The ability of central nervous systems to generate complex patterns of motor output without patterned input has now been clearly established. Some of the most thorough analyses of such centrally generated patterns have been made on the flight-control mechanisms of locusts (see Wilson, 1967, for a review) and calliphorid flies (Wyman, 1966, 1969; Mulloney, 1969). Each of these studies included a description of the normal output from the thoracic ganglia to the flight muscles during flight, in terms of the activity of the individual motor neurones. The patterns described for locusts and other neurogenic fliers such as moths (Kammer, 1967) are similar, suggesting that similar mechanisms are operating in these orders. The patterns described in flies are so different from those of locusts and moths that they are probably the products of very different mechanisms. This difference raises the possibility of many unrelated mechanisms generating flight, each restricted to a small group of animals, each of which would have to be examined before any generality would emerge.

This paper reports the results of a comparative study of the normal patterns of motor output to the indirect flight muscles during flight in Bombus californicus (Hymenoptera) and Oncopeltus fasciatus (Hemiptera). These species were chosen as representatives of two major orders of myogenic insects in the hope that the results would clarify the relation of the previously described dipteran motor patterns to those of the orthopterans and lepidopterans.

METHODS

Oncopeltus fasciatus came from stocks maintained by the Stauffer Chemical Co., Mountain View, Calif. Bombus californicus workers were caught before each experiment in the University of California Botanical Garden. Each insect was mounted with wax on a toothpick—the bees by the scutellum and the milkweed bugs by the prothoracic shield. The bees were prepared in a 5°C. cold room, but the bugs were prepared at normal room temperature. Subsequent experimental procedures were the same for both species.

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Wire electrodes, 50 μ in diameter and insulated except at the tip, were placed in the desired muscles through holes punched in the exoskeleton. The location of each electrode tip was ascertained after each experiment by dissecting the preserved insect. The extracellular electrodes detected muscle action potentials which were amplified differentially against a reference electrode in the animal's gut. The amplified potentials were displayed on an oscilloscope and stored on magnetic tape for later filming. Flight was elicited by placing the prepared animals in the working section of an open-jet wind tunnel whose wind speed could be controlled. The wind stimulus and the lack of tarsal contact were usually enough to sustain flight behaviour.

The time at which each spike in a series occurred was measured from the film. These data were analysed with a general-purpose digital computer using programs modified from those written by Robert Wyman (1965) and other programs written by the author. Graphic presentation of the results is much more easily understood than the equivalent statistical tables, so these tables are not included in the results of this paper. Nonetheless, a statistical analysis of the sort developed by Wyman has been carried out on each of the findings presented, and the results of Wyman's quantitative methods and the graphic methods are in agreement.

Interspike interval is the time in milliseconds between a spike in one unit and the next spike in the same unit. The latency of a spike is the time in milliseconds between its occurrence and the spike immediately preceding it in another unit, the reference unit. The phase of a spike is the fraction of the concurrent interspike interval of another unit, the reference unit, at which the spike occurred. For a fuller discussion of these measures see Wyman (1965).

RESULTS—BOMBUS

I will present the detailed characteristics of the motor neurones innervating one muscle, and then compare the properties of other sets of neurones with the exemplary set. The comparisons will stress those properties which are different, leaving the reader to generalize all common characteristics from the earlier detailed description. This organization will be repeated in the second section, which deals with the indirect flight motor neurones of Oncopeltus.

Neurones innervating one dorso-longitudinal muscle

The dorso-longitudinal muscles are a pair of large fibrillar muscles, and are the principal depressors of the wings. These muscles are each innervated by five motor neurones. Ikeda & Boettiger (1965) studied the neuromuscular junctions of these units in Bombus americanorum and found that each muscle fibre receives only one axon, and that each nerve spike elicited a large, over-shooting action potential in the muscle fibre. The muscle action potentials facilitated rapidly to a steady amplitude. Each lasted about 30 msec. I have assumed that the neurones innervating the dorso-longitudinal muscles of B. californicus have similar properties. On occasion, the recorded muscle spikes occurred in doublets or triplets, but these bursts are not homologous with those which occur regularly in orthopteran flight motor neurones. Ikeda & Boettiger found that the muscle fibre sometimes fired two or three spikes
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during a single junctional potential. The bursts which occur in Orthoptera are one-to-one repetitions of arriving nerve spikes.

