er responses but did not eliminate them.

The attractiveness of female models impregnated with the 22.8 FDE odor cue is decreased after contact with males. Since most *L. zephyrum* females mate only once but some (<36 percent) will mate again, the male donor of an antiaphrodisiac odor cue protects his mate from superfluous male responses and reduces the likelihood that she will mate again. A male that detects such a cue on a female would gain more fertilizations by avoiding her, especially in sites like a *L. zephyrus* aggregation where there are large numbers of other females.

The material deposited by males on females may be a specific pheromone or pheromone blend (an antiaphrodisiac) or it could be some multipurpose material present on the surface of males, such as cuticular hydrocarbons. Antiaphrodisiac pheromones are most likely to evolve in aggregated species, with low to moderate levels of polygamy and sperm mixing. *Lasioglossum zephyrum* is aggregated and appears to have low to moderate levels of polygamy (*18*). Whether there is sperm mixing is not known.

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References and Notes

1. G. M. Happ, *Nature (London)* **222**, 180 (1969).
2. C. J. August, *J. Insect Physiol.* **17**, 739 (1971).
3. M. C. Birch, in *Pheromones*, M. C. Birch, Ed. (North-Holland, London, 1974).
4. L. E. Gilbert, *Science* **193**, 419 (1976).
5. Male *Centris adani* may deposit a citrol-like odor on females during copulation; the response of other *C. adani* males to this odor is not known [G. W. Frankie, S. B. Vinson, R. E. Coville, *J. Kans. Entomol. Soc.* **53**, 837 (1980)].
6. The social behavior of *L. zephyrum* has been well studied. See C. D. Michener, *The Social Behavior of the Bees* (Belknap, Cambridge, Mass., 1975) chap. 24; M. D. Breed, *Insectes Soc.* **22**, 375 (1975); M. D. Breed, J. M. Silverman, W. J. Bell **24**, 351 (1977); L. Greenberg, *Science* **206**, 1095 (1979); P. F. Kukuk, M. D. Breed, A. Sobti, W. J. Bell, *Behav. Ecol. Sociobiol.* **2**, 319 (1977); G. Buckle, *Insectes Soc.* **29**, 125 (1982).
7. E. M. Barrows has described patrolling behavior (*13*) and pouncing behavior [*J. Kansas Entomol. Soc.* **49**, 105 (1976)].
8. E. M. Barrows, thesis, University of Kansas, Lawrence (1975).
9. ———, *Behav. Biol.* **15**, 57 (1975).
10. G. C. Eickwort and H. S. Ginsberg, *Annu. Rev. Entomol.* **25**, 421 (1980).
11. Electrophoretic examination of 31 apparently singly founded *L. zephyrum* colonies indicates that in 36 percent of the colonies either the founding female was doubly inseminated or there was more than one foundress.
12. Females were tethered by taping their wings to a 15-cm long applicator stick with Scotch brand strapping tape. Such a female was held by hand in an area containing an abundance of patrolling males. Five females were used in all. The field site for this and other experiments was the Monkey Run site, a steep, east-facing clay bank rising about 9 m above a stream (Fall Creek) in Tompkins County, Ithaca, N.Y. The *L. zephyrum* aggregation contains hundreds of nests, and thousands of males patrol the site in July and August.
13. E. M. Barrows, *Insectes Soc.* **22**, 307 (1975).
14. The odor cues consisted of: control, 50 μl of methylene chloride; standard, methylene chloride extract half of a *Colletes* sp. Dufour's gland; 5.7 FDE, 10 μl of vial rinse; 11.4 FDE, 20 μl of vial rinse; and 22.8 FDE, 40 μl of vial rinse; and 22.8 FDE, 40 μl of vial rinse plus male contact.
15. A methylene chloride extract of the Dufour's glands of six *Colletes* sp. was used as a standard because in the Collitidae the Dufour's gland secretions are dominated by macrocyclic lactones. Similarly, in the Halictidae, the Dufour's gland secretes macrocyclic lactones [C. D. Andersson, G. Bergstrom, B. Kullenberg, D. Stallberg-Stenhagen, *Ark. Kemi.* **26**, 191 (1966); G. Bergstrom, *Chem. Sci.* **5**, 39 (1974); A. Hefetz, H. M. Fales, S. W. T. Batra, *Science* **204**, 415 (1979); R. M. Duffield, A. Fernandes, S. McKay, J. W. Wheeler, P. R. Snelling, *Comp. Biochem. Physiol.* **67B**, 159 (1980); A. Hefetz, M. S. Blum. G. C. Eickwort, J. W. Wheeler, *Comp. Biochem. Physiol.* **61B**, 129 (1978); R. M. Duffield, A. Fernandes, C. Lamb, J. W. Wheeler, G. C. Eickwort, *J. Chem. Ecol.* **7**, 319 (1981)].
16. There were two instances in which males landed on a model, it was the one with the high female odor concentration. After the landings occurred, the contaminated model was removed and replaced with a fresh model. The time of the observation was extended to compensate for time lost between a male's landing and the replacement of the model.
17. R. A. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, ed. 1, 1969).
18. E. M. Barrows, W. J. Bell, C. D. Michener. *Proc. Natl. Acad. Sci. U.S.A.* **72**, 2824 (1975).
19. I thank G. C. Eickwort, W. L. Roelofs, and P. W. Sherman for reading an earlier draft of this manuscript. Supported by NIH-NRSA grant 1-F32-MH08722-01.

