

CHAPTER 8

# The visually responsive neuron and beyond: multisensory integration in cat and monkey

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## Introduction

Vertebrates possess an impressive array of highly specialized senses for which unique peripheral organs have evolved. The eye, with its ability to orient to external stimuli in ballistic fashion and to adapt to a wide range of changes in illumination, is a marvel of bioengineering. Its sensory receptors, like those in each of the other peripheral sensory organs, have evolved to transduce only specific kinds of environmental energy into the neural code used by the brain to detect and interpret external events. By being tuned to a different form of energy, each sensory system provides the organism with a different "view" of the world. These different views extend to the sensory impressions produced by activating one receptor system or another. Once the peripheral receptors of a given sensory modality provide input signals to the nervous system, events transpiring along its sensory pathway lead ultimately to a distinct perceptual experience, and there is no way to effectively compare among the sensory experiences from different modalities. Hue, pitch and tickle, for example, are experiences unique to the visual, auditory and somatosensory systems, respectively. Each exists as an independent experience without counterpart in any other modality.

Yet, despite the presence of subjective features unique to each modality, the brain is able to integrate the information derived from different

modalities into a meaningful reflection of its complex sensory environment. As one would expect of an integrative process, inputs from one sensory modality often alter the processing of information in another (see Welch and Warren, 1986, for a recent review). This can increase or decrease the effectiveness of specific sensory cues and enhance behavioral flexibility. Through the process of integration, multisensory stimulus complexes can take on meaning that their individual unimodal stimulus components do not have. Although much of what we are concerned with here pertains to higher mammals, the presence of multisensory processing per se antedates mammals, and even antedates the evolutionary invention of the nervous system. It is already present in unicellular organisms (e.g., paramecia, see Naitoh, 1968; Eckert et al., 1972) and appears to have been retained throughout multicellular speciation. It is present not only in comparatively simple organisms (e.g., flatworms, see Koopowitz et al., 1979), but also in the higher primates, and at all intervening levels of complexity. In fact, we know of no animal in which there exists a complete segregation of sensory processing.

It may seem surprising, then, that despite a voluminous literature dealing with the modality-specific properties of neurons at all levels of the nervous system in many different species, we remain largely ignorant of the processes by which simultaneous inputs from different modalities are dealt

with collectively. In large part this is because investigators interested in the properties of sensory neurons study them in laboratory conditions designed to minimize the possibility that extraneous stimuli can confound results. This strategy has provided a wealth of sensory data and a good deal of insight into problems of perception and sensorimotor behavior, as evidenced by much of the work reported in this symposium concerned with "the visually responsive neuron". However, because many areas of the brain that receive visual inputs also receive converging non-visual input, the visually-responsive neuron may also be an auditory and/or somatosensory-responsive neuron. Consequently, to understand its functional properties it is necessary to examine its responses to different sensory stimuli and to combinations of these stimuli. While multisensory convergence is especially prevalent outside the primary projection pathways, it is by no means unknown within seemingly dedicated unimodal regions such as the dorsal column nuclei, vestibular nuclei, and even striate cortex (e.g., Jabbur et al., 1971; Morrell, 1972; Fishman and Michael, 1973; Waespe et al., 1981; Noda, 1981; see also Meredith and Stein, 1986a).

Perhaps the best known site of multisensory convergence within the visual system is the superior colliculus (Stein, 1984), and its non-mammalian homologue, the optic tectum (Hartline, 1984), structures that play an integral role in attentive and orientation behaviors. Visual, auditory and somatosensory inputs project to the deep layers of the superior colliculus and do so in topographic fashion. Thus, each sensory representation is map-like and all of the maps are in spatial register with one another (see Stein and Meredith, 1990, for a brief review). In this way a sensory cue, regardless of modality, activates neurons in the same general location in the superior colliculus: the location corresponds to the position of the stimulus in sensory space. Cues positioned forward in space (or on the front of the body) activate rostral neurons, cues above the animal or on its upper body activate medial neurons, and so on. This is not only an

economical way to represent sensory space, but it is also an efficient way to match incoming sensory information with outgoing "motor" information, for these sensory maps are also in register with the motor maps found in the deep layers (e.g., Stein et al., 1976; Harris, 1980; Stein and Clamann, 1981; Jay and Sparks, 1984; Sparks, 1989). Because many of the different sensory inputs converge on the same neurons, some trimodal neurons and many bimodal neurons (of all sensory combinations) are produced. A single multisensory neuron will have its two or three sensory receptive fields in spatial register with one another, and this intraneuron spatial register is likely to play a significant role in the overall alignment of the visual and non-visual maps found here (Meredith and Stein, 1990).

