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Visual responses of neurons in somatosensory cortex of hamsters with experimentally induced retinal projections to somatosensory thalamus

(receptive field/plasticity/development/sensory)

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ABSTRACT **These experiments investigate the capacity of thalamic and cortical structures in a sensory system to process information of a modality normally associated with another system. Retinal ganglion cells in newborn Syrian hamsters were made to project permanently to the main thalamic somatosensory (ventrobasal) nucleus. When the animals were adults, single unit recordings were made in the somatosensory cortices, the principal targets of the ventrobasal nucleus. The somatosensory neurons responded to visual stimulation of distinct receptive fields, and their response properties resembled, in several characteristic features, those of normal visual cortical neurons. In the visual cortex of normal animals and the somatosensory cortex of operated animals, the same functional categories of neurons occurred in similar proportions, and the neurons' selectivity for the orientation or direction of movement of visual stimuli was comparable. These results suggest that thalamic nuclei or cortical areas at corresponding levels in the visual and somatosensory pathways perform similar transformations on their inputs.**

In thalamic nuclei and cortical areas of the visual and somatosensory systems, information about peripheral stimuli is abstracted by single neurons that respond preferentially to particular values of one or more stimulus parameters. To what extent is information processing in the two systems similar and how do these systems differentiate during ontogeny? To study these questions, we exploited the fact that in newborn hamsters, retinal ganglion cell (RGC) axons can be surgically induced to form permanent, retinotopic projections to the primary somatosensory (ventrobasal, VB) thalamic nucleus (1–5). We made neurophysiological recordings from single neurons in the principal targets of VB, the first and second somatosensory cortices (SI and SII, respectively), of neonatally operated, adult hamsters. We quantitatively compared the visually evoked responses of these neurons with those of single neurons in the primary visual cortex (VI, area 17) of normal, adult hamsters. We found that in operated hamsters, SI/SII neurons normally associated with somatic sensation have visual response properties that resemble those of neurons in VI of normal animals.

METHODS

Permanent retinal projections to VB were induced in anesthetized, newborn Syrian hamsters, as described (1–5). Two of the principal targets of RGC axons, the superior colliculus (SC) and dorsal lateral geniculate nucleus (LGd), were ablated. Heat lesions of SC were made bilaterally; unilateral, retrograde degeneration of LGd was induced by making a heat lesion of the ipsilateral occipital cortex. The VB ipsilateral to the cortical lesion was made an alternative target for RGC axons by making a midbrain hemisection to cut its ascending somatosensory afferents.

For recording experiments, adult hamsters were anesthetized with urethane and prepared as described (5). Physiological status and anesthesia level were assessed by continuous monitoring of the electrocardiogram. Recording micropipettes (4–6 MΩ impedance) containing 5% NaCl and 4% pontamine blue penetrated the dura, perpendicular to the cortical surface. Soma/dendrite recordings were distinguished from axon recordings by established criteria (6). Visual receptive fields (RFs) were plotted on a screen with a hand-held projector and then studied quantitatively using computer-generated, stationary or moving bars or spots, and drifting or alternating phase gratings of variable spatial and temporal frequencies, presented on a cathode ray tube. Single unit responses to visual stimuli were recorded and analyzed by computer; in some units, we qualitatively evaluated responses to light cutaneous stimulation. After recording, the anesthetized animals were intracardially perfused with 10% formalin. Brains were sectioned frozen at 50 μm and stained with cresyl violet. Visually responsive neurons in operated hamsters were shown to lie in SI and SII by two independent criteria (5). (*i*) Some recording sites were marked by iontophoresis of pontamine blue. Subsequent histological examination revealed that these and other sites were in SI or SII as cytoarchitectonically defined (7, 8). (*ii*) The neurons were within regions whose somatic representations had polarities characteristic of SI or SII (5).

We studied 35 visually responsive cells in SI/SII of 7 operated animals aged 9–18 months and, as controls, 48 visually responsive cells in VI of 12 normal animals aged 6–18 months. Of these cells, 26 in SI/SII and 41 in VI were fully characterized; partial data were obtained from the rest.

