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The influence of visual and auditory receptive field organization on multisensory integration in the superior colliculus

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Abstract The spatial register of the different receptive fields of multisensory neurons in the superior colliculus (SC) plays a significant role in determining the responses of these neurons to cross-modal stimulus combinations. Spatially coincident visual-auditory stimuli fall within these overlapping receptive fields and generally produce response enhancements that exceed the individual modality-specific responses and can exceed their sum. Yet, in this context, it has not been clear how “spatial coincidence” is operationally defined. Given the large size of SC receptive fields, visual and auditory stimuli could be within their respective receptive fields even when there are substantial spatial disparities between them. Indeed, previous observations have raised the possibility that there may be a second level of determinism in how SC neurons deal with the relative spatial locations of within-field cross-modal stimuli; specifically, that multisensory response enhancements become progressively weaker as the within-field visual and auditory stimuli become increasingly disparate. While the present experiments demonstrated that SC multisensory neurons have heterogeneous receptive fields, and that the greatest number of impulses evoked were by stimuli that fell within the area of cross-modal receptive field overlap, they also indicate that there is no systematic relationship between cross-modal stimulus disparity and the magnitude of multisensory response enhancement. Thus, two within-field cross-modal stimuli produced the same proportionate change (i.e., multisensory response enhancement) when they were widely disparate as they did when they overlapped one another in space. These

observations indicate that cross-modal spatial coincidence can be defined operationally by the borders of an SC neuron’s receptive fields regardless of the size of those receptive fields and/or the absolute spatial disparity between within-field cross-modal stimuli.

Keywords Multimodal · Polysensory · Cross-modal · Intersensory · Physiology · Cat

Introduction

The superior colliculus (SC) contains multisensory neurons that are created by the convergence of modality-specific afferents arising from a variety of sources (Edwards et al. 1979; Huerta and Harting 1984; Wallace et al. 1993). As a consequence of this convergence, each multisensory SC neuron has multiple receptive fields, one for each sensory modality to which it responds. These receptive fields represent similar regions of sensory space. For example, a visual-auditory neuron with a visual receptive field in central space will have an auditory receptive field in an overlapping region of central space (Meredith and Stein 1996).

The cross-modal register of receptive fields is critical for normal multisensory processes (Meredith and Stein 1986a, 1986b, 1996; Wallace et al. 1996). Under normal circumstances, multiple cues derived from the same event, such as an object striking a surface, are derived from the same location in space and will fall simultaneously within a given neuron’s overlapping receptive fields. The physiological result of this combination is a significant enhancement in the neuron’s response above that elicited by the most effective of those stimuli individually, and often one that is greater than their sum, an effect not obtained in these neurons when the same stimuli are presented as within-modality pairs (Stein and Meredith 1993). The corresponding behavioral consequence of these cross-modal stimulus conditions is a substantial increase in the probability of a correct response to an event (Stein et al. 1989) and a substantial

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decrease in reaction time (Simon and Craft 1970; Nickerson 1973; Hughes et al. 1994, 1998; Frens et al. 1995; Goldring et al. 1996; Frens and Van Opstal 1998; Harrington and Peck 1998; Schroger and Widmann 1998; Giard and Peronnet 1999; Taylor et al. 1999). On the other hand, cross-modal stimuli derived from unrelated events are likely to be spatially disparate. For any particular multisensory neuron, the likelihood is that only one of those stimuli (e.g., visual) will fall within the borders of its excitatory receptive field. The other (e.g., auditory) will fall outside the borders of its excitatory receptive field. The result of this cross-modal stimulus configuration is either the absence of multisensory integration in that particular neuron or multisensory response depression (Meredith and Stein 1986b, 1996; Meredith et al. 1987; Stein et al. 1993; Stein and Wallace 1996; Wallace et al. 1996, 1998). The latter occurs if the extrareceptive field stimulus falls into an inhibitory region, which borders the excitatory receptive field of some SC neurons. The input from this extrareceptive field stimulus suppresses the excitation generated by the within-field stimulus (Kadunce et al. 1997). Similar cross-modal effects are observed at the behavioral level when orientation responses to visual targets are rendered less likely by the presence of spatially disparate neutral auditory stimuli (Stein et al. 1989).

In previous studies of multisensory integration, cross-modal stimuli generally were presented either in very close spatial proximity or far enough apart so that one stimulus fell near the center of its excitatory receptive field and the other fell well outside its excitatory receptive field. Based on these observations, it is unclear whether spatial coincidence is defined operationally by the physical concordance of the stimuli in space, by a given neuron's area of cross-modal receptive field overlap, by the outer borders of its excitatory receptive fields, or by some combination of these factors. The present experiments were designed to examine these questions in visual-auditory SC neurons.