The typical visually-responsive superior colliculus neuron not only responds to inputs from non-visual modalities, but also integrates visual and non-visual information. The integration that occurs in response to combinations of visual and non-visual stimuli often results in a dramatic increase in the number of impulses evoked when compared with that elicited by either stimulus presented alone. This response enhancement is not merely a summation of the individual responses, but is a multiplicative increase in activity that can exceed 1200%. On the other hand, combinations of visual and non-visual cues can also evoke integrated responses that are significantly lower than those obtained from the individual stimuli. Although examples of response depression are not encountered as often as response enhancement, both forms of multisensory integration are frequently exhibited by the same neuron, as shown in Fig. 1.

The degree to which a non-visual stimulus can influence responses to visual stimuli varies not only from neuron to neuron, but can also change for a given neuron. The magnitude of these interactions is determined by a variety of factors inherent in the stimuli and the neurons themselves. The robust nature of these determinants of multisensory integration is so consistent that the determinants are referred to as "rules" for convenience.

### *The rules of multisensory integration*

(1) *Spatial factors.* As detailed above, the different receptive fields of a given multisensory neuron show a general spatial register. This spatial registry is a key determinant of the type of interaction that will be produced. For example, when a visual and an auditory stimulus originate from the same spatial location, they fall within the excitatory receptive fields of the same multisensory neuron. This combined stimulus enhances the neuron's responses far above that to either stimulus alone. If, however, the auditory stimulus originates from a location outside its excitatory receptive field, it can no longer enhance the neuron's activity, and if it falls within an inhibitory region, it will depress the neuron's responses to the visual stimulus (Meredith and Stein, 1986b).

(2) *Temporal factors.* The temporal "window" during which multisensory integration can take place is quite long (sometimes exceeding 1500 msec). Maximal interactive effects are produced during this window by overlapping the periods of maximal unimodal influence with one another. In this way simultaneous visual and non-visual stimuli often produce dramatic interactions despite their very different input latencies (Meredith et al., 1987).

(3) *Magnitude.* Multisensory interactions are multiplicative rather than additive. In the most dramatic examples, the combination of an ineffective visual stimulus and an ineffective auditory or somatosensory stimulus reliably evokes responses (Meredith and Stein, 1986a).

(4) *Inverse effectiveness rule.* Combinations of weak unimodal stimuli produce proportionately greater response enhancements than do combinations of strong stimuli. This indicates that multisensory enhancement is most effective when unimodal stimuli are poorly effective by themselves (Meredith and Stein, 1986a).

These observations have raised several additional questions. First, can a neuron's visual receptive field properties be affected by non-visual stimuli? And if so, what are the "rules" by which this is accomplished? Second, are the rules of multisensory integration specific to the superior colliculus of the cat, or

are they applicable to visually-responsive (or auditory-responsive and/or somatosensory-responsive) neurons in other structures and animals? These questions are addressed below.

### **Methods**

All procedures were performed in compliance with the *Guide for Care and Use of Laboratory Animals* (NIH publication no. 86-23) at Virginia Commonwealth University, which is accredited by the American Association for the Accreditation of Laboratory Animal Care. The methods for many of these experiments have been described in detail elsewhere (e.g., Meredith and Stein, 1986a), and are therefore described only briefly.

#### *Cat*

Recordings were made through a resealable recording well/head-holding device (see McHaffie and Stein, 1983) implanted 1 week or more prior to experimentation. The well was implanted over either the superior colliculus, the lateral suprasylvian (LS) cortex or the anterior ectosylvian sulcus (AES). For recording, anesthesia was induced with ketamine (30 mg/kg) and maintained with either ketamine (5–10 mg/kg per hour) or halothane (0.5–2.0%). Animals were paralyzed (pancuronium bromide, 10 mg/kg; 2–4 mg/kg per hour) and artificially respired. The optic discs were projected and focused onto a translucent plastic hemisphere and corrective contact lenses were applied. A calibrated X-Y slide was attached to the recording well to hold and guide the recording electrode (glass insulated tungsten, > 1 M $\Omega$  impedance). The location of each successful recording penetration was marked electrolytically and, after euthanasia (barbiturate overdose) and perfusion, reconstructed from histologically prepared sections.

