mark the relative frequencies of short IRTs which occurred on individual first, second, and third days after administration of the two highest doses. The combined results shown in the bottom panel of Fig. 2 are representative of the results obtained with the individual subjects shown in the upper panels. Relative frequencies of overestimation errors were low and stable on placebo-control days prior to Δ^9-THC administrations (black squares). When Δ^9-THC was given, overestimation errors increased in relative frequency with increasing dose level (black circles). This effect of Δ^9-THC on accuracy of timing performance diminishingly perseverated on days following drug administrations (open circles). Relative frequencies of overestimation errors were elevated up to 3 days after administrations of the higher doses of Δ^9-THC (numbered open triangles). The other timing error, A-B IRTs longer than 90 seconds in duration, were typically low in relative frequency, never exceeding 10 percent of the work output. The drug had no observable effect on this type of timing error.

These data are important for several reasons. The fact that doses of 1.0 mg/kg and larger decreased the frequency of food-reinforced operant behavior confirms effects that have been observed with other species (*4*). The finding that high doses of the drug continue to exert an effect for up to 3 days also is of interest in view of biochemical data indicating that metabolites of Δ^9-THC persist in the body for up to a week after ingestion (*5*). Finally, the fact that drug effects were obtained at the 0.25 mg/kg dose level, well within the effective dose range for humans, and the fact that the change in timing behavior appears to confirm data on humans, both suggest that the chimpanzee may be a useful animal in studies of marihuana.

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References and Notes

1. H. Isbel, G. W. Gorodetsky, D. Jasinski, U. Claussen, F. Spulak, F. Korte, *Psychopharmacologia* **11**, 184 (1967); L. E. Hollister, R. K. Richards, H. K. Gillespie, *Clin. Pharmacol. Ther.* **9**, 783 (1968); I. E. Waskow, J. E. Olsson, C. Salzman, M. M. Katz, *Arch. Gen. Psychiat.* **22**, 97 (1970); L. E. Hollister, *Science* **172**, 21 (1971).
2. In conducting this research, we adhered to the "Guide for Laboratory Animal Facilities and Care," as promulgated by the Committee on Revision of the Guide for Laboratory Animal Facilities and Care of the Institute of Laboratory Animal Resources, National Academy of Sciences–National Research Council.
3. E. G. Williams, C. K. Himmelsbach, A. Wikler, D. C. Ruble, B. N. Lloyd, *Public Health Rep.* **61**, 1059 (1946); F. Ames, *J. Ment. Sci.* **104**, 972 (1958); T. Petrzilka and C. Sikemeier, *Helv. Chim. Acta* **50**, 1416 (1967); A. T. Weil, N. E. Zinberg, J. M. Nelsen, *Science* **162**, 1234 (1968); L. D. Clark, R. Hughes, E. N. Nakashima, *Arch. Gen. Psychiat.* **23**, 193 (1970); L. E. Hollister and H. K. Gillespie, *ibid.*, p. 199; R. Mechoulam, *Science* **163**, 1159 (1970); Secretary, Department of Health, Education, and Welfare, *A Report to the Congress: Marihuana and Health*, 31 Jan. 1971 (U.S. Government Printing Office, Washington, D.C., 1971), document 0-415-832.
4. E. S. Boyd, E. D. Hutchinson, L. C. Gardner, D. A. Merritt, *Arch. Int. Pharmacodyn.* **144**, 533 (1963); E. A. Carlini, *Pharmacology* **1**, 135 (1968); D. E. McMillan, L. S. Harris, J. M. Frankenheim, J. S. Kennedy, *Science* **169**, 501 (1970); J. M. Cole, W. A. Pieper, D. M. Rumbaugh, *Commun. Behav. Biol.* **8**, No. 1 (July 1971).
5. L. Lemberger, S. D. Silberstein, J. Axelrod, I. J. Kopin, *Science* **170**, 1320 (1970); L. Lemberger, N. R. Tamarkin, J. Axelrod, I. J. Kopin, *ibid.* **173**, 72 (1971).
6. Synthetic Δ^9-THC was obtained from J. A. Scigliano (Center for Studies of Narcotics and Drug Abuse, National Institute of Mental Health, Chevy Chase, Md.). It was dissolved in absolute ethanol in a concentration of 0.2 g/ml, and was assayed to be 93 percent pure. It was administered as received or, for a dose of 1.0 mg/kg or lower, it was diluted with ethanol with the dose volume varying from a minimum of 0.07 ml up to 1.08 ml.

