and no aptation above the level of organisms; any resultant trends need not be adaptive, and the process is reducible to combinations of long-recognized microevolutionary processes. If we follow widely accepted analyses of what may not be termed group selection (*11, 22, 23*), then consistency demands recognition of effect macroevolution as separate from species selection.

There are suggestions that the frequency of certain variants available at genetic and phenotypic levels may be intrinsically determined (*10, 15*). The effect hypothesis translates this notion to variation among species. It suggests that life's diversity patterns, and through them some long-term directional tendencies, may be incidental nonadaptive consequences. The effect hypothesis is simpler and makes fewer assumptions than the hypothesis of species selection. The onus is on those who assert group selection in any particular case to show that the concept is demanded by the evidence—that is, that selection of genotypes and phenotypes or other lower level processes do not provide a sufficient explanation of the deterministic pattern among groups. The effect hypothesis is of particular relevance to analyses of species diversity in ecosystems. It recognizes hierarchy of biological organization. But a hierarchical approach, which addresses the causes of sorting among species, cannot "negate the importance of population level phenomena" (*30*). Testing for causes of macroevolutionary pattern may require studies involving many subdisciplines from genetics to paleontology.

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26. E. S. Vrba and N. Eldredge, in preparation.
27. A comparable *S* has been suggested for generalist and specialist species, with a high *E* of new generalist species resulting from large niche overlap (*8*, p. 310).
28. Species-selected trends represent new and improved efficiency (*5*); see also Stanley (*7*, p. 184).
29. Just as a claim of group aptation requires special argument (*11, 22*), so does a claim of species aptation (*26*). If all organisms in a species are black, black color is a species character. If black organisms are subsequently removed by selection, but those of different color in a related species survive, this is differential species extinction. Selection of organisms is enough to account for events, and there is no need for concepts of species aptation and selection.
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Interactions Among Converging Sensory Inputs in the Superior Colliculus

Abstract. *The responses of superior colliculus cells to a given sensory stimulus were influenced by the presence or absence of other sensory cues. By pooling sensory inputs, many superior colliculus cells seem to amplify the effects of subtle environmental cues in certain conditions, whereas in others, responses to normally effective stimuli can be blocked. The observations illustrate the dynamic, interactive nature of the multisensory inputs which characterize the deeper laminae of the superior colliculus.*

One assumption underlying neurophysiological studies of the superior colliculus has been that detailing the response properties of its constituent cells in the laboratory will give us insight into how these cells function under more "natural" environmental conditions. Investigators have usually determined the characteristics of a given superior colliculus cell by examining its responses to a modality-specific (for example, visual) stimulus whose physical parameters are systematically varied. In this manner, the investigator identifies the physical characteristics of those stimuli likely to have optimal access to the circuitry of the superior colliculus and, therefore, most likely to evoke an orientation response (*1*).

Table 1. Frequencies of superior colliculus neurons from cat (59 cells) and hamster (49 cells) by type of interaction (*9*) and laminar distribution (*8*). Numbers in parentheses are percentages.

Interaction	Cell location		Totals
	Superficial laminae	Deep laminae	
Enhancement	0	26 (29.2)	26
Depression	0	21 (23.6)	21
None	19 (100)	42 (47.2)	61
Totals	19	89	108

Yet during normal behavior an animal is confronted with a variety of simultaneous stimuli from different sensory modalities. The likelihood of an orientation response may depend as much (if not more) on the combination of stimuli as on the normal effectiveness of any individual stimulus. It is possible that this behavioral phenomenon occurs because the influence of a sensory stimulus on a given neuron can vary in the presence of cues from other sensory modalities. The substrate already exists and cells receiving two or more sensory inputs have been described both in the superior colliculus (*2*) and in its nonmammalian homolog, the optic tectum (*3*). However, with the exception of a report on the interaction of infrared and visual inputs to cells of the optic tectum of the rattlesnake (*4*), we have little information regarding the product of simultaneous sensory convergence onto these midbrain cells.

