

disulfides is well known (14), and it is likely that the activity of this fraction is due to a small amount of dimethyl disulfide formed from the trisulfide. The possibility remains, however, that there is an unidentified active compound in this fraction.

We conclude that dimethyl disulfide is present in the estrous hamster vaginal secretion. In addition, this compound, when present at stimulus intensities in the range of those to be expected from a receptive female, elicits approaching, digging, and sniffing behaviors similar to those elicited by the natural secretion. Consequently this compound is an active attractant and can be considered the likely factor in the normal attraction of the male hamster to the female. Other assay procedures will be required to determine whether this compound or some unidentified substance subserves the other behavioral responses evoked by the vaginal secretion.

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- Random-bred 115-g hamsters were obtained from Lakeview Hamster Colony. All animals were housed individually in single-sex colony rooms at 20° to 21°C with reversed 12:12 hour light-dark cycles. Each animal was supplied with nesting materials, unlimited rat and guinea pig chow, and thrice weekly feedings of carrots and sunflower seeds.
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- All gas chromatography was done on a Hewlett-Packard 5750B instrument equipped with a flame ionization detector, 1.8 m by 2 mm (inside diameter) glass columns packed with 10 percent Carbowax 20M (unless otherwise noted) on 80/100 mesh Chromosorb W HP, nitrogen carrier gas (15 cm³/min), and a capillary splitter which diverted 90 percent of the column effluent to an exit port on the side of the chromatograph.
- Mass spectra were obtained with a DuPont 21-492 double focusing mass spectrometer operating at a resolution of 1000, an ionization potential of 140 volts, and an ion accelerating potential of 1800 volts. The spectrometer scanned at 2 seconds per decade from *m/e* 600 to *m/e* 20. A new scan was initiated every 9 seconds. The data were collected on a VG 2040 data handling system. Gas chromatography peaks were identified by plots of total ion current or of selected ion currents against scan number and by the Mülheim algorithm [D. Henneberg, K. Casper, E. Ziegler, *Chromatographia* **5**, 209 (1972)] or the VG "mass max" algorithm. For each compound three mass spectra were obtained as the peak emerged from the GC. In each case, the four most intense ions matched the *m/e* and relative intensity observed for authentic dimethyl disulfide and dimethyl trisulfide, respectively. We obtained the spectra of the authentic compounds under experimental conditions identical with those used to obtain the spectra of the unknowns. The spectra of the compounds from the vaginal secretion also agree with those reported in the "Eight Peak Index of Mass Spectra," (Mass Spectrometry Data Centre, AWRE Aldermaston, England, ed. 2, 1974). Finally, the probability based matching algorithm of McLafferty was used for a computer search of a file of 35,700 mass spectra [F. W. McLafferty, R. H. Hertel, R. D. Villwock, *Org. Mass Spectrom.* **9**, 690 (1974)]. The highest confidence indices were given by dimethyl disulfide and dimethyl trisulfide. The major ions observed in the unknown spectrum identified as that of dimethyl disulfide are: *m/e* (intensity, percent) 94 (100), 79 (75), 45 (57), and 47 (21). The ions from the unknown spectrum identified as that of dimethyl trisulfide are: 126 (100), 79 (54), 45 (45), and 80 (39).
- Additional major components (0.5 to 30 µg per female) have also been identified from the whole volatile fraction. These include ethanol, 1-propanol, 1-butanol, 1-hexanol, and ethyl butyrate. Authentic samples of these compounds, at the appropriate intensities, proved inactive. In addition, a number of common odorants not present in the natural secretion have been examined in the usual male behavioral assay. For example, oleic and linoleic acids were inactive in milligram amounts whereas similar quantities of butyric acid and amyl acetate each elicited responses of less than 5 seconds' duration. Food odors were also inactive.
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Coordinated Activities of Middle-Ear and Laryngeal Muscles in Echolocating Bats