13 August 1971

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Attentiveness to Sensory Stimuli: Central Control in Locusts

Abstract. *Wind-angle changes evoke yaw-correcting deflections of the abdomen in tethered locusts, but only if the wings are beating. In flight, the central neuronal flight motor drives abdominal motoneurons in rhythmic bursts. Wind angle inputs, which are inadequate alone to drive these motoneurons, alter the number of spikes per burst, and the alterations are reciprocal in opposite nerves. Burst frequency and phase are unaffected.*

How an animal determines at any moment whether or not to respond to a given sensory stimulus is a long-standing problem in the study of animal behavior. In the past, this role of controlling responsiveness has often been relegated to an ill-defined "central excitatory state" or level of "arousal." In the desert locust (*Schistocerca gregaria* ph. *gregaria*), this process can be studied quantitatively in individually identified motoneurons.

A tethered locust responds to head-on wind from a miniature wind tunnel by lifting its abdomen, legs, and antennae into flight posture and beating its wings as in normal flight (*1*). Pivoting the wind tunnel in a horizontal arc about the head mimics most of the aerodynamic conditions of yaw in free flight. This stimulus, which the locust monitors with a bank of delicate cephalic wind-receptor hairs (*2*), evokes a complex yaw-correcting maneuver involving the wings (*3*), abdomen, legs, and head (*4*). If the locust spontaneously ceases flying in the maintained wind stream, none of these movable members respond to wind-angle changes, but all movements reappear in full measure the instant flight spontaneously resumes (*4*).

We have studied the motor mechanisms involved in yaw-correcting movements, and have focused on the switchlike mechanism whereby the insect attends to a flight-relevant stimulus (wind-angle change) during flight and apparently ignores the same stimulus during flightless intervals. In studying the abdomen's response—a lateral, rudderlike deflection determined by the wind angle (*4*)—we find that during flight, the central neuronal flight motor, known to coordinate the patterned wing movements, also drives abdominal motoneurons in synchronous impulse bursts. In a head-on wind, the bursts of both sides are of approximately equal strength and cause balanced rhythmic contractions of opposite abdominal muscles, which lift the abdomen into flight posture and cause a slight vertical vibration. Wind-angle changes modulate, in a bilaterally reciprocal fashion, the number of impulses per motoneuron burst and thereby unbalance the contractions of the two sides and cause a lateral deflection. The wind input, while sufficient to modulate ongoing neural activity, is inadequate by itself to activate the motoneurons.

During flight, the abdomen undergoes high-frequency, low-amplitude vibrations in the vertical plane. Mechanical recordings of this movement (Fig. 1A) show that the vibrations are synchronous with the wingbeat. To determine whether this vibration originates in the abdominal musculature or results passively from mechanical coupling to the vibrating thorax, we isolated the abdomen from the thorax and left the soft, pliable nerve cord as a bridge between the two body sections. The abdomen still vibrated synchronously with the wingbeat (Fig. 1B), while cold block applied to the nerve-cord bridge extinguished the vibration of the abdomen but left the thoracic movements apparently unaffected (Fig. 1C). This strongly implicates central or peripheral neurons of the flight system in the production of the abdominal vibrations (*5*).

We investigated the motor supply to the dorsal longitudinal (DL) muscles of the first abdominal segment, which is important in the abdomen's yaw-correcting responses (*6*). Metathoracic nerve 4 (*7*) innervates the abdomen, where its main terminal branch comprises the entire DL motor supply of the first segment. As determined by histological and physiological evidence, this terminal branch contains approximately 15 axons. One of these is the afferent fiber of a stretch receptor embedded within the muscle (*8*), and the remainder are efferent to the DL muscle.

