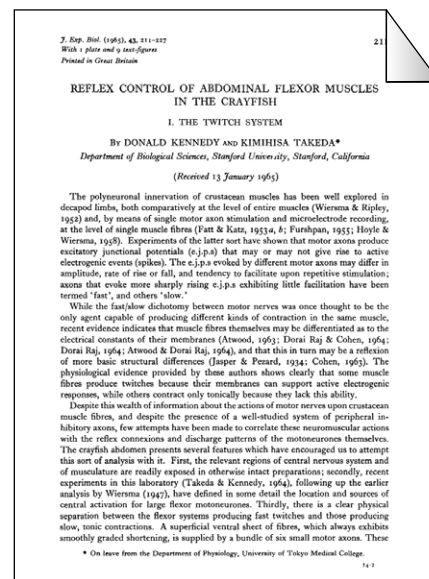


## PARALLEL 'PHASIC' AND 'TONIC' MOTOR SYSTEMS OF THE CRAYFISH ABDOMEN



Harold Atwood discusses Donald Kennedy and Kimihisa Takeda's 1965 papers describing the crayfish 'phasic' motor system, involved in escape behaviour, and the 'tonic' system, involved in postural control. Both papers can be accessed from <http://jeb.biologists.org/content/vol43/issue2>

The ground-breaking papers of Donald Kennedy and Kimihisa Takeda (Kennedy and Takeda, 1965b; Kennedy and Takeda, 1965a) on crustacean motor systems established a general principle of motor control: there is a division of labour among available motor neurons and muscle fibres. The investigators recognized two types of muscle in the crayfish abdomen, which they categorized as slowly contracting or 'tonic' (capable of sustained, fatigue-resistant, graded contractions), and rapidly contracting or 'phasic' (producing very rapid, twitch-like, non-sustained contractions). The two types of muscle are anatomically separated and supplied by two sets of motor neurons with very different physiological properties. The motor neurons of the tonic musculature exhibit a lot of spontaneous impulse activity and are responsible for postural adjustments and everyday locomotion. In contrast, the motor neurons of the phasic musculature are silent most of the time, but when recruited for vigorous escape activity they fire a few impulses at a time in intermittent bursts, producing relatively brief episodes of intense movement. Many variations on this theme have since been found throughout the animal kingdom, but in selecting the musculature of the crayfish

abdomen, Kennedy and Takeda presented an extremely clear-cut case of complete separation of phasic and tonic motor systems, with anatomically distinct sets of muscles innervated by separate groups of specialized motor axons (now often referred to as 'phasic' and 'tonic' motor axons).

To appreciate the significance of this major contribution, we have to go back to the era in which the study was developed. Earlier physiological work on crustacean muscles, starting in the 19th century, had been on limb muscles, each innervated by a small number of excitatory and inhibitory neurons. Several of these muscles receive dual excitatory innervation: two motor axons supply the entire muscle, one producing a faster contraction than the other [hence the terms 'fast axon' and 'slow axon' generally in use at the time (Wiersma, 1961a)]. Staining of crustacean muscle axons with Methylene Blue revealed profuse parallel branching of axon terminals, with all observed muscle fibres receiving both 'fast' and 'slow' axons, plus an inhibitory axon (van Harrevel and Wiersma, 1937). Electrical recordings from these muscles showed larger responses to 'fast' axon stimulation in the majority of dually innervated muscle fibres, and for a while it was accepted that all of the crustacean muscle fibres were similar, and could each produce a fast or slow contraction depending on which of the two axons was stimulated. This view was promoted in an influential monograph on comparative neuromuscular physiology by Graham Hoyle, in which he wrote: '... in arthropods there is in most, if not all, instances, only one kind of muscle fibre' (Hoyle, 1957). However, this assertion was soon disproved by the discovery of muscle fibres with different electrical properties in crab leg muscles (Atwood, 1963) and by the recognition of even more distinctive differences among muscle fibres of the crayfish abdomen (Abbott and Parnas, 1965; Kennedy and Takeda, 1965a; Kennedy and Takeda, 1965b). In limb muscles, fibres with different electrical and mechanical characteristics are often mixed together (Atwood et al., 1965) while in the crayfish abdomen, massive 'twitch' muscles form the bulk of the musculature, and a separate thin sheet of superficial muscle fibres, much different in properties and appearance, constitutes the 'tonic' musculature responsible for abdominal postural adjustments.

