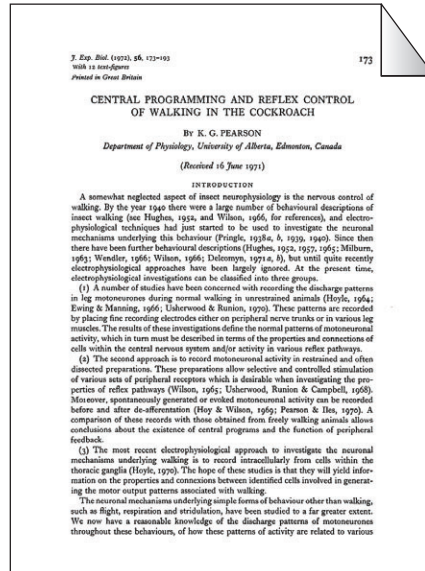


JEB Classics is an occasional column, featuring historic publications from *The Journal of Experimental Biology*. These articles, written by modern experts in the field, discuss each classic paper's impact on the field of biology and their own work. A PDF of the original paper is available from the JEB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

JEB CLASSICS

A SOMEWHAT NEGLECTED ASPECT OF INSECT NEUROPHYSIOLOGY



Tom Matheson discusses Keir Pearson's 1972 paper entitled 'Central programming and reflex control of walking in the cockroach'.

A copy of the paper can be obtained from <http://jeb.biologists.org/cgi/content/abstract/56/1/173>

Keir Pearson began his influential 1972 paper on cockroach walking with the statement that "a somewhat neglected aspect of insect neurophysiology is the nervous control of walking". He then proceeded to outline a series of experiments that, together with his earlier work (Pearson and Iles, 1970), helped to shape a very large body of subsequent research that has shown how the central nervous system and sensory signals act together to control limb movements. Almost 40 years later, his 1972 paper continues to be cited four or five times a year. The list of citing authors reads like a who's who of motor control and neuroethology, and the 240 or so citations span topics as diverse as vertebrate spinal cord pattern generation (Grillner, 1974), motor deficits in patients with large-fibre sensory neuropathy (Sanes et al., 1984), artificial neural nets for controlling legged robots (Cruse et al., 1995), and motor memories in foraging wood ants (Lent et al., 2009). This diversity is testament to the fundamental nature of the questions addressed by Pearson's experiments and to his clarity of expression, which makes his paper very accessible.

As Keir himself pointed out, by the early 1970s there was a growing body of work describing both central and peripheral neuronal contributions to the motor control of repetitive behaviours such as stridulation,

breathing and flight. Extracellular nerve and muscle recordings had been used since the 1940s – a great deal of the resulting work being published in *The Journal of Experimental Biology* by leaders in the field such as Pringle (e.g. Pringle, 1939) – and intracellular studies were beginning to appear (Hoyle, 1970).

For walking, however, there was considerable uncertainty about the relative roles of central and peripheral signals in generating the motor pattern. Charles Sherrington had shown that stepping reflexes could be elicited in cats whose spinal cords were severed (Sherrington, 1906); and, in locusts, the removal of leg sensory receptors was known to markedly disrupt leg movements (Usherwood et al., 1968; Wendler, 1966). Such experiments had given rise to a strong notion that walking rhythms were largely generated by sensory reflexes – although this view was beginning to lose favour (Wilson, 1966).

Pearson set out to resolve this question. To do so, he focussed on the hind legs of the cockroach *Periplaneta americana* and, in particular, on a subset of the muscles that raise (levate) and lower (depress) the limbs during the swing and stance movements of a step cycle, respectively. In 1970, he and John Iles had used restrained, headless and completely deafferented animals (i.e. lacking a brain or any sensory feedback from the leg) to demonstrate for the first time that alternating patterns of levator and depressor motor activity similar to those seen in walking were generated centrally in the absence of leg sensory feedback. Put simply, the basic motor pattern was generated within the central nervous system (Fig. 1). This decisive finding was a turning point because it laid to rest the idea that the motor pattern might be generated by a chain-reflex mechanism that was dependent upon the activation of sensory receptors in the limbs. Pearson's subsequent 1972 paper provided important additional experiments along with a lucid discussion that synthesised the two studies.