Just before entering the muscle, the terminal branch subdivides into three twigs. The spike of each motor axon can usually be recorded in each of these twigs, a result suggesting that every motor axon contributes a process to each twig. Since the relative spike heights of the different processes of any cell are nearly constant from one animal to another, and since several of the cells have characteristic firing patterns, we could usually identify each of ten or more individual motor axons in different animals, in spite of the relatively large neuron population sampled. To do this, we used an en passant suction electrode on the main terminal branch, plus suction electrodes on transsected stumps of at least two of the three twigs.

We have detected two major functional groups of motor axons (*9, 10*). In this report we treat a group consisting of the five axons of greatest diameter (5 to 8 μm), as measured in the main terminal trunk (*11*). This group, employed primarily in flight-associated movements, we call A fibers. We have also reported (*10*) on a second group, comprising about seven units of diameter 0.5 to 3 μm (*12*), which is involved both in flight and in ventilatory pumping (B fibers).

The A fibers are usually silent during flightless periods. In flight, however, they fire in bursts that are synchronous with the wingbeat (Fig. 2), and their activity evokes contractions at this frequency in the DL muscle. These twitches, along with those of other segmental DL muscles, are largely responsible for the abdominal vibrations recorded in Fig. 1, A and B. Since visual inspection indicates that the muscle remains partially contracted throughout a barrage of flight bursts, this activity probably also serves to raise the abdomen into flight posture.

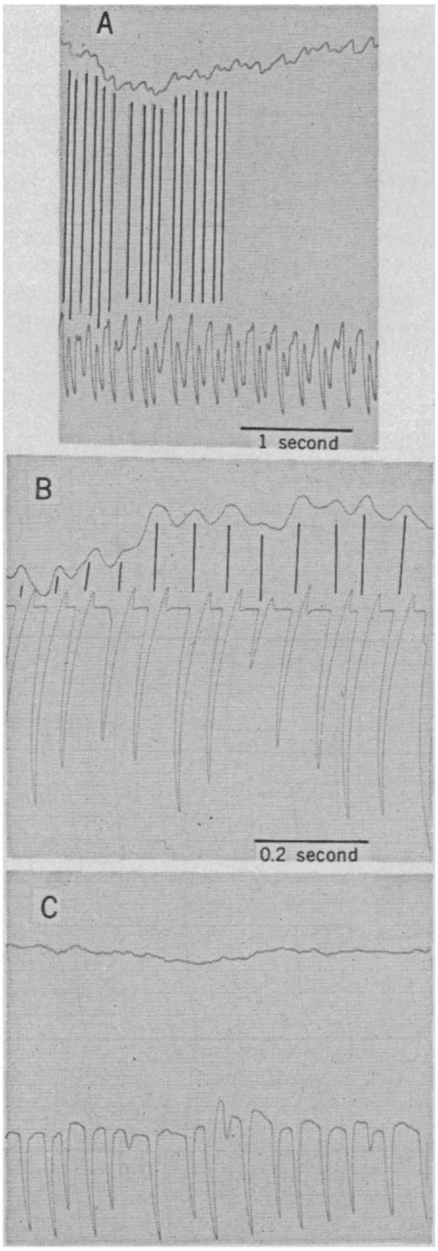


Fig. 1. Mechanoelectrical recordings made simultaneously from a locust's thorax (lower traces) and abdomen (upper traces) under three different conditions of tethered flight. (A) During normal tethered flight, recordings show vibrations of the abdomen synchronous with the wingbeat. (B) After the entire insect, except for the nerve cord, has been transsected between the thorax and abdomen, vibrations of the abdomen and wingbeat are still synchronous. (C) After cold block of the nerve cord bridging the thorax-abdomen gap, the wingbeat is normal, whereas vibration of the abdomen is blocked. Time scale for B and C is the same.

Figure 2 also shows that wind-angle changes, which in the intact insect evoke lateral posturing of the abdomen, also affect the number of spikes per burst. In this case, a 20° turn to the left totally suppressed one burst from the A fibers in the right nerve and greatly inhibited the next burst, after which there was considerable recovery. In the intact animal, this wind-angle change evokes an abdominal movement to the left.

