

Visual, Auditory, and Somatosensory Convergence on Cells in Superior Colliculus Results in Multisensory Integration

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SUMMARY AND CONCLUSION

1. Convergence of inputs from different sensory modalities onto individual neurons is a phenomenon that occurs widely throughout the brain at many phyletic levels and appears to represent a basic neural mechanism by which an organism integrates complex environmental stimuli. In the present study, neurons in the superior colliculus (SC) were used as a model to examine how single neurons deal with simultaneous cues from different sensory modalities (e.g., visual, auditory, somatosensory). The functional result of multisensory convergence on an individual cell was determined by comparing the responses evoked from it by a combined-modality (multimodal) stimulus with those elicited by each (unimodal) component of that stimulus presented alone.

2. Superior colliculus cells exhibited profound changes in their activity when individual sensory stimuli were combined. These "multisensory interactions" were found to be widespread among deep laminae cells and fell into one of two functional categories: 1) response enhancement, characterized by a significant increase in the number of discharges evoked; and 2) response depression, characterized by a significant decrease in the discharges elicited.

3. Multisensory response interactions most often reflected a multiplicative, rather than summative, change in activity. Their absolute magnitude varied from cell to cell and, when stimulus conditions were altered, within the same cell. However, the percentage change of enhanced interactions was generally inversely

related to the vigor of the responses that could be evoked by presenting each unimodal stimulus alone and suggests that the potential for response amplification was greatest when responses evoked by individual stimuli were weakest.

4. The majority of cells exhibiting multisensory characteristics were demonstrated to have descending efferent projections and thus had access to premotor and motor areas of the brain stem and spinal cord involved in SC-mediated attentive and orientation behaviors.

5. These data show that multisensory convergence provides the descending efferent cells of the SC with a dynamic response character. The responses of these cells and the SC-mediated behaviors that they underlie need not be immutably tied to the presence of any single stimulus, but can vary in response to the particular complex of stimuli present in the environment at any given moment.

INTRODUCTION

Most animals possess multiple sensory systems with which they can simultaneously sample a wide variety of physical changes in their environment. This not only increases the probability that relevant events will be detected, but makes possible the interweaving of sensory experiences into a multisensory perceptual fabric. In this manner, stimulus complexes can have effects or meanings that individual components would not have, as when an auditory and a visual stimulus produce a response that neither stimulus alone would evoke (74, 76).

Given the multitude of stimuli that normally impinge on freely moving animals, it is likely that multisensory integration is a critical and ongoing determinant of behavior. It is therefore surprising that, in contrast to the voluminous literature on the properties of cells in each of the individual sensory systems, we are largely ignorant of how the nervous system deals collectively with simultaneous inputs from different modalities. We do know, however, that inputs from different sensory modalities converge on individual cells in the brain. This phenomenon occurs in many areas of the central nervous system (CNS) (e.g., 11, 12, 24, 38, 40, 41, 53, 58, 61, 86, 102, 110, 117) and at many phyletic levels (e.g., 31, 39, 46, 48, 54, 67, 83, 91, 94).

Perhaps nowhere is the convergence of modalities more evident than in the superior colliculus (SC), a structure intimately involved in attending to, localizing, and orienting to sensory stimuli. Visual, auditory, somatosensory, vestibular, and proprioceptive inputs converge on cells in the deep laminae (ventral to stratum opticum) of the SC (1, 17, 25, 30, 31, 36, 40, 41, 43, 54, 62, 65, 66, 71, 74, 76, 98, 99, 102–105, 109, 115, 116) and many deep laminae cells project to motor and premotor areas that control orientation of the eyes, pinnae, and head (34, 42, 44, 59).

In the present study, we sought to determine some of the consequences of multisensory convergence in the brain by using the deep laminae SC cell as a model to compare the effects of unimodal and multimodal stimuli. Of specific interest was 1) whether combination of different sensory stimuli would evoke responses that differed substantially from responses to the stimuli individually, and 2) whether the SC cells most directly involved in orientation behaviors (e.g., with descending efferent projections) would behave in the same way as other SC cells. Preliminary results of these experiments have been reported (74, 76).

METHODS

Data were obtained using standard extracellular recording techniques from 22 chronically prepared adult cats.

Surgical preparation

Several days (5–7) before the first recording session, the animal was anesthetized with pentobarbital sodium (40 mg/kg) and its head was fixed in a ste-

reotaxic head holder. Aseptic conditions were maintained while a craniotomy (2 cm in diameter) was made to expose the cortical regions dorsal to the SC, and a hollow cylinder head-holding device (73) was stereotactically implanted over the opening and secured in place by anchoring screws and dental acrylic. The well of the cylinder was temporarily closed with a tight-fitting screw cap and the wound was sutured closed around the implant.

Recording experiments began with the administration of an anesthetic dose of ketamine hydrochloride (30 mg/kg). The well head-holding implant was attached to a mounting plate that supported the head without wounds or pressure points and without obstructing the eyes, pinnae, face, or body surface. The animal was intubated, paralyzed (a 1:1 mixture of gallamine triethiodide and d-tubocurarine; 10 mg/kg), and artificially respiration with a mixture of 75% N₂O and 25% O₂. Supplementary doses of the anesthetic (15 mg/kg) and the paralytic agent (0.6 mg/kg) were routinely administered. Expiratory CO₂ was monitored and kept between 4.0 and 4.7%. Body temperature was maintained at 37–38°C with a heating pad. The pupils were dilated with an ophthalmic solution of 1% atropine sulfate and the positions of the optic discs were projected onto a translucent 91-cm diameter Plexiglas hemisphere. The hemisphere was positioned at a distance of 45 cm from the eyes. Contact lenses were applied to prevent corneal drying and to correct retinoscopically determined refractive errors.

Recording

A calibrated X-Y slide was fitted over the recording cylinder to guide the glass-insulated tungsten recording electrode (tip, 1–2 μm; tip exposure, 12–20 μm impedance = >1 MΩ) to the surface of the SC (identified by visually elicited multiunit activity). The electrode was then advanced through the SC using a hydraulic microdrive. Neurons were identified by their spontaneous activity and by their responses to a variety of search stimuli (see below). Neuronal responses were amplified, displayed on an oscilloscope, and played through an audiometer. Since neuronal isolation was a critical factor for these experiments, only cells with a clear signal-to-noise ratio (at least 3:1) were evaluated, and their waveshapes were monitored before, during, and after each set of sensory tests (see below).

During recording, the depth of each neuron was indicated on the microdrive and recording sites were marked with small electrolytic lesions. At the conclusion of an experiment, the animal was given an overdose of pentobarbital sodium and perfused through the heart with physiological saline followed by 10% formalin. The brain was processed using routine histological procedures (50 μm frozen sections, cresyl violet staining) and recording sites were histologically verified.

Receptive field mapping and general sensory tests

Visually responsive cells were sought using flashed or moving slits or spots of light. Their receptive fields were then mapped using a hand held light source (pantoscope) that projected light spots or bars directly on the Plexiglas hemisphere. With the ipsilateral eye occluded by an opaque barrier, the borders of the visual receptive field were determined by moving the visual stimulus from the periphery inward from all directions until an enclosed responsive area was delimited. Next, a series of brief qualitative tests were conducted to determine the general visual responsiveness (e.g., response to flashed spots, preferences for velocity and direction of movement, preferences for stimulus size, binocularly, etc.) of the cell. Following each experiment, the size and location of each visual receptive field was transferred to a standardized representation of the visual field. The area of a visual receptive field was calculated as the area of a circle using half the average of the longest and shortest diameters as the radius.

Somatosensory cells were identified by their responses to mechanical stimuli (e.g., taps, strokes with a camel's hair brush, manual compression of the skin, air puffs). The minimum stimulus necessary to evoke a response was determined using calibrated von Frey hairs. This stimulus was then used to map the receptive field and to determine the cell's minimum velocity (slow, intermediate, or high), whether it was rapidly or slowly adapting, and if it was activated by hair displacement (guard hairs or sinus hairs) or required distortion of the skin or subcutaneous tissue. Cells were classified according to the criteria of Burgess and Perl (21) for primary somatosensory afferents. Receptive fields were transferred to a standardized representation of the cat body, drawn to scale from a 3-kg animal. This representation with the receptive field drawn on it was placed beneath a grid (each grid square represented 1 cm²) and the area of the receptive field was determined by counting the grid squares covering it.

Auditory cells were identified by their responses to complex manually presented stimuli, that included claps, hisses, whistles, and/or broad-band noise bursts. The receptive field was then mapped using an electronically controlled broad-band noise stimulus presented at predetermined points in space (elevation 0, 30–330°; azimuth 0, 22, 45, 67, 90, or . . . 360°). The stimulus was presented repeatedly (3 to 5 times) at each position and points at which discharges were elicited were plotted on a two-dimensional representation of auditory space. The area of auditory space that a stimulus produced a one standard deviation increment in the number of discharges was considered the auditory receptive field. Auditory receptive field areas were calculated

as the area of a circle in the same manner used to determine visual receptive field areas. With a speaker placed along the acoustical axis of each pinna, the free field binaural properties of a cell were examined by evaluating its responses to identical broad-band noise bursts from the contralateral speaker, the ipsilateral speaker, and then both speakers simultaneously. Although free-field stimuli (rather than a sealed stimulus delivery system) were used here, the data seemed to fall readily into the classification scheme of Wise and Irvine (118), determined using a sealed stimulus delivery system. Therefore, their criteria were used and binaural categories were assigned accordingly. No systematic attempt was made to determine the threshold levels for auditory cells or to evaluate their responses to pure tones.

Sensory stimulation for multisensory tests

Once a neuron was identified and isolated, quantitative sensory tests were conducted using reproducible, electronically controlled stimuli initiated by a trigger pulse from an Ortec programmer; the onset, duration, and physical parameters of each stimulus could be varied independently and are described below.