RESULTS

Spatial Organization of RFs. We recorded units with distinct visual RFs, in VI of normal and in SI/SII of operated hamsters. [Visually evoked responses cannot be obtained in SI/SII of normal hamsters (5).] These RFs showed zones from which responses were elicited by turning luminous spots or bars on, off, or both on and off (Fig. 1, upper frames). In VI of normal and SI/SII of operated hamsters, RFs had the

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Abbreviations: LGd, dorsal nucleus of the lateral geniculate body; RF, receptive field; RGC, retinal ganglion cell; SC, superior colliculus; SI, primary somatosensory cortex; SII, second somatosensory cortex; VB, ventrobasal thalamic nucleus; VI, primary visual cortex.

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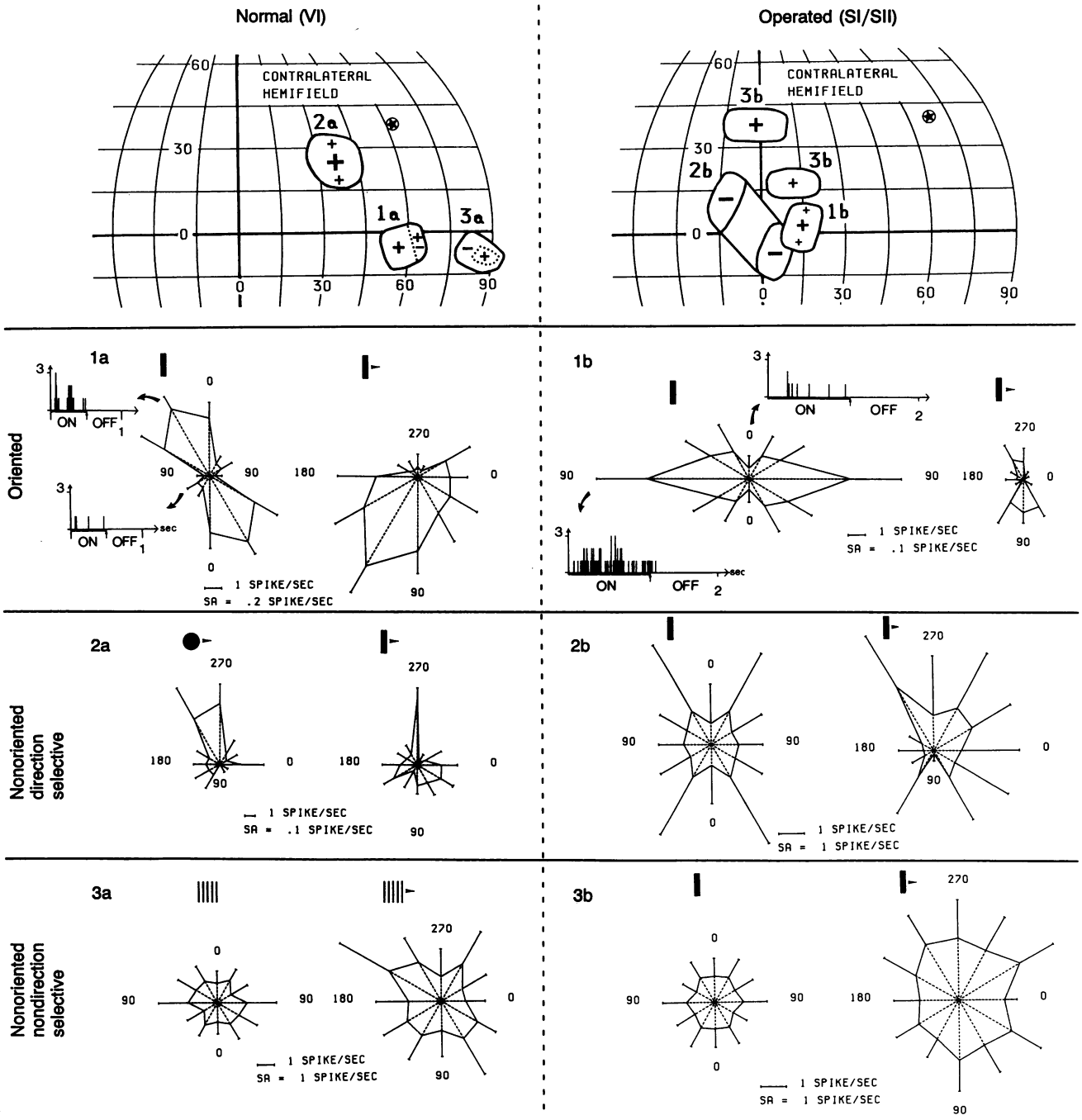