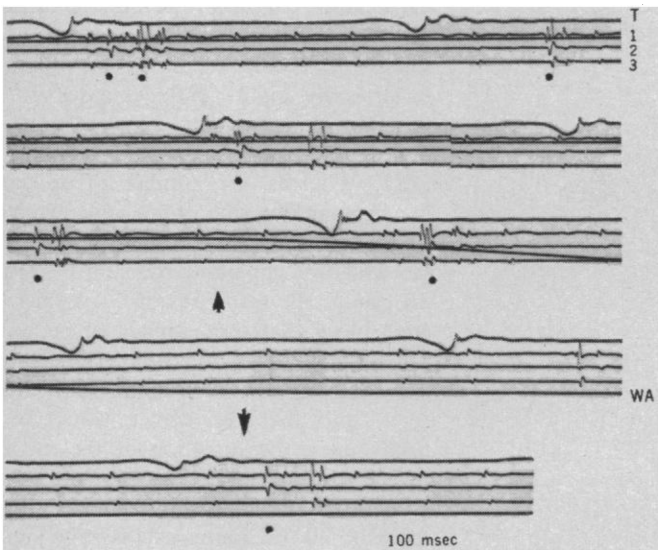
Figure 3A represents the separate wind-angle responses of the five A fibers for left and right turns about the head-on position. For all five units on the right side, the number of spikes per burst increases for turns toward the right and decreases for turns toward the left, with a latency of less than one wingbeat (100 msec) (*13*). Whereas the number of spikes per burst varies with wind angle, burst frequency and phase with respect to the wingbeat apparently do not. Figure 3B groups the responses of all A fibers and shows that the number of spikes per burst is least for wind from the left and greatest for wind from the right, and that the center value depends upon the direction of the most recent wind-angle change (*14*). These differences are generally greater for more rapid or more extensive wind-angle turns.

The modulation of ongoing burst activity by wind-angle changes suggests a simple explanation for the switching of the abdomen's controlling neurons from "attentiveness" to "inattentiveness," as detected at the behavioral level. The wind-angle inputs may contribute weak excitatory synaptic potentials to ipsilateral follower neurons and weak inhibitory potentials to contralateral follower neurons. In contrast, these follower cells may receive strong synaptic drive from the thoracic flight system. Although the excitatory wind inputs alone are inadequate to depolarize these follower cells to threshold, both excitatory and inhibitory wind inputs could modulate membrane potential (and therefore impulse frequency) of a follower cell that was already driven beyond threshold by the more potent synaptic drive of the flight system. The follower cells in this scheme are equated with either the motor or premotor neurons.

What is the source of the ongoing flight bursts in the abdominal DL muscles? The two most likely sources are the central flight motor of the meso- and metathoracic ganglia (*15*) and sensory feedback from some receptors signaling the phase of the wingbeat (*16*). We eliminated the latter possible source by cutting all peripheral nerves of the thorax and transsecting the ventral nerve cord between the metathoracic and first abdominal ganglia. These operations almost certainly eliminated all afferent input phased to the wingbeat. Recordings made under these conditions from cut central stumps of the nerve containing the A fibers of the first abdominal segment (this nerve is a root of the metathoracic ganglion) and from a motoneuron to wing-depressor muscles (thoracic DL's) show normally synchronous efferent bursts. Wind-angle changes have their usual effect on the A fibers while leaving the wing nerve essentially unaffected. These experiments strongly suggest that the A-fiber bursts are produced by the central flight motor.

Since the abdominal and thoracic DL muscles are serially homologous, it is meaningful to consider the degree of similarity between their neuronal controls. Both muscles are innervated by five large motor axons (*17*), although simultaneous recordings show that the abdominal and thoracic axons are separate units. While a group of smaller fibers (B fibers and others) also innervates the first abdominal DL muscle, small fibers that appear histologically to innervate the thoracic DL's are not known to make functional connections to the muscles. As indicated above, the burst rhythms during flight in the two muscles and their motoneurons are synchronous and nearly in phase. We have found further similarities with regard to respiratory function (*10*).