Visual stimuli were generated by a projector equipped with circular and rectangular diaphragms with which the shape and size of the stimulus could be varied. Spots or bars of light (luminance, 53 cd/m² against a background of 2.7 cd/m²) were projected through a rotating prism and reflected from a galvanometer-driven mirror onto the translucent Plexiglas hemisphere. The galvanometer was controlled by an electronic ramp generator that determined the amplitude (2–180° across the hemisphere) and velocity (2.7–555°/s) of stimulus excursions. Stationary flashed stimuli were presented with the use of an electronic shutter.

Somatosensory stimuli were delivered using an electronically controlled moving-coil vibrator (Ling 102A shaker) that was mechanically adapted to increase the amplitude of its excursion. The probe tip was loaded against a hair or group of hairs, or against the skin, and stimulation consisted of the initial displacement, a plateau phase, and a return to the original position. The amplitude (range of 0.05–5.0 mm) and velocity (range of 15–420 mm/s) of the somatosensory stimulus could be varied independently.

Auditory stimuli were broad-band noise bursts (10–250 ms, 200–20,000 Hz, 40- to 70-dB sound pressure level) presented through one of two speakers mounted on a hoop (50-cm diameter) that rotated around the animal's interaural axis. Changes in elevation of the auditory stimulus were effected by moving the hoop around the interaural axis, whereas changes in azimuth were made by moving the speaker along the hoop. The onset, duration, and intensity of the stimulus were controlled in-

dependently by an electronically triggered broadband noise generator. The hoop, speaker, and animal were contained in a three-sided chamber, the fourth side of the chamber was closed by the Plexiglas hemisphere (except during auditory receptive field mapping); the chamber and the ipsilateral inner surface of the hemisphere were lined with a corrugated sound-absorbing material. In a few early experiments, acoustic stimuli were generated by gating (with an electronically controlled solenoid valve) a controlled (by a flowmeter) air flow through a hose whose open end was constricted by a glass pipette.

Experimental trials

Single-modality (control) stimulation consisted of the presentation of modality-specific stimuli for each sensory modality. These tests consisted of the repeated presentation ($n = 8-16$) of the optimal stimulus (e.g., evoking the highest discharge frequency) for that modality (e.g., visual alone, auditory alone) within the appropriate receptive field. Stimuli from modalities that did not excite the cell when presented alone were located in their 'presumptive' receptive fields, i.e., they were placed within receptive fields of other cells that were responsive to these stimuli in the same electrode penetration and/or they were placed in topographic register with other effective modalities in that specific cell (40, 77, 104).

Combined-modality (test) stimulation consisted of the repeated ($n = 8-16$) simultaneous presentation of stimuli from more than one modality (e.g., visual and auditory). Combined-modality stimuli were presented coincident in space or in close topographic register. These tests utilized the identical stimuli presented during single-modality stimulation, but were now in pairs or, less frequently, in triplets.

Data analysis

For each single and combined-modality test, the mean, standard deviation and standard error of the mean were calculated for the number of spikes evoked for the duration of the discharge train by a DEC MINC 11/23 computer and stored on disc. A multimodal interaction was defined as a significant ($P < 0.05$, two-tailed t test) change in the number of impulses elicited by combined-modality stimulation when compared with the number evoked by single-modality tests (specifically, the most effective or "best" single-modality stimulus). Interactions were further subdivided: a significant increase in the number of discharges was defined as "response enhancement", and a significant decrease was defined as "response depression". The following formula was used to calculate the magnitude of an interaction as a percentage

$$[(CM - SM_{\max}) \times 100]/SM_{\max} = \%$$

where CM is the number of impulses evoked by combined-modality stimulus, and SM_{\max} is the number of impulses evoked by best single-modality stimulus.

Assessment of efferent status

Antidromic activation of identified neurons was used to determine whether a given cell sent its axon out of the SC via the midbrain tegmentum. This was accomplished by electrically stimulating the descending efferent pathways of the SC through electrodes implanted in 13 out of 22 cats. Each set of stimulating electrodes consisted of three sharpened (tips of 2–5 μm) isonel-insulated tungsten wires (uninsulated 0.2–0.5 mm up the shaft) spaced 1 mm apart, with their tips staggered at 1-mm intervals in the A-P plane. One electrode set was stereotactically implanted in the lateral efferent bundle (LEB) and one in the medial efferent bundle (MEB) using a rostral or caudal approach that was angled to avoid traversing the SC. By alternately recording and stimulating, the final position of each electrode set was determined on the basis of sensory responses and evoked movements. The electrodes were cemented in place using dental acrylic on the same day that the cylinder head-holding device was implanted.

A cell was classified as a descending efferent if it was antidromically activated by electrical stimulation (monopolar cathodal pulses, 50- to 300- μA intensity and 0.1-ms duration) delivered through any one of the implanted electrodes. Criteria for antidromic activation were responses showing <0.2 ms latency variation on successive tests, responding consistently to both pulses of a double shock at frequencies > 300 Hz, and demonstrating a reliable threshold for activation by stimulus currents of <300 μA .

RESULTS

Responses to visual, auditory, and somatosensory stimuli and to combinations of these stimuli were examined in 489 SC neurons. As noted previously (see Ref. 101 for review) cells responsive to visual stimulation were encountered in all laminae, whereas those responsive to acoustic, somatosensory, and multisensory stimuli were found only in laminae ventral to the stratum opticum (i.e., in the "deep" laminae). Responses to all combinations of visual, auditory, and somatosensory stimuli were observed among these deep laminae cells. However, not only were some cells excited by inputs from more than one modality as previously reported (see Ref. 101 for review) but others were excited by one modality and depressed

by another, or even were depressed by both afferent sources. Therefore, any neuron that was influenced (either excited or depressed) by inputs from more than one sensory modality was classified as multisensory. Nearly half of the cells identified in the deep laminae ($n = 169/344$; 49%) were multisensory (see Fig. 1), and their activity was profoundly influenced by the combination of stimuli from different sensory modalities.

Modality-specific response properties

SUPERFICIAL LAMINAEE. Although reports exist indicating a few scattered nonvisual cells in the superficial laminae (1, 65, 66), none of the 145 cells examined here in the superficial layers were influenced by auditory or somatosensory stimuli. The overwhelming majority were responsive to visual stimuli (visual, 142; unresponsive, 3), were binocular ($n = 120/122$; 98%), were best activated by a moving visual stimulus that was smaller than the receptive field, had restricted receptive fields (average diameter, 23° ; range of 4 to 60°), and nearly half ($n = 57/115$; 49%) showed a strong preference for direction of movement.

DEEP LAMINAEE. Of the deep laminae cells evaluated, 70% ($n = 242/344$) received visual

inputs, 49% ($n = 170/344$) received auditory inputs, and 26% ($n = 88/344$) somatosensory inputs; only 10% ($n = 35/344$) were unresponsive. Response properties were examined in 74% ($n = 254/344$) of the cells and these properties are described below.

VISUAL. All deep laminae visual cells responded to a light stimulus moved across the receptive field and most ($n = 58/73$; 79%) were activated by flashing stimuli as well. The majority of these cells were best activated by stimuli smaller than their receptive fields and, as noted in Table 1, were best activated by stimuli that moved in a specific direction (direction selective cells, $n = 96/165$; 58%) at velocities $> 10^\circ/\text{s}$ (e.g., high velocity versus low velocity, $< 10^\circ/\text{s}$) ($n = 101/160$; 63%). Nearly all were binocular ($n = 181/195$; 93%), and although the visual receptive fields of unimodal cells (mean = 58° diameter; $n = 40$) were significantly ($P < 0.01$, one tailed t test) smaller than those of multimodal cells (average = 78° diameter; $n = 77$), no other major distinctions between the populations of unimodal and multimodal visual cells were noted. The receptive fields of both unimodal and multimodal cells exhibited the same topographic organization and increased in size with increasing depth in the SC.

AUDITORY. A total of 170 acoustic-sensitive neurons (both unimodal and ultimodal) were identified and most ($n = 98/170$; 58%) responded vigorously (3 to 30 spikes/response) to contralateral stimuli. The binaural responses of 109 auditory cells were evaluated and are displayed in Table 2 (according to the classification scheme of Wise and Irvine (118)).

Response profiles were determined and receptive fields plotted for 28 auditory neurons with receptive field diameters ranging from 75° to the entire auditory field (average diameter, 140°). The majority of these ($n = 24/28$; 86%) had receptive fields that were primarily contralateral, and four had fields restricted to a small portion of the region anterior to the interaural axis (e.g., frontal). As was the case for visual cells, no significant differences between unimodal and multimodal auditory cells were apparent in this sample.

SOMATOSENSORY. A total of 88 cells received somatosensory inputs and 78 could be broadly classified by receptor type according to the criteria established for first order afferents by

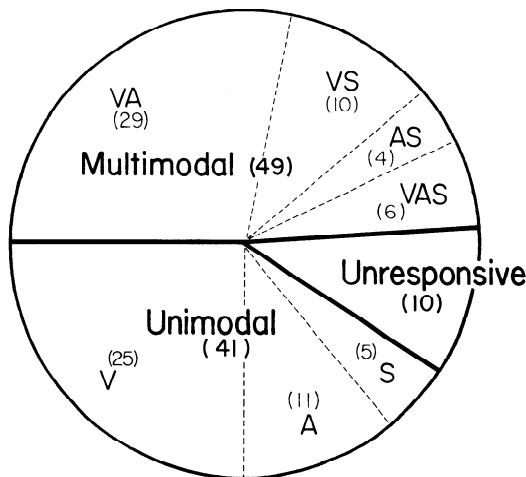


FIG. 1. Proportion of unimodal, multimodal, and unresponsive cells encountered in the deep laminae of the superior colliculus are depicted here. Unimodal and multimodal segments are further subdivided according to the relative incidence of each cell type. V, visual, A, auditory, S, somatosensory; combinations refer to specific multimodal cell types. Numbers in parentheses represent percentages based on the entire deep laminar cell population studied.

