peak value of venous blood oxygen saturation during reaction was not more than 68% HbO_2, venous outflow constantly increased. When the peak value reached 70 to 85% HbO_2, the venous outflow either decreased or increased. When venous blood oxygen saturation reached, under stimulation of sympathetic nerves, the value of 85% HbO_2 or more, the venous outflow decreased. We revealed as well reversed line correlation between initial level of venous blood oxygen saturation and the character of venous outflow from an organ under electrical stimulation of sympathetic fibres (Figure 2b). It turned out that if the initial level venous blood oxygen saturation was small, i.e. the oxygen consumption by the tissue of an organ was high, venous outflow as a rule was increased. On the contrary, the more the venous blood oxygen saturation before stimulation, the more evident was the tendency to the decrease of the venous outflow under electrical stimulation of sympathetic fibres.

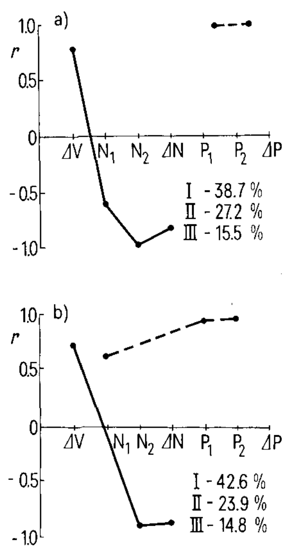

Fig. 3. Results of the factor analysis of vasomotor reactions and dynamics of venous blood oxygen saturation changes in the spleen (a) and intestine (b) under electrical stimulation of sympathetic fibres. Abszissa, analyzed priznacs; ordinate, means of coefficient of correlation. Line, I factor; interrupt line, II factor; point, III factor. Weights of factors: a) I, 38.7%; II, 27.2%; III, 15,5%. b) I, 42.6%; II, 23.9%; III, 14.8%. V, venous outflow (ml); N_1, initial level of the venous blood oxygen saturation (%Hb O_2); N_2, peak means of the venous blood oxygen saturation (%Hb O_2); N, venous blood oxygen saturation changes; P_1, initial level of the perfusion pressure; P_2, peak means of the perfusion pressure; P, the perfussion pressure changes.

To elucidate the relation between both the value and character of capacitance vessel responses of spleen and intestine and all the parameters recorded, we used one of the methods of the factor analysis – method of chief components. It was shown (Figure 3) that the most essential factor was the close negative correlation between magnitude and character of capacitance vessel responses from one side and dynamics of venous blood oxygen saturation from another.

Thus the results of the analysis permit us to suggest that the more intensive the oxygen exchange in spleen and intestine before and during the sympathetic stimulation, i.e. the more is venous blood desaturated with oxygen, the more frequent the constrictory response of capacitance vessels. On the contrary, the lower the oxygen exchange in spleen and small intestine, i.e. the more the venous blood saturated with oxygen, the more frequent is dilatory response of capacitance vessels.

It is necessary to emphasize, however, that this correlation was obtained in experiments with sympathetic fibres cut, i.e. when the organs investigated were practically deprived of neurogenic control. Whether this correlation exists in the normally functioning spleen and small intestine will be shown in further investigations.

Coordinated Activation of Muscle Fibres by Different Conduction Velocities in Branches of a Crustacean Motor Axon

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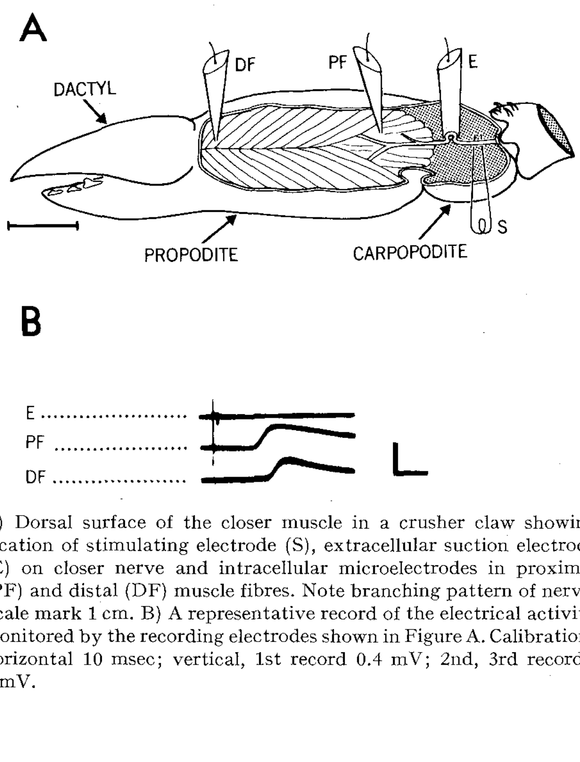
Summary. Higher conduction velocities in branches of the fast excitor axon to distal muscle fibres ensure that these fibres are activated almost simultaneously with proximal fibres in the claw closer muscle of lobsters, producing a contraction of maximal force.

In muscle contraction, maximal force is exerted when all fibres within a muscle (or motor unit) are excited simultaneously. The resulting coordination problem is accentuated in crustaceans, in which entire muscles are innervated by few (1–4) excitatory motor axons, so each neuron serves a large number of muscle fibres. In addition, the muscle fibres are arranged in pinnate fashion resulting in a wide separation between proximal and distal fibres (Figure A). What is the mechanism for exciting the fibres within such muscles so that they contract almost simultaneously? In the lobster claw closer muscle, different conduction velocities in the branches of a single excitatory axon allow widely separated muscle fibres to be activated within a few milliseconds of one another.