Most previous studies on neuromuscular systems of crustaceans had been concerned with the details of innervation and synaptic transmission. While these features were assessed in the abdominal flexor muscles

by Kennedy and Takeda in their 1965 JEB publications (Kennedy and Takeda, 1965a; Kennedy and Takeda, 1965b), they also had a larger aim: to discover the uses to which the two systems are put during normal behaviour, and the mechanisms of their recruitment in the central nervous system. The investigators demonstrated the different behavioural roles of the two motor systems through simple but elegant experiments. When they cut all the nerve branches supplying the superficial (tonic) flexor muscles in an isolated abdomen, all abdominal flexor tone disappeared and the abdomen became limp and passive. Conversely, when they cut the nerve branches to the deep (phasic) flexors in a separate specimen, the rapid tail flip (normally used in backward escape swimming) could not be elicited, but slow abdominal flexion persisted. The two motor systems are clearly linked to different behavioural acts: postural adjustments and reflexes for the tonic system, and vigorous escape responses for the phasic system.

The isolated crayfish abdomen also proved to be an excellent experimental preparation for investigation of synaptic transmission at neuromuscular junctions and of nerve impulse traffic in identified motor axons. In unstimulated abdomens, Kennedy and Takeda observed continuous ongoing action potentials in the motor nerves to the slow flexor muscles, and complete silence in the much larger nerves to the fast flexor muscles (Kennedy and Takeda, 1965a). Having made this observation, Kennedy and Takeda went on to record the action potentials from exposed intact nerves and showed that slow flexor axons could be induced to change their activity by various stimuli applied to the abdomen, demonstrating that the central nervous system mediates a wide range of reflexive control (motor responses elicited by sensory stimulation).

The fast flexor axons are recruited by a completely separate interneuron network, the 'giant fibre' interneurons, within the central nervous system. These interneurons form four axon tracts, and it is their large size that ensures the rapid impulse conduction velocity required for fast reflexes. Stimulation of any one of these large interneurons (or very strong sensory input to head or tail of intact animals) commands a tail-flip response due to direct and rapid excitation of the 'phasic' motor neurons (Wiersma, 1961b). Hence, these giant interneurons are often termed 'command' interneurons because they 'command' a well-defined behavioural act (for reviews, see Kupfermann and Weiss, 1978; Wine and Krasne, 1982). The interneuronal networks that regulate the

tonic system's reflexes do not excite the 'phasic' motor neurons. Thus, the two motor systems are controlled by separate groups of interneurons, and form two parallel control systems with very little interaction, either peripherally or centrally.

Elucidation of the mechanisms through which interneurons activate motor neurons was an obvious additional target for research, and the crayfish 'phasic' motor system rapidly yielded results. Takeda and Kennedy began investigations into the activation of flexor motor neurons within the central nervous system by recording from their cell bodies *in situ* with sharp intracellular microelectrodes, and observing their electrical responses to the stimulation of input pathways (Takeda and Kennedy, 1964). They and subsequent investigators found that other interneurons besides the 'giant' interneurons could activate the 'phasic' motor neurons. Eventually it was determined that the rapid flexion involved in the escape responses shows variation according to which central pathways are active. In an intact animal, strong stimulation of the tail produces a different swimming response from stimuli applied to the head, because different interneuronal pathways are activated (reviewed in Wine and Krasne, 1982). Many additional details of central control were added over the next two decades (for reviews, see Wine and Krasne, 1982; Page, 1982). Behaviourally, escape swimming is generally more stereotyped and rapid than the much more variable and subtle movements that are regulated by the tonic axons and their associated networks of interneurons.