Methods

All procedures were carried out in strict accordance with the guidelines of the Wake Forest University School of Medicine and the National Institutes of Health, and followed the *Principles of laboratory animal care* (NIH publication No. 86-23, revised 1985).

Surgical and recording preparation

Five cats were used in the present experiments. Each was rendered tractable with a combination of ketamine hydrochloride (30 mg/kg i.m.) and acepromazine maleate (0.2–0.4 mg/kg i.m.). After endotracheal intubation, the animal was anesthetized and maintained during surgery with isoflurane (0.5–2.0%). Body temperature was maintained with a circulating heating pad. The animal was then fixed in a stereotaxic head holder, and a craniotomy was performed in order to gain access to the SC. A stainless steel recording well was positioned over the craniotomy, secured to the skull with stainless steel screws and cemented into place with dental acrylic (McHaffie and Stein 1983). The skin was then

sutured into place around the well and the animal was allowed to recover for 7–10 days. Postoperative care was carried out according to NIH and Institutional guidelines.

Before each recording experiment the animal was anesthetized with an initial dose of ketamine hydrochloride (30 mg/kg i.m.) and acepromazine maleate (0.2–0.4 mg/kg i.m.). Its head was secured by attaching the implanted well to a mount, which provided support without the presence of pressure points or obstruction of the eyes, auditory canals, or body surface. The animal was intubated and artificially respired. Expiratory CO₂ was monitored and maintained between 3.8 and 4.5%. The saphenous vein was cannulated and fluids (4–6 ml lactated Ringer/h), paralytics (0.1 mg pancuronium bromide/kg, initial dose, followed by supplements of 0.06 mg · kg⁻¹ · h⁻¹) and anesthetic (10 mg ketamine hydrochloride · kg⁻¹ · h⁻¹) were administered intravenously. Body temperature was maintained with a heating pad, the pupils were dilated with a 1% ophthalmic atropine solution and the positions of the optic discs were back-projected and focused either onto a 92-cm diameter translucent hemisphere or onto a tangent screen. The hemisphere and tangent screen were each placed 40 cm from the eyes. A corrective lens was applied to focus the contralateral eye on the screen and the ipsilateral eye was covered with an opaque lens. The animal was positioned within an auditory hoop apparatus so that its interaural axis was aligned with the axis of rotation of the hoop and perpendicular to the visual vertical meridian.

Recording procedures

Single-neuron extracellular recordings were carried out with epoxyite-insulated tungsten microelectrodes (1–3 MΩ at 1 kHz). The electrode was lowered manually through the cortex to the surface of the SC and then moved in small steps (5–15 μm) with a hydraulic microdrive. Neurons were identified by their spontaneous activity and by their responses to a variety of search stimuli. Neural activity was amplified, displayed on an oscilloscope and played through an audio monitor. Neural responses were collected using the Spike2 (Cambridge Electronic Design) data acquisition system, and the amplitude and waveshape of each neuron were evaluated on-line via this system to ensure single-neuron isolation. Each neuron was examined for its responses to visual and auditory stimuli. Responses to stimuli were first established qualitatively to determine the nature of the stimuli to be presented for quantitative analysis. Each animal was used in one or two recording sessions per week for approximately 6 months. Following a recording session, paralysis was reversed and anesthesia discontinued. Upon return of stable respiration and locomotion the animal was returned to its home cage.

Sensory classification

Visually responsive neurons were sought using a variety of moving and stationary flashed stimuli. Visual stimuli were generated by a Silicon Graphics Indigo workstation and projected via a BARCO graphics 701S video-projector. Once a visually responsive neuron was isolated, its receptive field was mapped. Stimulus shape, size, location and movement were computer-controlled. Bars and spots of light were 1–3° in diameter and 53 cd/m² against a background of 2.7 cd/m². Stationary flashed stimuli were used in most cases and were generally effective. However, in a few experiments a moving visual stimulus was required in order to generate responses from the neuron. In these cases a high-velocity (300°/s) stimulus was moved through a very small area (approximately 3°) of the receptive field.

Auditory responsive neurons were identified by their responses to a variety of complex auditory stimuli, which included hisses, claps, whistles, and broad-band (20–20,000 Hz, less than 70 dB SPL) noise bursts. Their receptive fields were mapped with computer-controlled broad-band sound bursts delivered via 16 stationary speakers (Optimus Pro-25 Titanium) positioned around the animal at 15° intervals on a hoop whose axis of rotation was in line with the animal's interaural axis. Stimulus parameters (i.e., intensity, duration, timing, etc.) were computer-controlled.