Responses to unimodal (visual, auditory or somatosensory) stimuli were first established to determine which stimuli would be presented during tests for multisensory interactions. All quantitative sensory tests were then conducted using reproduci-

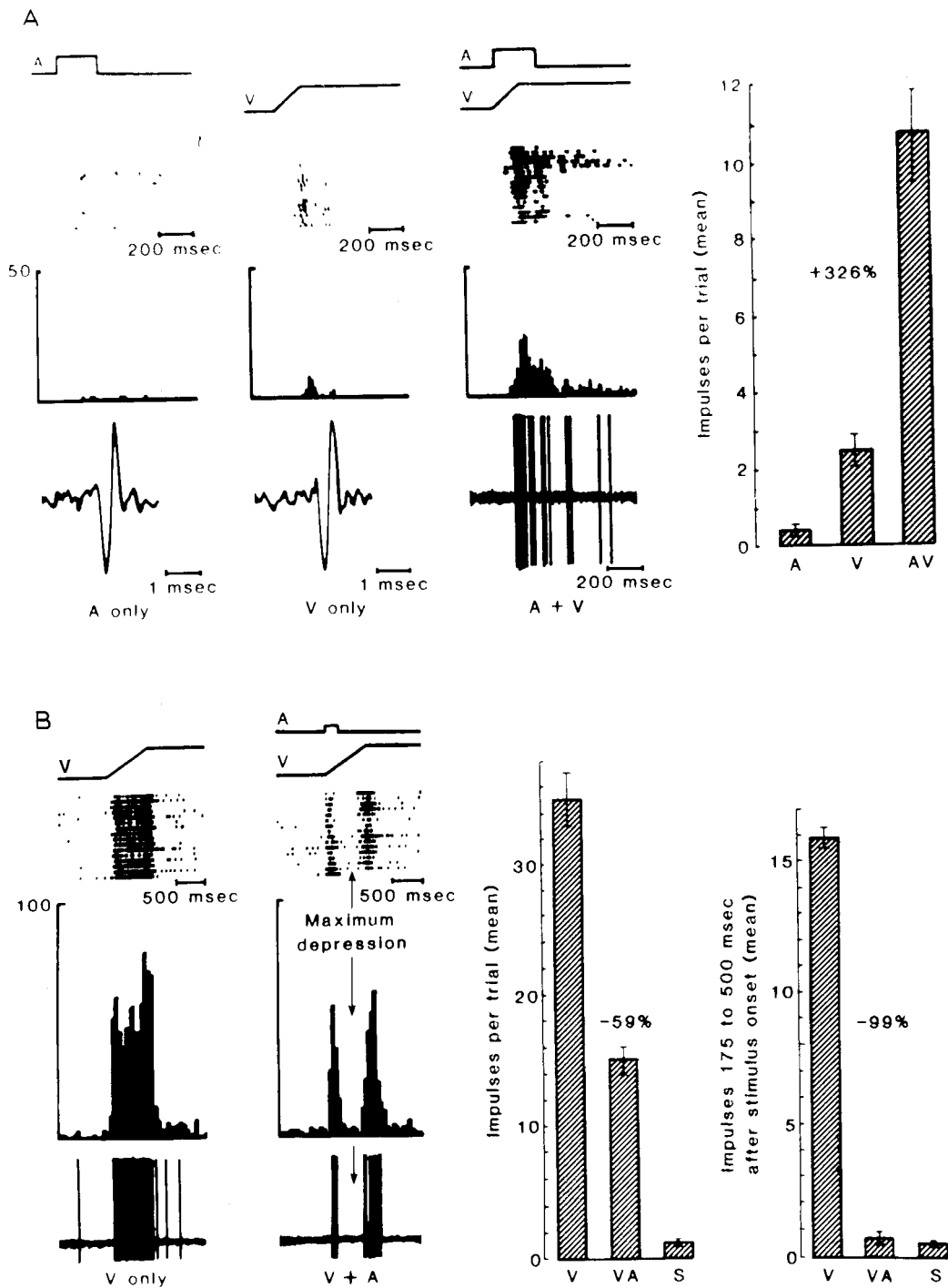


Fig. 1. *A*. Response enhancement in a bimodal (visual-auditory) neuron in cat superior colliculus. The auditory stimulus is represented by a square wave (A) and the visual stimulus by a ramp (V). The rasters below show the neuron's responses to 16 successive stimuli (each dot is one impulse). Matched peristimulus time histograms (bins = 10 msec) and oscillograms are shown below each raster. From left to right: few impulses were evoked by the auditory stimulus (200 msec, broadband noise burst) when presented alone. The visual

ble, electronically controlled stimuli initiated by a computer; the onset, duration and physical parameters of each stimulus are varied independently.

Once a neuron was isolated and its receptive field(s) mapped, multisensory tests were performed. Single-modality (e.g., visual alone, auditory alone) and multisensory (e.g., visual and auditory) stimuli were presented repeatedly (8–16 times) within their respective receptive fields in an interleaved manner at long interstimulus intervals (10–30 sec). Responses elicited by combining the stimuli were compared statistically (paired *t*-test) to those elicited by the single-modality presentations to determine if there was a significant ( $P < 0.05$ ) increase (response enhancement) or decrease (response depression) in the number of impulses. By using this manner of analysis, the total product resulting from a combination of stimuli is emphasized, and arbitrary, mathematically constrained categories (i.e., inhibition, occlusion, summation, facilitation) are avoided. The magnitude of the interaction is calculated as:

$$(\text{CM} - \text{SM}_{\text{max}}) / (\text{SM}_{\text{max}}) \times 100 = \% \text{ interaction}$$

where CM is the mean number of impulses evoked by the combined-modality stimulus, and  $\text{SM}_{\text{max}}$  is the mean number of impulses evoked by the most effective single-modality stimulus.

