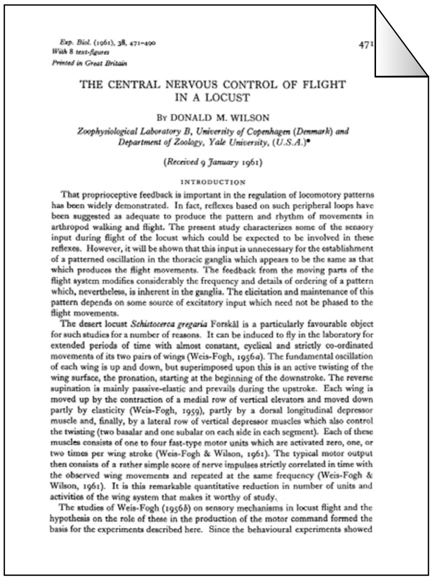
JEB Classics is an occasional column, featuring historic publications from *The Journal of Experimental Biology*. These articles, written by modern experts in the field, discuss each classic paper's impact on the field of biology and their own work. A PDF of the original paper is available from the JEB Archive (http://jeb.biologists.org/).

THE CENTRAL NERVOUS CONTROL OF INSECT FLIGHT



Exp. Biol. (1961), 38, 471–490
With 8 text-figures
Printed in Great Britain

471

THE CENTRAL NERVOUS CONTROL OF FLIGHT IN A LOCUST

BY DONALD M. WILSON

*Zoophysiological Laboratory B, University of Copenhagen (Denmark) and Department of Zoology, Yale University, (U.S.A.)**

(*Received 9 January 1961*)

INTRODUCTION

That proprioceptive feedback is important in the regulation of locomotory patterns has been widely demonstrated. In fact, reflexes based on such peripheral loops have been suggested as adequate to produce the pattern and rhythm of movements in arthropod walking and flight. The present study characterizes some of the sensory input during flight of the locust which could be expected to be involved in these reflexes. However, it will be shown that this input is unnecessary for the establishment of a patterned oscillation in the thoracic ganglia which appears to be the same as that which produces the flight movements. The feedback from the moving parts of the flight system modifies considerably the frequency and details of ordering of a pattern which, nevertheless, is inherent in the ganglia. The elicitation and maintenance of this pattern depends on some source of excitatory input which need not be phased to the flight movements.

The desert locust *Schistocerca gregaria* Forskål is a particularly favourable object for such studies for a number of reasons. It can be induced to fly in the laboratory for extended periods of time with almost constant, cyclical and strictly co-ordinated movements of its two pairs of wings (Weis-Fogh, 1956*a*). The fundamental oscillation of each wing is up and down, but superimposed upon this is an active twisting of the wing surface, the pronation, starting at the beginning of the downstroke. The reverse supination is mainly passive-elastic and prevails during the upstroke. Each wing is moved up by the contraction of a medial row of vertical elevators and moved down partly by elasticity (Weis-Fogh, 1959), partly by a dorsal longitudinal depressor muscle and, finally, by a lateral row of vertical depressor muscles which also control the twisting (two basalar and one subalar on each side in each segment). Each of these muscles consists of one to four fast-type motor units which are activated zero, one, or two times per wing stroke (Weis-Fogh & Wilson, 1961). The typical motor output then consists of a rather simple score of nerve impulses strictly correlated in time with the observed wing movements and repeated at the same frequency (Weis-Fogh & Wilson, 1961). It is this remarkable quantitative reduction in number of units and activities of the wing system that makes it worthy of study.

The studies of Weis-Fogh (1956*b*) on sensory mechanisms in locust flight and the hypothesis on the role of these in the production of the motor command formed the basis for the experiments described here. Since the behavioural experiments showed

A copy of Wilson's 1961 classic paper 'The central nervous control of flight in a locust' can be accessed from http://jeb.biologists.org/cgi/content/abstract/38/2/471

It seems that the workings of the human mind thrive on polarities; us *vs* them for example, or good *vs* evil, preformation *vs* epigenesis, nature *vs* nurture. But reality generally lies between the poles. So it is with the history of ideas about the control of rhythmic locomotion, a function that is the very essence of animaldom. The polarity in the present case is the issue of peripheral *vs* central control of rhythmic locomotion.

Why is Don Wilson's classic 1961 paper a pivot point in the history of this question? Before 1961 the predominant concept was that rhythmic locomotor behaviour, such as swimming, flying or breathing, is maintained and regulated by a chain of reflexes, that proprioceptive feedback at one instant shapes motor output at the next. The evidence came primarily from direct observation of normal and modified motion in numerous metamerically segmented animals, especially annelids, arthropods and fish. The concept of peripheral control of rhythmic locomotion was epitomized by Sir James Gray – a founder of *The Journal of Experimental Biology* – in his Croonian Lecture to the Royal Society (Gray, 1939). His model proposed that the muscular rhythms of locomotion that issue from the central nervous system are controlled and maintained by rhythmical input from peripheral sense organs in the musculature or the integument. Charles Sherrington's work on vertebrate proprioceptors (Sherrington, 1906) gave the model a plausible mechanism. It was accepted that some degree of intrinsic central patterning must be present in fish and amphibian locomotion (e.g. Lissman, 1946a,b) but proprioceptive feedback was thought to be essential for the generation of motor output in rhythmic locomotion. Erich von Holst saw an interplay between peripheral and central control (von Holst, 1935) and later, with cybernetics newly in vogue, this was named the Reafference Principle by Mittelstaedt and von Holst, in which they addressed what happens in the central nervous system where sensory feedback from muscles impacts motor output (Mittelstaedt and von Holst, 1950). By introducing cybernetic control theory to concepts of central nervous function they went beyond prevalent simplistic reflex concepts.

