

Table II

Perfusion fluid	No. of experiments	Net glucose transport ($\mu\text{moles g}^{-1} \text{ h}^{-1}$)	ω of thiourea ($\text{mmoles g}^{-1} \text{ h}^{-1} \text{ Atm}^{-1}$) in the absence of drag flow	ω of thiourea ($\text{mmoles g}^{-1} \text{ h}^{-1} \text{ Atm}^{-1}$) in the presence of a maximal theoretical drag flow
Krebs and Henseleit added with glucose 13.9 mM and thiourea 10 or 20 mM	9	276.9 ± 37.4	0.56 ± 0.03	0.61 ± 0.04
Same fluid NaCl substituted with Tris-HCl	6	164.8 ± 45.1	0.42 ± 0.05	0.43 ± 0.05
Same fluid NaCl substituted with Choline-HCl	8	149.2 ± 34.6	0.42 ± 0.02	0.44 ± 0.02

Thiourea, mol. wt. 76.12; semistarved rats, average percent weight decrease $24.2 \pm 2.0\%$.

nation is that sodium choline and tris affect, directly unspecifically and in a different way the physico-chemical properties of the cell membrane. Another possible explanation of our data is that of an indirect effect of the decreased Na^+ concentration on the membrane permeability. We have previously demonstrated that glucose transport depends on the intracellular concentration of glucose, i.e. the higher the intracellular concentration of glucose, with a consequent swelling of the cell, the more the glucose transport¹⁵. In the absence of sodium chloride, the intracellular accumulation of glucose is lower as well as the swelling of the cell. Now the hypothesis may be put forward that the degree of swelling is parallel with the permeability of the cellular membrane.

Zusammenfassung. Der Einfluss des Natriums auf die passive Permeabilität der Jejunum-Schleimhaut der La-

boratoriumsratte gegenüber wasserlöslichen, nichtmetabolisierbaren und elektroneutralen Substanzen (Thioharnstoff, Azetamid) wurde untersucht. Wird das Natrium des NaCl in der Perfusionsflüssigkeit durch Tris- oder Cholin-Kationen ersetzt, so nehmen sowohl der transepitheliale Glukosetransport wie auch die Mobilität der geprüften Substanzen ab.

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¹⁵ A. FAELLI, G. ESPOSITO and V. CAPRARO, *Archo Sci. biol. Bologna* 50, 234 (1966).

Muscle Spindle Innervation in the Intertransverse Caudal Muscles of the Rat

The intertransverse caudal muscles in rat are interesting physiologically because β -axon excitation of the muscle spindles they contain results in an unusually intense and prolonged response from primary endings¹. β -axons are motor to both intra- and extra-fusal muscle fibres, and their conduction velocities are intermediate to α -(purely skeletomotor), and γ -(purely fusimotor)axons.

These muscles are also useful experimentally since their conformation permits intramuscular structures to be studied with relative ease^{2,3}. The histological work described here was done with the aim of explaining previous findings and of extending the usefulness of the preparation.

This paper has a precedent in the study of rat lumbrical muscles recently published in this journal by PORAYKO and SMITH⁴, who justifiably state that there has been relatively little work on rat muscle spindles as compared with those of cat. This is particularly true of rat fusimotor innervation.

Method. The intertransverse muscles of adult albino rats were stained with methylene blue (BOYD⁵), and gold

chloride (BOYD⁶), but most of the work was done on preparations stained with silver (IP and BARKER⁷). Some muscles were stained for anticholinesterase activity, using acetyl thiocholine and butyryl thiocholine as substrates⁸, and were subsequently stained with silver (IP⁹). Nerve branches to the muscle were stained with buffered osmium tetroxide, sectioned and the component axon

¹ G. L. KIDD, in *Control and Innervation of Skeletal Muscle* (Thomson and Co. Ltd., Dundee 1966), p. 83.

² I. GURUMURTHY and G. L. KIDD, *Lab. Practice* 16, 34 (1967).

³ M. H. GLADDEN and G. L. KIDD, *J. appl. Physiol.*, in press (1969).

⁴ O. PORAYKO and R. S. SMITH, *Experientia* 24, 588 (1968).

⁵ I. A. BOYD, *J. Physiol.* 144, IOP (1958).