Abstract. *The middle-ear muscles and laryngeal muscles of the little brown bat (*Myotis lucifugus*) are highly developed. When the bat emits orientation sounds, action potentials of middle-ear muscles appear approximately 3 milliseconds after those of the laryngeal muscles; this activity of middle-ear muscles attenuates the vocal self-stimulation and improves the performance of the echolocation system. When an acoustic stimulus is delivered, both types of muscles contract; action potentials of the laryngeal muscles appear approximately 3 milliseconds after those of the middle-ear muscles. These two groups of muscles are apparently activated in a coordinated manner not only by the nerve impulses from the vocalization center, but also by those from the auditory system.*

In the echolocating bat, the cricothyroid muscle and middle-ear muscles (MEM's) are enormously hypertrophied. In man, the inferior laryngeal nerve, innervating all extrinsic laryngeal muscles except for the cricothyroid muscle, is essential for speech (1). In the bat, the superior laryngeal nerve innervating the cricothyroid muscle is indispensable for the emission of orientation sounds. The bat's laryngeal mechanism for the production of sound is different from that of man (2). Unlike man, the echolocating bat has large MEM's which appear to be powerful in controlling the transmission of sound energy across the ossicular chain. The contraction-relaxation time of the MEM's is of very short duration. The tetanus fusion frequency of the stapedius muscle ranges between 260 and 320 sec⁻¹ (3). When the bat emits a short frequency-modulated (FM) orientation signal, the MEM's start to contract 6 to 8 msec before vocalization and usually contract maximally during vocalization. Then, these muscles relax within 2 to 8 msec after vocalization. These muscles are specialized for selective attenuation of the vocal self-stimulation, which can theoretically improve echo detection (3, 4). The vocal MEM activity—that is, the MEM activity synchronized

with vocalization—indicates that the MEM's and laryngeal muscles (LM's) are activated in a coordinated manner by the nerve impulses originating from the vocalization center. During further experiments on the vocal MEM activity in the little brown bat (*Myotis lucifugus*) (3), we found that not only the MEM's but also the LM's responded to acoustic stimuli. These two groups of muscles are apparently activated by nerve impulses from the auditory system. We describe here the coordinated activities of the MEM's and LM's that appear when the bat vocalizes and when it receives acoustic stimuli.

Eighteen *M. lucifugus* were studied. With the animal under ether anesthesia, the flat head of a nail 1.8 cm long was mounted against the dorsal surface of the skull of each animal with glue and dental cement. The animal was placed ventral side up in a body-sized oblong box made of wire mesh. Its head was then held motionless by locking the shank of the nail into a metal rod with a set screw. Both the MEM's and LM's were then exposed. An indifferent electrode (silver wire) was placed on the subcutaneous tissue, and recording electrodes (sharpened tungsten wires) were inserted into the MEM's and cricothyroid muscle or inferior laryngeal

nerve for recording of action potentials. The action potentials were displayed on the screen of a cathode-ray oscilloscope and were averaged with a computer (Nicolet 1070) to show the response pattern quantitatively. Orientation sounds were elicited from the bat by pulling its tail with forceps and were picked up with a Brüel and Kjaer $\frac{1}{4}$ -inch microphone. The electronic instruments used to generate acoustic stimuli have been described (5, 6). Since the duration of the orientation sound was shorter than 4 msec, short tone bursts were delivered as stimuli. The tone bursts had a 0.5-msec rise-decay time and a 4-msec duration and were delivered at a rate of 1.5 sec⁻¹ from a condenser loudspeaker placed 60 cm in front of the animal. The loudspeaker was calibrated with the microphone placed at the bat's ears and its output was expressed in decibels sound pressure level (db SPL) referred to 0.0002 dyne/cm² root mean square.

When the bat emitted orientation or nonorientation sounds, both the MEM's and LM's discharged before vocalization. The cricothyroid muscle always became active a few milliseconds earlier than the stapedius muscle (Fig. 1A). When the animal emitted an orientation sound (average duration, 2.9 ± 0.7 msec) action potentials from the cricothyroid and stapedius muscles appeared 11.4 ± 2.2 and 8.8 ± 2.2 msec, respectively, before vocalization. The activity of the stapedius muscle thus followed that of the cricothyroid muscle by about 2.6 msec. When the animal emitted nonorientation sounds (average duration, 31.3 ± 7.1 msec), the action potentials of the cricothyroid and stapedius muscles appeared 52.8 ± 4.1 and 38.4 ± 6.7 msec, respectively, before vocalization. That is, the activity of the stapedius muscle followed that of the cricothyroid muscle by about 14.4 msec. The tensor tympani muscle became active 1.9 msec after the stapedius muscle when the bat emitted orientation sounds (3). The coordination of the activities of the LM's and MEM's was different depending upon the types of sounds emitted by the bat. The cricothyroid muscle, the most essential muscle for the emission of orientation sounds (2), begins to contract earlier than the MEM's. However, the MEM's can attenuate vocal self-stimulation, because the emission of sounds follows cricothyroid muscle activity by about 11.4 msec and stapedius muscle activity by about 8.8 msec (3, 4).