Each of the dorso-longitudinal motor neurones fired regularly during flight. Figure 1 is a section of the film recording the activity recorded by three electrodes during a long flight. The single unit whose spike appears on line 1 is an example of a dorso-longitudinal unit. The duration of the muscle action potentials is about 25 msec. Figure 2a is an example of the histograms of interspike intervals which result from

the analysis of such records. The intervals are approximately normally distributed about their mean value, which is consistent with the fact that the neurone innervating this muscle fibre was firing regularly and not in a bursting pattern as do the motor neurones of these muscles in locusts and moths.

The different motor neurones innervating one dorso-longitudinal muscle did not fire in any fixed temporal pattern relative to one another. Figure 2b is a histogram of the latencies of the spikes of one left dorso-longitudinal unit relative to the spikes of another unit in the same muscle, the reference unit. These two units fired synchronously more frequently than they did with any other latency. Except for this tendency to fire synchronously, no latency was preferred more than another (see Wyman, 1965, for a discussion of the shapes of latency histograms). At the longer latencies—those near the mean interspike interval of the reference unit—the latency histogram drops gradually to zero, as is expected in such histograms if no latency value is preferred over others. In all cases, latency was positively correlated with the length of the concurrent interval of the reference unit, which means that usually latency increased as
Fig. 2. Temporal and phasic properties of Bombus motor neurone discharge. (a) A histogram of the interspike intervals of a left dorso-longitudinal unit recorded during flight. (b) A histogram of the latencies of a left dorso-longitudinal unit relative to another unit in the same muscle. (c) A histogram of the phases of a left dorso-longitudinal unit relative to another unit in the same muscle. (d) A histogram of the phases of a right dorso-ventral unit relative to another unit in the same muscle. (e) A histogram of the latencies of a left dorso-ventral unit relative to another unit in the same muscle. (f) A histogram of the phases of a left dorso-longitudinal unit relative to a right dorso-longitudinal unit.
the interspike interval increased, and therefore there is no latency-fixing mechanism operating among these neurones.

All possible phases occurred between units in the same dorso-longitudinal muscle. Figure 2c is a histogram of the phases of a unit relative to another unit in the same muscle. Phases of 0.0 and 1.0 were most common, which is consistent with the tendency to fire synchronously seen in the latency histograms, but except for these peaks all phases occurred in about equal numbers. Figure 3 is a plot of a portion of these

![Figure 3](image)

Fig. 3. The phases of a left dorso-longitudinal unit in *Bombus* relative to another unit in the same muscle plotted against the time at which each of the interspike intervals of the reference unit began. Each point represents the phase of one spike.

same phase data against the time at which the interval from which each phase was calculated began. One cannot see any steady trend or stable phase pattern. Pairs of neurones whose firing frequencies differed by a greater amount than these, and which fired very steadily, showed a steady progression of constantly increasing or decreasing phase. This phenomenon is an artifact of the frequency difference between the two units, and is discussed at length by Wyman (1969). No other phase patterns were observed in these experiments. Phase has nearly zero correlation with the length of the concurrent interval of the reference unit.

Units in the same dorso-longitudinal muscle shared both long-term and interval-to-interval changes in frequency. The range of observed mean frequencies in all experiments was from 6.6 to 23.8 spikes per second, but in any one flight the frequency
domain was much more restricted. Figure 4 is a plot of the interspike intervals of two left dorso-longitudinal units against the time at which each interval began. Changes in average frequency lasting several seconds and brief oscillations of intervals about their mean occurred simultaneously and in the same direction in both units. It is surprising that two units could share interval-to-interval frequency variations so closely without having phase-regulating or latency-regulating mechanisms. However, similar findings have been reported in flies (Wyman, 1969), in locust preparations (Wilson & Wyman, 1965) and in crayfish claw motor neurones (Wilson & Davis, 1965). The mean frequencies of units recorded simultaneously from the same dorso-longitudinal muscle rarely differed by more than 5%. The mean wingbeat frequencies of bumblebees in these experiments ranged from 115 to 240 cycles per sec. These statistics were closely correlated with the mean frequencies of action potentials in the indirect flight muscles.