Receptive field mapping

The borders of the visual receptive fields were first mapped manually and then were determined quantitatively using a computer-controlled sequence of stimulus presentations that spanned their presumptive borders. The operational border of the excitatory receptive field was defined as a region from which responses could be elicited on 50% or more of the trials. Although inhibitory regions bordering the receptive field were often noted, their borders were not mapped in detail. A more in-depth exploration of the differential areas of responsiveness within the receptive field was conducted by varying the location of a stimulus systematically in azimuth along a particular elevation. In this way it was possible to construct a spatial response profile based on the mean number of impulses evoked by ten stimulus repetitions at each site.

Auditory receptive fields were mapped in similar fashion and the same criteria were applied. The receptive field borders were first defined qualitatively. Once the receptive fields were roughly delimited, their borders were examined quantitatively using broadband noise bursts delivered from hoop-mounted speakers. The auditory hoop was aligned along the horizontal meridian, and responses to each of the individual speakers were recorded. The hoop was then rotated about the animal's interaural axis and the procedure repeated at other elevations with selected speakers. The map was explored in greatest detail at azimuths at 0° elevation (i.e., along the interaural plane). The intensity of the auditory stimulus used in an individual experiment was varied (range of 53–65 dB SPL on a background of 42–45 dB SPL), depending on the dynamic properties of the neuron. In all cases, the stimulus intensity chosen was maintained throughout the study of the neuron.

Stimulus delivery, data acquisition, and analysis

Visual-auditory multisensory neurons were defined as those that responded to stimuli from both modalities or whose responses to one modality-specific stimulus were altered by the presence of a stimulus from the other (Meredith and Stein 1983). Once such a neuron was encountered and its visual and auditory receptive fields were mapped, responses to each single-modality stimulus and to the multisensory combination were determined quantitatively. This was accomplished by randomizing the presentation of the stimulus or stimulus combination in the relevant receptive fields 8–12 times at 6–10 s intertrial intervals. During multisensory trials the two sensory stimuli were generally presented simultaneously or within 50–200 ms of one another. The specific temporal interval between stimuli that produced the greatest interaction for each neuron was determined during an initial set of test trials that preceded the interleaved trials used in the data set.

Neuronal responses to each modality-specific stimulus and stimulus combination were assessed and analyzed statistically to determine whether a significant (two-tailed *t*-test, $P < 0.05$) change (increase = enhancement; decrease = depression) in the number of impulses occurred with combined stimuli when compared with the most effective single-modality stimulus. The magnitude of this change was calculated by the following formula:

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

where CM is the mean number of impulses evoked by the combined-modality stimulus and SM_{max} is the mean number of impulses evoked by the most effective single-modality stimulus.

Evaluation of differences between groups of tests in which the stimuli were: (a) both within the area of receptive field overlap, (b) one within the area of overlap and the other outside, and (c) both outside the area of overlap (i.e., IN-IN, IN-OUT, OUT-OUT) employed standard analysis of variance (ANOVA) methods. In addition, to compare across these different groups, pairwise comparisons using Tukey HSD tests were conducted.

Histology

In the last several experiments in each animal, locations of interest were marked with electrolytic lesions (10–12 μ A; 12 s). After the

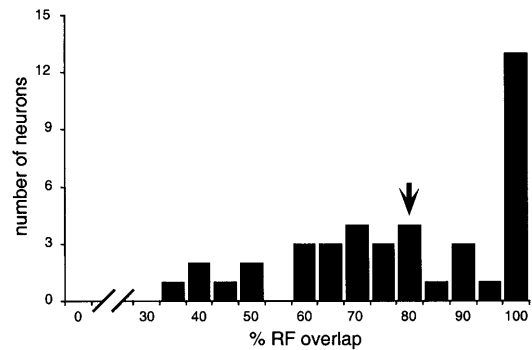


Fig. 1 A high degree of cross-modality spatial overlap is present between the visual and auditory receptive fields (RFs) of multisensory SC neurons. The arrow depicts the population mean

final experiment, the animal was killed with an overdose of pentobarbital sodium (100 mg/kg i.v.) and perfused transcardially with saline followed by 10% formalin. The midbrain was blocked stereotaxically and was then removed and placed in a sucrose solution (25%) overnight. Frozen sections (50 μ m thickness) were cut in the coronal plane, counterstained with cresyl violet, and electrode penetrations were reconstructed based on marking lesions.