Our results show that the central flight motor is used by the locust nervous system as an indicator of flight activity. In this capacity, the flight motor serves two functions, apart from patterning the wingbeat—it lifts the abdomen into flight posture (partially through mechanically summating ver-



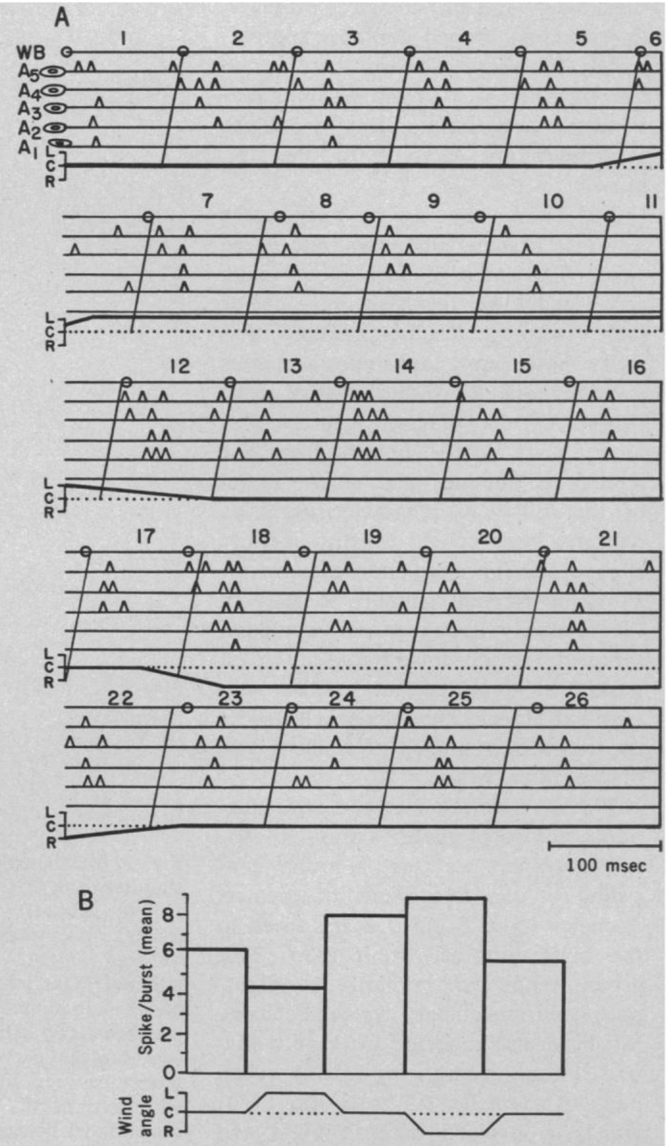


Fig. 2 (left). Simultaneous recordings from terminal twig 1, 2, and 3 of the nerve to the right DL muscle of segment A_1. These twigs have been cut near the entrance to the muscle, and the insect has been pinned to a wax block. Also shown is a phonocartridge recording of the thoracic movements (*T*), which are in fixed phase with the wingbeat. A 20° change in wind angle to the left, achieved by rotating a miniature wind tunnel, is indicated by trace *WA* (arrows indicate the beginning and end of the wind tunnel's rotation). Impulses of four different A fibers register the largest spikes in twig 1. (One of these fibers, A_5, is indicated by a dot under the records for each of its seven impulses shown.) Smaller spikes are from B fibers or other axons (*10*). The figure shows that A fibers have a fixed phase with respect to the wingbeat, and that a wind-angle change away from the side recorded suppresses burst activity. Fig. 3 (right). (A) Activity during flight of the five right-side A fibers (A_1 to A_5, in order of decreasing spike size). Wind flow is from the center (*C*) (burst 1 to 5), from 15° left (*L*) (burst 7 to 11), again from the center (burst 13 to 17), from 15° right (*R*) (burst 18 to 21), and again from the center (burst 24 to 26). Data are from the experiment shown in Fig. 2. Compared to activity in wind from the center, activity in all cells is depressed in wind from the left and enhanced in wind from the right. A fixed point of the wingbeat (*WB*), determined by a phonocartridge recording from the thorax, is shown by circles on the top trace. Parallel oblique lines, drawn as regression lines to these circles, are reference markers to show that wind angle does not affect frequency or phase of the A-fiber bursts. Wind-angle changes are shown in the bottom trace. (B) The mean number of spikes per burst for all right-side A fibers for wind-angle sequences in (A). Firing activity is lowest for wind from the left and highest for wind from the right. Activity in wind from the center is greater when wind direction has returned from the left than when it has returned from the right or has remained constant at center (first bar on graph).

tical vibrations), and it sensitizes the A fibers or their premotor cells to wind-angle inputs. Neurons employed in other specific flight orientations may be similarly affected by the flight motor (*4, 18*). Therefore, this central oscillatory network is multifunctional.