**Neurones innervating one dorso-ventral muscle**

The dorso-ventral muscles are a pair of large, fibrillar muscles which elevate the wings. Their innervation is more complex than that of the dorso-longitudinal muscles. The number of neurones innervating each of the dorso-ventrals is not known, but the activity patterns of these neurones during flight can be described. Ikeda & Boettiger (1965) found that some of the dorso-ventral fibres are multiply innervated. The post-junctional responses of these fibres to stimulation of different axons fell into four distinct classes, three of which could be distinguished by extracellular recording.
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methods. The first class of responses (class 1) occurred in all fibres, and was the same as the large spikes seen in dorso-longitudinal fibres. The spikes showed little facilitation and lasted about 30 msec. The second class of responses showed considerable facilitation, a marked tendency to fire repetitively from one junctional potential, and was restricted to a set of fibres in the anterior region of the muscle. The junctional potentials lasted about 60 msec., and were an important component of the recorded spikes. The third class of responses is also restricted to the anterior section of the muscle, and to a very small number of fibres. This class is distinctive because its

Fig. 5. The output of several dorso-longitudinal units in Bombus recorded simultaneously during flight. These spikes were somewhat distorted by the amplifiers. Channels 1 & 2: left dorso-longitudinal units; channel 3: a right dorso-longitudinal unit; channel 4: the location of this electrode was not clearly established. One hundred millisecond time mark.

responses last only 5 to 8 msec. and have almost no junctional component. Judging from the amplitude, duration and lack of facilitation shown by the recorded spikes, from the position of the recording electrodes, which in most cases were located in the posterior region of the muscle, it is likely that the dorso-ventral motor neurones whose activity has been analysed here are class 1 motor neurones.

The activity of these dorso-ventral motor neurones during flight resembled that of dorso-longitudinal motor neurones in all ways but one. All possible phases occurred between these units, but they tended to fire nearly synchronously more often than they fired exactly synchronously. This tendency produced phase relations such as that seen in Fig. 2d, where there is a peak at about 0.1. However, plots of phase against time showed that these units do not have any stable phase patterns which are not an artifact of slight frequency differences. Figure 2e is a histogram of the latencies of a left dorso-ventral unit relative to another unit in the same muscle. The peak at 14 msec. confirms the tendency to fire most often near synchrony but not synchronously, but
other than this peak there is no strong preference for any latency. Neither phase nor latency was significantly correlated with the length of the concurrent intervals of the reference unit in these cases.

*Neurones innervating contralateral homologues*

Contralateral neurones did not fire in any preferred or fixed temporal or phasic pattern. Figure 2f is a histogram of the phases of a left dorso-longitudinal unit relative to a unit of the right dorso-longitudinal muscle. Unlike neurones innervating the same muscle, these neurones did not tend to fire synchronously, and therefore the histogram is flat. Contralateral units shared both long-term and interval-to-interval frequency changes, but not as precisely as units in the same muscle. The mean frequencies of units in contralateral synergists varied by up to 10%. However, Fig. 5 shows sections of a record of one flight in which the only recorded right dorso-longitudinal unit at first fired at a slightly lower frequency than the left dorso-longitudinal units, and as all the units decreased their firing rates, stopped firing for longer and longer periods. The occurrence of these quiet intervals was not regular, nor was their duration exactly proportional to the interspike intervals of the left dorso-longitudinal units. The point is that at low frequencies some units did not fire for many hundreds of milliseconds during which synergistic units were firing normally, and during which flight continued apparently unhindered. This loss of some units at low frequencies resembles the situation in locusts when the animals are generating less lift than is needed to keep them in the air but wing movements are continuing. Under these conditions, some units fail to fire for many wingbeats (Wilson & Weis-Fogh, 1962). Unlike any published records from the flight muscles of dipterans, this shows that recruitment of motor neurones can occur in myogenic insects.