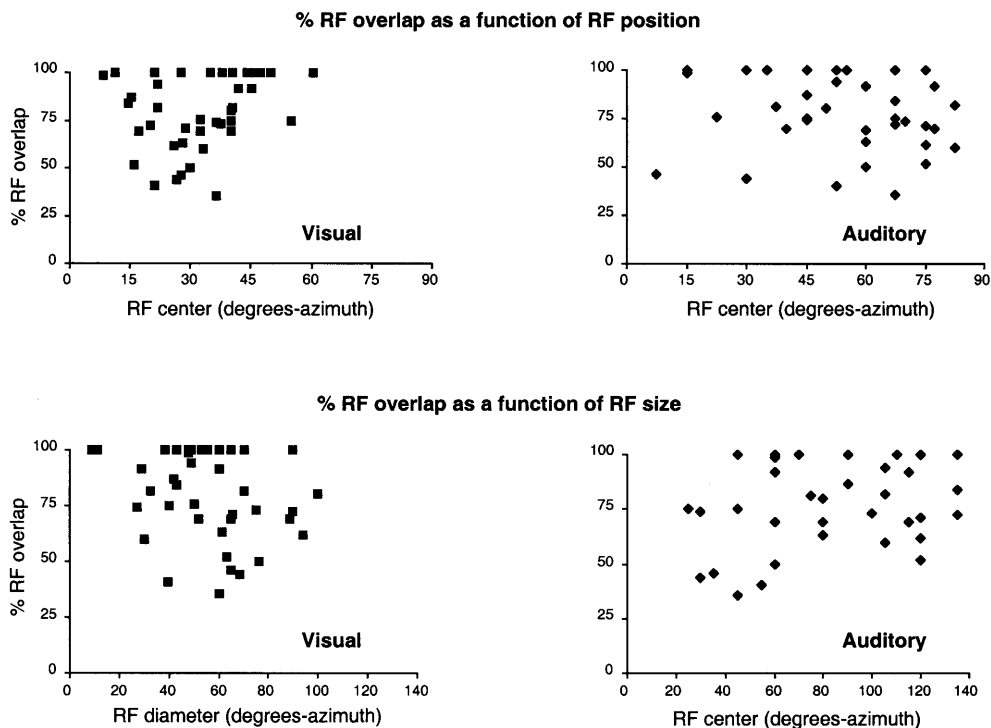
Results

One hundred fifty-four multisensory neurons were sampled in the deep laminae of the SC. Forty-one of these were bimodal visual-auditory neurons and were isolated for sufficient periods of time to examine their modality-specific responses to stimulation of multiple receptive field sites. In 34 of these neurons, a detailed examination of their multisensory response profiles at multiple receptive field locations was also conducted. These data provided the basis not only for examining the effects of cross-modal spatial disparity on multisensory integration, but also for examining the possibility that the area of visual-auditory receptive field overlap provided an especially effective region for multisensory integration.

Spatial organization of visual-auditory receptive fields

In the rostral portion of the SC, multisensory neurons generally had visual receptive fields that ranged from less than 10° to approximately 40° in diameter, and auditory receptive fields that ranged from less than 20° (typically measured at 0° elevation) to approximately 60° in diameter. These receptive fields were located in frontal space. Multisensory neurons in the caudal SC had larger (40–100° visual receptive field diameters and 60–135° auditory receptive field diameters) and more temporal or peripheral receptive fields. Although a systematic examination of neurons at all SC locations was not conducted, there was a high degree of spatial correspondence between the visual and auditory receptive fields of multisensory neurons at all tested locations

Fig. 2 The degree of visual-auditory receptive field overlap in multisensory neurons did not vary as a function of the location or size (i.e., diameter) of their respective receptive fields



(see also Middlebrooks and Knudsen 1984; King and Palmer 1985; Meredith and Stein 1996; Wallace et al. 1996; Wallace and Stein 1997).

Despite this general rule of cross-modal receptive field correspondence, in any given multisensory neuron the degree of overlap between its visual and auditory receptive fields could vary considerably. In order to gain a quantitative measure of this variability, the area of overlap between receptive fields was calculated for every visual-auditory neuron studied. Because auditory receptive fields were always larger than their visual counterparts, the degree of receptive field overlap was expressed as the percentage of the visual receptive field subsumed within the auditory receptive field (Meredith and Stein 1996). As can be seen in Fig. 1, the majority of visual-auditory neurons exhibited a high degree of overlap, with 71% (29/41) having greater than 70% of their visual receptive field contained within the area of the auditory receptive field. The mean overlap for the entire population was 80%. In 13 neurons the visual receptive field was completely contained within the receptive field of its auditory counterpart (i.e., 100% overlap). Receptive field overlap did not vary significantly as a function of either receptive field location or size (Fig. 2).

