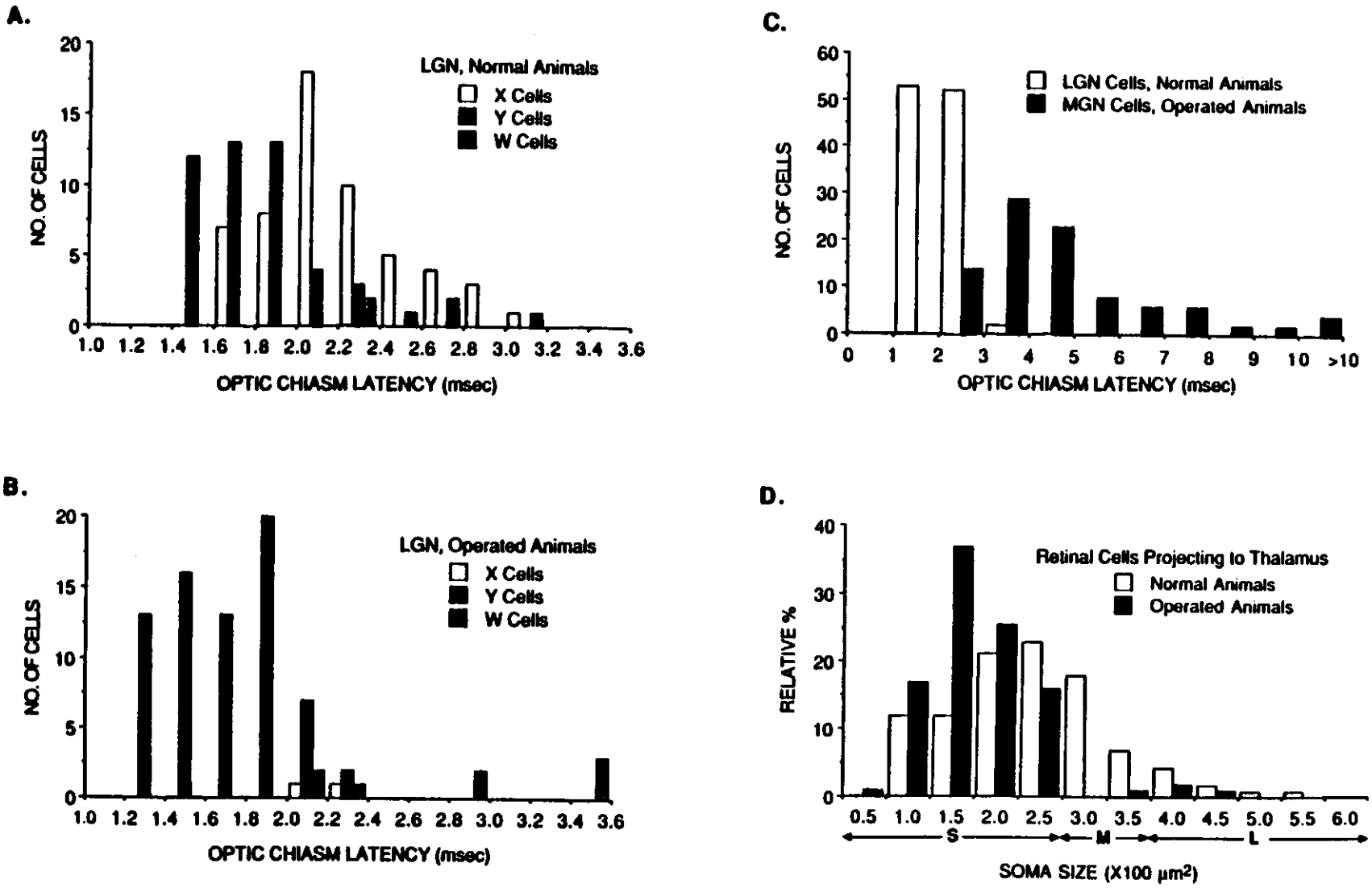
98
Medial
LGd
MGd
88
Dorsal
Anterior
LGd
POl
MGd
MGv