FIG. 1. Visual RFs and response properties of three neurons in VI of normal hamsters and three neurons in SI/SII of operated hamsters, stimulated through the contralateral eye. RFs and polar histograms with the same number were obtained from the same neuron. (*Upper two frames*) Spatial organization of visual RFs. Spherical representations of part of the visual field; vertical meridian (0) is the projection of the body plane of symmetry; horizontal meridian (0) is the projection of the horizontal plane containing the eyes. "30," "60," and "90" are eccentricities of meridia and elevation lines in degrees. Circled star is the projection of the optic disk. RF borders were determined by using small, stationary, flashed stimuli. "+," "−," and "±" indicate zones in which responses were evoked by luminous stimuli turned on, off, or on and off, respectively. Response intensity in unizone RFs occasionally varied with position in the RF, as indicated in 2a and 1b by large and small symbols. (*Lower six frames*) Three functional categories of visual RFs. Same neurons as above in VI (1a–3a) and SI/SII (1b–3b). Symbols above each polar histogram indicate stimulus used to evoke responses illustrated. "▮" and " |||| " correspond, respectively, to *stationary*, flashed bars and to stationary, alternating phase gratings of six orientations separated by 30° (0° = vertical, 90° = horizontal) and presented randomly in a sequence repeated ≥5 times. Orientation of each dotted radius on polar plot indicates stimulus orientation; length of dotted radius gives mean response rate (spikes sec^{-1}) at that orientation. Solid line segments show standard deviation of each response. "▮►," "●►," and " ||||►" correspond, respectively, to bars, spots, and sinusoidal gratings, *moving* in 12 directions separated by 30° (0° = nasal to temporal, 90° = superior to inferior) and repeatedly presented in a random sequence. Bars and gratings moved in directions perpendicular to their long axes. Orientations of radii on polar plots indicate direction of stimulus movement; lengths of radii give mean response rate; solid line segments indicate standard deviation. SA indicates mean spontaneous activity rate. 1a and 1b: orientation-selective units. Units were considered to be orientation selective if their orientation bias, B, was ≥0.7. ($B = 1 - R_{min}/R_{max}$; R_{min} and R_{max} are the mean firing rates evoked by stationary bars at orientations producing the weakest and strongest responses, respectively. For units responding equally at all orientations, $B = 0$, whereas for those giving no response at the least effective orientation, $B = 1$). Poststimulus time histograms (PSTHs) are for responses to stationary flashed bars with the preferred

Table 1. Distribution of single unit visual RF types in VI of normal and SI/SII of operated hamsters

	Single unit visual RF type, %		
		Nonoriented	
Hamsters	Oriented	D	ND
Normal (VI) (41)	37 (15)	24 (10)	39 (16)
Operated (SI/SII) (26)	31 (8)	19 (5)	50 (13)

The number of units of each type is given in parentheses. Percentages are based on the number of units classified; 7/48 units in VI and 9/35 units in SI/SII were not sufficiently studied to be classified. D, directional; ND, nondirectional.

same three types of spatial organization: (*i*) "unizone" RFs had one on, off, or on/off zone that could be homogeneous (Fig. 1, RFs 2b and 3b) or, occasionally, heterogeneous (Fig. 1, RFs 2a and 1b) with respect to the intensity of the response evoked by stimulating different subregions of the RF; (*ii*) "concentric" RFs had on or off centers and antagonistic surrounds (Fig. 1, RF 3a); (*iii*) "multizone" RFs had adjacent, nonconcentric zones of on and off or of on and on/off response (Fig. 1, RF 1a).