TABLE 1. *Visual response properties of deep laminae cells*

	Directional		Velocity		Flash		Ocularity	
	Yes	No	Low	High	Yes	No	Mo	Bi
Unimodal	37	24	21	34	23	4	2	72
Multimodal	59	45	38	67	35	11	12	109

Burgess and Perl (21). Once again, no obvious differences among unimodal and multimodal cells were noted. As shown in Table 3, the majority ($n = 67/78$; 86%) were activated by hair displacement and, of these hair-activated cells, most ($n = 60$) responded with a brief burst of impulses to movement of guard hairs away from, and often returning to the rest position; seven hair cells responded with a brief burst of impulses to the displacement of facial sinus hairs (e.g., vibrissae), and the remaining 11 were either unresponsive or were poorly activated by hair displacement, but responded with a short burst of discharges to rapid indentation of the skin. All somatosensory cells were activated by stimulation of the contralateral body surface and seven had receptive fields that crossed the midline (usually on the face or head) to occupy a comparatively small area of the ipsilateral body surface. The average somatosensory receptive field was $\sim 270 \text{ cm}^2$ (range of 4 to 760 cm^2). Although somatosensory receptive fields of unimodal cells tended to be somewhat larger than those of multimodal cells (average, 347 versus 226 cm^2 , respectively), the difference was not statistically significant.

Result of modality convergence

The functional consequences of multisensory convergence in the SC were quantitatively evaluated in 154/489 neurons. At least two single-modality tests and one combined-modality test (average 7.5 tests per cell; range of 3–42), consisting of 8 to 16 stimulus presen-

tations each, were delivered to each of these cells. All of the 18 superficial laminae cells examined in this manner responded only to stimuli from one modality (visual). Of the 136 deep laminae cells examined in this manner, 37 responded only to stimuli from one modality, and 11 cells did not produce a statistically significant change in response during combined-modality stimulation, although they did exhibit responses to more than one modality. In contrast, 88 deep laminae cells demonstrated profound changes in their activity when stimuli from two or more sensory modalities were combined. Two functional categories were identified among these cells: 1) response enhancement ($n = 61$), and 2) response depression ($n = 27$).

Multimodal interactions

Response enhancement was demonstrated in 45% ($n = 61/136$) of the deep laminae cells quantitatively studied and Fig. 2 illustrates a typical example. This cell responded weakly to a visual or an auditory stimulus presented alone (Fig. 2, A and B) but showed a striking ($>1,200\%$) response increment when those same stimuli were combined (Fig. 2C). Response enhancement was a characteristic of many deep laminae cells and was evoked by all possible modality combinations. Figures 3, 4, and 5 illustrate that this phenomenon was independent of a specific combination of modalities: the responses of 37 cells were enhanced by simultaneous visual and auditory cues (Fig. 2), 5 by auditory-somatosensory cues

TABLE 2. *Binaural categories*

	EO/I	EO/F	EO/O	EE/F	OO/F	NT	Total
Unimodal	3	1	1	1	1	14	21
Multimodal	22	3	15	2	3	43	88

First two characters represent, respectively, responses to contralateral and ipsilateral free field cues presented alone. E, excitement; O, no response. The third character refers to the response elicited by simultaneous presentation of contra- and ipsilateral cues. I, inhibition; F, facilitation; O, no binaural interaction; NT, not tested.

TABLE 3. Somatosensory receptor types

	Guard Hair	Vibrissa	Skin	Total
Unimodal	13	1	2	16
Multimodal	47	6	9	62

(Fig. 3), 11 by visual-somatosensory cues (Fig. 4), and 8 by visual-auditory-somatosensory stimulus combinations (Fig. 5). Although the majority ($n = 57/61$) of these cells showing response enhancement responded to each of the stimuli presented alone, the multisensory properties of some ($n = 4$) cells became ap-

parent only during combined-modality tests. In these specific cases, an auditory stimulus that seemed ineffective in single-modality tests markedly facilitated responses to the visual cue (somatosensory stimuli failed to influence any of these four cells either when presented alone or in combination with a visual or an auditory stimulus).

RESPONSE DEPRESSION. Twenty-seven (20%) of the deep laminae cells studied quantitatively responded to combined-modality stimulation with significantly fewer impulses than were elicited by single-modality cues. A typical example of response depression is illustrated in

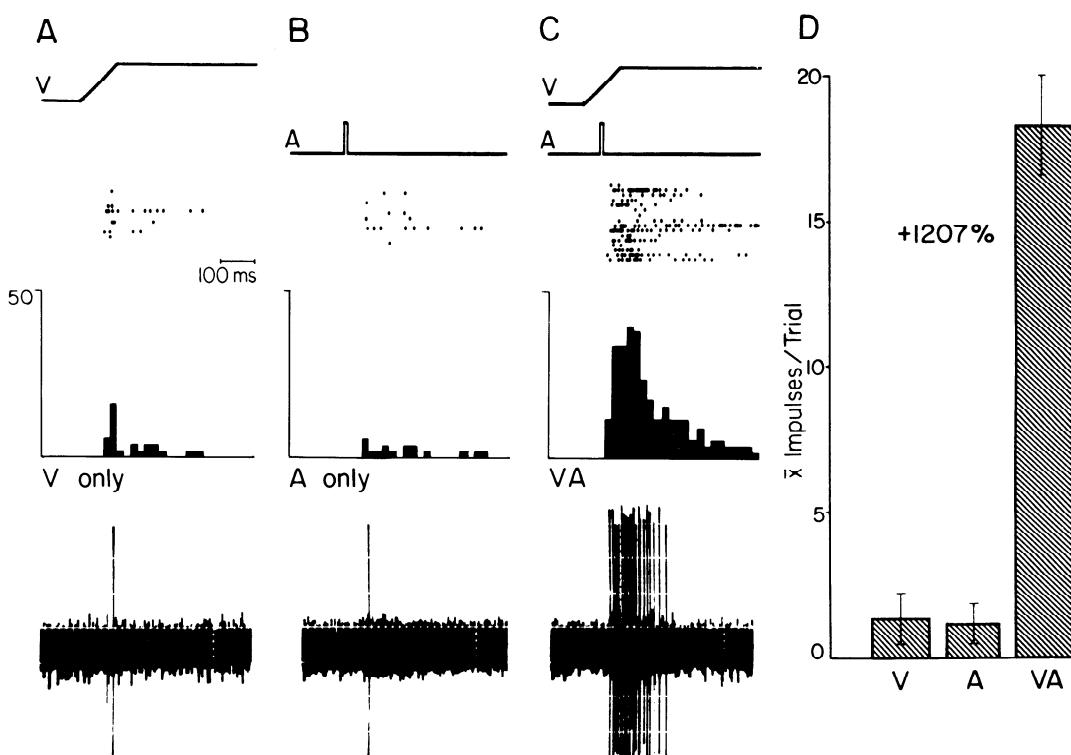


FIG. 2. Convergence of inputs from different sensory modalities onto individual neurons produces dramatic changes in their activity. *A*: a visual stimulus, size = $1 \times 1^\circ$ (ramp "V"), was moved through visual receptive field at $350^\circ/\text{s}$ in the preferred direction. Visual stimulus evoked few impulses on 6/16 presentations and are represented in the raster and histogram below the stimulus trace. Each dot in the raster represents 1 impulse. These same conventions are used in *B*, *C*, and subsequent figures. Oscillogram illustrates discharge of the cell in response to one stimulus presentation. *B*: an auditory stimulus (square wave "A" representing a 10-ms broad-band noise burst; <60 dB SPL) also evoked few impulses when presented alone and also had a low response probability. *C*: when visual and auditory stimuli were presented together, a profound response interaction occurred: responses were now evoked on every presentation and usually consisted of long discharge trains. *D*: mean number of impulses (standard error of the mean is vertical line through each bar) evoked in *A*, *B*, and *C* is compared in a bar histogram. A 1,207% increase ($P < 0.001$ two tailed t test) in mean number of impulses evoked by the combined-modality stimulus was exhibited when compared with the response to the visual stimulus alone (most effective single-modality stimulus). Time scale in *A* also applies to *B* and *C*.

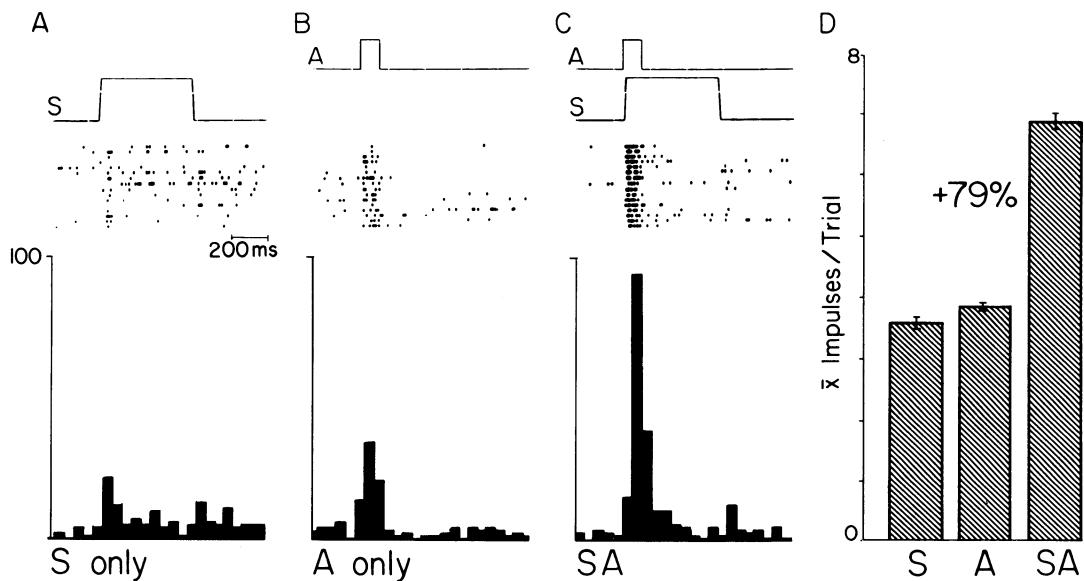


FIG. 3. Response enhancement was produced in this cell by combining somatosensory and auditory stimuli. *A*: a weakly effective somatosensory stimulus that indented the skin (square wave "S", velocity = 400 mm/s) and a somewhat more effective (*B*) auditory stimulus (square wave "A"; duration = 100 ms; <60 dB SPL) were combined (*C*). Note response enhancement generated by the combination, so that a 79% increase ($P < 0.001$) in mean number of impulses was evoked (*D*).