### Monkey

A monkey scheduled for euthanasia was obtained for terminal experimentation. The recording and stimulation paradigms were the same as in cat, but

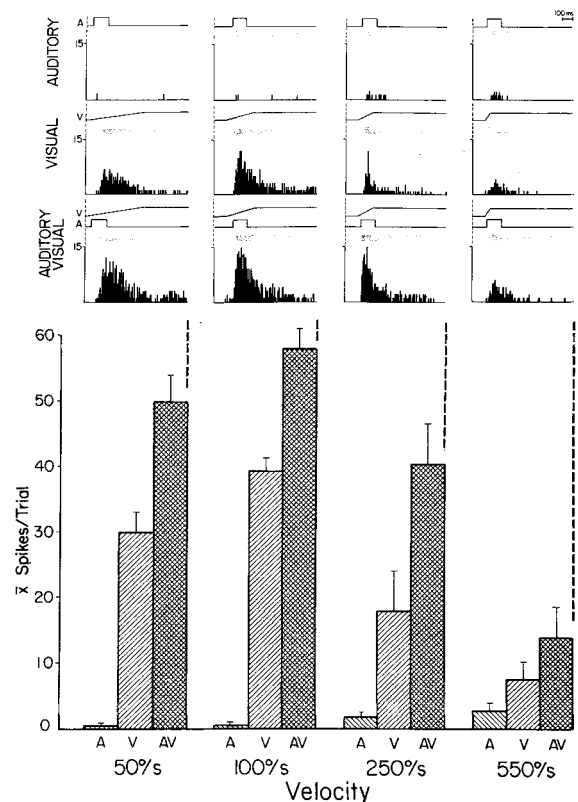


Fig. 2. Maintenance of velocity selectivity by a visual-auditory neuron in the superior colliculus during multisensory integration. As shown by the rasters and peristimulus time histograms at the top, an auditory stimulus was unreliable in activating this neuron, and generally evoked few impulses. In contrast, a moving visual stimulus was quite effective, and the neuron showed a reliable preference for movement at 100°/sec. When the auditory and visual stimuli were combined at each velocity, the auditory stimulus significantly ( $P < 0.001$ ) enhanced responses but did not alter velocity selectivity. This is most apparent in the graph at the bottom. Note that the relative velocity preferences remained despite the response enhancement induced by the auditory stimulus.

stimulus ( $1^\circ \times 2^\circ$  bar, moved at 300°/sec in the preferred direction across the receptive field) evoked impulses on 69% of the trials. When, however, the visual and auditory stimuli were presented in close temporal sequence, the combined stimulus evoked vigorous responses on every trial. Histogram on the right shows the mean response for each stimulus condition. The number of impulses evoked by the combined stimulus was significantly enhanced (paired *t*-test,  $P < 0.001$ ). Vertical lines represent standard errors of the mean. **B.** Response depression in a bimodal (visual-auditory) neuron in cat superior colliculus. From left to right: a  $2^\circ \times 4^\circ$  bar of light moved at 125°/sec evoked vigorous responses. However, no response was elicited by auditory or by somatosensory stimuli when presented alone. When an auditory stimulus (200 msec, broadband noise burst) was presented during visual stimulation, it significantly inhibited responses to the visual stimulus ( $P < 0.001$ ). The inhibitory effect was nearly complete from 175 to 500 msec after auditory onset. Peristimulus time histograms are calibrated for 100 impulses and 50 msec time bins. (Reproduced with permission from Meredith and Stein, 1983.)

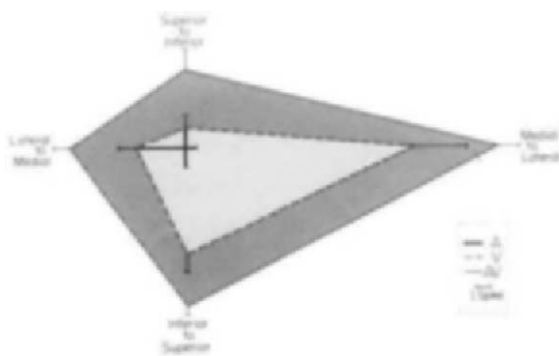


Fig. 3. Maintenance of direction selectivity by a visual-auditory neuron in the superior colliculus during multisensory integration. A polar coordinate plot illustrates the direction preferences of this neuron. The lengths of the lines reflect the mean number of impulses evoked (standard error bars are shown). The most vigorous responses were evoked when the visual stimulus moved from medial to lateral along a horizontal trajectory through the receptive field. An auditory stimulus (broadband noise burst) that was minimally effective alone produced significantly ( $P < 0.001$ ) enhanced responses to the visual stimulus regardless of the direction of visual movement, but had no effect on the relative preference for one direction of movement over another. The crossed bars representing the mean auditory responses were obtained from four separate sets of trials with the auditory stimulus alone. Each set of auditory trials was interleaved with visual and visual-auditory trials.