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Descending Efferents from the Superior Colliculus Relay Integrated Multisensory Information

Abstract. *By means of their efferent projections to motor and premotor structures, the cells in the deep superior colliculus are intimately involved in behaviors that control the orientation of the eyes, pinnae, and head. These same efferent cells receive multiple sensory inputs, thereby apparently enabling an animal to orient its receptor organs in response to a wide variety of cues. This sensory convergence also provides a system in which motor responses need not be immutably linked to individual stimuli but can vary in reaction to the multitude of stimuli present in the environment at any given moment.*

That the superior colliculus (SC) plays a role in visual orientation has been known since the late 19th century (*1*), but only recently has its multisensory nature been demonstrated. Behaviorally, it is evident as a tendency to neglect contralateral sensory stimuli after the removal of one SC (*2*)—an observation that prompted investigators to explore the organization and properties of its constituent neurons. Consequently, the organization of the sensory (visual, auditory, and somatosensory) and motor representations in the SC has been described in detail, and these representations have been shown to be in register with one another (*3*). For example, the upper portions of visual, auditory, and body space are represented in the same region in the SC, and electrical stimulation here produces upward movement of the eyes, pinnae, and head—an elegant yet simple organizational plan.

For the SC to transform sensory input into motor output, sensory input ultimately must reach the deep efferent cells that produce orientation by way of projections (Fig. 1) to the brainstem and spinal cord (*4*). Yet with few exceptions (*5*) little attention has been directed to-

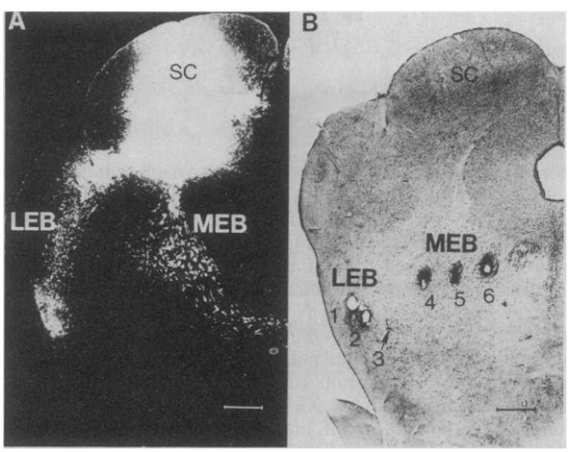

Fig. 1. (A) Dark-field micrograph showing the two descending efferent pathways labeled with tritiated leucine [the medial efferent bundle (*MEB*) and the lateral efferent bundle (*LEB*)], as they exit from the superior colliculus (*SC*) and course toward their brainstem and spinal cord targets. Calibration bar, 1 mm. (B) SC neurons with descending efferent axons were activated antidromically by electrical stimulation delivered through arrays of implanted electrodes. The tips of the electrodes in each array were spaced approximately 1 mm apart in the anterior-posterior and medial-lateral planes to permit the delivery of discrete electrical stimuli at a variety of points within each of these efferent SC pathways. This micrograph illustrates the most caudal point at which the electrical stimuli were presented (electrode 3). The tips of the remaining electrodes (1 and 2 and 4 to 6) were located in sections as far as 1.0 mm rostral to the one shown here [corresponding to levels depicted in (A)]. Calibration bar, 1 mm.

