Spatial factors determine the activity of multisensory neurons in cat superior colliculus

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The responses of a neuron to stimuli from one sensory modality can be profoundly influenced by inputs from other sensory modalities. The present experiments demonstrate that the nature and the magnitude of these multisensory interactions depend on the positions of the stimuli in relation to their respective receptive fields. The spatial rules governing these interactions underscore the significance of the alignment of sensory maps in the brain.

Casual observers of animal behavior are often struck by their exquisite sensitivity to subtle changes in environmental stimuli. Yet such sensitivity is a common endowment in predator and prey alike and insures the survival of species living with widely different ecological stresses. Many vertebrates maximize their ability to detect meaningful external stimuli by monitoring their environment through a variety of seemingly independent, but simultaneously active, sensory channels: visual, auditory, somatosensory, etc. Although separate in the peripheral nervous system, the inputs from these different sensory systems converge on individual neurons (i.e. multisensory neurons) in a variety of locations in the brain (see for examples refs. 1, 3, 17, 20, 23, 25). According to at least one speculation12,21, such convergence may enable different sensory systems to interact in order to generate neuronal and behavioral responses that are dependent on the complex of stimuli present.

Perhaps nowhere are multisensory cells more evident19 or more relevant to this issue than in the superior colliculus (SC), a midbrain structure involved in transforming sensory cues into motor responses8,27 and in effecting an organism’s rapid orientation to environmental stimuli18. Recent experiments have shown that the convergence of inputs from different sensory modalities can interact to enhance or depress the activity of many deep laminae SC cells11,16 and thus the data are consistent with the postulate mentioned above. Most intriguing is the observation that these interactions occur predominantly in those SC cells that are directly involved in motor responses12 (see also ref. 8).

In the present experiments we sought to determine if there are definable rules by which interactions take place in multisensory SC cells. Because the effective stimulus location (for each cell and each sensory modality) is determined by a cell’s receptive fields, these experiments were directed toward evaluating how the relative spatial positions of stimuli from two different sensory modalities would influence the responses they elicited. The results show that dramatically different response interactions can be evoked from the same cell by the combination of two sensory stimuli depending on the spatial locations of each of these stimuli. A critical factor governing these interactions in all the cells studied was the location of the stimuli relative to their respective receptive fields.

A chronic recording chamber was surgically mounted on the skull of each cat (n = 10) a week

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prior to the recording session so that its head could be held from the mount during recording without introducing wounds or pressure points. For recording, each animal was anesthetized (ketamine-HCl, 30 mg/kg), paralyzed (gallamine triethiodide, 5 mg/kg with D-tubocurarine, 5 mg/kg) and respired with N₂O 75%:O₂ 25%. Neuronal activity was recorded extracellularly with glass-insulated tungsten microelectrodes. When a cell was isolated, its receptive field for each effective modality was mapped, and precisely controlled electronically generated stimuli were presented to evaluate its response properties. Visual cues consisted of flashing or moving spots or bars of light projected on a translucent hemisphere located in front of the animal. Acoustic stimuli were broadband noise bursts (2–20 kHz; 35–55 dB sound pressure level) delivered from a hoop-mounted speaker that was movable in elevation and azimuth. The visual axis was aligned perpendicular to the horizontal plane of the interaural axis so that visual and auditory coordinates were in register. Somatosensory stimuli consisted of hair or skin displacement by a probe attached to a moving-coil vibrato. The position of the eyes, pinnae and body remained fixed during the experiment. Repeated (8–16) presentations of visual, auditory and/or somatosensory stimuli were used in the following tests. (A) Single-modality tests: one stimulus from one sensory modality (e.g. visual) and then a second stimulus from another modality (e.g. auditory); (B) Combined-modality tests: simultaneous presentation of spatially coincident stimuli, one from each of two modalities (e.g. visual and auditory); (C) Disparate combined-modality tests: the same stimulus pair as in (B) but while one maintained its original spatial location, the other was displaced to a new location after each presentation series. This allowed a comparison to be made of the effectiveness of stimulus pairs at different spatial locations and disparities. Responses (i.e. number of neuronal discharges) to combined-modality tests that were significantly (P < 0.05, two-tailed t-test) greater (or less) than those evoked by the most effective single-modality test were considered to reflect response interactions.

Forty multisensory SC cells were studied in detail. In each cell, the sign of the response interaction (i.e. enhancement or depression) as well as its absolute amplitude (i.e. number of impulses) proved to be dependent on the spatial relationship of the stimuli to their respective receptive fields. Consequently, the following response phenomena were observed. (A) When combined-modality stimuli were presented within their receptive fields, response enhancement was evoked. These enhancements usually reflected an interaction that was greater than the sum (i.e. multiplicative) of responses evoked by either stimulus alone and could exceed 1200%. (B) The highest levels of response enhancement were produced when the stimuli were presented so that they were coincident in space and within their receptive fields. This was best observed in auditory–visual cells and is likely due to the observation that the most effective or ‘best’ area of a multimodal cell’s auditory receptive field is usually in topographic register with its visual receptive field. (C) When one of the stimuli was presented outside the borders of its receptive field, either no interaction was produced or response depression was elicited. Response depression could be powerful enough to eliminate a vigorous discharge to one stimulus alone and was found in cells receiving binaural auditory inputs identified as EO/I (representing contralateral monaural excitation, no ipsilateral monaural response and an inhibitory binaural interaction) and OO/F (representing no monaural responses, but binaural facilitation) according to the criteria of Wise and Irvine. These response phenomena are illustrated in Fig. 1. For this cell, coincident visual and auditory stimuli evoked a 235% response enhancement. However, separating these stimuli significantly degraded the response enhancement elicited, and when the auditory stimulus was displaced far enough (so that it was outside its excitatory receptive field), response depression (to −68%) was evoked from many locations. Thus a multisensory neuron can show a dramatic range of response that includes both response enhancement and response depression.