the anesthetic condition was different. The animal was initially anesthetized with ketamine hydrochloride, and then maintained during surgery and recording by inhalation anesthesia using 0.5–2.5% halothane. A craniotomy was performed to expose the intraparietal sulcus; the wounds were infiltrated with Xylocaine and the cortex was covered with agar. Electrode penetrations were made along the intraparietal sulcus to sample neurons in both banks and the fundus. In the rostral aspect of the sulcus the electrode penetrations were extended deep to the fundus in order to sample neurons in the superior temporal sulcus.

## Results

### *Visual receptive field properties and multisensory integration in cat superior colliculus*

A number of properties characterize visually-

responsive neurons in the superior colliculus, including: velocity tuning, directional selectivity, spatial summation and spatial inhibition. These properties are as common among unimodal visual neurons as among multisensory neurons (Meredith and Stein, 1986a). To determine if these properties are altered by the presence of non-visual stimuli, each property was explored by varying the parameters of the visual stimulus when it was presented alone, and then in a matching trial in which the visual stimulus was paired with a non-visual stimulus.

The neuron whose responses are documented in Fig. 2 was best activated by a visual stimulus moved across the receptive field at approximately  $100^\circ/\text{sec}$ . Combining the moving visual stimulus with a brief, broad-band, stationary auditory stimulus (the auditory stimulus was poorly effective on most trials when presented alone) significantly enhanced the neuron's responsiveness, but did not alter its selectivity with regard to the speed of the moving visual stimulus. Its best response was still evoked at  $100^\circ/\text{sec}$ . In this neuron, as well as in the others examined ( $n = 4$ ), the presence of a non-visual stimulus did not alter its tuning for a particular velocity of moving visual stimuli.

The same effect was noted on directional selectivity ( $n = 9$ , an example is shown in Fig. 3), spatial summation ( $n = 7$ , Fig. 4, top), and spatial inhibition ( $n = 7$ , Fig. 4, bottom). In each case the magnitude of the response was altered significantly by the presence of a non-visual stimulus, but there was no effect on the selectivity of the visual response.

### *Multisensory integration in cortex*

Although the characteristics of multisensory integration, including those described above, have been well established in the superior colliculus, their occurrence and general applicability for other areas of the CNS had yet to be determined. Therefore, we examined neurons in several cortical regions believed to be multisensory.

*Cat.* The cat's lateral suprasylvian (LS) cortex is

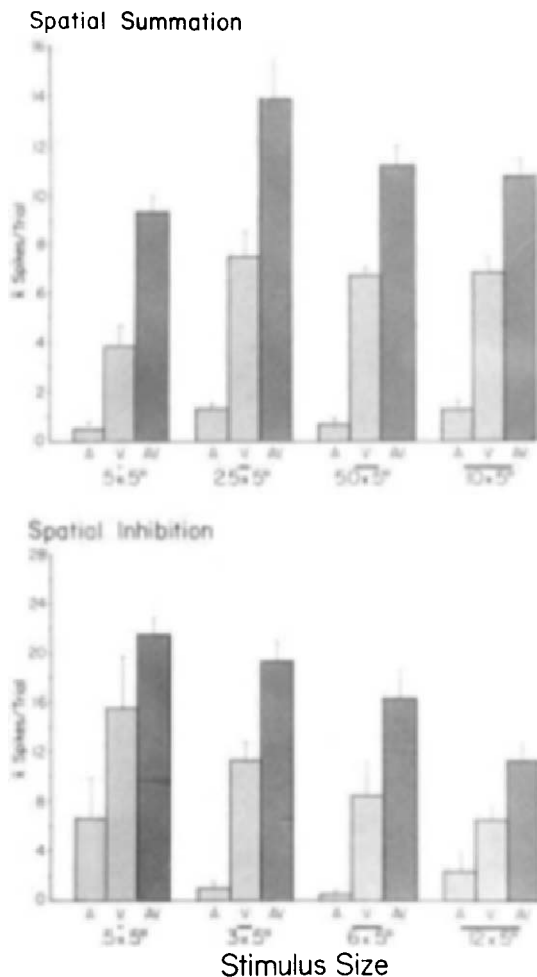


Fig. 4. Spatial summation and spatial inhibition are maintained in superior colliculus neurons during multisensory integration. The effectiveness of an auditory stimulus (A) presented alone and of visual stimuli (V) of various sizes moved across the receptive field are plotted. All stimuli were smaller than the diameter of the receptive field. Note the presence of significant ( $P < 0.001$ ) spatial summation. The presence of a spatially coincident auditory stimulus enhanced responses to each visual stimulus (trials labeled "AV"), but did not alter the relative effectiveness of stimuli of different sizes. A similar effect is shown at the bottom for a different neuron in which smaller stimuli produced greater responses than larger stimuli despite the fact that all stimuli were confined within the borders of the excitatory receptive field (within-field spatial inhibition).