Effect of spatial disparity on multisensory interactions

To examine whether the proximity of the visual and auditory stimuli within their receptive fields played a significant role in the response enhancement generated by their combination, their disparity was systematically varied. In

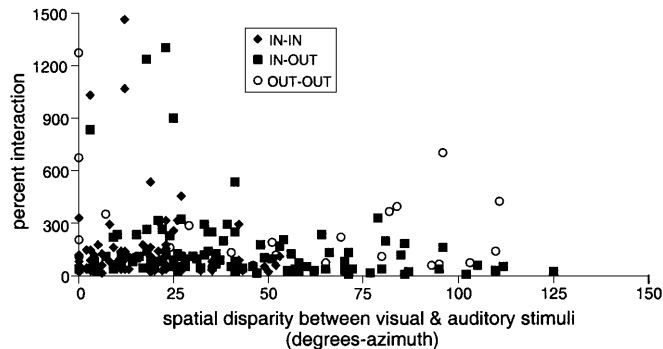


Fig. 3 The magnitude of the multisensory response change was not systematically related to the disparity between the visual and auditory stimuli. (*IN-IN* both stimuli were presented within the area of receptive field overlap, *IN-OUT* one stimulus was presented within and the other outside the area of receptive field overlap, *OUT-OUT* both stimuli were presented outside the area of receptive field overlap)

conducting these tests, visual-auditory stimulus pairs were presented in one of three disparity configurations: (1) both stimuli within the area of receptive field overlap (*IN-IN*), (2) one stimulus within and the other stimulus outside the area of overlap (*IN-OUT*), and (3) both stimuli outside the area of overlap (*OUT-OUT*). No relationship was found between the spatial disparity of the visual and auditory stimuli and the magnitude of the multisensory interaction (i.e., a proportionate measure referred to as “multisensory response enhancement”) generated by their combination in any of these configurations. The data from these tests were, therefore, combined and are presented in Fig. 3.

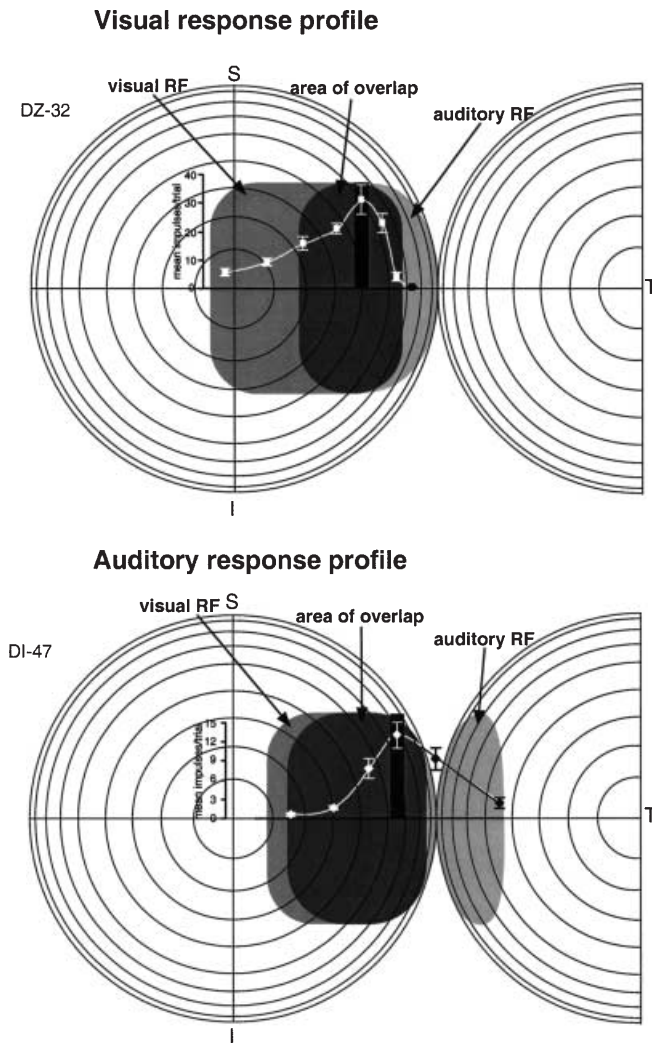


Fig. 4 The most vigorous modality-specific responses were generally evoked by multisensory SC neurons by a stimulus located within the area of cross-modal receptive field overlap. At the *top* are shown the receptive fields (*shading*) and the visual response profile of a visual-auditory neuron. The region of cross-modal receptive field overlap (*darkest shading*) is shown on standard representations of visual and auditory space. In this convention the horizontal and vertical lines depict meridians; each *concentric circle* represents 10°, and the caudal half of contralateral auditory space is represented by a *half-circle* that has been folded forward. Overlaid on these representations is a graph representing the responses obtained to the same visual stimulus at various locations (*circles*). Note that the peak response was obtained within the region of receptive field overlap (*black bar*). *Error bars* represent standard errors of the mean. At the *bottom* are shown the receptive fields and auditory response profile for a second visual-auditory neuron. The same conventions are used as above. Note that the maximum modality-specific auditory response was obtained at a point within the region of receptive field overlap (S, superior; I, inferior; T, temporal)