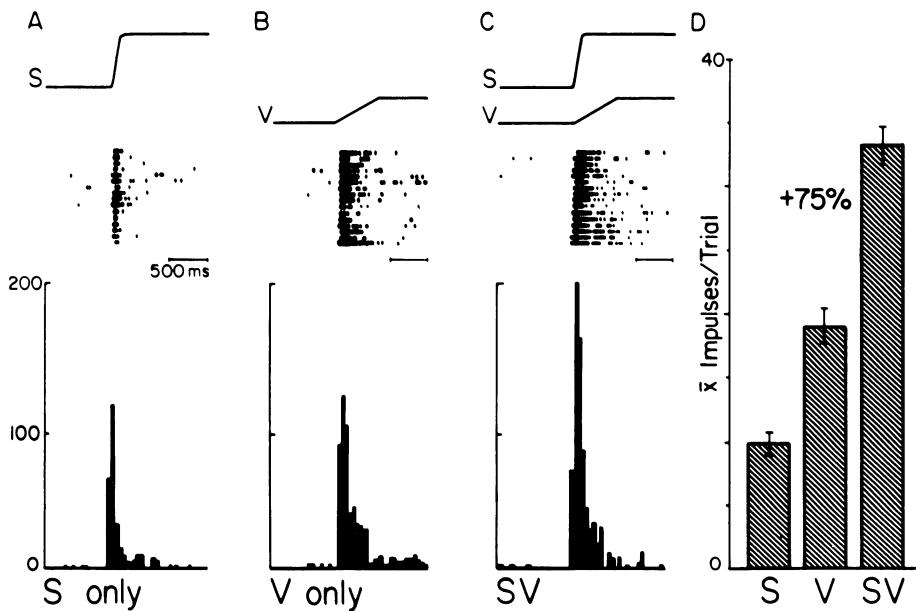
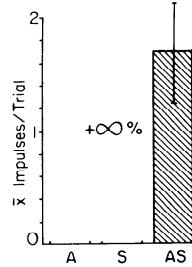
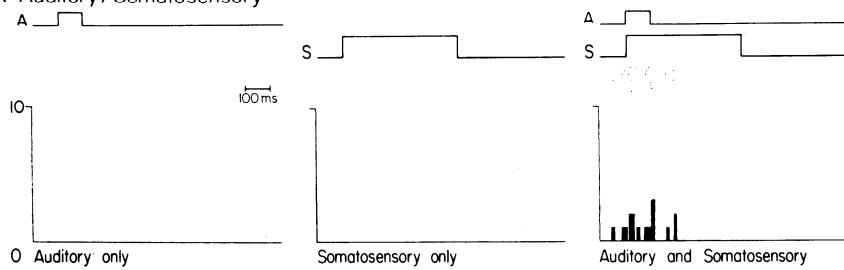


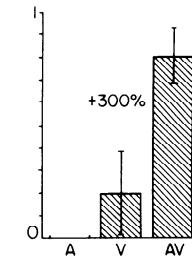
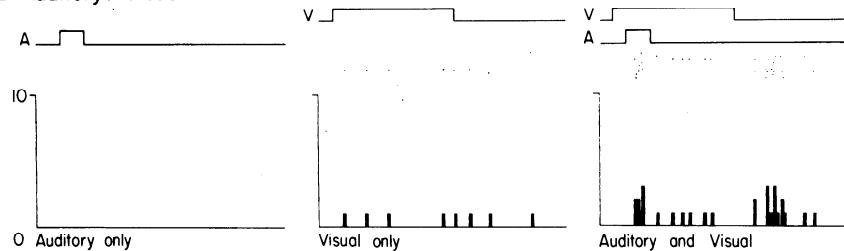
FIG. 4. Response enhancement was generated by combining somatosensory and visual stimuli. *A*: vigorous discharges are evoked by a somatosensory stimulus that displaced guard hairs (square wave "S", 400 mm/s) or (*B*) by a moving visual stimulus (ramp "V") ($1 \times 3^\circ$, velocity = $13^\circ/\text{s}$) alone, and their combination produces even more vigorous activity (*C*). This response enhancement represents a 75% increase (*D*) ($P < 0.01$) in the number of impulses elicited.

Trimodal cell:

A Auditory/Somatosensory



B Auditory / Visual



C Somatosensory / Visual

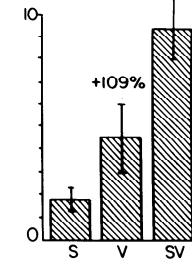
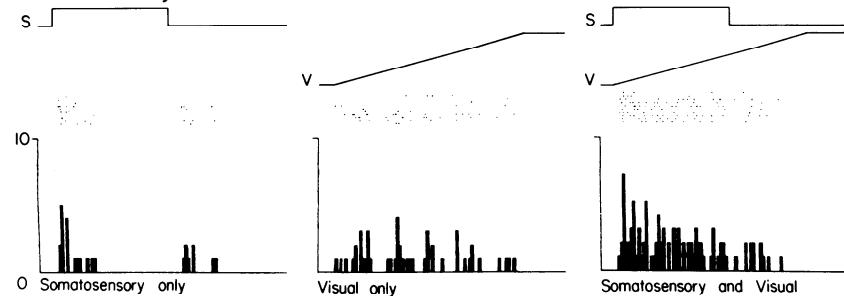


FIG. 5. Response enhancement in a trimodal cell that could be produced by any combination of auditory, somatosensory, and visual stimuli. *A*: although the auditory (duration = 100 ms, <60 dB SPL) and somatosensory (guard hair displacement, velocity = 275 mm/s) stimuli presented alone were insufficient to activate the cell, combining them evoked responses on 8/10 stimulus presentations. As indicated by the bar graph, these subthreshold inputs from the different modalities interacted to generate a suprathreshold response (percent enhancement is infinite). *B*: subthreshold auditory (100 ms; <60 dB SPL) stimulus is paired with a weakly effective visual stimulus ($6 \times 10^\circ$, flash duration = 500 ms), and their combination generated a 300% response enhancement. *C*: an effective somatosensory stimulus (same stimulus as in *A* but located in a different position of the receptive field; velocity = 275 mm/s) or a moving visual stimulus ($2 \times 4^\circ$, velocity = 55°/s) each activated the cell when presented alone. However, combining the somatosensory and visual stimuli increased response reliability to 100% and evoked a significantly more vigorous response (109%).

Fig. 6, where combined auditory and visual cues evoked substantially fewer impulses than elicited by the visual (the most effective single-modality stimulus) stimulus alone. The majority of cells ($n = 21/27$; 78%) exhibiting response depression to combined-modality stimuli appeared to be influenced by stimuli from only one modality in single-modality tests. Among the cells studied, auditory stimuli

most often effected response depression ($n = 22/27$; 81.5%), but the phenomenon was also produced by all modality combinations. As was true for a few cells exhibiting response enhancement (see above), multisensory properties were apparent here only during combined-modality tests during which the inhibitory influence of a seemingly "ineffective" stimulus became evident. Although it is reasonable to

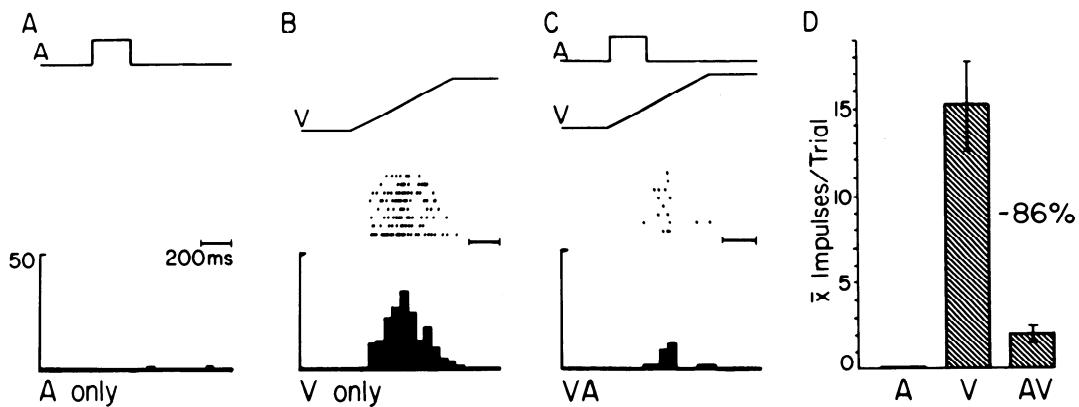


FIG. 6. Responses to a visual stimulus can be depressed by the presence of an auditory stimulus. *A*: an auditory stimulus (A) (duration = 200-ms broad-band noise burst, <60 dB SPL) presented in contralateral auditory space failed to activate this cell. On the other hand, a visual stimulus (V) ($5 \times 10^\circ$ dark bar, velocity = $100^\circ/\text{s}$) moved through the visual receptive field evoked a vigorous discharge on every presentation. Combining the auditory and visual stimuli (C) produced a significant ($P < 0.001$) reduction (-86.2%) in the number of discharges evoked by the visual stimulus (D).

assume that the apparently ineffective stimulus had an inhibitory influence on the cell's activity when presented alone, the absence of spontaneous activity in these cells precluded observing it. On the other hand, in six cells ($n = 6/27$; 22%), response depression was evident during combined-modality tests even though each of the stimuli could excite the cells when it was presented alone. In these cases, excitatory responses to one stimulus modality appeared to be followed by a period

of postexcitatory inhibition. During combined-modality stimulation the postexcitatory inhibition profoundly depressed the cell's response to any stimulus. In Fig. 7, a cell responds to a somatosensory stimulus with a brief excitatory response followed by a powerful inhibitory period, and also showed a delayed inhibitory response to a visual stimulus. The activity of the cell was depressed even further when combined visual-somatosensory stimuli were presented (Fig. 7C).

