

This Week's Citation Classic

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Atwood H L. Crustacean neuromuscular mechanisms. *Amer. Zool.* 7:527-52, 1967.
[Dept. Zoology, Univ. Toronto, Toronto, Ontario, Canada]

Speed and strength of muscular response in crustaceans is attributable to inherent electrical and mechanical properties of muscle fibers, and in part to quantitative aspects of transmitter release at nerve terminals. Peripheral inhibitory synapses modulate muscular contractions through pre- and post-synaptic mechanisms. [The SC¹® indicates that this paper has been cited over 120 times since 1967.]

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"Studies summarized in this paper were originally prompted by observations of G. Hoyle and C.A.G. Wiersma,¹ who measured contractions and electrical events evoked by stimulation of isolated motor neurons supplying crustacean limb muscles. Some muscles innervated by two excitatory motor neurons showed, with stimulation of a 'fast' motor neuron, large electrical events in individual muscle fibers, but a small contraction of the entire muscle. Conversely, identical stimulation of the companion 'slow' motor neuron elicited small electrical events in the same muscle fibers, accompanied by strong muscular contraction.

"They concluded that 'fast' and 'slow' axons released different transmitter chemicals that acted directly on the contractile machinery of the muscle fiber to produce characteristic contractions, independently of membrane electrical events.

"This bold idea, which was at variance with accepted dogma of excitation-contraction coupling in vertebrate muscles, attracted me into graduate work in comparative neuromuscular physiology. I went to work with Hoyle at the University of Glasgow in 1960, convinced that the hypothesis of Hoyle and Wiersma¹ was correct, and determined to strengthen it with further experimental evidence. However,

Hoyle soon left Glasgow for the University of Oregon. I stayed on; Peter Usherwood, another graduate student, became my chief mentor. I worked in relative isolation in a dark basement laboratory in Glasgow. There were very few distractions.

"While recording with microelectrodes from crustacean muscle fibers, I began to make findings at variance with my preconceptions. Although electrical events evoked by stimulation of the 'slow' axon were smaller than those of the 'fast' axon in accessible muscle fibers, a group of less accessible fibers showed the reverse pattern: much larger electrical events during stimulation of the 'slow' axon. These muscle fibers had distinctive membrane electrical properties² and were physiologically specialized for slow, powerful contractions. Other fibers in the same muscle were specialized for fast contractions. Thus, the distinctive contractile responses evoked by the two motor axons were due to differential recruitment of specialized groups of muscle fibers, rather than to differences in transmitter chemicals. The mechanism of excitation-contraction coupling was found to be under electrical control, as in vertebrate muscle.³

"Few papers in comparative physiology become highly cited. Perhaps the reason is that comparative physiologists are more often concerned with divergent details than with generalities. The 1967 review counteracted this tendency by demonstrating features shared by neuromuscular systems of vertebrates and arthropods: elaboration of physiologically distinct muscle fibers for different functions, specialization of motor neurons into 'phasic' and 'tonic' types, matching of motor neurons and muscle fibers to form functionally diverse working units, and generally similar excitation-contraction coupling mechanisms. The reasons for the many citations of this review are several: it established some general features of crustacean neuromuscular systems, emphasized the utility of these systems for research on synaptic mechanisms akin to those in central nervous systems, and provided a timely summary of a rapidly developing field of research. A more recent review⁴ has extended these themes."

1. **Hoyle G & Wiersma C A G.** Coupling of membrane potential to contraction in crustacean muscles. *J. Physiol. London* 143:441-53. 1958.
2. **Atwood H L.** Differences in muscle fibre properties as a factor in "fast" and "slow" contraction in *Carcinus*. *Camp. Biochem. Physiol.* 10:17-31, 1963.
3. **Atwood H L, Hoyle G & Smyth T.** Electrical and mechanical responses of single innervated crab-muscle fibres. *J. Physiol. London* 180:449-82. 1965.
4. **Atwood H L.** Organization and synaptic physiology of crustacean neuromuscular systems. *Progr. Neurobiol.* 7:291-391, 1976.