*Neurones innervating antagonistic muscles*

The results of comparisons of antagonistic units are the same as those of contralateral synergists in all respects but their frequency characteristics. Dorso-ventral units always fired at lower frequencies than dorso-longitudinal units—up to 25% lower. In this they resemble the antagonists in calliphorid flies (Wyman, 1965). In flights where no long-term changes in firing frequency occurred other than at the start and stop, and in flights in which only monotonic frequency trends occurred, antagonistic units shared the frequency trends but did not follow the same interval-to-interval oscillations. In flights in which spike frequencies varied irregularly, antagonistic units did not follow the same frequency trends.

*Seldom-observed activity patterns*

In one very long flight, the two left dorso-longitudinal units began late in the flight to alternate with the three dorso-ventral units. Figure 6 is a section of the film of this flight. The alternation was not precise, and periods of more ordinary activity were interspersed among the bursts of dorso-longitudinal and dorso-ventral spikes. The bursts lasted about 400 msec. The firing rate of the dorso-ventral units accelerated within each burst, as does the rate of units within the bursts seen in the firing patterns of locusts and moths (Waldron, 1967; Kammer, 1967), but the rate of the dorso-longitudinal units decreased when the dorso-ventrals were silent. This alternation
Fig. 6. A peculiar output pattern in Bombus, in which antagonistic units fired in alternating bursts which were interspersed among periods of more normal activity. The bracket a marks a period in which the dorso-ventrals were silent. The bracket b marks a period in which the dorso-longitudinals were silent. Channel 1: two left dorso-longitudinal units; channels 2 & 3: left dorso-ventral units; channel 4: this electrode was on the interface of the left dorso-longitudinal and dorso-ventral muscles. The large spike is a dorso-longitudinal unit, and the small spike is a dorso-ventral unit.

Fig. 7. The transition from warm-up to flight in Bombus. During warm-up the units fired synchronously, and the thorax did not move. In the interval marked by the arrow, the bee extended its wings and began to fly. The output pattern beyond this point appeared normal. Channels 1 & 2: left dorso-longitudinal units; channel 3: a right dorso-longitudinal unit. One hundred millisecond time mark.
between dorso-longitudinal and dorso-ventral units may be related to the fact that they are antagonists, but the alternation occurs on a time scale orders of magnitude greater than the wingbeat period.

The dorso-longitudinal motor neurones, at least, can fire in patterns associated with activity other than flight. Figure 7 is a section of a film recording the activity of three units during the time the bee was warming up after being brought out of the cold room. All three units fired in near-perfect synchrony at high frequency for over a minute. Then, at the pause marked by the arrow, the bee opened its wings and began to fly. The flight continued for another minute and a half, during which the units fired in the normal flight pattern. This sudden change of firing pattern associated with the transition from warm-up to flight is very similar to some shifts of pattern associated with warm-up in moths (Kammer, 1968).

RESULTS — ONCOPELTUS

Again, I will describe in detail the properties of the motor neurones innervating one dorso-longitudinal muscle, and use this description as the background for the discussion of the properties of other sets of neurones, and of the comparisons of neurones in different sets. *Oncopeltus fasciatus* has three pairs of indirect flight muscles.

Neurones innervating one dorso-longitudinal muscle

The dorso-longitudinal muscles are a pair of large, fibrillar muscles, and are the principal depressors of the wings. I have not counted the axons innervating each of these muscles, but Barber & Pringle (1966) reported five or more units in each dorso-longitudinal of a related hemipteran family (Belostomatidae), and when these muscles in *Oncopeltus* are fixed in situ with Kahle's fluid they shrink into five distinct bundles.