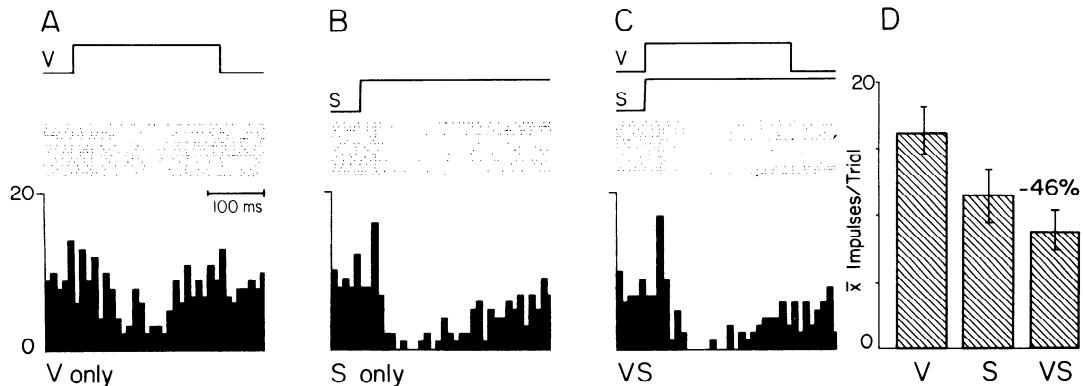


FIG. 7. Spontaneous activity of this cell was diminished by the presence of (*A*) a visual (V) ($2^\circ \times 5^\circ$, 275 ms-flash) or (*B*) a somatosensory (S) (velocity = 260 mm/s) stimulus (after a brief period of excitation to the somatosensory stimulus), and their combination (*C*) produced even greater suppression. This response depression was apparent as a significant ($P < 0.05$) reduction (-46%) in the number of impulses elicited (D).

Variation of the magnitude of response interactions

The degree of response interaction varied widely among cells and for those exhibiting response enhancement the percentage change ranged from +20.1% to infinity (see Fig. 5A). These percentage changes appeared to be inversely related to the vigor of the responses

evoked by single-modality stimulation. When weakly effective stimuli were combined a proportionately greater increase in activity was produced than that by combinations of more effective stimuli. This will be apparent by comparing Figs. 2 and 4. The cell in Fig. 2 exhibited a weaker response to single-modality stimuli than that in Fig. 4, but showed a con-

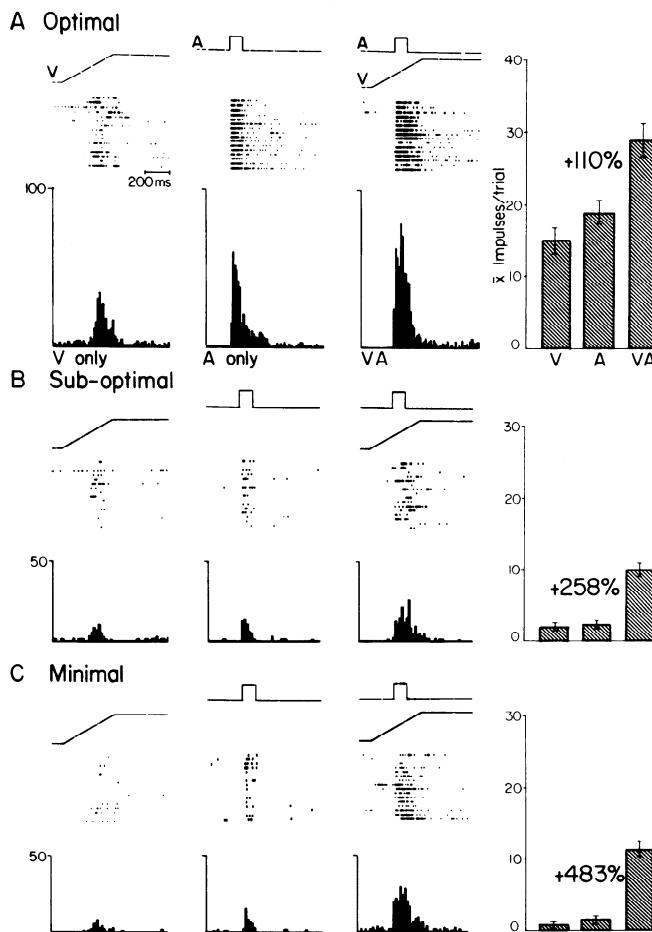


FIG. 8. Different magnitudes of response interaction can be elicited within the same cell by varying the effectiveness of the individual stimuli. As the physical parameters of the single-modality stimuli are systematically changed [e.g., size of visual stimulus (V), intensity of auditory stimulus (A)] so that progressively fewer discharges are evoked, the percentage of response enhancement produced by combining the stimuli increases. In A, B, and C the size of a moving visual stimulus (velocity = 115°/s) was progressively reduced (A, $2 \times 4^\circ$; B, $1 \times 1^\circ$; C, $0.5 \times 0.5^\circ$), and produced reductions in the number of discharges that corresponded to the reductions in stimulus size. Likewise, in A, B, and C the intensity of an auditory stimulus was progressively reduced by lowering the flow rate of air through a constricted tube. These reductions in airflow produced changes in sound intensity and elicited a progressive decrement in the number of impulses evoked by the auditory stimulus alone in A, B, and C. Combining these same stimuli (e.g., "optimal" visual with "optimal" auditory in A) generated response interactions under each condition, although the vigor (number of impulses) of the interaction was different in each case. As can be seen by comparing bar graphs in A, B, and C, there tended to be an inverse relationship between unimodal effectiveness and the percentage of enhancement evoked by combining those same stimuli.

siderably greater (1,207 versus 75%) level of response enhancement. Conversely, the neuron illustrated in Fig. 4 responded with many discharges to both single-modality tests (Fig. 4, A and B), but combined-modality stimulation generated a relatively low degree of response enhancement (75%, Fig. 4C).

To examine whether relative increases in activity are intrinsic properties of specific cells or can be attributed to the effectiveness of the stimuli presented, the following tests were administered. First, the stimuli that evoked the most vigorous responses were determined for each effective modality, and single and combined-modality tests were conducted using these optimal stimuli. Next, a single parameter of each of the stimuli was systematically altered (e.g., size of a visual stimulus, intensity

of an auditory stimulus, etc.) so that the numbers of impulses evoked in single-modality tests were progressively reduced until the single-modality cues were just above threshold. In the example illustrated in Fig. 8, this produced a progressive increment, from 100 to 438%, in the interaction generated. Similar results were obtained in other cells with other stimulus combinations and these data indicate that, for a given cell, the percentage of response enhancement is related to the effectiveness of the single-modality stimuli in an inversely proportional fashion. In contrast, the degree of response depression (range of -25.3 to -91.4%) appeared to be directly dependent on the efficacy of the depressing stimulus. However, since the depressive effect of most stimuli could be observed only when presented in

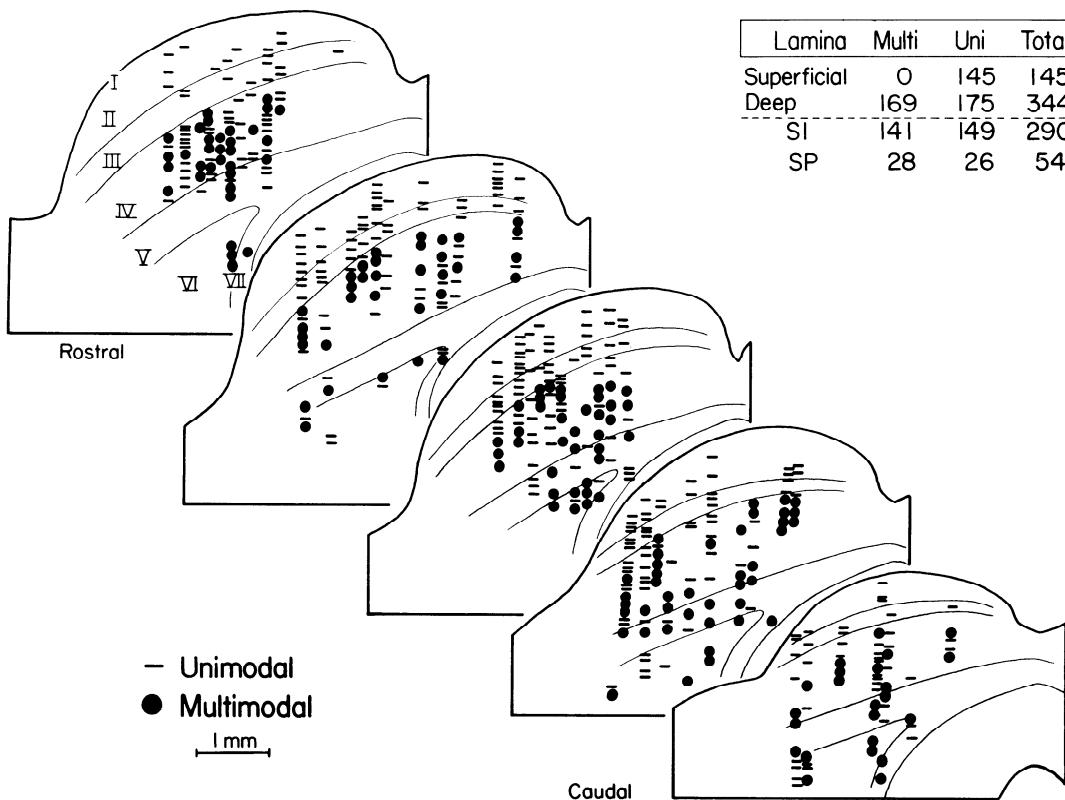


FIG. 9. Location of the neurons identified in this study are plotted on representative sections taken at 600–800 μm intervals through the superior colliculus (SC). Closed circles indicate the location of multimodal cells, and dashed lines represent the location of unimodal cells (includes 35 unresponsive cells). Roman numerals identify the laminae of the SC. Table (upper right) shows the frequency where multimodal and unimodal cells were encountered in the different laminae. Note the absence of multimodal cells in the superficial laminae. SS, superficial strata (laminae I, II, and III); SI, stratum griseum and stratum album intermediale (IV, V); SP, stratum griseum and stratum album profundum (VI, VII).

combination with an excitatory stimulus (especially when a cell had little spontaneous activity), it was difficult to relate the physical properties of a depressing stimulus to the degree of depression it evoked when presented alone.