best known as a "visual" area, and has been subdivided on the basis of its multiple representations of visual space (Palmer et al., 1978). However, in the

anterior LS, near the confluence of cortical areas devoted to visual, auditory and somatosensory representations, we have found scattered multisensory neurons ( $n = 8$ ). Similarly, multisensory neurons were found in the cat's anterior ectosylvian sulcus (AES). The AES is generally characterized as an "association" cortex, but is comprised of distinct unimodal regions that include: a somatosensory area (SIV, Clemo and Stein, 1982), an auditory region (Field AES, Clarey and Irvine, 1986), and a visual area (anterior ectosylvian visual area, AEV or EVA, see Mucke et al., 1982; Olson and Graybiel, 1987). The multisensory neurons ( $n = 24$ ) were found near the borders of these unimodal areas (Clemon et al., 1991).

Multisensory neurons in cat cortex appear to integrate sensory information in a manner virtually indistinguishable from neurons in the superior colliculus. In the example from LS depicted in Fig. 5, the neuron responded to a visual stimulus as well as to a somatosensory stimulus. Although the receptive field for each modality was rather large, they were in good spatial register, a feature commonly observed in multisensory neurons in the superior colliculus. When visual and somatosensory stimuli were presented together within their respective receptive fields, a strong enhancement of activity was produced. As with multisensory neurons in the superior colliculus, the temporal relationship between the two unimodal stimuli was an important factor in determining the level of interaction that would take place. By timing the multimodal stimuli so that the unimodal discharge trains would be overlapping, enhancement was maximized (see also Meredith et al., 1987).

The integrative properties of multisensory neurons were much the same in the AES. This is evident from the example shown in Fig. 6. The neuron responded to auditory stimuli in contralateral space and to gentle cutaneous stimulation of the contralateral body. The auditory and somatosensory receptive fields had similar spatial features: both were quite large, but excluded the most rostral and caudal areas of auditory and body space. Once again, the weak response to each unimodal stimulus

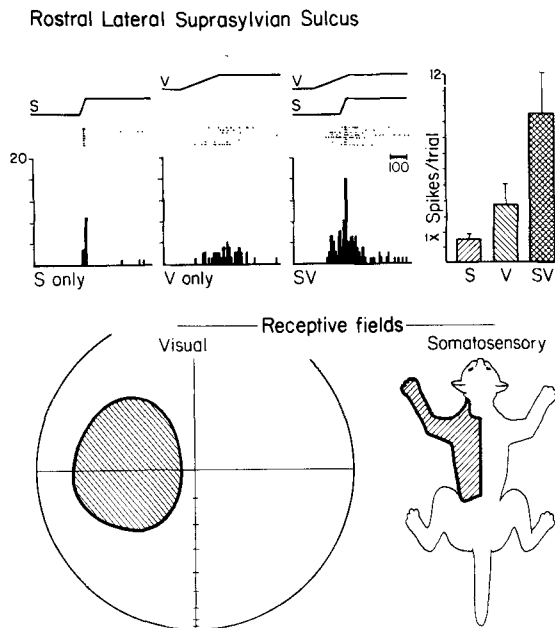


Fig. 5. Response enhancement in a visual-somatosensory neuron in cat lateral suprasylvian (LS) cortex. The visual receptive field of this neuron is depicted at bottom left, and its somatosensory receptive field at bottom right. A somatosensory stimulus (S) that indented the skin on the mid-region of the dorsal trunk elicited a brief, short latency response. A visual  $2^\circ \times 5^\circ$  stimulus (V) moved across the visual receptive field at  $100^\circ/\text{sec}$  also produced a weak response. However, combining the two stimuli (SV), so that the tactile stimulus came on 160 msec after the visual stimulus, resulted in a significant ( $P < 0.001$ ) enhancement of neuronal responses that exceeded the sum of the two unimodal responses.

was significantly enhanced by their combination, and this enhanced response exceeded the sum of the two unimodal responses. The same spatial rules for multisensory integration detailed in the superior colliculus were operative in this neuron. When the auditory stimulus was presented outside its receptive field, and thus out of register with the somatosensory stimulus, combining the two stimuli produced significant response depression.