![Fig. 8. The activity of three left dorso-longitudinal units (labelled a, b, and c on the first section) recorded during flight in *Oncopeltus fasciatus*. The recording was made with one electrode in the muscle and a reference electrode in the animal's gut. Ten millisecond time mark.](image-url)
The neurones innervating these muscles fired at less than one-tenth the wingbeat frequency and with no preferred phase relative to the position of the wings. Each motor neurone fired regularly during flight. The muscle action potentials which followed the nerve spikes lasted about 10 msec. They showed no facilitation or antifacilitation in the range of frequencies encountered. Figure 8 is a section of the film recording the activity of three left dorso-longitudinal units during a long flight. The three units could be distinguished reliably by the amplitude of their spikes. Figure 9a is an example of the histograms of the interspike intervals of these units. There is but one peak, and the intervals are approximately normally distributed about their mean value. This regularity resembles that seen in the flight motor neurones of bumblebees and dipterans, and is unlike the bursting patterns seen in moths and locusts.
Except for a tendency to fire synchronously, the different motor neurones innervating the same dorso-longitudinal muscle did not have any preferred or fixed temporal patterns. Latency histograms associated with these units resembled their counterparts in bumblebees. Latency was positively correlated with the length of the concurrent interval of the reference unit, which confirms the lack of a fixed interval between spikes in different units. The three units in Fig. 8 had slightly different firing frequencies, and so their spikes drifted slowly past one another.

All possible phases occurred between units in the same muscle, but zero phase was most common. Figure 9b is an example of a histogram of the phases of one unit relative to another unit in the same muscle. There is a sharp peak at zero phase, the result of the tendency of these two units to fire synchronously. Plots of phase against time showed, however, that these units do not hold any stable phase pattern.

Neurones innervating the same dorso-longitudinal muscle fired at nearly the same frequency, and shared both long-term and interval-to-interval changes in frequency. Figure 10 is a plot against time of the interspike intervals of two left dorso-longitudinal units. The oscillations of interval were similar in amplitude and direction for both units. In flights in which the firing frequencies varied over many seconds, units in the same muscle shared each of these changes very precisely. In their phase and frequency characteristics, neurones innervating an *Oncopeltus* dorso-longitudinal muscle are remarkably similar to their counterparts in *Bombus*. 

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**Fig. 10.** The interspike intervals of two left dorso-longitudinal units in *Oncopeltus* plotted against the time at which each began. The intervals of one unit are marked with squares, the other with circles.
Neurones innervating one dorso-ventral muscle

The dorso-ventral muscles are a pair of large, fibrillar muscles, and are the principal elevators of the wings. The number of neurones innervating each dorso-ventral in *Oncopeltus* is not known. The temporal and phasic patterns of these neurones were the same as those of the neurones innervating dorso-longitudinal muscles. In this similarity, they differ from the dorso-ventral motor neurones of *Bombus*, where dorso-ventral units tended to fire approximately synchronously more frequently than they fired synchronously. In *Oncopeltus*, synchronous firing was most common, so the phase histograms showed a peak at zero phase.

Neurones innervating one dorsal oblique muscle

The dorsal obliques are a pair of rather small, fibrillar muscles lateral to the dorso-longitudinal muscles. Their function is unknown in *Oncopeltus*, but Barber & Pringle (1966) suggest that in belostomatids these muscles are mainly supinators of the wings. Kammer (1967) concluded that in Lepidoptera these muscles are wing elevators.

The motor neurones of the dorsal oblique muscles had the same temporal and phasic properties as dorso-longitudinal motor neurones. They tended to fire synchronously more frequently than did any of the other sets of neurones innervating indirect flight muscles, but, nonetheless, all possible phases occurred between the units in each flight. Dorsal oblique motor neurones had a wider range of firing frequencies than any of the other sets of motor neurones, ranging from lower than the frequency of the dorso-ventral units to slightly above that of the dorso-longitudinals. I do not know the behavioural significance of the wide range, but it is consistent with the suggestion that they are wing supinators.