There was good neurophysiological evidence for central pattern generation dating back to the classic work of E. Adrian who showed that isolated ventral nerve cords of a water beetle *Dytiscus marginalis* produced rhythmic output (Adrian, 1931). Similarly Peter Miller showed that respiratory rhythms in the migratory locust do not depend on phasic input (Miller, 1960).

Technical advances in electrophysiology during post-World War II decades, especially the refinement of the cathode ray oscilloscope, made extracellular recording a powerful tool for the neural basis of behaviour, and Wilson was poised to make the most of these new and powerful techniques. Some 20 years after Gray's Croonian Lecture, Wilson's paper provided evidence to reject the proprioceptive chain reflex model by rigorously demonstrating that the full motor pattern of locust flight could be generated by fully deafferented thoracic ganglia, which could not receive the inputs required by the proprioceptive chain model.

Don Wilson, a student of one of the greatest comparative neurobiologists, the late Ted Bullock, had already established a reputation for comparative neurobiology with studies on sea anemonies, annelids and octopus before he joined Torkel Weis Fogh's lab in the Zoophysiological Institute at the University of Copenhagen. Weis Fogh had been pursuing a meticulous analysis of flight mechanics in the desert locust *Schistocerca gregaria* and had developed an experimental system in which a tethered locust could be induced to fly persistently in the controllable output of a wind tunnel and to maintain strictly coordinated movements of the two pairs of wings over long time periods (Weis Fogh, 1956a). Having developed the flight system, Weis Fogh explored aspects of sensory input relevant to flight and, reflecting the general paradigm of the time, developed a model consistent with the idea that proprioceptive feedback generated the cycle of motor commands, but the search for the critical phasic input was unavailing (Weis Fogh, 1956b). Wilson and Weis Fogh then began a fruitful neurophysiological collaboration (Wilson and Weis Fogh, 1962) that led to the publication of Wilson's classic paper. First they built a detailed picture of neural output to the flight muscles, and then compiled a catalog of phasic and tonic sensory inputs to the thoracic ganglia. They concluded that the input could potentially '*allow of a purely reflex integration of the flight pattern*'. So far the model was orthodox feedback-based.

Then came a series of skilful experiments in which Wilson successively eliminated sensory input to the thoracic ganglia while recording motor output in increasingly cut-away preparations in order to evaluate the influence of sensory feedback (Fig. 1). First the head and suboesophageal ganglion were removed and, despite the absence of the wind-sensitive head sensory hairs that normally activate flight after the locust jumps, normal though slowed flight could be initiated by means of the tarsal reflex and maintained in an airstream. Following on with a series of further operations in which thoracic connectives in the ventral nerve cord, and sensory nerves were selectively severed built a catalogue of the numerous sources of sensory input that could be taken to imply a purely reflex integration of the flight motor.

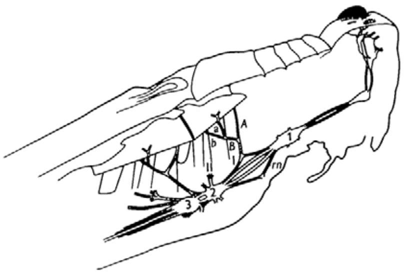


Fig. 1. Diagram of a dissection of *Schistocerca.* The dorsal tegmentary nerve supplying the head hairs is indicated as a solid line. The nerves and ganglia are numbered as in Ewer (Ewer, 1953; Ewer, 1954). *rn* indicates recurrent nerve. The positions of the dorsal longitudinal muscles and elevator muscles are indicated. The controller depressors lie behind the elevators *rn* this view. Many non-flight structures are omitted.

The next series of operations were crucial. They opened the way to a new paradigm for they showed that total removal of the sources of periodic input did not abolish patterned motor output. Deafferentation slowed the flight sequence but the cycle otherwise resembled the normal intact pattern closely. If flight was not maintained by reflex feedback then the motor pattern must have originated within the ganglia. The requisite mechanism was certainly there, for Wilson showed the presence of '*a multiplicity of oscillators*' in the flight control system. Thus he proposed that '*the basic co-ordination of flight is an inherent function of the central nervous system but that peripheral feedback loops influence the frequency of operation and details of pattern.*'