In response to an acoustic stimulus, the stapedius and tensor tympani muscles of *M. lucifugus* discharge with a minimum latency of 3.4 and 4.4 msec, respectively (3). This is the acoustic MEM reflex. When recordings of action potentials were made from the cricothyroid muscle and inferior

laryngeal nerve, both of them responded to acoustic stimuli (Fig. 1, B to D). The minimum latencies of these responses were 6.2 msec for the cricothyroid muscle and 6.7 msec for the inferior laryngeal nerve. Since the inferior laryngeal nerve innervates all extrinsic muscles except the cricothyroid muscle, not only the cricothyroid muscle but also other LM's show the reflex activity. We thus call the reflex the acoustic LM reflex. In terms of latency, the reflex arc of the LM's contains a neural chain longer

than that of the MEM's. The muscular contractions due to the acoustic LM reflex were observed under a dissection microscope, but the vocalization related to the reflex was not detected by a microphone placed near the mouth.

The threshold curve of the acoustic MEM reflex is broad. The Q-10 db values (best frequency divided by bandwidth of tuning curve at 10 db above the minimum threshold) of 22 single stapedius muscle fibers ranged between 6.6 and 10.

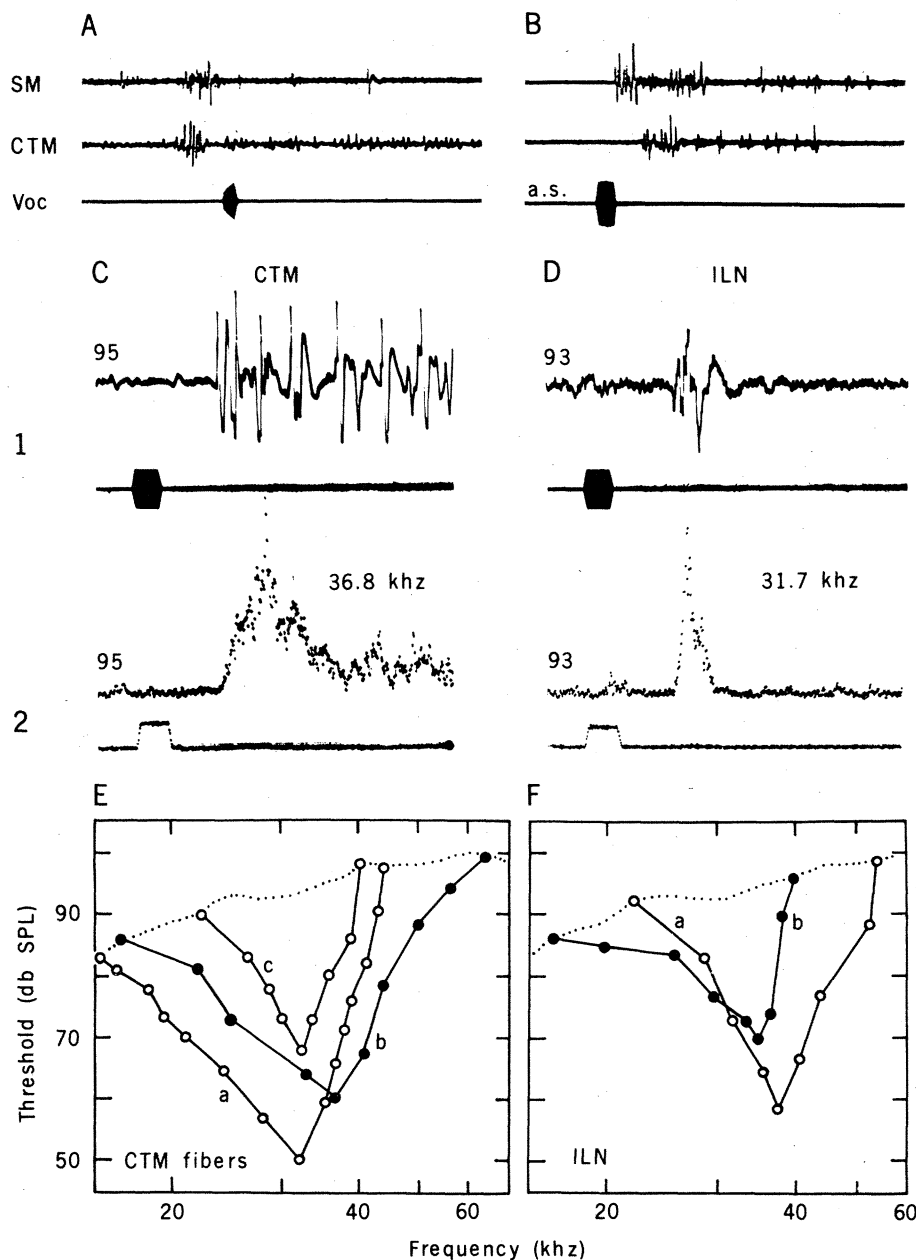


Fig. 1. (A) Electrical activities of the stapedius muscle (SM) and cricothyroid muscle (CTM) when the bat emitted a 3.5-msec orientation sound (Voc). (B) Responses of the two muscles to a 4-msec tone burst (a.s.) at 94 db SPL and 32.1 kHz. The rise-decay time is 0.5 msec. (C and D) Responses of the cricothyroid muscle and inferior laryngeal nerve (ILN), respectively, to 4.0-msec tone bursts with a 0.5-msec rise-decay time. The upper traces in section 1 represent action