Neurones innervating contralateral homologues

Contralateral dorso-longitudinal and dorso-ventral units had no preferred or fixed temporal or phasic patterns. I was not able to record simultaneously from both dorsal oblique muscles, but Barber & Pringle (1966) reported that in belostomatids contralateral dorsal oblique motor neurones fired without any preferred phase. Figure 9c is a histogram of the phases of a dorso-longitudinal unit in intervals of a contralateral dorso-longitudinal unit. The histogram is flat; there is no tendency for the two units to fire synchronously, unlike the tendency characteristic of units in the same muscle. The frequency-sharing characteristics of contralateral dorso-longitudinal and dorso-ventral units were different. Contralateral dorso-longitudinal units followed frequency trends and interval-to-interval oscillations nearly as well as did units in the same muscle, although their frequencies differed by up to 12%. Contralateral dorso-ventral units did not follow the same frequency trends, nor did they follow the same interval-to-interval oscillations of their interspike intervals. This absence of frequency sharing is similar to the properties of contralateral dorso-ventral units in *Bombus* during flights in which spike frequencies varied over many seconds. Mean frequencies of contralateral dorso-ventral units differed by up to 30%.
Neurones innervating antagonistic muscles

Motor neurones innervating antagonistic muscles—dorso-longitudinals versus dorso-ventrals versus dorsal obliques—had no preferred or fixed temporal or phasic patterns. Comparisons of antagonistic units gave the same results as comparisons of contralateral homologues. There was no difference between the results of comparisons of ipsilateral and contralateral antagonists. In very steady flights, antagonistic units shared the minor frequency changes which occurred, but did not follow the same interval-to-interval oscillations. Figure 11 is a plot against time of the interspike intervals of a left dorso-longitudinal unit and a left dorso-ventral unit. During the section of the flight from which the sample was selected, the frequency of the dorso-ventral unit was increasing while the frequency of the dorso-longitudinal unit dropped slightly. In no case was the degree of frequency sharing among antagonistic units as strong as that among units in the same muscle, or among contralateral dorso-longitudinal units. Dorso-longitudinal units usually fired at about a 25% greater frequency than dorso-ventral units. Dorsal oblique units had widely varying firing frequencies.

**DISCUSSION**

First, a summary of those results which apply to both *Bombus* and *Oncopeltus*:

1. Units in the same muscle fire regularly, not in patterned bursts (Figs. 1, 2a, 8, 9a).
2. Units in the same muscle have a weak tendency to fire synchronously, but do not have any other fixed or preferred phasic or temporal pattern relative to one
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another (Figs. 2b, 2c, 3, 9b). Dorso-ventral units in Bombus are an exception (Figs. 2d, e).

(3) Units in the same muscle share frequency changes very precisely (Figs. 4, 10).
(4) Units in different muscles have no preferred or fixed temporal patterns relative to one another (Figs. 2f, 9c).
(5) Units in contralateral homologues share frequency changes to a much lesser degree than do units in the same muscle, and in erratic flights may change independently (Fig. 5).
(6) Units in antagonistic muscles change frequency independently (Fig. 11).

The first three points distinguish the properties of units in the same muscle from the properties of neurones innervating different muscles sufficiently so that these functional groups form real subsets of the pool of motor neurones driving the indirect flight muscles. This distinction holds true both in bees and bugs, and resembles the organization of the flight motor neurones of flies, where units in the same muscle maintain precise, non-synchronous phase patterns (Calliphoridae) or tend to fire asynchronously even though all possible phases do occur between units in the same muscle (Syrphidae). In flies, units in different muscles normally do not have any preferred or fixed timing relative to one another, or relative to the position of the wings (Wyman, 1969; Mulloney, 1970). The point that units in a dorso-longitudinal muscle tend to fire synchronously is consistent with the results of Barber & Pringle (1966), who found this to be true in *Lethocerus maximus* (Belostomatidae, Hemiptera). It differs from the report of Esch & Bastian (1968) that the dorso-longitudinal motor units of *Apis mellifera* fire in a random phase distribution during flight. My few recordings from the dorso-longitudinal muscles of flying honeybees show that, just as in bumblebees, units within one muscle tend weakly to fire synchronously although all possible phases occur in long flights (cf. Figs. 2c, 9b).