A host of subsequent studies on annulates and vertebrates, too many to mention here, have confirmed Wilson's conclusion; the control of numerous rhythmic behaviours, not only locomotion, proved to be at neither pole, neither peripheral input nor central programs alone. Instead, central pattern generators are modulated by tonic and phasic sensory feedback, which serves to adapt motions to the real heterogeneous world of errors in genetically determined motor programs, of bumps, turbulence, injury and aging. Wilson's breakthrough paper was followed by another important contribution with a clear demonstration that the bifunctional muscles that effect two distinct patterns, walking and flying, in the locust were under independent control and thus not subject to a fixed set of connexions (Wilson, 1962). His view of the role of sensory feedback in diverse behaviour patterns is summed up in a paper completed shortly before his death (Wilson, 1972), in which he emphasizes the corrective role of sensory feedback: '*the importance of sensory feedback in behavior patterns appears not to lie in the cueing of sequences but rather in the correction of errors inherent in genetically determined motor programs*'. Recognition that neurohormonal modulation of central circuits added a further complex layer to the control of rhythmic behaviour emerged later but was built on the foundation concept of the central pattern generator (Marder and Calabrese, 1996).

It may be simplistic to cite one paper as the *fons et origo* of an entire field but, as Graham Hoyle has pointed out, Wilson's paper not only established the role of central patterning in rhythmic behaviour but also gave direct experimental support to the ethological concept of the *genetically determined fixed action pattern* that is released by appropriate input (Hoyle, 1980). Thus it can be argued that Wilson's search for the neurophysiological basis of rhythmic locomotor behaviour led directly to the emergence of neuroethology as a discrete, if eclectic, discipline.

A note on Don Wilson himself: His writing was of a piece with the man; he was spare, muscular, and entirely without pretence. Besides his intensive research activity he was actively engaged in the social movements of the sixties; his equipment at Berkeley included a bullhorn with which to address student rallies. He was a skilled and graceful rock climber. I had the pleasure of making an easy climb with him in Yosemite not long before his untimely death in 1970 at 36 years of age by drowning in a rafting accident on the notorious Middle Fork of the Salmon River in Idaho. As with Mozart, one can only wonder what he might have achieved given a longer life.

10.1242/jeb.02592

John S. Edwards
University of Washington
hardsnow@u.washington.edu

References

Adrian, E. D. (1931). Potential changes in the isolated nervous system of *Dytiscus marginalis*. *J. Physiol*. **72**, 132-151.

Ewer, D. W. (1953). The anatomy of the nervous system of the tree locust, *Acanthaeris ruficornis.* I. The adult metathorax. *Arm. Natal Mus.* **13**, 467-481.

Ewer, D. W. (1954). The anatomy of the nervous system of the tree locust, *Acanthaeris ruficorms.* II. The adult mesothorax. *J. Ent. Soc. S. Afr.* **17**, 27-37.

Gray, J. (1939). Croonian Lecture. Aspects of animal locomotion. *Proc. Roy. Soc. B* **128**, 28-62.

Hoyle, G. (1980). Neural mechanisms. In *Insect Biology in the Future* (ed. M. Locke and D. S. Smith), pp. 635-665. Academic Press.

Lissman, H. W. (1946a). The neurological basis of the locomotory rhythm in the spinal dogfish (*Scyllium canicula, Acanthius vulgaris*). I. Reflex behaviour. *J. Exp. Biol.* **23**, 143-161.

Lissman, H. W. (1946b). The neurological basis of the locomotory rhythm in the spinal dogfish (*Scyllium canicula, Acanthius vulgaris*). II. The effect of deafferentation. *J. Exp. Biol.* **23**, 162-176.

Marder, E. and Calabrese, R. L. (1996). Principles of rhythmic motor pattern generation. *Physiol. Rev.* **76**, 687-717.

Miller, P. L. (1960). Respiration in the desert locust. I. The control of ventilation. *J. Exp. Biol.* **37**, 224-236.

Mittelstaedt, H. and von Holst, E. (1954). Reafferenzprinzip und Optomotorik. *Zool. Anz.* **151**, 253-259.

Sherrington, C. S. (1906). On the proprioceptive system, especially in its reflex aspect. *Brain* **29**, 467-482.
von Holst, E. (1935). Die Koordination der Bewegung bei den Arthropoden in Abhangigkeit von zentralen und peripheren Bedingungen. *Biol. Rev.* **10**, 2234-2261.
Weis Fogh, T. (1956a). Biology and physics of locust flight. II. Flight performance of the desert locust (*Schistocerca gregaria*). *Phil. Trans. B* **239**, 459-510.
Weis Fogh, T. (1956b). Biology and physics of locust flight. IV. Notes on sensory mechanisms in locust flight. *Phil. Trans. B* **239**, 553-584.
Wilson, D. M. (1961). The central nervous control of locust flight. *J. Exp. Biol.* **38**, 471-490.
Wilson, D. M. (1962). Bifunctional muscles in the thorax of grasshoppers. *J. Exp. Biol.* **39**, 669-677.
Wilson, D. M. (1972). Genetic and sensory mechanisms for locomotion and orientation in animals. *Am. Sci.* **60**, 358-365.
Wilson, D. M. and Weis Fogh, T. (1962). Patterned activity of co-ordinated motor units, studied in flying locusts. *J. Exp. Biol.* **39**, 643-667.