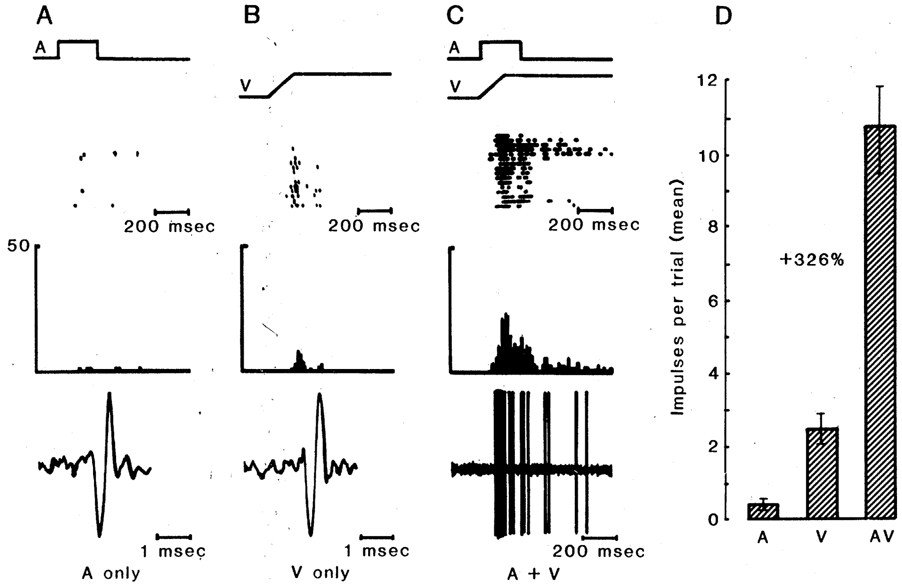

Fig. 1. Response enhancement in the superior colliculus of the cat. The cell responded to auditory (*A*) and visual (*V*) stimuli. A square wave represents the auditory stimulus and a ramp the visual stimulus. The raster below each stimulus trace displays the cell's responses to 16 successive stimulus presentations. Each dot represents one neuronal impulse, and the trials are ordered from bottom to top. Peristimulus time histograms (bins are 10 msec wide) are presented below each raster, and representative oscillograms below each histogram. (A) The auditory stimulus (200-msec hiss) was nearly ineffective when presented alone. Responses were elicited on 25 percent of the trials and consisted of few impulses. (B) The visual stimulus (a 1° by 2° bar of light moved across the receptive field at 300° per second in the preferred direction) elicited responses in 69 percent of the trials and was somewhat more effective. (C) When the two stimuli were presented in close temporal sequence, however, vigorous responses were elicited in 100 percent of the trials. (D) The increase in the number of impulses was significant (paired *t*-test, $P < 0.001$) (*9*). The vertical lines are standard errors of the mean.

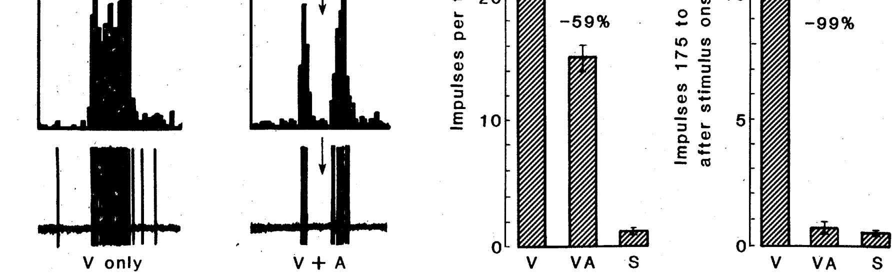

Fig. 2. Response depression. (A) The cell responded vigorously to a 2° by 4° bar of light moved across its visual receptive field at 125° per second. No response was elicited by auditory or by somatosensory stimuli. (B and C) An auditory stimulus (200-msec hiss) inhibited the response to the visual stimulus ($P < 0.001$). The depressive effect was virtually complete during the period from 175 to 500 msec after the onset of the auditory stimulus (B and D), reducing the cell's activity to its spontaneous (*S*) level. Peristimulus time histograms (A and B) are calibrated for 100 impulses and 50-msec time bins.

We have found a dramatic difference between the responses of superior colliculus cells when a combination of sensory cues was presented and when these stimuli were presented individually (*5*). Often we could not predict the effect of combinations of sensory stimuli on a cell's response, even when we knew the effectiveness of each stimulus individually. Thus, stimuli that appeared to be ineffective when presented alone could significantly alter the effectiveness of other stimuli when combined with them.

Eight cats were prepared for long-term study, and 19 hamsters for single experiments (*6*). Standard single-unit recording techniques were used. Once a cell was isolated, its receptive field was mapped and its responses to controlled visual, auditory, or somatic stimuli (*7*) were tested. These are referred to hereafter as separate-modality tests. The effective modalities and the optimal stimulus for each modality (that stimulus which evoked the greatest frequency or number of discharges) were identified. Then, combinations of sensory stimuli were presented simultaneously and at various predetermined intervals. These tests were referred to as combined-modality tests. The responses evoked by combined-modality stimulation were then compared with the responses evoked by separate-modality tests.