The activity patterns of the neurones innervating the indirect flight muscles of bees and bugs resemble those of locusts and moths in that units in the same muscle tend to fire synchronously (Wilson, 1966; Kammer, 1967). They also resemble the activity patterns of flies in that units in different muscles have no fixed or preferred phase relations (Wyman, 1965, 1969; Mulloney, 1970).

Several lines of evidence suggest that the flight-control mechanisms of these different orders have a common anatomical substrate and a common evolutionary origin. The indirect flight muscles of these different orders are derived from the same embryological origins (Neville, 1963; Nuesch, 1957; Tiegs, 1955), and the nerves innervating them follow the same course in the thorax if one allows for the condensation of ganglia which has occurred in Hymenoptera, Hemiptera, and Diptera (Markl, 1966; Johansson, 1957; Power, 1948). Furthermore, at least the dorso-longitudinal muscles are innervated by the same number of motor neurones (five) in three of these orders (Neville, 1963; Kammer, 1967). The exception is the Diptera, where these muscles are innervated by six motor neurones (Tiegs, 1955; cf. Mulloney, 1969). The anatomical differences which occur seem to be the result of the loss of particular pairs of muscles and the development of the mesothorax as the main source of power for both the meso- and metathoracic wings of bees and bugs. No newly evolved muscles appear in the flight motor of the myogenic orders. Thus, the musculature, the course of the nerves, and the number of motor neurones involved all
suggest that these orders are evolutionary developments of one basic flight mechanism.

If this postulate is correct, what can be said about the source of the output rhythm of the flight motor neurones in these orders? The neural control of flight in Orthoptera and Lepidoptera is much more complex than in the three myogenic orders because in the neurogenic system the relative timing of contractions in the muscles must be signalled by the nervous system.

One group of workers has suggested that the rhythmic bursts in the motor neurones of neurogenic fliers are the product of electrotonic coupling and mutual synaptic excitation of synergistic motor neurones, and that antagonistic motor neurones alternate because of inhibitory coupling between them or antecedent drivers (Wilson & Waldron, 1968; Kammer, 1968; Bentley, 1969a, b). Kendig (1968) established that both electrotonic and synaptic excitation exists between motor neurones innervating each mesothoracic dorso-longitudinal muscle in locusts, but concluded that the interactions were not strong enough to account for the observed behaviour patterns. Bentley (1969a, b) found in crickets both electrotonic coupling among units innervating the same muscle and inhibitory interactions between antagonistic units. Another author suggests that the motor neurones are driven by higher inter-neurones which are spontaneous pacemakers and the source of the flight rhythm (Svidersky, 1967). The work on which this hypothesis is based has the serious flaw that there is no evidence that the units from which Svidersky recorded are part of the flight system. However, Bentley (1969b) also has indirect evidence of an interneuronal pacemaker driving the motor neurones. Kammer (1968) and Wilson (1961) showed that there would have to be several such pacemakers to account for the pattern changes which occur in Lepidoptera and locusts.

The myogenic orders need not be precise about the relative timing of nerve impulses to different muscles because the timing of contractions is dictated by the resonant properties of the thorax. Diptera show the widest range of phase relations among units in one muscle and between units in different muscles. The normal patterns of calliphorids and syrphids have been described at the start of this discussion. D. M. Wilson (personal communication) reports that in some cases in flies units in the same muscle showed a strong tendency to fire synchronously, but that in these cases also all possible phases occurred between the units during the flight. This pattern is like that characteristic of bees and bugs, and a notable contrast with the normal constant, non-synchronous pattern of units in the same muscle in calliphorids (Wyman, 1965). However, Mulloney (1970) reported an exceptional case in Calliphora vicina in which contralateral dorso-longitudinal units locked in synchrony after two non-synchronous spikes at the start of the flight. Before the unusual flight, the units involved did not hold a fixed phase. The patterns reported in the present paper also resemble closely the normal patterns of Eristalis tenax (Syrphidae) with the difference that while units in the same muscle in E. tenax tend to fire asynchronously, units in the same muscle in bees and bugs tend to fire synchronously (Mulloney, 1970).