**Monkey.** The superior temporal sulcus (STS) and portions of the intraparietal sulcus (IPS) of the rhesus monkey's cortex have been shown to be "polymodal" (e.g., Bruce et al., 1981; Duhamel et

al., 1991). Therefore, we sought to determine whether neuronal responses would be enhanced and/or degraded here by multisensory stimuli as in cat superior colliculus and cortex. Sensory driving was excellent in these regions, with the medial bank of IPS most responsive to contralateral tactile stimuli, the lateral bank most responsive to contralateral visual stimuli, and STS exhibiting excellent bilateral auditory and tactile driving. A curious feature of many somatosensory neurons in STS was the presence of "split" receptive fields. The best examples of this were neurons from which

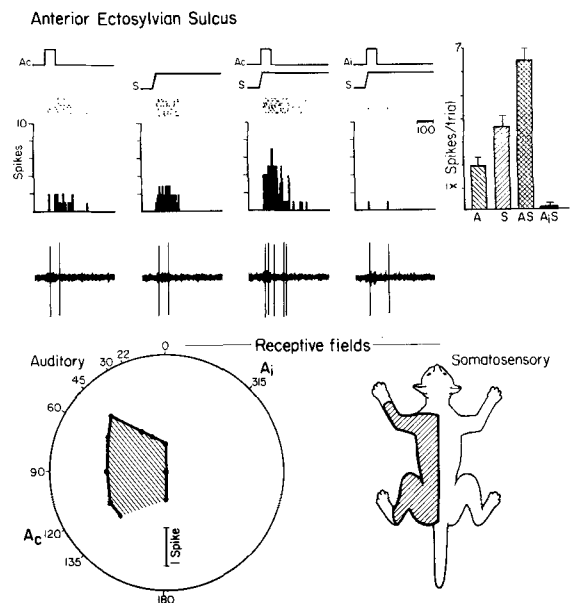


Fig. 6. Multisensory integration in a bimodal (auditory-somatosensory) neuron in cat anterior ectosylvian sulcus (AES). A broadband noise burst produced responses at each point tested (represented by closed circles) from  $0^\circ$  to  $135^\circ$  along the contralateral horizontal meridian as shown in the schematic at lower left. This is the horizontal extent of the auditory receptive field. The somatosensory receptive field encompassed the contralateral trunk and portions of the two limbs as shown on the figurine in the lower right. Presenting the contralateral auditory (Ac) or somatosensory (S) stimulus alone evoked comparatively weak responses, but the auditory-somatosensory combination produced a significantly ( $P < 0.01$ ) more vigorous response that exceeded the sum of the two unimodal responses. When, however, the auditory stimulus was presented in ipsilateral space (Ai) it significantly ( $P < 0.001$ ) depressed responses to the somatosensory stimulus.



vigorous driving was elicited by gentle cutaneous stimulation of either hand, but not the intervening body.

Although an exhaustive study remains to be conducted, it was interesting to note that among the neurons studied in monkey cortex ( $n = 15$ ), those identified as responsive to only one modality (i.e., unimodal) during casual qualitative examination ( $n = 9$ ) exhibited no response enhancements during extensive quantitative combined-modality testing. Thus, as in cat superior colliculus, qualitative tests are quite effective in identifying modality convergence patterns (though in neither case are inhibitory inputs effectively identified in this way). The sample of neurons in monkey cortex that were found to respond to more than one sensory stimulus during initial examination ( $n = 6$ ) also showed multisensory enhancement and/or depression during quantitative evaluation. Both visual-somatosensory and auditory-somatosensory neurons were encountered.

The responses of two neurons from the TPO sub-

division of the superior bank of STS (e.g., see Seltzer and Pandya, 1978) are shown here. In the auditory-somatosensory example shown at the top of Fig. 7 a somatosensory stimulus was moderately effective when presented on the lateral aspect of the face and an auditory stimulus was weakly effective when presented from the same region (i.e., 90° in contralateral space). Combining the somatosensory and auditory stimuli produced a markedly enhanced response that far exceeded the response to either stimulus alone. In the neuron depicted at the bottom of Fig. 7 a gentle somatosensory stimulus on the side of the face produced a reliable short-latency response, whereas visual stimuli, regardless of their location in space, were without apparent effect. However, when the visual stimulus was swept across central visual space at the same time the tactile stimulus was presented, a marked depression of the neuron's response to the somatosensory stimulus was observed. This indicated that the visual stimulus produced subthreshold (inhibitory) influences when presented alone.