Distribution of cells

The location of each cell studied was plotted (Fig. 9) and the distribution of these cells within the SC was evaluated, according to the laminae, rostrocaudal, and mediolateral distribution. Except for the well-documented superficial/deep laminae dichotomy of visual and nonvisual representations, the distribution of cell types in the SC showed only a limited tendency for unequal distributions (see below), and all regions of the SC contained all cell types.

DISTRIBUTION OF MODALITIES. Visually responsive cells were found in all laminae, but

decreased in frequency with increasing depth in the SC. Yet, as shown in Fig. 10A, visually responsive cells predominated throughout the rostrocaudal and mediolateral extent of the deep SC laminae. Responses to auditory and/or to somatosensory stimuli were observed only in the deep laminae and increased in frequency with increasing depth. Similar proportions of auditory cells were encountered throughout most of the SC, dipping slightly in its lateral and caudal aspects. On the other hand, the percentage of somatosensory cells increased from rostral to caudal. Nonresponsive cells were encountered infrequently throughout the SC (Fig. 10A).

DISTRIBUTION OF MULTIMODAL CELLS. Multimodal cells represented nearly half the cell population ($n = 169/344; 49\%$) in the deep laminae and were encountered in all but one electrode penetration (see Fig. 9). Despite dif-

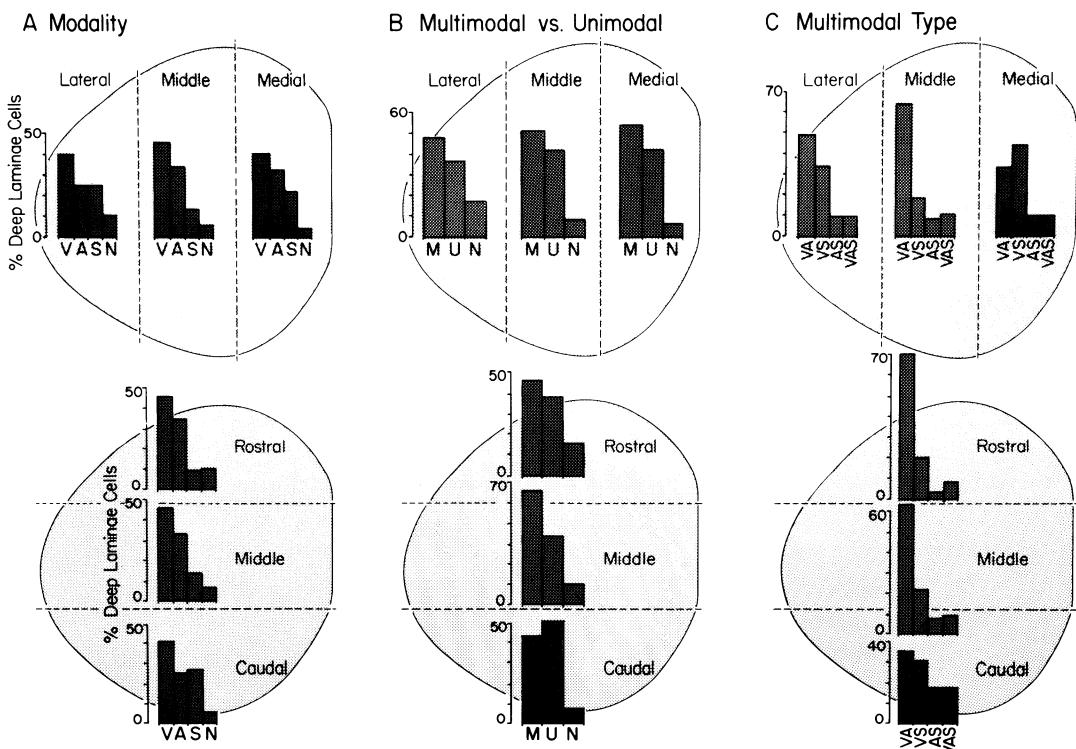


FIG. 10. Mediolateral (top) and rostrocaudal (bottom) distribution of deep laminae cells according to their modality (A), multimodal/unimodal nature (B), and pattern of modality convergence (multimodal type) (C). In a schematic representation of the dorsal surface of the superior colliculus (SC), the proportion of cells in a given region (SC divided into thirds) showing a particular property are plotted as a bar graph in that region. V, visual; A, auditory; S, somatosensory; N, unresponsive; M, multimodal; U, unimodal.

ferences in the numbers of multimodal cells in the stratum griseum intermediale/stratum album intermediale (collectively referred to as strata intermedium = SI) ($n = 141/290$) and stratum griseum profundum/stratum album profundum (strata profundum = SP) ($n = 28/54$), they constituted nearly identical proportions of cells in each (SI = 49%; SP = 52%).

As shown in Fig. 10B, multimodal cells predominated in all areas of the SC except its caudal-most region, with visual-auditory cells (see Fig. 10C) constituting the greatest proportion of multisensory cells in nearly every region. The proportion of cells that demonstrated interactions of any form, (e.g., enhancement or depression) was nearly equal in SI and SP throughout the SC.

Multisensory cells are SC efferents

Antidromic activation via stimulation of the LEB and MEB was attempted in 204 cells (see Fig. 11C for examples of stimulation sites).

Few of the superficial laminae cells ($n = 3/49$) responded to antidromic stimulation, but almost half ($n = 72/155$; 46%) of the deep laminae cells were identified as efferent using these tests. The two cells illustrated in Fig. 12 are representative of the majority of efferent SC cells encountered. These cells were activated by stimulation of one (Fig. 12A) or both (Fig. 12B) of the descending efferent bundles; both cells responded to sensory stimuli and exhibited multisensory response interactions. As shown in the table in Fig. 13, nearly all efferent cells demonstrated sensory responses ($n = 69/72$; 96%) and almost three-fourths of them ($n = 51/72$; 71%) were influenced by more than one sensory modality. In contrast, unimodal cells constituted the majority ($n = 55/83$; 66%) of those that failed to be activated by antidromic stimulation.

It could not be predicted on the basis of modality-specific response properties whether a given cell was a descending efferent. Regardless of the pattern of convergence, 54% of

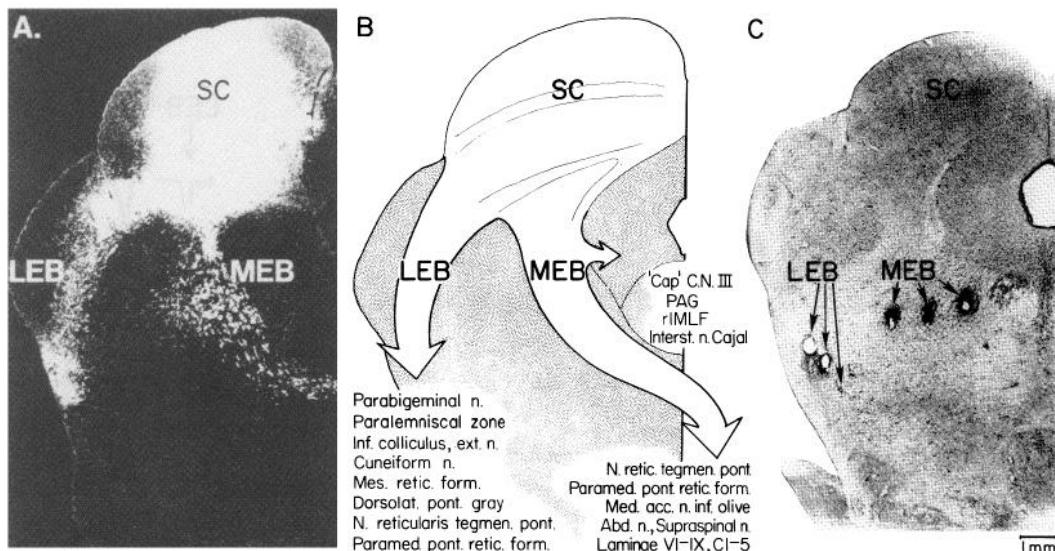
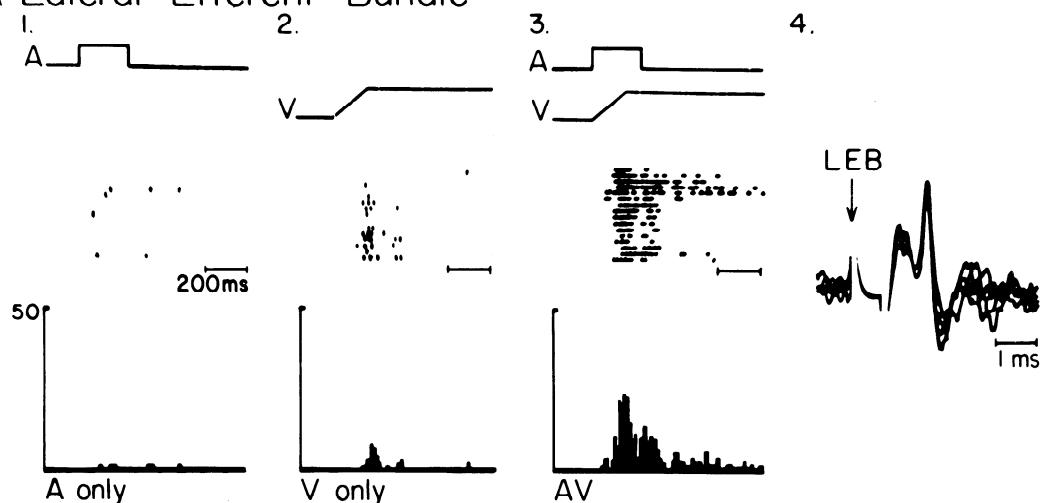