The responses of 108 superior colliculus neurons were examined. All cells exhibiting multimodal interactions ($N = 47$) were located within the deeper laminae (*8*) (Table 1) and fell into two functional categories: response enhancement and response depression (*9*). The degree of response alteration resulting from these interactions ranged from +326 percent to −99 percent and depended upon both the stimuli presented and the timing of their presentations. The most profound interactions occurred when combined-modality cues were presented within 100 msec of one another (*10*).

Cells exhibiting response enhancement showed the same general characteristics as the example provided in Fig. 1. A unimodal auditory or a unimodal visual stimulus often failed to evoke discharges, and even on those trials in which these stimuli did produce a response, the response consisted of relatively few impulses. When the two stimuli were presented together, however, a vigorous response was evoked on every stimulus presentation. Other cells exhibited similar response enhancements to combinations of visual-somatic, auditory-somatic, and visual-auditory-somatic stimuli. When individual stimuli were just above threshold for eliciting discharges, the enhancement was greater than when the individual stimuli were highly effective. Thus, as the effectiveness (number of discharges elicited) of the individual stimuli increased, the percentage of enhancement produced by combining them decreased.

The cell illustrated in Fig. 2 is a typical example of response depression: it responded vigorously to a visual stimulus but not to an auditory or a somatic stimulus. When the auditory stimulus was presented with the visual stimulus, however, the cell's ability to respond to the visual stimulus was profoundly inhibited (*11*). In other cells, response depression was observed in response to visual-somatic and to auditory-tactile stimulus combinations.

The capability of a stimulus to enhance or depress the response of a given cell could not be predicted on the basis of separate-modality tests; it became apparent only when paired with an appropriate second stimulus. Therefore, to characterize cells of deep laminae on the basis of their responses to unimodal stimulation may give an inaccurate picture of their functional properties under nonlaboratory conditions, when many sensory cues are present. Rather than having a static set of response properties that relate only to the physical parameters of a single sensory stimulus, the response properties of superior colliculus neurons in the deep laminae are dynamic; their responses depend on (i) which stimulus combinations are present, (ii) the physical properties of the different sensory stimuli impinging upon the organism, and (iii) the timing of their occurrences.

It seems likely that by pooling a variety of sensory inputs, one population of superior colliculus cells may amplify the effects of subtle environmental changes to ensure an appropriate behavioral response even when individual cues are near threshold. Since there is no need to pool the various inputs for this purpose when each input by itself is highly effective, the degree of response enhancement decreases as the effectiveness of the individual stimuli increases.

On the other hand, some superior colliculus cells may pool sensory inputs in order to act as response inhibitors, thereby ensuring the absence of inappropriate responses. In these cases, a stimulus that usually evokes vigorous neuronal activity in the superior colliculus and ultimately a behavioral response, can be rendered ineffective in the presence of certain other sensory signals.

The principles underlying these interactions are not yet clear. However, multisensory interactions are restricted to cells of the deep superior colliculus, where visual, auditory, and somatic inputs converge (*2*). Since the final superior colliculus arbiter of an orientation response may reside in the deeper laminae, it is these interactions that may determine whether a behavioral change takes place.

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7. Quantitative tests were conducted with electronically controlled stimuli. Visual stimuli were stationary and moving spots or bars of white light projected onto a translucent plexiglass hemisphere positioned in front of the animal. Auditory stimuli were hisses delivered by a solenoid-controlled airstream or clicks from an audio amplifier. Somatosensory stimuli were airpuffs gated by a solenoid and a probe controlled by a moving coil vibrator.
8. Superficial layers include the stratum opticum and above and deep layers include the stratum griseum intermedial and below.
9. Response enhancement (and response depression) was defined as a significant (paired t-test, $\alpha = .05$) increase (or decrease) in the number of impulses elicited by combined-modality stimulation when compared with the number of impulses evoked by the most effective separate-modality stimulus. Sixteen stimulus repetitions were presented in each test. The percentage of enhancement or suppression was calculated as $(CM - SM_{\max})/SM_{\max} \times 100$, where CM is the response to the combined-modality stimulus and $SM_{\max}$ is the response to the most effective separate-modality stimulus.
10. Different stimulus modalities evoked responses of different latencies and time courses. Thus, even though stimuli of different modalities were presented simultaneously, their inputs did not necessarily reach a given cell at the same time nor did their effects persist for the same periods. Yet for all stimulus combinations, effects were greatest when stimuli were presented within 100 msec of one another.
11. The somatic stimulus did not influence the cell (Fig. 2).
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