## Discussion

The present experiments demonstrate that despite the profound influences of multisensory integration on superior colliculus neurons, their unimodal receptive field properties are preserved during combined-modality stimulation. A visual neuron retains its directional and velocity selectivity, as well as its specificity for stimulus size, despite having its overall activity level significantly altered by a non-visual stimulus. The preservation of unimodal receptive field properties appears to be an additional "rule" of multisensory integration that may be added to the list presented in the Introduction. It ensures that a neuron's selectivity for specific stimulus features in one modality is unimpaired in the presence of stimuli from other modalities. This invariance in receptive field properties seems essential for the nervous system to maintain a constant code for stimulus features in an ever-changing sensory world.

Although the cat superior colliculus neuron is a

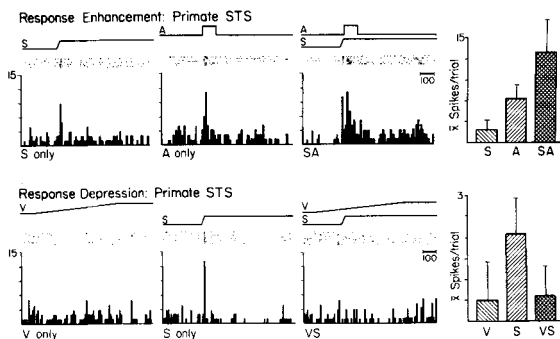


Fig. 7. Multisensory integration in bimodal neurons of monkey superior temporal sulcus (STS). Response enhancement: the neuron shown in the upper set of rasters and histograms was activated by a somatosensory (S) stimulus that indented the skin on the contralateral cheek. It was also activated by a broadband noise burst (A) originating from the same general spatial location (i.e., 90° contralateral). When the two stimuli were combined (SA), responses were significantly ( $P < 0.01$ ) enhanced. Response depression: the neuron shown at the bottom responded to a somatosensory stimulus, but a visual stimulus was without apparent effect. When, however, the visual stimulus was combined with the somatosensory stimulus it significantly ( $P < 0.01$ ) inhibited the neuron's responses.

major site for the convergence and integration of multisensory information (Stein, 1984; Meredith and Stein, 1986a,b; Stein and Meredith, 1990; Wallace et al., 1991), it is only one of many central nervous system sites in many species where information from several modalities converges. In the current study, single cells in cat LS and AES and in monkey IPS and STS were examined in the same fashion as were superior colliculus neurons in previous studies and found to adhere to the same set of basic integrating principles. Although the spatial, temporal and multiplicative characteristics of multisensory integration were most closely examined in cat cortex, all of the observations in monkey were consistent with those described in cat. The multisensory receptive fields of a single neuron overlapped one another in space, so that sensory stimuli that were in close spatial register fell within their excitatory receptive fields and enhanced the neuron's activity; spatially disparate stimuli produced either no interaction or depressed responses. The timing of the stimuli was a critical determinant of the interaction produced. Stimuli presented so that their unimodal discharges would overlap evoked maximal response enhancements. These interactions were multiplicative in nature and were not specific for the modality combinations examined; the same rules appeared to be operative among any combination of visual, auditory and somatosensory stimuli.

The rules of multisensory integration evident at the level of the single neuron are also consistent with studies of intact behaving animals. The attentive and orientation responses cats make to visual and auditory stimuli were predictable based on the reactions of superior colliculus neurons to these stimuli (Stein et al., 1988, 1989). When the auditory stimulus was spatially and temporally coincident with the visual stimulus, the animal's responses to the visual stimulus were enhanced in a multiplicative fashion. In contrast, when the visual and auditory stimuli were spatially disparate, responses to the visual stimulus were depressed.

It is unlikely that these complex overt behaviors depend solely on mechanisms involving the superior colliculus and/or its afferent systems. It seems far

more likely that the rules of multisensory integration extend well beyond the midbrain and its afferent systems to represent a general set of principles by which multisensory neurons operate throughout the brain. Thus far the data are consistent with this postulate in cat LS and AES, as well as in the parietal and temporal cortices of the monkey. They are also consistent with behavioral and event-related potential data in human subjects (Costin et al., 1991). However, these similarities should not be taken to mean that multisensory integration in structures with different roles does not have a very different impact on behavior and perception. Surely it must, but it is likely that similar integrative processes are necessary to link immediate overt responses (e.g., mediated by the superior colliculus), cognition (mediated by cortex), and even emotive processes (e.g., mediated by the limbic system). In this way the same combinations of stimuli that enhance or degrade responses in one area of the brain will enhance or degrade responses in other areas of the brain, with the probable result being an increase or decrease in the salience of a stimulus at all levels of information processing. Yet, changes in the magnitude of the signal via multisensory integration appear to be accomplished without altering the unimodal receptive field properties that may be necessary for coding specific stimulus features.

These data indicate that the visual responses of many neurons, whether in the superior colliculus or cortex, represent only one facet of their sensory coding capabilities. Thus, the rubric "visually-responsive neuron" is particularly apt as a general designation. It is far less exclusive than the more commonly used category: "visual neuron".

### Acknowledgements

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