In the first part of the 1972 paper, from work carried out in restrained cockroaches, Pearson confirmed the 1970 observation that deafferented animals could produce centrally generated reciprocal patterns of activity in the coxal motor neurones. But, this new work also addressed a problem of the earlier study using headless animals: that it had not been possible to fully disentangle the effects of descending brain signals from those of sensory signals from the legs – a problem that had left some ambiguity in the interpretation of the earlier results. The 1972 experiments also extended the earlier result by showing that

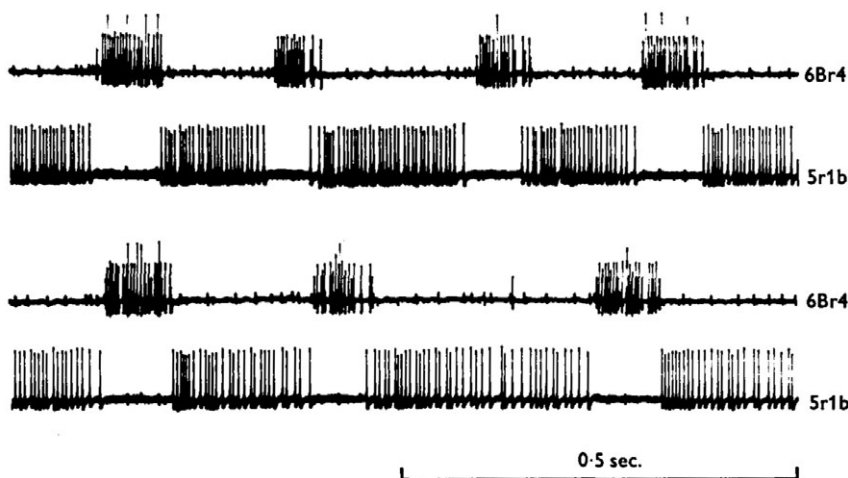


Fig. 1. A reproduction of figure 9 from Pearson and Iles' 1970 paper (Pearson and Iles, 1970), demonstrating that reciprocal patterns of leg motor activity could be generated centrally in a headless and, more importantly, deafferented cockroach. The upper trace of each pair (labelled 6Br4) shows coxal levator activity, whereas the lower trace (labelled 5r1b) shows coxal depressor activity, over seven consecutive cycles. A single motor neurone (the slow depressor coxae D_s) was active in the nerve 5r1b recording, whereas at least four were seen in the 6Br4 recording.

removal of leg sensory signals led to changes in the motor pattern; most notably an increased activation of one of the motor neurones, the slow depressor coxae D_s . This second important result provided strong evidence that sensory feedback acted to modify the centrally generated pattern of activity.

To determine whether his results were meaningful in freely walking cockroaches, Pearson recorded the motor neurone signals using flexible electromyogram wires inserted directly through the cuticle into the muscles of interest. The cockroaches were able to walk or run freely in an arena, and could be given weights to carry or pull in different ways. Pearson's recordings provided beautifully clear examples of alternating activity in the antagonistic levator and depressor coxae motor neurones during real walking, and formed the basis for quantitative analyses of specific relationships between the bursts of motor activity.

These analyses gave important insights into the detailed action of individually identified motor neurones during walking. The electromyogram recordings showed that changes in walking and running speed were associated with the recruitment of different motor neurones. The first of several further key observations was that as walking speed changed, the durations of the bursts of activity in the depressor motor neurone D_s changed much more than did those of the levators. This correlated well with contemporary behavioural data for walking

(Delcomyn, 1971), which showed that changes in walking speed affected the stance phase (to which the depressor contributes) much more markedly than the swing phase. Pearson was also able to describe how the motor activity was patterned within a burst, and to show how this changed with walking speed or experimental manipulation. Crucially, loading the animals led to alterations of motor activity, so sensory feedback here – as in the dissected preparations – clearly influenced the overall pattern. Moreover, Pearson deduced that the sensory feedback was much less important at the fastest walking speeds. One of the nicest lines of argument employed in this part of the paper was that the stance phase coxal depressor motor activity was intensified at times when there was self-induced loading of the leg as the other ipsilateral legs entered the swing phase and thus no longer contributed to the support of the body mass (Fig. 2). Now, almost 40 years later, it is becoming