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References and Notes

→ T. Weis-Fogh, *Proc. Roy. Soc. Ser. B* **239**, 459 (1956).
2. J. M. Camhi, *J. Exp. Biol.* **50**, 335 (1969); *ibid.* **52**, 519 (1970); T. Weis-Fogh, *Nature* **164**, 873 (1949).
3. I. Waldron, *J. Exp. Biol.* **47**, 213 (1967).
4. J. M. Camhi, *ibid.* **52**, 519 (1970).
5. Ventral abdominal muscles and at least one fiber in the abdominal nerve cord are active in flight rhythm [I. Waldron, *ibid.* **47**, 201 (1967)].
6. Most of the yaw-correcting deflection of the abdomen occurs at this joint (*4*).
7. Also called the "tergal nerve of the first abdominal segment" [F. O. Albrecht, *The Anatomy of the Migratory Locust* (Athlone, London, 1953), p. 80].
8. E. H. Slifer and L. H. Finlayson, *Quart. J. Microsc. Sci.* **97**, 617 (1956).
9. These two fiber groups are more properly viewed as two extremes of fibers having a continuous range of properties (*10*).
10. M. Hinkle and J. H. Camhi, *Science* **175**, 553 (1972).
11. Relative sizes of different units were determined by comparing their spike heights in the main terminal trunk. That this measurement reflects relative sizes is indicated by two findings. (i) We could always record five large A-fiber spikes, and nerve cross sections show five large axons. (ii) There is a close correspondence between spike height and conduction velocity, a property generally strongly correlated with axon diameter.
12. Usually one or two axons show responses that are not consistent with this grouping into A and B units. A very common example is a small unit which is tonically active all during flight but is not active in the rhythmic firing pattern (Fig. 2). Embryos of this species have only seven or eight axons innervating the homologous muscle of the fourth abdominal segment. These may be B fibers, which are needed throughout life for respiration, while the flight-associated A fibers may develop closer to adulthood (M. Tyrer, personal communication.)
13. The unusually low frequency of wingbeats of 10 sec^{-1} rather than the normal 17 sec^{-1} (*1*) resulted from the necessity to remove the wings or wax them in place during recording periods. Stretch-receptor feedback, which normally doubles the wingbeat frequency [D. M. Wilson and E. Gettrup, *J. Exp. Biol.* **40**, 171 (1963)] was thereby largely lacking.
14. Though the effects of wind angle shown here are not overwhelming, the differences are larger if one considers only the first few bursts after a wind pivot. Also, since wind angle effects are bilaterally reciprocal, the actual magnitude of the effect is twice that shown here.
15. D. M. Wilson, *J. Exp. Biol.* **38**, 491 (1961).
16. E. Gettrup, *Acta Physiol. Scand.* **59** (Suppl. 213), 46 (1963).
17. A. C. Neville, *J. Exp. Biol.* **40**, 123 (1963).
18. A similar effect of central projections in determining the responsiveness level of sensory interneurons has been reported in crayfish. The origin of the central command is unknown but complex, and is correlated with the general level of limb motor activity [C. A. G. Wiersma and T. Yamaguchi, *ibid.* **47**, 409 (1967)].
19. Supported by NIH grant NS-09083 to J.M.C. We thank W. J. Davis and G. Wyse for their helpful comments and C. Monroe for technical assistance.