Figure 3


A.
LGN, Normal Animals
X Cells
Y Cells
W Cells
NO. OF CELLS
OPTIC CHIASM LATENCY (msec)
B.
LGN, Operated Animals
X Cells
Y Cells
W Cells
NO. OF CELLS
OPTIC CHIASM LATENCY (msec)
C.
LGN Cells, Normal Animals
MGN Cells, Operated Animals
NO. OF CELLS
OPTIC CHIASM LATENCY (msec)
D.
Retinal Cells Projecting to Thalamus
Normal Animals
Operated Animals
RELATIVE %
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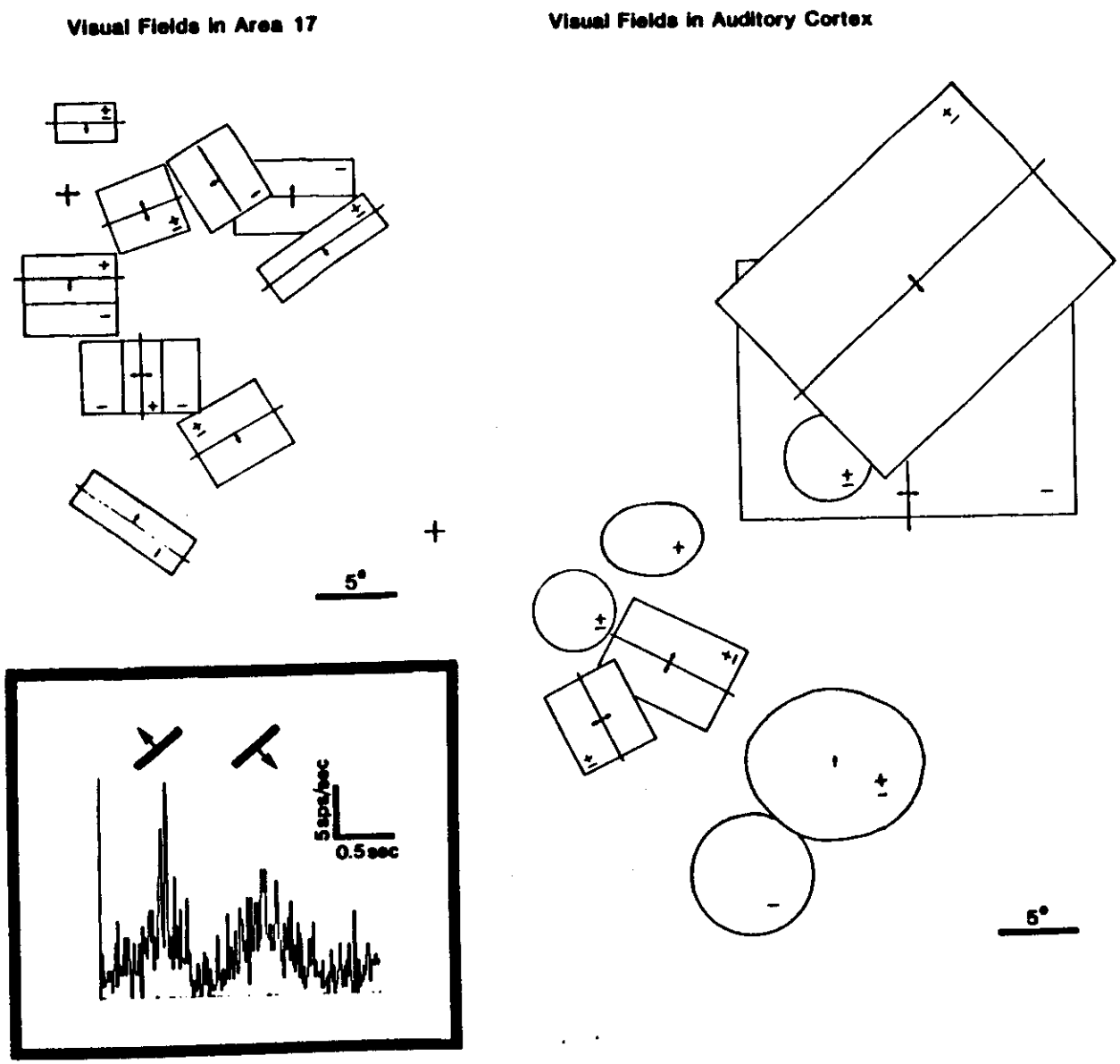
SOMA SIZE (X100 μm²)

Figure 4


Visual Fields in Area 17
5°
5 sps/sec
0.5 sec
Visual Fields in Auditory Cortex
5°