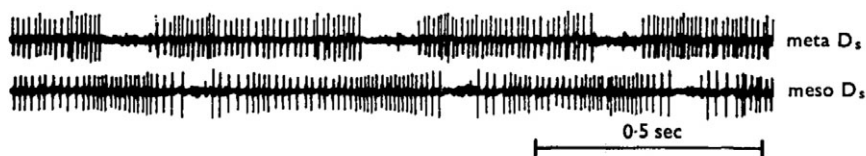


Fig. 2. A reproduction of figure 10 from Pearson's 1972 paper (Pearson, 1972), demonstrating that activity of the mesothoracic depressor coxae motor neurone D_s (lower trace) was enhanced at times when the ipsilateral prothoracic and metathoracic legs were in swing phase and thus not contributing to support of the body weight. Prothoracic and metathoracic swing phase occurred at the times when the metathoracic D_s was silent (upper trace), and this was associated with an increase of firing rate within each ongoing burst of activity in the mesothoracic D_s .

increasingly clear that passive biomechanical properties of the limbs provide additional mechanisms for stabilising limb movements alongside sensory feedback (Zakotnik et al., 2006; Proctor and Holmes, 2010). Such mechanisms might dominate at high stepping frequencies when there is insufficient time for sensory signals to reach the central nervous system and exert their influence.

To identify the sensory signals that might contribute to the load-induced changes in motor activity, Pearson carefully denervated different regions of the leg before observing whether or not an added load could still influence the motor pattern. These experiments ruled out major contributions from some of the coxal receptors, and led Pearson to suggest that the trochanteral campaniform sensilla might be responsible. These small dome-like sensory receptors on the leg were already known to excite the depressor motor neurone D_s in response to strain in the leg cuticle (Pringle, 1940), but nobody knew whether they actually responded to limb forces during normal walking. More recent work on these and other leg campaniform sensilla has provided strong indications that they do respond during walking (e.g. Hofmann and Bässler, 1982; Delcomyn, 1991; Noah et al., 2001), and their artificial stimulation has now been shown to affect ongoing walking motor patterns (Schmitz, 1993; Akay et al., 2007).

Pearson's 1972 paper was presented in an exceptionally clear and lucid style of writing, which remained tightly focussed on the questions at hand. Its accessibility has undoubtedly contributed to the paper's long-lasting influence on the field. It touched on several key questions that have exercised sensory motor neurophysiologists of both vertebrate and invertebrate persuasions over the subsequent 40 years: load compensation, gating of reflexes during active behaviour, and the site and nature of feedback influences on central networks. Pearson provided a concise

summary of the rapidly changing state of knowledge at the time. For instance, he proposed a model for the observed patterns of coordination of the coxal depressor and levator motor neurones in the cockroach, and used this to explain possible mechanisms by which limb proprioceptors of locusts might have caused the profound effects of sensory manipulation seen by Usherwood et al. (Usherwood et al., 1968). In the light of subsequent intracellular studies and an increased understanding of the patterns of connectivity between the various motor neurones and interneurons involved in leg movements, some details of Pearson's basic model seem now to be incorrect – and others remain untested (e.g. Burrows, 1996) – but it nevertheless provided a significant stimulus and focus for much subsequent work.

An important area of modern biomedical research is the design of effective limb prostheses controlled by brain signals ('neural prostheses' or 'brain-machine interfaces, BMIs'). Despite remarkable progress in this area (e.g. Velliste et al., 2008), one fundamental remaining problem is how best to incorporate sensory signals into control systems driven by brain activity: a question that was already at the

forefront of Pearson's mind some 40 years ago – albeit in a rather different context.