FIG. 11. Descending efferent projections and connections of the deep SC laminae. *A*: dark-field photomicrograph showing the two descending efferent pathways labeled with tritiated leucine [MEB, medial efferent bundle (that becomes the tectospinal tract); LEB, lateral efferent bundle] as they exit the SC and course toward their brain stem and spinal cord targets. *B*: targets of the descending efferent bundles (see Ref. 34, 50, 59) are listed. *C*: SC neurons with descending efferent axons were antidromically activated by electrical stimulation delivered through arrays of implanted electrodes, reaching the bundles via a caudal-to-rostral approach through the cerebellum and the brain stem tegmentum. Tips of the electrodes were spaced ~ 1 mm apart in the A-P and M-L planes to allow the delivery of discrete electrical stimuli at a variety of points within each of these efferent SC pathways. *C*: photomicrograph illustrates the most caudal point where the electrical stimuli were presented (note that the hole made by the most medial LEB electrode is barely visible) and the tips of the remaining electrodes ascended the brain stem ventral to the SC for as far as 1 mm anterior to the section shown here (corresponding to the level depicted in *A*).

A Lateral Efferent Bundle



B Medial and Lateral Efferent Bundles

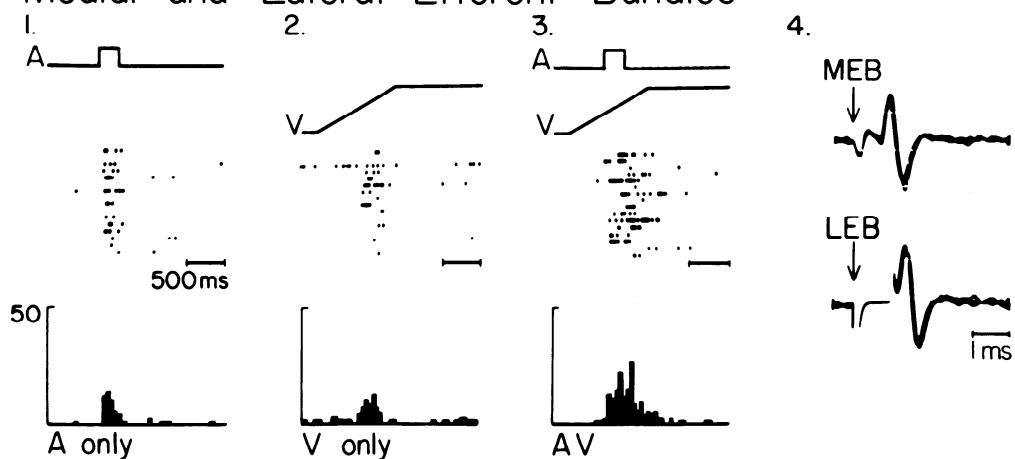


FIG. 12. Superior colliculus (SC) cells with descending efferent projections integrate multisensory inputs. The majority of multisensory cells had axons that exited the SC by way of the lateral efferent bundle (LEB) or medial efferent bundle (MEB). Examples shown here were typical of this population. *A*: weakly effective auditory (A) and visual (V) stimuli, when combined, produced a significant response enhancement in this cell, which was also antidromically activated by electrical stimulation (arrow) of the LEB ($2 \times$ threshold current ($120 \mu\text{A}$); 0.1 ms ; $n = 5$). MEB stimulation was ineffective, even at high current intensities ($>600 \mu\text{A}$). *B*: a cell exhibiting similar response enhancement is antidromically activated from either descending efferent bundle (MEB = $2 \times$ threshold current $95 \mu\text{A}$; 0.1 ms ; $n = 5$; LEB = $2 \times$ threshold current, $110 \mu\text{A}$; 0.1 ms ; $n = 5$).

the efferent cells received visual inputs, 59% received auditory inputs, and 50% received somatosensory inputs. Similarly, the specific response properties of visual (e.g., direction selectivity, velocity selectivity, response to moving versus stationary light), auditory (e.g., binaural properties, receptive field type, or size), and somatosensory (e.g., receptor type,

receptive field location, or size) cells were distributed in similar proportions among the efferent and nonefferent populations.

Efferent cells were encountered throughout the rostrocaudal extent of the SC, as shown in Fig. 13 and cells were identified with similar frequency in SI ($n = 61/132$; 46%) and SP ($n = 12/23$; 51%), with multimodal cells constitut-

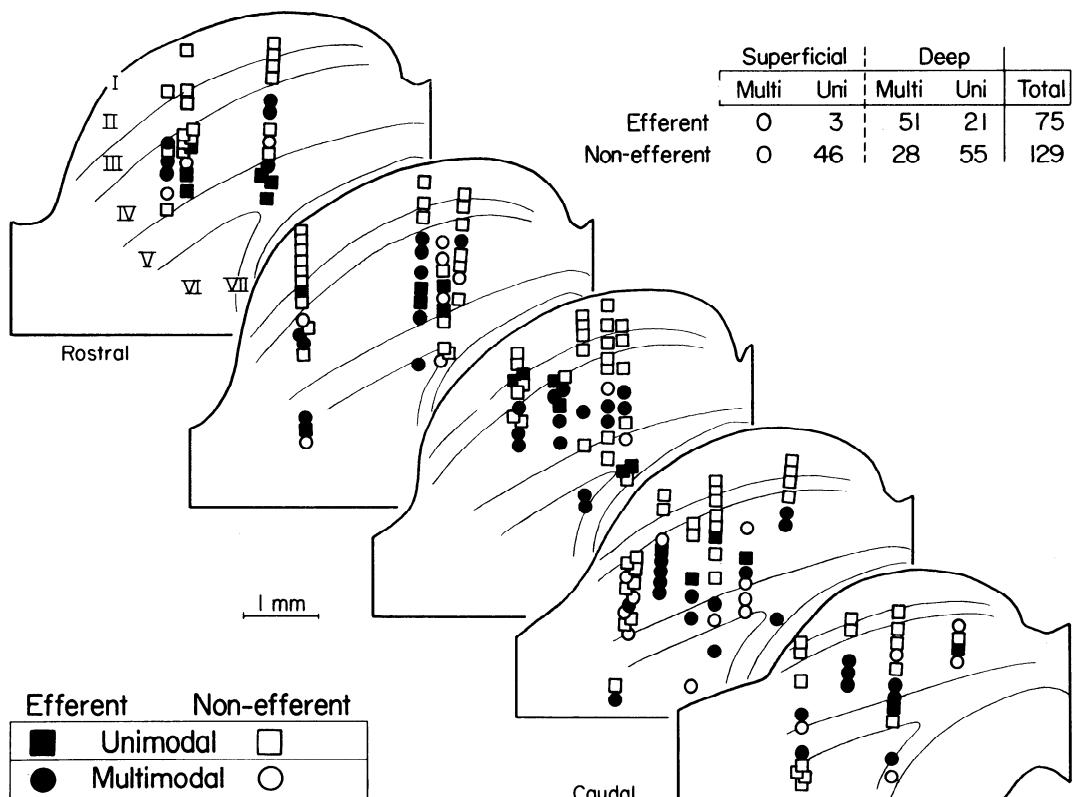


FIG. 13. Location of neurons that were evaluated for their descending efferent projections are plotted on representative sections taken at 600- to 800- μm intervals through the superior colliculus (SC). All cells depicted here are also included in Fig. 9. Closed circles and squares represent multimodal and unimodal (includes 14 unresponsive) cells, respectively, that were antidromically activated through the medial efferent bundle (MEB), lateral efferent bundle (LEB), or both. Open symbols represent cells where no descending efferent projections could be demonstrated (nonefferent). Roman numerals identify the SC laminae. Table in the upper right shows the frequency where multimodal and unimodal cells were identified as descending efferents.

ing the majority of efferents in each ($SI = 71\%$; $43/61$; $SP = 73\%$; $8/11$). The majority of efferent cells (73%) were activated by electrical stimulation of the MEB, whereas a smaller proportion (43%) via the LEB and only a few (16%) by both the MEB and LEB. However, this difference may only reflect the efficacy of stimulating one bundle over the other, or an electrode bias if neurons projecting in one bundle differ in size from those in the other rather than an actual distinction in the routes of specific efferent cells.

These data indicate that the majority of the output cells of the SC with descending projections are multisensory. Furthermore, the majority of such efferent cells exhibit multimodal interactions; thus their responses and their influences on premotor and motor cells of the

brain stem and spinal cord, are determined by the complex of multisensory stimuli present.

DISCUSSION

The present study demonstrates that individual neurons not only receive convergent inputs from different sensory modalities, but also integrate those inputs to provide a dynamic response flexibility. The interactions generated by multisensory integration are powerful enough to produce vigorous responses to stimuli that are only minimally effective when presented alone, or to eliminate the discharges normally evoked by an effective unimodal stimulus. Neurons in the deep laminae of the SC were used to evaluate the process of multisensory integration, and a description of

their response properties, patterns of convergence, interactive nature and possible functional roles are described below.