The spatial organization of unit RFs in SI/SII of operated hamsters differed from that of unit RFs in VI of normal hamsters in two respects. First, unit RFs in VI consist of a single responsive region; 57% of the visual RFs in SI/SII of operated animals consisted of two responsive regions, 20°–40° apart, either completely separated (Fig. 1, RF 3b) or, less often, linked by a region of weak, irregular response (Fig. 1, RF 2b). Usually, one responsive region gave much more robust visual responses than the other; unit response properties were tested only in the former. Second, units in SI/SII had visual RFs that were larger than those of units in VI. The mean RF area in VI was 93°^{2}. In SI/SII, the mean was 274°^{2}, considering only the more responsive region, and 416°^{2}, summing the two responsive regions, for units with more than one.

Functional Categories of RFs. We distinguished three functional categories of neurons in VI of normal hamsters (Fig. 1, lower frames 1a–3a); the same three types of visually responsive neurons were present in SI/SII of operated hamsters (Fig. 1, lower frames 1b–3b), in proportions not significantly different from those in VI (χ^2 test, $P = 0.7$; Table 1). (*i*) *Orientation selective* (Fig. 1, 1a and 1b). These units had a preferred orientation when stimulated with a stationary, flashed bar. There was no significant difference in orientation bias (defined in Fig. 1 legend) between orientation-selective units in VI and in SI/SII (two-tailed Mann–Whitney *U* test; $P > 0.1$). The best response to a moving bar was obtained when a bar of the preferred orientation moved along one direction (for unidirectional units—e.g., 1a) or both directions (for bidirectional units—e.g., 1b) orthogonal to the preferred orientation. These units gave stronger responses to optimally oriented bars than to spots with the same area, intensity, and velocity of motion (not shown), but preferred directions were similar for bars and spots. (*ii*) *Nonoriented, direction selective* (Fig. 1, 2a and 2b). These units had no orientation preference for stationary bars (2b) or gratings (not shown) nor did they give stronger responses to a moving bar than to a moving spot of the same area, intensity, and velocity (2a). However, these units preferred movement in one (2a and 2b) or both (not shown) directions along a particular axis.

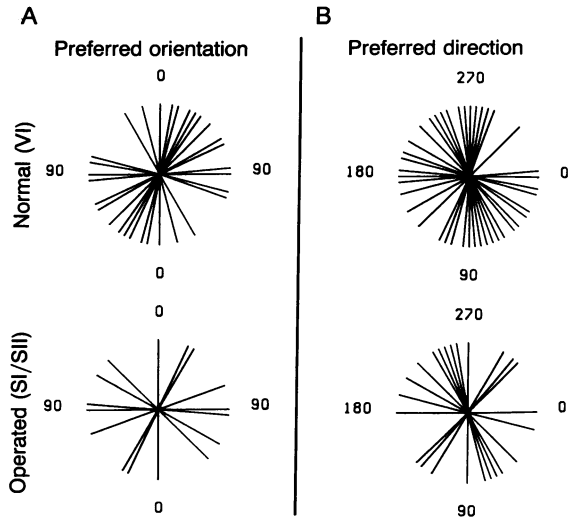

FIG. 2. (*A*) Preferred stimulus orientations of 15 cells in VI of normal hamsters and 8 cells in SI/SII of operated hamsters. Each diameter represents the preferred orientation of one cell. (*B*) Preferred directions of movement for orientation-selective and nonoriented, direction-selective cells. For each unidirectional neuron, preferred direction is represented by a radius pointing in that direction. For each bidirectional neuron, preferred axis of movement is represented by a diameter parallel to that axis. Conventions as in Fig. 1.

(*iii*) *Nonoriented, nondirection selective* (Fig. 1, 3a and 3b). These units had no preferred orientation when stimulated with stationary gratings (3a) or bars (3b) and no preferred direction of movement when stimulated with moving gratings (3a), bars (3b) or spots (not shown).