10.1242/jeb.034918

Tom Matheson
University of Leicester
tm75@le.ac.uk

References

- Akay, T., Ludwar, B. Ch., Goritz, M. L., Schmitz, J. and Büschges, A.** (2007). Segment specificity of load signal processing depends on walking direction in the stick insect leg muscle control system. *J. Neurosci.* **27**, 3285-3294.
- Burrows, M.** (1996). *The Neurobiology of an Insect Brain*, 682 pp. Oxford: Oxford University Press.
- Cruse, H., Bartling, C., Cymbalyuk, G., Dean, J. and Dreifert, M.** (1995). A modular artificial neural-net for controlling a 6-legged walking system. *Biol. Cybern.* **72**, 421-430.
- Delcomyn, F.** (1971). The locomotion of the cockroach, *Periplaneta americana*. *J. Exp. Biol.* **54**, 443-452.
- Delcomyn, F.** (1991). Activity and directional sensitivity of leg campaniform sensilla in a stick insect. *J. Comp. Physiol. A* **168**, 113-119.
- Grillner, S.** (1974). Generation of locomotion in spinal dogfish. *Exp. Brain Res.* **20**, 459-470.
- Hofmann, T. and Bässler, U.** (1982). Anatomy and physiology of trochanteral campaniform sensilla in the stick insect, *Cuniculina impigra*. *Physiol. Entomol.* **7**, 413-426.
- Hoyle, G.** (1970). Cellular mechanism underlying behaviour – neuroethology. *Adv. Ins. Physiol.* **7**, 349-444.
- Lent, D. D., Graham, P. and Collett, T. S.** (2009). A motor component to the memories of habitual foraging routes in wood ants? *Current Biol.* **19**, 115-121.
- Noah, J. A., Quimby, L., Frazier, S. F. and Zill, S. N.** (2001). Force detection in cockroach walking reconsidered: discharges of proximal tibial campaniform sensilla when body load is altered. *J. Comp. Physiol. A* **187**, 769-784.
- Pearson, K. G.** (1972). Central programming and reflex control of walking in the cockroach. *J. Exp. Biol.* **56**, 173-193.
- Pearson, K. G. and Iles, J. F.** (1970). Discharge patterns of coxal levator and depressor motoneurons of the cockroach, *Periplaneta americana*. *J. Exp. Biol.* **52**, 139-165.
- Pringle, J. W. S.** (1940). The reflex mechanism of the insect leg. *J. Exp. Biol.* **17**, 8-17.
- Proctor, J. and Holmes, P.** (2010). Reflexes and preflexes: on the role of sensory feedback on rhythmic patterns in insect locomotion. *Biol. Cybern.* **102**, 513-531.
- Sanes, J. N., Mauritz, K. H., Evarts, E. V., Dalakas, M. C. and Chu, A.** (1984). Motor deficits in patients with large-fiber sensory neuropathy. *Proc. Natl. Acad. Sci. USA* **81**, 979-982.
- Schmitz, J.** (1993). Load-compensating reactions in the proximal leg joints of stick insects during standing and walking. *J. Exp. Biol.* **183**, 15-33.
- Sherrington, C. S.** (1906). *The Integrative Action of the Nervous System*. New Haven, CT: Yale University Press.
- Usherwood, P. N. R., Runion, H. I. and Campbell, J. I.** (1968). Structure and physiology of a chordotonal organ in the locust leg. *J. Exp. Biol.* **48**, 305-323.
- Velliste, M., Perel, S., Spalding, M. C., Whitford, A. S. and Schwartz, A. B.** (2008). Cortical control of a prosthetic arm for self-feeding. *Nature* **453**, 1098-1101.
- Wendler, G.** (1966). The coordination of walking movements in arthropods. *Symp. Soc. Exp. Biol.* **20**, 229-250.
- Wilson, D. M.** (1966). Insect walking. *Ann. Rev. Entomol.* **11**, 103-122.
- Zakotnik, J., Matheson, T. and Dürr, V.** (2006). Co-contraction and passive forces facilitate load compensation of aimed limb movements. *J. Neurosci.* **26**, 4995-5007.