potentials originating from several muscle fibers or nerve fibers, and those in section 2 represent the average of responses to the tone bursts delivered 32 times at a rate of 1.5 sec⁻¹. The lower traces show the tone bursts in section 1 and the half-wave-rectified envelopes of the tone bursts in section 2. The frequencies of the tone bursts are given in kilohertz, and the amplitudes are given by the numbers at the left in decibels SPL. (E) Threshold curves of three single cricothyroid muscle fibers (a, b, and c) obtained from a single bat. (F) Threshold curves of the inferior laryngeal nerves obtained from two different bats (a and b).

The best frequency and the minimum threshold of the MEM reflex are 25 to 40 kHz and 20 db SPL, respectively (3). For comparison, the threshold curve of the acoustic LM reflex was measured with a 40-msec tone burst as the responses of the cricothyroid muscle and the inferior laryngeal nerve (Fig. 1, E and F). The threshold curve was of triangular shape and was narrower than that of the acoustic MEM reflex. The best frequency was between 30 and 40 kHz, similar to that of the acoustic MEM reflex, and the lowest threshold was 50 db SPL, about 30 db higher than that of the acoustic MEM reflex. The Q-10 db values of threshold curves of 68 single cricothyroid muscle fibers ranged from 1.3 to 10 (average, 3.1). For FM sounds similar to orientation sounds of *M. lucifugus*, the threshold of the acoustic LM reflex was about 20 db lower than that for pure tones. The vocal self-stimulation in terms of N_1 (the summated auditory nerve response to an acoustic stimulus) is 80 to 90 db SPL when the bat emits orientation sounds (6), so that the acoustic LM reflex could be evoked by vocal self-stimulation and also intense echoes.