The normal calliphorid pattern is probably the result of lateral inhibition among the motor neurones innervating each muscle (Mulloney, 1970). How are the motor patterns of Bombus and Oncopeltus generated? I suggest that each subset of the flight motor neurone pool receives excitation from one or many interneurones or sensory neurones whose function is to modulate the firing frequency of the neurones in the
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subset. Neurones innervating contralateral synergists would be modulated by similar interneurones, possibly by a bilateral set of such interneurones. This system would account both for the high degree of frequency sharing seen in each subset of motor neurones and for the less strong but still similar frequency characteristics of several of the contralateral synergistic subsets. Shared excitation would also account, at least in part, for the tendency of neurones in a subset to fire synchronously, since an arriving excitatory spike would raise the probability of firing in all members of a subset at the same time; but it is equally possible that electrotonic coupling of the sort which occurs in locusts and crickets is the cause of the tendency of these neurones to fire synchronously. According to the hypothesis being presented, the independent frequency changes of antagonistic subsets would be caused by the different properties of the postulated sets of excitatory interneurones.

The normal flight patterns of bees and bugs does not suggest any interaction among antagonistic subsets of the flight motor neurones, except in the case of the alternation between antagonists seen once in bees. In crickets, the rhythmic alternation of bursts in antagonistic units is caused by inhibitory interactions affecting the antagonistic subsets (Bentley, 1969b). Perhaps such inhibitory interactions exist between the antagonistic subsets of the indirect flight motor neurones in bees and bugs, but their effect is detectable only under special circumstances.

The known output patterns of the neurones innervating the indirect flight muscles of myogenic insects could be generated by one basic mechanism. In one such scheme, the pool of motor neurones is divided into functional subsets, each of which innervates one muscle. Each subset receives excitatory input which is shared among the members of the subset, and which modulates their firing frequencies. Different subsets are to some degree separately modulated. The motor neurones of each subset are electrotonically coupled, which produces the tendency of neurones in the subset to fire synchronously in bees, bugs and some flies. There is a lateral inhibitory network among the motor neurones, strongest between those of a single subset, and with a strength which varies in different groups of insects. This lateral inhibition produces the phase patterns of some dipterans, and the alternation between antagonists seen occasionally in bees.

In conclusion, the patterns of impulses in the motor neurones driving the indirect flight muscles of bees and bugs share some of the characteristics of the patterns known from other work on flies, moths and locusts. These common features encourage speculation about the possible common features of the pattern-generating mechanisms in these orders. Through further studies of this sort we should be able to reconstruct not only the morphological evolution of insect flight mechanisms, but also the neurological changes which have occurred as these systems evolved.

SUMMARY

1. Each of the motor neurones innervating the indirect flight muscles of Bombus and Oncopeltus fire regularly during flight, not in patterned bursts. The several motor neurones innervating one muscle fire at about the same rate and have a weak tendency to fire synchronously, but all possible relative timings occur in each flight. Neurones innervating different muscles have no preferred relative timing, and may have different frequencies.
2. The motor patterns of *Bombus* and *Oncopeltus* are very similar. These patterns could be generated by a model including common excitatory input to each of the neurones innervating one muscle and by weak electrotonic short-latency synaptic coupling between the motor neurones. Different sets of neurones would receive different excitatory input, and antagonistic sets seem to be coupled by a weak inhibitory mechanism.

3. Recruitment of motor units was observed in *Bombus* during low-frequency activity.

4. Synergistic units in *Bombus* fire in near-perfect synchrony during periods when the bee is warming up but not flying. When the bee begins to fly, there is a sudden shift to the output pattern characteristic of flight.

5. The patterns of impulses in these insects have characteristics shared by both dipteran patterns and by orthopteran and lepidopteran patterns. The flight systems of Orthoptera, Lepidoptera, Hemiptera, Hymenoptera and Diptera also have many anatomical similarities. The anatomical similarities and the several common characteristics of the motor output patterns in these orders support the hypothesis that there was one primordial flight mechanism common to the origin of these orders, from which the different mechanisms which exist today have evolved.

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REFERENCES


Motor neurone activity during flight in bees and bugs