The claw closer muscle in lobsters is the largest limb muscle and is innervated by 2 excitatory (fast and slow) axons and an inhibitory axon[3]. The fast axon is the major motor fibre to the dorsal surface of the muscle, although all regions of the muscle are innervated by both axons to some extent[4]. Furthermore, it is possible to selectively stimulate the fast axon, since it invariably has the lowest threshold of all 3 axons[4]. We therefore examined the temporal differences in excitation of widely separated dorsal fibres when the fast excitor was stimulated.

In a typical experiment, the dorsal surface of the closer muscle was exposed by removing the opener muscle. A proximal and a distal fibre were penetrated simultaneously with conventional 3 *M* KCl filled glass microelectrodes (Figure A). The closer nerve, which was isolated from the main leg nerve, was stimulated with brief (< 0.1 msec) square pulses via platinum wire electrodes. The resulting spikes were monitored distal to the stimulating electrodes by a suction electrode recording 'en-passant' (Figure A). The distances between electrodes were measured using an ocular micrometer. This experimental design provided a record of the extracellular spikes in the fast axon and the resultant excitatory postsynaptic potentials (EPSPs) in the muscle fibres (Figure B). The time taken from the axon spike to the beginning of each EPSP, together with the distance separating the electrodes recording these events, gave an average conduction velocity for those branches of the fast excitor axon which supplied the muscle fibres. These conduction velocities enabled us to compare the latencies for activation in widely separated muscle fibres.



A) Dorsal surface of the closer muscle in a crusher claw showing location of stimulating electrode (S), extracellular suction electrode (E) on closer nerve and intracellular microelectrodes in proximal (PF) and distal (DF) muscle fibres. Note branching pattern of nerve. Scale mark 1 cm. B) A representative record of the electrical activity monitored by the recording electrodes shown in Figure A. Calibration: horizontal 10 msec; vertical, 1st record 0.4 mV; 2nd, 3rd records, 4 mV.

Comparison of conduction velocities (CV) in the fast excitor axon to proximal (PF) and distal (DF) fibres in the lobster claw closer muscle

CV (m/sec)		Differences in CV between PF and DF		Differences in time of EPSP initiation between PF and DF (msec)	Distance between PF and DF (mm)
PF	DF	DF–PF	$\frac{DF-PF}{PF} \times 100$ (%)		
1.4	2.1	0.7	50	6.5	20
1.1	1.9	0.8	73	4	16.6
0.6	1.2	0.6	50	5.6	12.5
0.7	2.0	1.3	186	5	24.1
2.0	2.5	0.5	25	2.2	10.1
1.3	2.4	1.1	85	2.5	15
0.7	2.0	1.3	186	2.5	15
2.0	3.0	1.0	50	4	28

The results from 8 separate closer muscles (5 crusher and 3 cutter claws) are summarized in the Table. Impulse propagation in axon branches to the distal fibres was consistently faster (25% to 186%) than in branches to proximal fibres. Even though the fibres were widely separated (10.1 to 28 mm), the EPSP to the distal fibre was only a few msec (2.2 to 6.5) behind that in the proximal fibre. In the example given in Figure B, though the 2 muscle fibres are separated by 28 mm, there is only a 4 msec lag in the initiation of an EPSP in the distal fibre. When the distance between fibres was less than 5 mm, the conduction velocity in axonal branches to the 2 fibres did not differ significantly. Clearly, faster impulse propagation to the distal fibres ensures that they are activated almost simultaneously with the proximal fibres. This coordination is particularly important for the fast axon of the cutter claw, which can cause claw closure in approximately 20 msec[4].

It should be borne in mind that whereas contraction, of a vertebrate twitch type muscle fibre depends on an all-or-nothing action potential generated by the EPSP, contraction of a crustacean striated muscle fibre is graded according to the rate and degree of depolarization of the fibre resulting from the EPSP. The size of EPSP varies considerably amongst fibres of the dimorphic claw closer muscle with the fast axon generating relatively small EPSPs in the crusher claw (1–3 mV as in Figure B), and larger EPSPs in the cutter claw (4–15 mV)[4]. Facilitation and summation of EPSPs leads to larger depolarization of the fibre and may lead to an all-or-nothing action potential. The latter is certainly the case in some fibres of the cutter claw where stimulation of the fast axon with paired pulses results in an overshooting action potential which produces a twitch contraction[4]. In this case coordinated activation of widely separated muscle fibres would ensure the maximal twitch contraction.

What is the basis for the different rates of impulse propagation in branches of a single motor axon? Conduction velocity varies directly with axon diameter, hence differences in diameter may explain differences in conduction velocity. It is therefore instructive to consider the branching pattern of the closer nerve in the lobster claw (Figure A). The closer nerve divides into 2 primary branches, which innervate fibres on either side of the tendon along the length of the muscle. Proximal to this major bifurcation is a branch which is much thinner than the primary branches and which supplies the proximal muscle fibres. Presumably impulse propagation along this fine branch would be slower than along the large primary branches producing coordinated activation of proximal and distal muscle fibres.

Alternatively the excitatory axon may take a more circuitous route to the proximal muscle fibres, so that the pathway to these fibres is strictly via fine axon branches. In contrast the distal fibres may be innervated by small axon branches that travel only short distances from the large primary branch.

[1] Supported by Muscular Dystrophy Association and National Research Council of Canada.

[2] Supported by National Institute of Health and Muscular Dystrophy Association of America.

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