In both normal and operated hamsters, RF category and RF spatial organization were correlated: all oriented and nonoriented, direction-selective units were either unizone or multizone; 27 of 29 nonoriented, nondirection-selective units were either unizone or concentric, whereas 2 were multizone. In normal and operated hamsters, the distributions of preferred orientations (Fig. 2*A*) and directions of movement (Fig. 2*B*) were both random. The depth distributions of the different types of visually responsive neurons were similar in normal and operated hamsters: orientation-selective neurons predominanted in the supragranular cortical layers of VI and SI/SII (6/10 = 60% and 5/10 = 50%, respectively, of neurons physiologically characterized and histologically localized in layers II–III) but were less common in deeper layers (4/24 = 17% and 3/13 = 23%, respectively, of neurons characterized and localized in layers IV–VI).

The mean latency of response to a visual stimulus (Fig. 3*A*) was 198 msec in VI and 209 msec in SI/SII; a *t* test showed no significant latency difference between neurons in VI and in SI/SII ($P = 0.569$). Neurons were divided into three groups according to their preferred stimulus velocity. Slowly moving stimuli (0–15° sec^{-1}) were preferred by relatively fewer neurons in SI/SII than in VI, whereas stimuli of medium velocity (15–60° sec^{-1}) were relatively more often preferred in SI/SII than in VI; neurons preferring high velocities (>60° sec^{-1}) were about equally common in VI and SI/SII (Fig. 3*B*). To perform a χ^2 test on the preferred velocity distributions, we had to combine the medium and high velocity

orientations (150° and 90°, respectively) and with orthogonal orientations (60° and 0°, respectively). PSTHs show that the on response to an optimally oriented, flashed bar was phasic in unit 1a and more tonic in unit 1b. In both cases, the on response strongly decreased when the units were stimulated with bars orthogonal to the preferred orientation. 2a and 2b: nonoriented, direction-selective units. Both were unidirectional. 2a preferred 270° movement, whereas 2b preferred upward nasal movement. 3a and 3b: nonoriented, nondirection-selective units. They showed no preferred orientation when stimulated with stationary gratings (3a) or bars (3b) and no preferred direction of movement when stimulated with moving gratings (3a) or bars (3b).

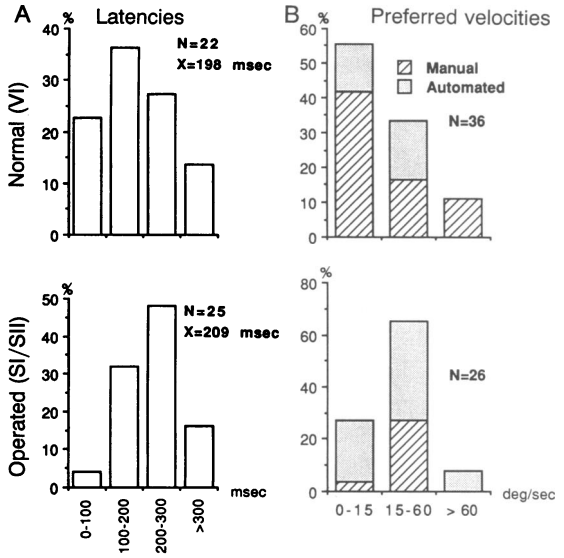

FIG. 3. Response latencies (*A*) and preferred stimulus velocities (*B*) for neurons in VI of normal and in SI/SII of operated hamsters. Latencies were measured from onset of optimal stimuli to the first peak in a unit's response. Preferred velocities were determined manually or by using the computer. In manual tests (hatching), an otherwise optimal stimulus was swept across the RF at speeds in the ranges of 0–15°/sec, 15–60°/sec, or >60°/sec; in automated tests (stippling), a grating of optimum orientation and spatial frequency was swept across the RF at one of 16 different velocities, separated equally on a logarithmic scale from 0.5° to 25°/sec and presented repeatedly in pseudorandom order; the preferred stimulus velocity was that which evoked the greatest mean firing rate. Vertical axes, percentage of neurons tested of a given category; horizontal axes, latency or velocity category. N = number of neurons tested; X = mean latency in msec.

categories because of the small number of units in the latter; the distributions for VI and SI/SII were significantly different ($P = 0.025$) when tested this way.