Best points were contained within the area of receptive field overlap

Nevertheless, the locations of the stimuli within their respective receptive fields were not irrelevant. Modality-specific receptive fields were heterogeneous such that

Table 1 Pairwise comparisons of the probability of multisensory response enhancement based on stimulus location. Evaluated here are the group means based on the location of the stimuli with respect to the area of receptive field overlap. Comparisons were conducted using Tukey's honestly significant differences. (*In-In* Both stimuli are within the area of overlap, *In-Out* one stimulus was within the area of overlap and the other was outside this area, *Out-Out* both stimuli were outside the area of overlap)

Groups	t_s	P	P
(In-In) vs (In-Out)	2.08	<0.05	
(In-In) vs (Out-Out)	3.61	<0.05	<0.01
(In-Out) vs (Out-Out)	1.53		

Table 2 Pairwise comparisons of the magnitudes of multisensory response enhancements based on stimulus location relative to the area of receptive field overlap. All conventions and statistical tests are the same as in Table 1

Groups	t_s	P
(In-In) vs (In-Out)	0.75	
(In-In) vs (Out-Out)	4.44	<0.001
(In-Out) vs (Out-Out)	3.69	<0.001

the responses evoked with the same stimulus varied widely as its position changed (Fig. 4). Although in the examples presented, and in a number of other instances, a maximal response (i.e., a "best point") was flanked on either side by areas of progressively lower response, in other cases the spatial response profile showed less regularity. Generally, best points were located within the area of receptive field overlap. This was the case for visual best points in 90% (37/41) of the neurons examined, and for auditory best points in 61% (25/41) of the neurons studied. For the majority of neurons (59%; 24/41), the best points of both receptive fields were located within the area of receptive field overlap. Furthermore, in a number of neurons (12/41; 29%), the visual and auditory best points were at the same location in space, thereby underscoring a cross-modal correspondence in receptive field organization.

The impact of the area of receptive field overlap on multisensory responses

The importance of the area of overlap was also apparent in the multisensory responses evoked by stimulus combinations. Just as the absolute magnitude (i.e., total number of impulses) of modality-specific responses was greatest when stimuli were located in this area, so was the absolute magnitude of the responses to cross-modal stimulus combinations. Indeed, these two measures were positively correlated (Figs. 5, 6). Furthermore, the probability of generating an enhanced multisensory response was significantly affected by where the stimuli were relative to the area of overlap (ANOVA, $F=3.32$, $P=0.043$; Table 1). This probability was highest (52%) when at least one of the stimuli was within the area of

Fig. 5 The multisensory response profile is dependent upon the modality-specific response profiles. On the *top* are shown the receptive fields of a visual-auditory neuron and the stimulus locations used for modality-specific and multisensory tests. Receptive field conventions are the same as in Fig. 4. Icons depict the positions of the auditory (speakers) and visual (bars) stimuli. Stimuli were presented both individually and together at a total of 6 locations (numbers 1–6). Histograms in the middle illustrate this neuron’s response to the visual (*Vis*), auditory (*Aud*) and combined (*VA*) stimuli at each of these locations. Summary graph at the *bottom* shows the mean response for each of these conditions, with the best point highlighted within the *gray bar*. Error bars represent standard errors of the mean