⁶ I. A. BOYD, *Stain Technol.* 37, 225 (1962).

⁷ D. BARKER and M. C. IP, *J. Physiol.* 169, 73P (1963).

⁸ R. E. COUPLAND and R. L. HOLMES, *Q. Jl microsc. Sci.* 98, 327 (1957).

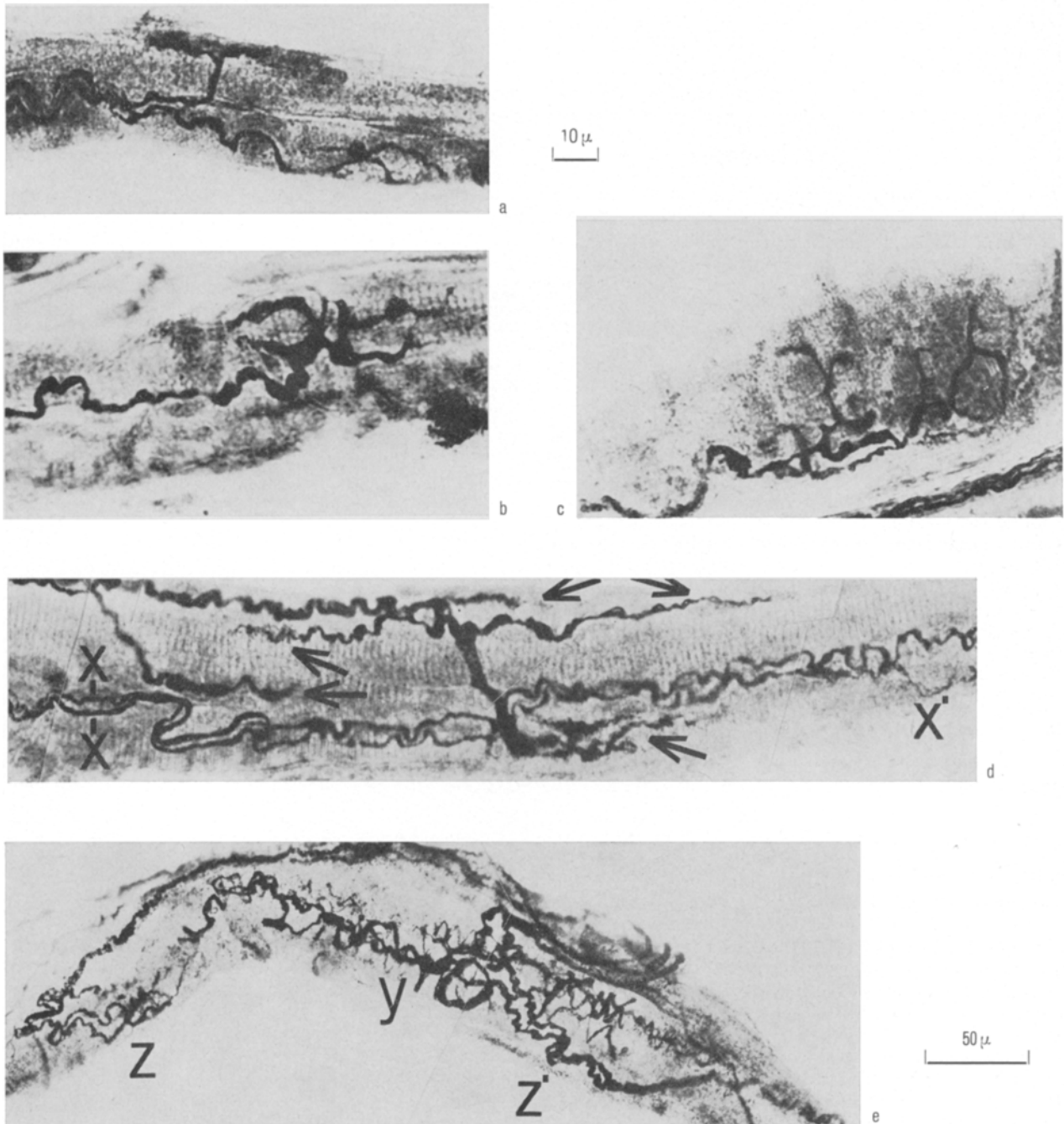
⁹ M. C. IP, *J. Physiol.* 192, 801 (1967).

diameters were measured. This was done in normal and de-efferented preparations. All denervations were carried out at least 35 days before removal of the muscle.