ward determining the physiological properties of deep SC cells identified as efferents and whose activity is most closely associated with SC-mediated orientation responses. Studies of the sensory properties of these cells have been limited to their visual characteristics, while studies of the motor properties of deep-layer SC cells (many of which undoubtedly were efferents) have largely been restricted to their role in eye movements (*6*). Yet many of the deep SC cells that exhibit presaccadic activity do not respond to visual stimuli (*7*). Thus, one might suspect that many SC cells have motor-related properties but no sensory inputs to elicit their motor-related activity. However, since many SC cells receive auditory or somatosensory inputs (or both) (*3*), perhaps the activity of these presaccadic cells is triggered by nonvisual signals (*8*). Moreover, the activation of descending SC efferents produces orientation not only of the eyes, but of other receptor organs as well (*3*). If the same SC-mediated orientation response (for example, eye or pinna movement) can be elicited by the different sensory modalities represented in the SC (*3*), these modalities all must have access to SC efferent cells. Perhaps these sensory inputs even converge on the same efferent cells, thereby influencing the orientation of the various receptor organs by way of the same SC circuits. We began to examine these questions by determining which sensory inputs have access to which descending efferent SC cells. We found that (i) nearly all the descending efferent cells (usually regarded as "motor") have sensory properties that are indistinguishable from those of "nonefferent" cells, and (ii) it is on these descending efferents that sensory modalities normally converge (*9*), thereby producing integrated multimodal output signals that are striking transformations of the individual sensory inputs (*10*). Preliminary results of this work have been presented (*11*).

Once a cell was isolated (*12*), its efferent status was established by recording its antidromic responses (*13*) to electrical stimulation of the medial efferent bundle (MEB) and the lateral efferent bundle (LEB) (Fig. 1B) (*14*). Cells antidromically activated by stimulation of MEB, LEB, or both were classified as "efferent" (*15*). We then determined which sensory stimuli could influence the cell. This was accomplished by repeatedly (8 to 16 times) presenting controlled, reproducible visual, auditory, and somatosensory stimuli (*16*) individually (for example, visual alone, auditory alone: single-modality tests) and then together in various combinations (combined-modality tests). The number of impulses evoked during each test was recorded and the results compared; cells were then grouped into one of three functional categories: (i) unresponsive to sensory stimulation, (ii) unimodal (influenced by stimuli of only one sensory modality), and (iii) multimodal (influenced by stimuli of more than one sensory modality).

Of the 153 deep lamina SC cells studied, almost half (47.7 percent, $N = 73$) were antidromically activated from one (MEB, 42; LEB, 19) or both (MEB + LEB = 12) of the descending efferent bundles. Nearly all the antidromically activated (efferent) cells (95.9 percent, $N = 70$ of 73) were responsive to one or