What is the function of the acoustic LM reflex? *M. lucifugus* emits FM orientation sounds 3 to 4 msec in duration at a rate of 10 to 15 sec⁻¹ during searching or cruising flight. When the bat finds a target and approaches it, the duration of orientation sounds decreases and the rate of sound emission increases. In the terminal phase of echolocation, the duration is often as short as 0.5 msec and the rate as high as 200 sec⁻¹ (7). If emitted sounds and echoes are both considered, the rate of stimulation of the auditory system goes up to 400 sec⁻¹. The acoustic LM reflex may play some role in rapid sound emission. In order to find the possible roles of the reflex, the FM sound comparable to the natural orientation sound was elicited from the bat by electrically stimulating a certain part of the midbrain reticular formation (8), and the effect of an acoustic stimulus on the emission of the FM sound was examined. When a 4-msec tone burst was delivered before the vocalization and the acoustic LM reflex was evoked, the following vocalization was slightly reduced for 150 msec. When the tone burst was delivered after the vocalization, the acoustic LM reflex evoked by the tone burst was augmented for 70 msec. These data suggest that vocalization augments the echo-evoked LM reflex occurring within 70 msec, and the reflex in turn suppresses vocalization following it within 150 msec. In other words, the acoustic LM reflex works as a weak negative feedback for vocalization. A negative feedback in the motor system has been

considered to stabilize the operation of the system. The primary function of the acoustic LM reflex is probably the stabilization of the performance of the vocalization system.

In the above experiment, the electric stimulus that elicited vocalization and the tone burst that evoked the reflex were delivered at a rate of 2 sec⁻¹. Since *M. lucifugus* emits orientation sounds at rates higher than 10 sec⁻¹, we tried to explore the functional role of the acoustic LM reflex with the bat vocalizing at rates higher than 10 sec⁻¹, but we could not obtain data to make any conclusions beyond those given above. It also remains to be determined whether the acoustic LM reflex exists in other mammals or is unique in echolocating bats. As far as we know, this is the first description of the acoustic LM reflex (9).

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9. We presented these findings at the 1975 spring meeting of the Acoustical Society of America [P. H.-S. Jen and N. Suga, *J. Acoust. Soc. Am.* **57**, S42 (1975)]. A. Yanovitz, J. Lozar, and C. W. Mitchell then repeated the same experiment with rats and found the acoustic LM reflex. Their preliminary experiments were reported at the 1975 fall meeting of the Acoustical Society of America [*J. Acoust. Soc. Am.* **58**, S123 (1975)]. Thus the acoustic LM reflex may be common in mammals.
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Perceptual Illusion of Rotation of Three-Dimensional Objects

Abstract. *Perspective views of the same three-dimensional object in two orientations, when presented in alternation, produced an illusion of rigid rotation. The minimum cycle duration required for the illusion increased linearly with the angular difference between the orientations and at the same slope for rotations in depth and in the picture plane.*

Shepard and Metzler (1) found that the time required to determine whether two perspective views portray the same three-dimensional object is a linear function of the angular difference between the two orientations portrayed. The decision time is the same for rotations in depth and rotations in the two-dimensional picture plane. They proposed that subjects make the comparisons by carrying out a mental analog of the actual physical rotation of one object into congruence with the other and, further, that the mental representations that are internally transformed in this way are more akin to the three-dimensional objects portrayed than to the two-dimensional retinal projections of those objects.

To say that the internal process is a mental analog of an external process is, in part, to say that the internal process is similar in important respects to the perceptual process that would take place if a subject were actually to watch the corresponding physical rotation (2). We investigated a perceptual illusion of apparent rotational movement in order to further explore the possible role of perceptual mechanisms in mental rotation. By alternately presenting two of the Shepard-Metzler perspective

views of a three-dimensional object, we created the appearance of a single object rotating back and forth either (i) in depth about the vertical axis of the object or (ii) around a circle in the two-dimensional picture plane.

Presumably the rotational trajectory through which the object seemed to move as a result of these alternations is the same path through which subjects imagined one object moving into congruence with the other in the mental rotation task. The distinguishing factor is that, in the present case of apparent movement, the subjective experience is of a much more clearly perceptual nature. Instead of actively having to imagine one object rotated into the other, possibly step-by-step or even piece-by-piece, subjects effortlessly experienced the object rapidly and smoothly rocking back and forth as a rigid whole. This phenomenon of apparent rotation thus seems to be less readily accounted for in terms of theories—currently popular in cognitive psychology and artificial intelligence—that emphasize processes of sequential search, recoding, and discrete manipulation of symbolic or propositional structures.

In classical studies of apparent movement, a simple stimulus (for example, a lu-