An additional goal of Kennedy and Takeda's work (Kennedy and Takeda, 1965a; Kennedy and Takeda, 1965b) was to clarify the functional role of peripheral inhibition. Most crustacean muscles are innervated by one or two inhibitory axons, but the biological functions of peripheral inhibition were not very well understood in the early 1960s. An important JEB paper by Brian Bush showed that reflexes involved in claw opening and closing include firing of peripheral inhibitory axons to weaken contractions of antagonistic muscles that would interfere with the reflex activity (Bush, 1962). Kennedy and Takeda found that both phasic and tonic flexor muscles receive inhibitory innervation, and they addressed the question of the role of these inhibitory axons by recording from them and their innervated muscles during reflex activities (Kennedy and Takeda, 1965a; Kennedy and Takeda, 1965b). In both sets of muscles, peripheral inhibition did not have much effect on the amplitude of excitatory postsynaptic potentials (the electrical responses of the muscle fibre

membrane, generated by neurotransmission at excitatory synapses, that are responsible for eliciting contraction of the muscle fibre), but it did shorten their time courses. This observation led to the conclusion that inhibition serves to repolarize the muscle fibres following excitation, thereby speeding muscle relaxation in preparation for a subsequent contraction, and improving the temporal precision of movement. The inhibitory axon of the slow flexor muscles is often recruited during central suppression of activity in the excitatory axons (Kennedy and Takeda, 1965b), indicating central inhibition of excitatory motor neurons along with central activation of the inhibitory neurons, and also a major role for the inhibitory neuron in the rapid termination of ongoing contractions. Improvement of temporal precision is also attributed to inhibitory axons of crustacean limb muscles (Bush, 1962), which suppress electrical activity most strongly in slowly contracting muscle fibres (Atwood, 1973). Although central mechanisms of recruitment for peripheral inhibitory neurons differ in limb and abdominal motor systems, the general role of improving the temporal precision of movement can be assigned to inhibitors in both cases.

The parallel phasic and tonic motor systems of the crayfish abdomen were not the first to be discovered, since it had been known for some time that slow (tonic) and fast (twitch) muscle fibres with separate innervation occur in muscles of amphibians (Kuffler and Vaughan Williams, 1953; Tasaki and Mizutani, 1944). However, the amphibian studies lacked a behavioural context, which the crustacean studies supplied. The principle of differential recruitment of phasic and tonic motor systems for specific acts was subsequently found to apply in mammals as well. For example, in the medial gastrocnemius muscle of the cat, only about 25% of the motor unit pool innervating slow-twitch muscle fibres is used for posture and walking; about 60% of the motor unit pool innervating 'fast fatigable' muscle fibres is used only for demanding efforts such as jumping (Burke, 1980). Apparently, evolutionary forces have resulted in this disproportionate allocation of muscle fibre types in many muscles of different species. A premium is put on large fast muscles or motor units that can be kept in reserve for demanding situations.

Many studies on reflex control of swimming and abdominal movement followed the initial studies of Kennedy and Takeda (Kennedy and Takeda, 1965a; Kennedy and Takeda, 1965b). Gradually, a fairly complete circuit for crayfish escape behaviour, mediated by the phasic motor

system, was worked out by a number of investigators, many of whom worked in Donald Kennedy's laboratory at Stanford University (reviewed by Wine and Krasne, 1982). Details of circuits involved in postural control were also elucidated (reviewed by Page, 1982). In addition to stimulating research on dual motor systems, their regulation by the central nervous system, and patterns of connectivity between motor neurons and muscle, the studies on the crayfish abdomen launched by Kennedy and Takeda (Kennedy and Takeda, 1965a; Kennedy and Takeda, 1965b) also gave rise to easily made preparations widely used in teaching laboratories as an introduction to hands-on neurophysiology. This lasting legacy has been invaluable for many generations of students, and will continue.

10.1242/jeb.010868

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