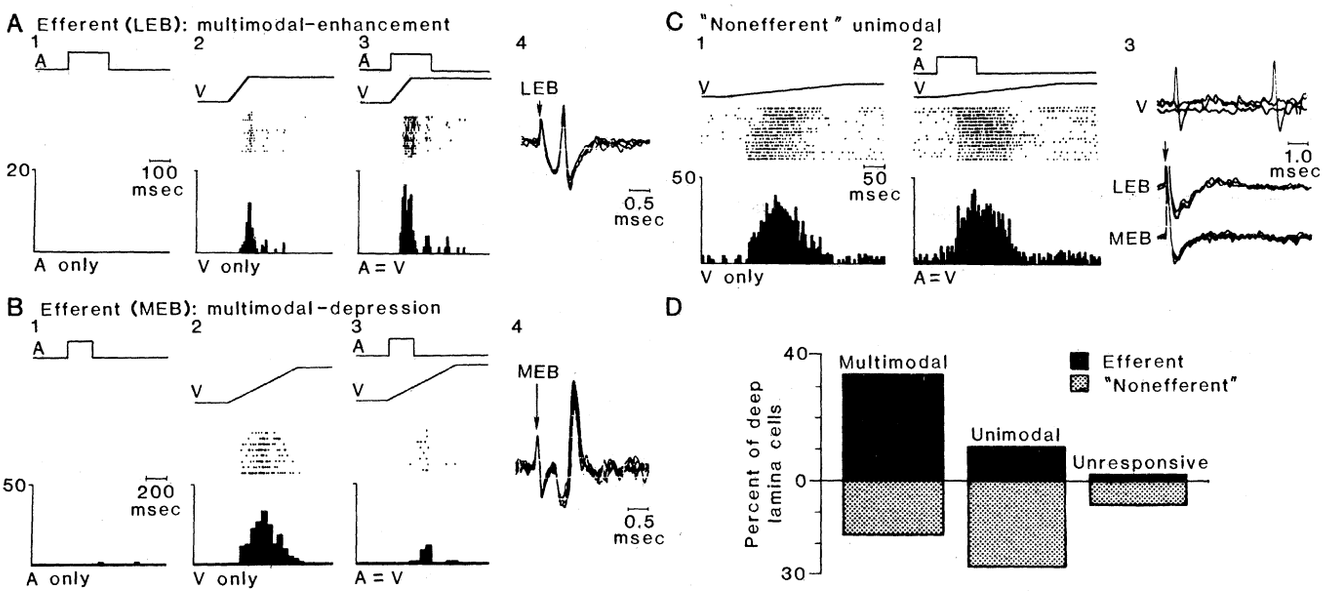

Fig. 2. Three SC cells that characterize efferent and nonefferent cells. (A) An efferent cell that receives converging sensory inputs and exhibits response enhancement projects out of the SC through the LEB. An auditory stimulus (*A*) alone is not effective, but it enhances responses to a visual stimulus (*V*) when they are presented together ($A = V$). The raster and histogram (10 msec per bin, 20 events per bin) below stimulus traces display the cell's responses to 16 successive trials. (1) The auditory stimulus (200 msec of white noise) alone did not elicit discharges. (2) The visual stimulus (1° by 3° bar of light moved at 500 deg/sec across the receptive field in the preferred direction) evoked 3.3 spikes per trial with a standard error of the mean of ±0.6. (3) Combining the two stimuli enhanced the response to 7.7 ± 0.65 spikes per trial [$t(15) = 5.1$, $P < 0.001$]. (4) Electrical stimulation of the LEB (arrow) (85 μA, 0.1 msec, $N = 5$) antidromically activated this cell. MEB stimulation was ineffective, even at high current intensities (>600 μA). (B) A cell that receives multimodal inputs that interact to effect response depression projects out of the SC through the MEB. (1) An auditory stimulus (250 msec white noise) was ineffective, but (2) a 3° by 6° dark bar moved through the receptive field at 100 deg/sec in the preferred direction produced a vigorous response (15.2 ± 1.4 spikes). However, when the auditory and visual cues were combined (3), the cell exhibited response depression (2.1 ± 0.3 spikes per trial) [$t(7) = 6.7$, $P < 0.001$]. (4) Electrical stimulation of MEB (arrow) (100 μA, 0.1 msec, $N = 5$) antidromically activated the cell, but LEB stimulation was ineffective, even at >600 μA. (C) A nonefferent unimodal visual cell. (1) This cell was excited by a 1° by 3° bar of light moving at 85 deg/sec across the visual receptive field in the preferred direction (25.3 ± 1.4 spikes per trial). (2) When this visual stimulus was combined with an auditory stimulus (200 msec of white noise), no significant change in the number of impulses was evoked (29.1 ± 1.3 spikes per trial). Similarly, pairing a somatosensory cue with the visual stimulus had no influence on the cell's response. (3) The oscillogram labeled "V" illustrates action potentials evoked by a visual stimulus. No potentials were elicited antidromically by stimulation of the LEB or the MEB (arrow), even at >600 μA. (D) Frequency (percent of deep lamina cell population) with which multimodal, unimodal, or unresponsive cells were encountered within the efferent and nonefferent populations.

more sensory modality, with the majority (74.3 percent, $N = 52$ of 70) responding to two or three modalities. The majority of multimodal cells (65.8 percent, $N = 52$ of 79) were efferent (Fig. 2D), and the majority (71.3 percent, $N = 52$ of 73) of the efferents were demonstrably multimodal. In contrast, only 33.7 percent ($N = 27$ of 80) of the nonefferent cells were multimodal.