Subsequent to neonatal midbrain hemisections, ascending somatosensory afferents grow rostral to the cut and reinvade VB (D.O.F., unpublished data). Thus, 22 visually responsive neurons in SI/SII were tested for somatosensory responsiveness. Eight (36%) responded to somatosensory stimulation; their response properties were qualitatively similar (unpublished data) to those of neurons in SI/SII of normal animals. One of the bimodal neurons was oriented; 1 was nonoriented, direction selective; 5 were nonoriented, nondirection selective; and 1 was uncategorized.

Neurons in SI/SII often responded less intensely to visual stimuli than did neurons in VI. Furthermore, for units that responded to visual and somatosensory stimulation, the somatosensory response was generally more robust. There was no correlation, however, between the intensity of a unit's visual response and its selectivity for various stimulus parameters. For example, in Fig. 1, although unit 1b in SI/SII does not respond to moving bar stimuli as well as unit 1a in VI, it is more sharply tuned for the direction of stimulus movement; in addition, unit 1b responds more robustly to stationary, optimally oriented bars.

DISCUSSION

In hamsters with abnormal retino-VB projections, somatosensory cortical neurons have visual response properties that resemble, in several characteristic features, those of normal visual cortical neurons. These data support the hypothesis that at the thalamic and cortical levels, the somatosensory and visual systems use similar neuronal circuits to perform similar transformations on their inputs,[§] a possibility raised on the basis of a common organizational plan of the thalamus (9) and neocortex (10, 11). We first consider several issues related to alternative interpretations.

In operated hamsters visual information almost certainly reaches SI/SII via the retino-VB projection. (*i*) Visually evoked responses cannot be obtained in SI/SII of normal hamsters (5). (*ii*) RGC axons make synapses in VB (1). (*iii*) Intraocular injections of ^{3}H-labeled amino acids label parts of VB and topographically corresponding regions of SI/SII; in SI/SII, the laminar distribution of label corresponds to the distribution of thalamocortical axons (3). (*iv*) The topography of the visual field representations in SI/SII is predicted by the topographies of the retino-VB and VB to SI/SII projections (5). (*v*) The somatosensory RFs of bimodal units were always on the mystacial vibrissae, head, or ears; these regions are represented on the lateral aspect of VB (12), which is also the site of termination of the retino-VB projection.

Our data from single neurons in VI are consistent with those of previous studies in rodents (13–15). There are qualitative and quantitative differences between the visual response properties of neurons in VI of normal hamsters and neurons in SI/SII of operated hamsters. Although some of these may reflect differences in the intrinsic circuitry of the visual and somatosensory thalamic nuclei or cortices, some probably have other causes. (*i*) The multiple responsive regions and supranormal areas of the visual RFs of some neurons in SI/SII arise because, unlike LGd and VB of normal animals, in which relay neurons that project to the same cortical loci get input from the same point on the receptor surface, in VB of operated animals neurons projecting to the same cortical locus get input from multiple retinal loci.[¶] (*ii*) The differences in latency and velocity preference between neurons in SI/SII and those in VI may reflect differences in the proportions of various RGC types that project to VB and LGd, respectively. In carnivores and primates, there are distinct classes of RGCs that differ with respect to multiple response parameters, including conduction velocity and preferred stimulus velocity (17). A transient retinal projection to VB in normal neonatal hamsters (18) contributes to the permanent projection in operated animals (4) and arises from RGCs that do not project to the thalamus in normal, adult animals (19).