These data indicate that the spatial principles of multisensory integration do not supersede the factors governing responses to single modality cues. Rather they appear to be based on them. For example, a visual SC receptive field typically consists of an excitatory region and a suppressive surround, and stimuli present simultaneously within these two regions antagonize one another. In a similar fashion, auditory receptive fields are determined by binaural inputs
Fig. 1. Multisensory response interactions are determined by the spatial relationships of the components of a multisensory stimulus. In A the visual and auditory receptive fields of a single SC cell are drawn in a schematic of visual and auditory space. The circle represents both the visual field and the auditory space anterior to the interaural axis. Visual and auditory space are aligned since the visual axis corresponds to 0° elevation and azimuth in auditory coordinates. First, a visual stimulus (1 x 3° bar of light) was moved through the visual receptive field at 22 degrees/s, 16 times. Then an auditory stimulus (1 s broad-band noise at 0° elevation and 45° azimuth) was presented in its receptive field 16 times. The responses evoked during each of these tests are displayed in the upper right of B. The square wave here represents the auditory stimulus (A), the ramp represents the visual stimulus (V), and the time scale (bar) equals 500 ms for all tests. These same stimuli were then presented simultaneously for 16 repetitions, and the resultant peristimulus time histogram (50 ms/bin) is presented in B at the intersection of the 0° (elevation) and 45° (azimuth) axes. Note the dramatic and multiplicative response enhancement (235%). When the auditory stimulus was displaced upward or laterally at each of the asterisks in A, the corresponding histograms were generated in B. Clearly, the magnitude of the enhanced interaction is degraded as the auditory stimulus is displaced toward the periphery of its receptive field. When the auditory stimulus is outside its receptive field response depression is produced in most instances. In C these interactions are displayed in perspective in order to admit a third axis: the percentage of response enhancement or depression plotted at the location at which the auditory stimulus was presented. These values were calculated as follows: \[ \frac{(CM - SM_{max}) \times 100}{SM_{max}} \] where CM is the response to the combined-modality stimulus and SM_{max} is the response to the most effective single-modality stimulus.
which frequently are also characterized by spatial antagonism\textsuperscript{9,13,26}. A multisensory cell with this combination of receptive fields will have its activity enhanced by two stimuli (of different modalities) centered within the excitatory regions of their receptive fields and inhibited if one stimulus is in the suppressive region of its receptive field. What remains most impressive, however, is the magnitude that these interactions attain: most such interactions are multiplicative rather than additive and combinations of stimuli can evoke responses in some cells unresponsive to the individual stimulus components\textsuperscript{11,16}. Furthermore, the magnitude of these interactions could be degraded when the multisensory stimuli were presented at increasingly greater temporal disparities\textsuperscript{2,15}.

It has been suggested that the alignment of multisensory maps is the simplest and most economical way to allow multiple sensory inputs access to the same motor outputs to produce coordinated orientation of the different receptor organs\textsuperscript{4,21}. However, the present observations indicate that a major consequence of this alignment is also to provide an enormous degree of sensitivity, resolution and flexibility in this system. As a result of the alignment of multisensory maps in the brain (see, for reviews, refs. 7, 19) there is substantial overlap of excitatory regions among a multisensory cell's receptive fields. This hardly seems serendipitous; since natural multisensory stimuli are often closely related in space due to common causality (e.g. sight and sound of an insect), receptive field alignment provides a mechanism by which combinations of stimuli originating from the same location can enhance responses in SC cells and thereby increase stimulus detection\textsuperscript{11,12,16}. Disparate, or large multisensory stimuli can evoke response depression by encroaching on suppressive regions — a mechanism of response inhibition and multisensory spatial resolution substantially the same as that known to exist within modalities\textsuperscript{10,14}.

Given that these interactions take place in the SC cells that project to premotor and motor areas of the brainstem and spinal cord to effect movement\textsuperscript{12}, they can play a significant role in determining whether or not an orientation response will occur and thus provide a great deal of flexibility in this sensorimotor system. Since multisensory interactions in SC cells are dynamic and depend on both the combinations of stimuli present and their specific spatial properties, the neural responses of SC cells and the behaviors they influence need not be immutably tied to the presence of an individual stimulus. Rather they can vary in relation to the particular complex of stimuli present at any given moment. The presence of multisensory convergence and aligned multisensory maps in organisms of various phyletic levels\textsuperscript{4,19} suggests that this mode of multisensory integration is adaptive in a host of ecological situations.

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