Yet, regardless of a cell's classification as unimodal, multimodal, efferent, or nonefferent, it fell in the same latency range and shared most of its receptive field properties with cells in all other categories influenced by the same sensory modality or modalities. For example, most cells responsive to visual stimuli were binocular; they also preferred stimuli that were smaller than their receptive fields and that moved in specific directions at low (10° to 50° per second) velocities. Similarly, most cells responsive to somatosensory stimuli were activated by displacement of guard hairs on the contralateral body surface, preferred rapid movement and responded in a transient fashion even to maintained stimuli. Most of the acoustically sensitive cells were binaural, responded to a white noise stimulus presented in contralateral auditory space, and had large receptive fields. Furthermore, all these cell types exhibited a tendency for response attenuation at high iterative rates of stimulation (6 to 8 per minute).

Substantial differences between the efferent and nonefferent populations were observed only when patterns of modality convergence were compared. The majority of efferent cells were multimodal as revealed by combined-modality tests. Furthermore, these combined-modality tests elicited responses that were often dramatically different from their responses to the same stimuli presented individually. The number of impulses evoked in efferent cells by combined-modality stimulation was significantly greater (or less) than that evoked by the most effective unimodal stimulus (Fig. 2, A and B). These response interactions were multiplicative: in some cells, they were great enough to enhance responses by more than 900 percent, whereas in others, responses were eliminated. On the other hand, nonefferent cells infrequently responded to more than one sensory modality, and comparatively few (8 of 27) demonstrated multimodal interactions (*17*).

There were almost equal proportions of efferent cells in intermediate (46.8 percent, $N = 60$ of 128) and deep (52 percent, $N = 13$ of 25) layers, and most were multimodal (intermediate = 70 percent, $N = 42$ of 60; deep = 76.9 percent, $N = 10$ of 13).

These data indicate that the vast majority of the SC cells projecting to motor and premotor areas have sensory properties and might best be designated as "sensorimotor." The results support the hypothesis that different sensory modalities can produce the orientation of the different receptor organs by way of the same SC-related circuits. Such a system would greatly simplify the task of coordinating the various components of an orientation response.

Not only may these sensorimotor cells provide a bridge between sensory and motor activities of the SC, but also as the sites at which different unimodal inputs converge, they are able to integrate the multitude of sensory cues impinging on the organism at any given moment. Their output messages, therefore, represent a synthesis of multimodal cues whose product depends on the spatial (*18*) and temporal (*19*) characteristics of the stimulus modalities. Apparently, this provides a neural mechanism that allows response flexibility, so that a given unimodal stimulus that evokes an orientation response under one set of circumstances need not evoke this response under all circumstances. By virtue of the interactions that occur in efferent SC cells during multisensory stimulation, a complex environmental stimulus may influence orientation behaviors very differently from any of its individual components.