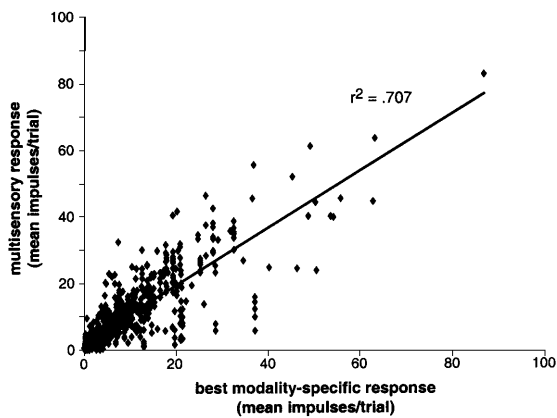
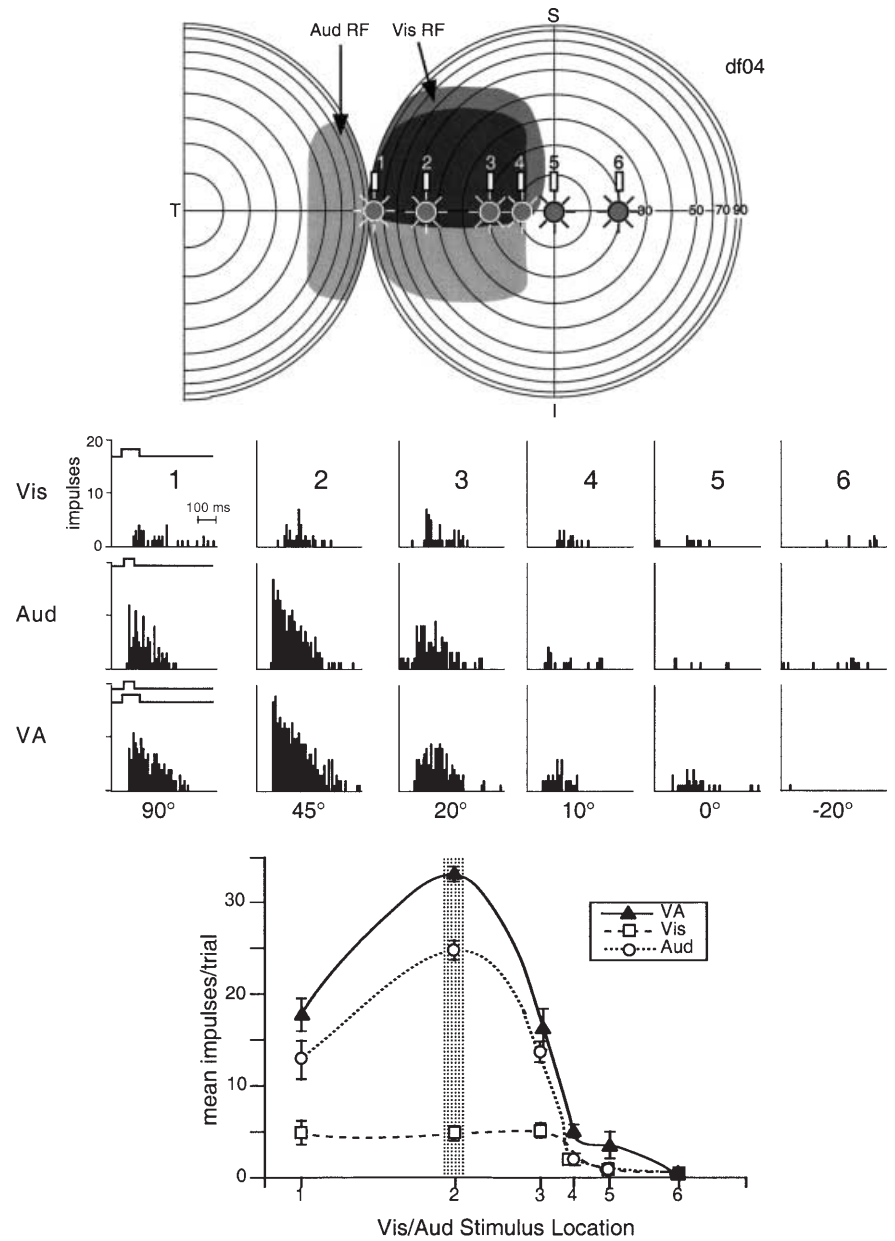


Fig. 6 At the population level it was evident that there was a positive correlation between modality-specific and multisensory responses

receptive field overlap and lowest (32%) when both stimuli were outside the area of overlap. Yet, despite this lower probability and the lower absolute magnitudes of the multisensory response, in those instances in which cross-modal stimulus combinations outside the area of overlap did yield a multisensory enhancement, their proportionate changes were typically larger than those produced by stimulus combinations within the area of receptive field overlap (ANOVA, $F=3.93$, $P=0.021$; Fig. 7, Table 2). This relationship is in keeping with the principle of inverse effectiveness (Meredith and Stein 1986a), whereby combinations of weakly effective modality-specific stimuli generally give rise to the largest proportionate response enhancements.

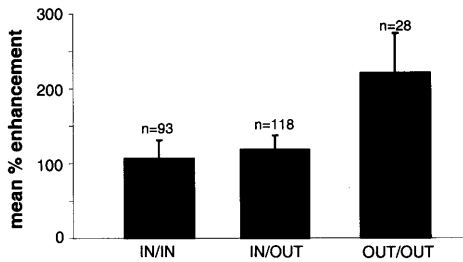


Fig. 7 Multisensory response enhancements of the greatest proportionate size were generated by stimulus combinations in which both stimuli were outside the area of receptive field overlap (*OUT/OUT*)

Discussion

The high degree of spatial overlap among the visual and auditory receptive fields of multisensory SC neurons was found to be maintained across much of the SC despite substantial changes in receptive field size and shifts in receptive field position. The area of receptive field overlap was also found to be the most responsive region of the receptive field. Thus, the highest absolute response magnitudes were evoked from this region by both modality-specific and cross-modal stimuli. But most significant in the current context is that the probability of obtaining an enhanced multisensory response was also highest if the cross-modal stimuli were within this region.