Modality-specific properties and multisensory convergence in deep SC

The distribution, response properties, and receptive field characteristics of cells activated by visual, auditory, and somatosensory stimuli were in general agreement with those of previous reports (e.g., 40, 52, 77, 80, 99, 102, 104, 115, 118). The majority of visually responsive cells were binocular and preferred stimuli that were substantially smaller than their receptive fields and that moved in a specific direction at velocities $> 10^\circ/\text{s}$. Most neurons that were sensitive to auditory stimuli were activated by a contralateral stimulus, had a "best" area within the receptive field, exhibited a train of discharges to an auditory stimulus, and received contralateral excitatory and ipsilateral inhibitory inputs. The presence of a train of discharges in auditory cells contrasts with several earlier findings in which few impulses could be evoked by an auditory stimulus (53, 118), but this discrepancy may be due to the difference in anesthetics used. Cells responsive to somatosensory stimuli were activated by displacement of hair or skin located primarily on the contralateral body surface and responded most vigorously to high-velocity stimuli in a transient manner even to maintained stimuli. These properties of visual, auditory, and somatosensory responses had similar distributions among unimodal and multimodal cells.

One of the striking features of the deep laminae is their rich endowment of cells receiving inputs from two or more sensory modalities, which, in the present study, represented $\sim 50\%$ of the sample. Yet estimates of the incidence of multisensory convergence based on current techniques are almost certainly gross underestimates, not only because a weakly effective modality may be overlooked even when it is included in the tests to which a cell is subjected, but also because certain sensory stimuli are rarely presented in these tests (e.g., vestibular, proprioceptive, noxious).

The presence of different types of multisensory cells (e.g., visual-auditory, visual-somatosensory, etc.) is characteristic of the SC in the various mammals that have been stud-

ied (1, 17, 25, 28, 30, 31, 36, 40, 41, 43, 54, 62, 66, 70, 71, 74, 76, 100–105, 109, 115) as well as in the nonmammalian homologue of the SC, the optic tectum (9, 39, 45–49, 67, 82). Cell types, convergence patterns, and incidence of multisensory cells in the midbrain appear to vary in different species and seem to reflect ecological distinctions. For example, somatosensory-visual cells predominate among multisensory cells in the rodent (31, 109), where the exquisitely organized vibrissal system is a significant aid to orientation and object identification, whereas visual-infrared cells are common in rattlesnake, a species that uses thermal cues to facilitate location and capture of warm-blooded prey (48, 82). In the present study (see also Ref. 115), the predominant multisensory cell type was visual-auditory in an animal (cat) that relies heavily on these sensory modalities for orientation and localization behaviors.

Although multisensory visual receptive fields are significantly larger than those of deep laminae unimodal visual cells and multisensory cells are distinct from unimodal cells when combinations of stimuli are present, they are quite similar in all other ways; the distribution and modality-specific features of multisensory cells cannot be distinguished from those identified as unimodal. Presumably then, and at least for the modalities evaluated in the present study, there is no differentiation of the various sensory afferents destined for deep laminae unimodal or multimodal cells.

Multisensory convergence: physiological consequences

The functional consequences of multisensory convergence are dramatically evident when two different sensory stimuli are present, and clearly distinguish multisensory cells from their unimodal neighbors. Two interactions were observed to result from multisensory convergence: 1) response enhancement, and 2) response depression. Response enhancement usually was observed in cells that could be activated by either of the stimuli (i.e., one of the individual modality components of a multisensory stimulus) presented alone, whereas most cells exhibiting response depression did so when an effective stimulus was paired with the one having no apparent influence. In both cases multisensory inter-

actions did not represent a simple sum of the activity elicited by the two stimuli alone, but showed a multiplicative relationship. It is important to note that any significant change in response during combined-modality stimulation from that evoked by the most effective single-modality stimulus was attributed to the presence of the two stimuli and, therefore, represented a multisensory interaction.

Although the effects of intramodal interactions (e.g., binocular, binaural), as well as some multimodal interactions (64, 66, 82, but also see 6, 32, 33), have been classified using such terms as inhibition, occlusion, summation, and facilitation, this nomenclature has been avoided here. Manipulation of the physical properties of the same stimuli produces interactions within the same cell that can fall into all of these categories and "inhibition" (response depression) and "occlusion," "summation" and "facilitation" (response enhancement) appear to reflect levels of multisensory interactions along the same continuum.

The magnitude of response interaction varied widely among cells and within the same cell with different stimulus parameters. In addition, the cells examined had very different response levels (i.e., number of impulses evoked). To compare interactions among these cells, the product of an interaction was calculated as a percentage of responses to the most effective unimodal stimulus. Despite the wide variability among responses there was a consistent inverse relationship between the percent response enhancement a stimulus produced when combined with another and its effectiveness when presented alone. Therefore, pairing weaker unimodal stimuli produced proportionately greater response enhancements than pairing more effective unimodal stimuli. Intuitively, this relationship seems reasonable. If a unimodal stimulus is highly effective, it is likely to produce a response via the SC, and the enhancing influence of a stimulus from another modality may be quite negligible. On the other hand, response interactions may serve to amplify the effects of minimal stimuli to increase the probability that a response will be elicited even when individual cues are near threshold.

It is unlikely that random interactions among modalities could provide the nervous system with meaningful information about the

external world. Rather, for any given cell or population of cells, these interactions must follow specific rules that are predicated on the physical properties of the external stimuli and their relationships to one another. In this way similar interactions will occur in these cells when the same stimulus conditions are present. That these effects did not reflect some generalized arousal or depressive phenomena was apparent because the position of the stimuli with respect to a cell's multisensory receptive fields was critical. In addition, neighboring unimodal or multimodal cells of a different type demonstrated no response interactions with these same stimulus combinations. Preliminary observations (75, 81) indicate that at least two specific stimulus factors, temporal and spatial, are critical in determining 1) whether enhancement or depression results from a multisensory stimulus combination, and 2) the magnitude of the resultant interaction.

Multisensory SC cells have descending efferent projections

Even though the activity of deep laminae cells under multisensory stimulus conditions differed from that of premotor cells of the SC by being time locked to the onset of the stimulus rather than to the onset of a (putative) motor response (e.g., an eye movement) (78), multisensory cells are likely to be intimately involved in SC-mediated behaviors. SC-mediated orientation and localization responses are effected through the descending efferent projections of deep laminae cells to premotor and motor areas of the brain stem and spinal cord (34, 42, 44, 50, 59). A comparatively simple way for these descending efferents to influence orientation responses, based on the sensory input that reaches the SC, is by integrating this sensory information. In the present study >90% of the cells identified as descending efferents also responded to sensory stimuli (see also 1, 16, 26, 79, 87) and >70% were multisensory. The sensory involvement of these cells, coupled with their presumptive role in motor responses, make it seem likely that they play an integral part in SC-mediated sensorimotor transduction.

The observation that widespread multisensory convergence takes place on descending output cells of the SC suggests that the cells influencing the movement of a given sensory

organ (e.g., eye movement) are themselves affected by many different sensory inputs (e.g., visual, auditory, somatosensory). This same conclusion was reached by Jay and Sparks (63), who showed that presaccadic-burst cells in the monkey SC are activated by visual as well as auditory stimuli. The present data are also consistent with the speculation that coordinated movements of the different sensory organs are produced via the SC because each of the sensory modalities has access to the same efferent circuits (104). This would be accomplished most readily by the collateralization of individual multisensory efferent fibers to the various premotor and motor areas that control the different sensory organs. Recent experiments by Grantyn & Grantyn (44) demonstrated that such collateralization is characteristic of at least one population of deep laminae cells, tectobulbo-spinal neurons.

Multisensory convergence/integration in the CNS

The observation that multisensory interactions often determine the final output signal of SC cells indicates that a given unimodal stimulus need not be immutably linked to a given SC-mediated response; rather, SC-mediated behaviors should vary depending on the context in which that stimulus is present. Pooling excitatory inputs from two or more sensory modalities may markedly increase the likelihood that an orientation response will be evoked by otherwise minimally effective stimuli. Alternatively, inhibitory interactions in SC cells might decrease the probability that responses will be elicited under certain conditions. The specific multisensory stimulus parameters that determine the nature of the interactions and the resultant overt behaviors are currently being investigated.

It is doubtful that the multisensory interactions described here in cat SC cells are unique to this species or structure. The SC is only one of many CNS structures containing multisensory cells. Inputs from different sen-

sory modalities (exteroceptive, enteroceptive, or both) have been demonstrated to converge on cells in the cerebral cortex (12, 13, 15, 20, 22, 27, 32, 33, 35, 37, 53, 60, 64, 68, 69, 72, 88–90, 92, 95, 97, 108, 110, 111, 114, 119), thalamus (3, 7, 14, 18, 23, 24, 56–58, 85, 113), hypothalamus (29), basal ganglia (51, 96, 106, 117), hippocampus (86), inferior colliculus (2, 107), reticular formation (4, 11, 93), cerebellum (5, 6, 8, 38), and primary sensory nuclei (19, 55, 61). This phenomenon also occurs broadly across phylogeny and has been documented in primates (28, 88, 89, 112), cats (4, 23, 69, 102), rodents (25, 30, 55, 66, 116), birds (9, 67), reptiles (39, 47, 48, 82), amphibia (5, 6, 45, 46), fish (49, 84, 94), and invertebrates (83, 91). On the basis of single-unit (7, 10, 12, 17, 20, 30, 32, 33, 35, 53, 56, 57, 64, 66, 70, 74–76, 81, 82, 94) studies in which multisensory interactions were observed, it is reasonable to conclude that multisensory integration is a ubiquitous neurological phenomenon that may represent a basic mechanism by which the brain integrates complex environmental stimuli. Whether the rules governing the nature of these interactions supersede species and structure remains to be determined. However, regardless of the principles by which different multisensory cells deal with their various inputs, it seems likely that the results of their combined activity will have profound influences on perception as well as on overt behavior.

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