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References and Notes

1. E. Adamuk, *Arch. Ophthalmol.* **18**, 153 (1872).
2. J. M. Sprague and T. H. Meikle, Jr., *Exp. Neurol.* **11**, 115 (1965); G. E. Schneider, *Science* **163**, 895 (1969); V. A. Casagrande *et al.*, *ibid.* **177**, 444 (1972).
3. See B. E. Stein [in *Comparative Neurology of the Optic Tectum*, H. Vanegas, Ed. (Plenum, New York, 1984), p. 819; *Annu. Rev. Neurosci.* **7**, 95 (1984)] for a recent review.
4. See M. F. Huerta and J. K. Harting [in *Comparative Neurology of the Optic Tectum*, H. Vanegas, Ed. (Plenum, New York, 1984), p. 687] for a recent review.
5. V. C. Abrahams and P. K. Rose, *J. Neurophysiol.* **38**, 10 (1975); D. M. Berson and J. T. McIlwain, *ibid.* **47**, 700 (1982); G. Chevalier, S. Gacher, J. M. Deniau, *Exp. Brain Res.* **53**, 320 (1984); R. W. Rhoades and D. R. Dellacroce, *Exp. Neurol.* **67**, 163 (1980).
6. R. H. Wurtz and J. E. Albano, *Annu. Rev. Neurosci.* **3**, 189 (1980).
7. P. H. Schiller and F. Koerner, *J. Neurophysiol.* **34**, 920 (1971); D. L. Sparks, *Brain Res.* **90**, 137 (1975); M. Straschill and F. Schick, *Exp. Brain Res.* **27**, 131 (1977).
8. M. F. Jay and D. L. Sparks, *Nature (London)* **309**, 345 (1984); B. E. Stein, H. P. Clamann, S. J. Goldberg, *Science* **210**, 78 (1980).
9. B. E. Stein and M. O. Arigbede, *Exp. Neurol.* **36**, 179 (1972).
10. E. A. Newman and P. H. Hartline, *Science* **213**, 789 (1981); M. A. Meredith and B. E. Stein, *ibid.* **221**, 389 (1983).
11. M. A. Meredith and B. E. Stein, *Soc. Neurosci. Abstr.* **9**, 817 (1983).
12. For recording, cats ($N = 12$) were anesthetized (ketamine hydrochloride, 30 mg per kilogram of body weight), intubated, paralyzed, and connected to a respirator (75 percent N_2O and 25 percent O_2). No wounds or pressure points were present. Glass-insulated tungsten electrodes were used for recording. "Search" stimuli consisted of electrical stimulation of the MEB or LEB, flashed or moving spots or bars of light projected on a translucent hemisphere positioned 45 cm in front of the animal (visual); complex sounds (auditory); and taps, brushes, or air puffs (somatosensory).
13. Monopolar cathodal pulses (50 to 300 μA, 0.1 msec) antidromically activated SC cells. Criteria were <0.2 msec latency variation, consistent responses to both double-shock pulses at >300 Hz, and threshold lower than 300 μA [mean effective stimulus current, 175 ± 72 (standard deviation) μA]. Current spread was minimal, as evidenced by (i) despite a major SC (superficial layers) projection to the parabigeminal nucleus, few superficial layer cells (3 of 67) were antidromically activated by LEB stimulation delivered approximately 1 mm caudal to the parabigeminal nucleus, and (ii) in each electrode penetration, antidromically activated cells were often separated by nonactivated (nonefferent) cells.
14. Electrode implantations were performed under pentobarbital anesthesia (40 mg/kg) several days before a recording session. Sets of tungsten stimulating electrodes were implanted through the use of either a rostral or caudal approach to reach the midbrain tegmentum without traversing the SC. A cylindrical well–head-holding device was implanted over a midline craniotomy to support the head without obstructing the eyes, pinnae, or face.
15. "Nonefferent" refers to our inability to demonstrate a descending axon, and does not preclude the possibility that a cell has an ascending, or intertectal, axon. It is also possible that some cells were incorrectly classified as nonefferent because the entire descending bundle was not activated. This would not obscure the dichotomy between multimodal (the majority are efferent) and unimodal (the majority are nonefferent) cells, but could contribute to underestimating the dichotomy.
16. Sensory stimulation during single- and combined-modality tests was electronically controlled: spots and bars of light were presented by a galvanometer-driven mirror system; white noise bursts (10- to 250-msec duration, 35- to 50-dB sound pressure level) were delivered through a piezoelectric speaker mounted on a movable hoop; and displacement of the skin or hair was accomplished with a moving probe controlled by a magnetic-coil vibrator. During combined-modality stimulation, stimuli from different modalities were presented simultaneously in close spatial register.
17. The low incidence of multimodal convergence in nonefferent cells makes generalizations about interactions in these cells premature at present (*15*).
18. M. A. Meredith and B. E. Stein, *Soc. Neurosci. Abstr.* **10**, 298 (1984).
19. J. W. Nemitz, M. A. Meredith, B. E. Stein, *ibid.*, p. 298.
20. We thank A. M. Clarke for his design and maintenance of the electronic equipment. Supported by NIH grant EY04119.

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