In sensory thalamic nuclei and cortical areas, the differentiation of some biochemical and morphological features underlying normal function may reflect the modality of the sensory input. Although sensory input of the appropriate modality clearly influences the development of sensory systems (20, 21), there are few data on how the differentiation of sensory systems depends on the *modality* of their input. Available evidence argues against such a dependence: retino-VB axons participate in synaptic complexes that morphologically resemble those of normal, somatosensory, rather than visual, thalamic afferents (1). This datum also suggests that the morphological features of thalamic synaptic complexes may not determine the parameters of cortical neuronal responses assayed in our visual RF studies.

[§]"Transformation" denotes the relationship between the information flowing into and out of a neural structure.

[¶]In normal mammals, orderly maps of the retina and body in VI and SI/SII, respectively, arise because in LGd and VB, "lines of projection" (the zones of termination of afferents representing a restricted region of the receptor surface) are congruent with the set of relay neurons that project beneath a single locus on the cortical surface (review in refs. 7 and 16). VB relay neurons projecting beneath a single cortical locus are distributed in arcs that lie in a plane approximately orthogonal to the lines of projection defined by retino-VB afferents in operated hamsters (2) and, therefore, intercept multiple, but not necessarily contiguous, lines of projection.

Neonatal lesions of SC and the brachium of the inferior colliculus produce abnormal retinal projections to the medial geniculate nucleus (MG), the principal thalamic auditory nucleus (1–4, 22–24). In operated ferrets with retino-MG projections, some neurons in the auditory cortex (AC) respond weakly to visual stimulation from large, poorly defined RFs (24). The reasons for the differences between our results and those obtained in ferret AC are unclear.

Three lines of evidence support the hypothesis that thalamic nuclei and cortical areas at corresponding levels in the visual and somatosensory systems perform similar transformations on their inputs:

(*i*) The visual and somatosensory systems use similar information processing strategies, based on similar morphological substrates. In these systems, the internal anatomical and functional organization of thalamic nuclei (9) and cortical areas (10, 11) are similar: each cortical area consists of uniform, multiply replicated modules that are basic units of information processing. In both systems, there are (*a*) orderly maps of the receptor surface at the thalamic (9) and cortical (25, 26) levels, (*b*) multiple, hierarchically organized, reciprocally connected cortical areas (27, 28), (*c*) similar laminar segregations within the cortex of various classes of afferent axons and efferent neurons (27–30), and (*d*) parallel pathways for processing information concerning distinct submodalities (27, 31).

(*ii*) Orientation-selective neurons occur with equal frequency and are equally sharply tuned in VI of normal and SI/SII of operated hamsters.[‖] The similar depth distributions of orientation-selective units in VI and SI/SII give further evidence of the similarity of circuitry in these cortical regions.

(*iii*) The similarity of the visual and somatosensory response properties of bimodal neurons in SI/SII of operated hamsters to those of single neurons in VI and SI/SII, respectively, of normal hamsters suggests that similar circuits in the visual and somatosensory thalamic nuclei and cortices can generate visual and somatosensory responses.

It is not known if the visual and somatosensory systems use similar strategies to accomplish similar tasks. Although neurons in somatosensory cortex of normal animals are selective for the direction and velocity of stimulus movement (34), orientation selectivity is rare (35) and these features may not be abstracted by the same mechanisms as in the visual system. Even if these stimulus parameters are not analyzed similarly in the two systems, the visual and somatosensory cortices may perform a common operation—e.g., selectively filtering their inputs so as to emphasize changes in the spatial or temporal domains. The hypothesis that visual and somatosensory forebrain structures perform similar transformations on their inputs implies that differences in information processing strategy between the two systems occur principally at prethalamic levels.

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[‖]This datum supports the hypothesis if either of two explanations of cortical orientation selectivity is correct. (*i*) It was originally suggested that the orientation preference of visual cortical neurons is an emergent property of thalamocortical connectivity or cortical circuitry (32). (*ii*) It is now known that in carnivores, RGCs and LGd neurons show weak orientation biases, although the contribution of these biases to the orientation preferences of cortical neurons is controversial (33). There has been no systematic study in rodents to determine where in the visual pathway different stimulus features are first abstracted. Thus, in rodents, carnivores, and other orders, the response preferences of RGCs or thalamic neurons may be sharpened by the cortex.