Although there are few previous instances in which cross-modal stimuli have been presented at various spatial disparities within their overlapping receptive fields, in at least one case such a test series showed that increasing disparities produced proportionately smaller multisensory enhancements (see Fig. 1 by Meredith and Stein, 1986b). This observation suggested that there may be more flexibility and/or a second level of determinism in the spatial principle of multisensory integration than is first apparent, and prompted some of the present tests to examine this possibility. However, little evidence was obtained to support such an organizational feature, and only in isolated examples were proportionately smaller multisensory response enhancements obtained at increasing within-field cross-modal stimulus disparities. Yet, even in these cases this relationship invariably failed at still larger disparities and/or when the same disparities were tested along another axis. For the purposes of multisensory response enhancement, it appears that individual neurons treat cross-modal stimuli within their receptive field borders largely the same regardless of whether they are spatially coincident or separated by significant disparities. At the level of the individual neuron, then, the borders of its excitatory receptive fields must be taken as operationally defining cross-modal spatial coincidence.

Despite the lack of a systematic effect of within-field cross-modal spatial disparity on multisensory response enhancement, the absolute position of each stimulus within its receptive field was not irrelevant. The differential sensitivity of receptive field loci underscores the internal complexity of the receptive fields of multisensory

neurons (perhaps a consequence of the multiple sources of modality-specific input to these neurons). In terms of multisensory enhancement, stimulus combinations located outside the area of receptive field overlap, where the responses evoked were generally weaker, had a comparatively low likelihood of producing response enhancement. Consequently, despite the fact that the outer borders of the receptive fields define the absolute limits of what must be operationally defined as spatial coincidence, the area of cross-modal receptive field overlap appears to be the major site at which multisensory enhancement is generated. Yet, in light of previous studies, it was surprising to note that there were a high number of receptive field sites at which cross-modal stimuli failed to produce a significantly greater response than did the best of the modality-specific stimuli alone. Previous studies of multisensory integration generally relied on moving visual stimuli, to which SC neurons are particularly responsive, and which are likely to obscure the within-field spatial heterogeneity that is exposed with stationary flashing stimuli or stimuli with very short traverses, such as those used here. In this context it is important to note that multisensory enhancement in SC neurons is dependent on the substantial corticotectal inputs derived from the anterior ectosylvian (AES) and rostral suprasylvian (rLS) sulci (Stein et al. 1983; McHaffie et al. 1988, 1993). When these cortices are deactivated, multisensory SC neurons continue to respond to their various modality-specific inputs, but lose the capacity to integrate them (Wallace and Stein 1994; Jiang et al. 2001). Thus, the failure of any particular receptive field sites to support SC multisensory integration may result from a failure to activate the requisite number of AES and/or rLS corticotectal inputs. Whether this is due to the spatial patterns with which corticotectal influences are exerted on individual SC neurons, the activation selectivity of the relevant corticotectal neurons, or some combination of the two remains to be determined.

The large receptive field sizes of multisensory SC neurons and absence of cross-modal spatial disparity coding suggests that the cross-modal spatial resolution at the level of the individual multisensory SC neurons is quite coarse. However, the spatial resolution of such integration at the population level is likely to be far greater. Because of the high degree of spatial overlap among SC receptive fields, spatially coincident cross-modal stimuli will fall within the excitatory receptive fields of the largest possible number of multisensory SC neurons. Presumably, such a combination of cross-modal cues will, thereby, evoke the largest multisensory population response. On the other hand, progressive increases in cross-modal spatial disparity have two effects that progressively minimize multisensory population responses. First, increasing cross-modal disparity decreases the likelihood of the two stimuli encroaching on the two excitatory receptive fields of the same neurons, thereby decreasing the incidence of multisensory enhancement and lowering the magnitude of the population response. Second, increasing cross-modal spatial disparity increases

the incidence of multisensory inhibition, an interaction produced when the excitatory inputs initiated by one stimulus (within its receptive field) conflict with the inhibitory inputs initiated by the other stimulus (outside its receptive field; see Kadunce et al. 1997). Consequently, the multisensory population response may reflect an underlying spatial resolution that is greater than that predicted by the absolute size of the multiple sensory receptive fields of individual SC neurons or even their areas of receptive field overlap. In behavioral experiments it has been shown that displacing an auditory stimulus as little as 15° medial to a visual stimulus is sufficient to eliminate multisensory enhancements in orientation and approach behavior (Stein et al. 1989). It is likely that the cross-modal spatial resolution of this system is even finer, but the effect of smaller cross-modal spatial disparities on behavioral responses has not yet been tested. Presumably, then, a 15° (or less) cross-modal spatial disparity should be sufficient to shift the neural population response in the SC from one that is dominated by multisensory enhancement to one in which multisensory enhancement is countered by multisensory depression. However, this assumption requires empirical testing.

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