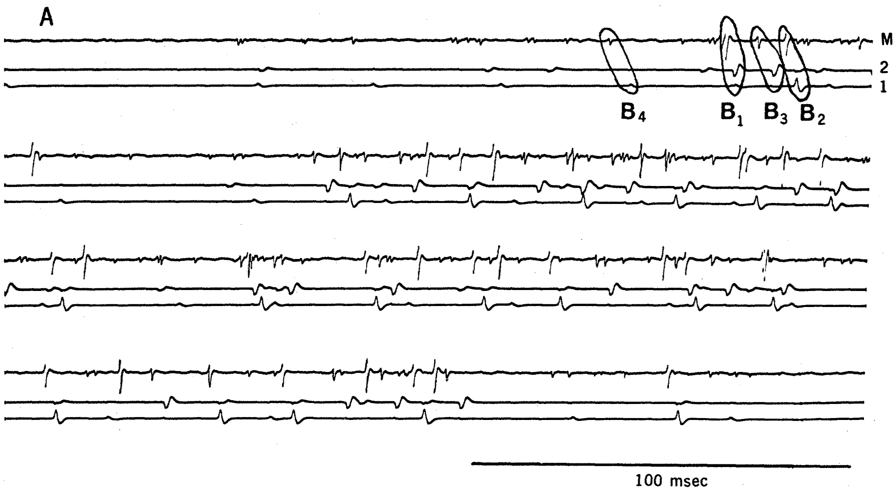
22 October 1971; revised 26 November 1971

Locust Motoneurons: Bursting Activity Correlated with Axon Diameter

Abstract. *A group of abdominal motoneurons in the locust can be driven by either or both of two central neuronal oscillators of different characteristic frequencies. Much of the motor cells' complex activity can be explained by the varying strengths of activation from these two rhythmic sources and by a cell-to-cell gradation in sensitivity to driving inputs, a property that is correlated with axon diameter.*

A current goal of behavioral neurophysiologists is to define the causal factors for specific patterns of output from an animal's nervous system. In most studies one or more natural or electrical stimuli are employed as inputs, and their interacting effects are studied as outputs at the motoneuron, muscle, or behavioral level. In many invertebrates, however, rhythmic motor activity can be produced independently of sensory stimuli by definable central networks, which comprise an important part of the neuronal machinery. We have studied the interaction of two such central neuronal oscillators on a specific group of locust motoneurons. We find that each of several output conditions is explained on the basis of summation of the two oscillatory signals, each with a range of possible amplitudes. The responsiveness of each motoneuron to this summed signal is correlated with its axon diameter.

The abdomen of the desert locust (*Schistocerca gregaria* ph. *gregaria*) engages in several stereotyped behaviors. During flight it (i) assumes a rigid horizontal posture about which it vibrates slightly in synchrony with the wingbeat, (ii) performs lateral yaw-correcting deflections, and (iii) performs vertical stall-avoidance deflections (*1*). At all times except approximately the first 10 seconds of flight, the abdomen also undergoes rhythmic ventilatory pumping motions (*2*). All of these behavior patterns result in part from contractions by the powerful dorsal longitudinal (DL) muscles in each



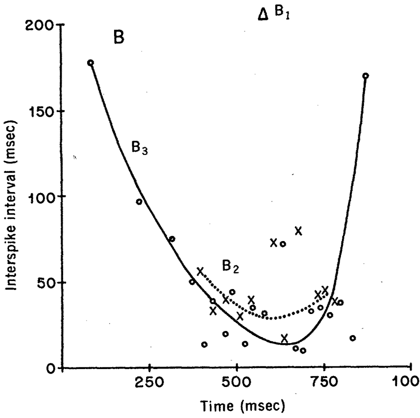


Fig. 1. Ventilatory bursting activity of abdominal B fibers. (A) A continuous record of a strong ventilatory burst was recorded from three points on the nerve: the main terminal trunk (*MT*), branch 1, and branch 2. One spike of each specifically identified B fiber is labeled. The recording shows that smaller spikes begin earlier and end later in the burst than larger spikes. (B) Graph of interspike interval as a function of time for units B_1 (△), B_2 (×), and B_3 (○) during a weak ventilatory burst. Unit B_3, first and last to fire, shows a smooth initial increase in frequency. Unit B_2, firing over the next longest interval, attains a slightly lower maximum frequency. Unit B_1 fires only twice and has a long interspike interval.