The muscle consists of many fusiform slips 1.0–1.5 cm in length arranged in parallel, with a fleshy origin from the vertebral transverse processes and inserted by long

tendons into more distal caudal transverse processes. It is innervated by branches from the lateral caudal nerve which runs along the superior surface of the muscle.

Results. Each nerve branch was found to innervate 0–9 spindles and 0–7 tendon organs, and often supplied several adjacent muscle slips. The most caudal branches



Photomicrographs of intrafusal muscles in rat, stained with silver. Magnification is the same for a, b, c and d, while e is at a lower power (a) 2 examples of 1st form of fusimotor ending described; (b) 2nd form of fusimotor ending; (c) skeletomotor ending for comparison; (d) rd form of fusimotor ending with terminals indicated by arrows. 2 axons (x-x) run across this ending; they terminate in the first form of ending and the termination of one is shown (x'); (e) de-efferented spindle showing one primary sensory ending (y) and 2 secondaries (z and z'), one of which (z') occupies the same area as the primary.

are the most useful experimentally (KIDD and KUČERA¹⁰) because these usually supply only 1–3 spindles. Tandem spindles do occur in these muscles. PORAYKO and SMITH⁴ found no tandem spindles in rat lumbricals. Axon diameters in supplying branches varied from 2–12 μ in normal and de-efferented preparations.

Sensory innervation. The central placing and form of the primary receptor ending do not differ from those in cat. Secondary receptor endings are found in a zone 100 μ long on either side of the primary. As in cat those secondaries next to the primary may take the form of rings and spirals, but most simply branch to end in fine filaments. Branches from some secondary endings appear to end in the region occupied by the primary. Only 10% of spindles have a single primary, while 10% have one secondary, 60% two secondaries and 20% three secondaries.

Motor innervation. Three forms of fusimotor ending are present in this muscle.

(1) A plate ending confined to the polar regions is structurally similar to extrafusal motor end plates, though less than half their size. There is a nucleated sole plate and a discrete subneural apparatus is revealed by cholinesterase staining. The axons supplying these plates have a diameter less than half that of axons supplying extrafusal muscles, but occasionally axons of similar diameter may supply extrafusal end plates. Axon diameter at the level of the spindle may bear no relation to that in the nerve trunk.

(2) Another form of plate ending occurs in the juxtaequatorial region, and is twice the size of the polar plates, has no nucleated sole plate and is supplied by an axon twice the diameter of axons supplying polar plates. The ending takes the form of several short tapering branches and knobs.

(3) Typically this is a multiterminal ending, occurring in the juxtaequatorial region. However, the ending is pleomorphic and may range from a single filament to many ramifying branches of different diameter. The whole juxtaequatorial region stains diffusely for cholinesterase activity, like those first found by CÖERS^{11,12} in rat rectus abdominis spindles. Some more intensely stained areas

are associated with the terminals of the 2nd and 3rd endings described above.

Discussion. These motor endings presumably correspond to the p_1 , p_2 and trail endings described in cat by BARKER¹³. The conformation of endings in rat spindles is however less elaborate than those in cat. PORAYKO and SMITH⁴ found only 2 forms of fusimotor endings in rat lumbricals. STEG¹⁴ working on other caudal muscles more distal than the intertransverse found spindles innervated by single γ -efferents.

BARKER^{13,15} states that p_1 plates are supplied by mixed (β) axons. Mixed innervation of the first plate endings described above has not yet convincingly been demonstrated in this muscle. This does not preclude the possibility as the techniques used will not demonstrate axon branching in the nerve trunk. These plate endings are however often supplied separately from the rest of the spindle by nerve branches which otherwise supply solely skeletomotor end plates.

Zusammenfassung. In den Muskelspindeln der Quermuskulatur im Rattenschwanz kam eine einzige primäre sensorische Endung in 10% der Spindeln vor, die übrigen hatten 1–3 sekundäre Endungen, 2 platte Endungen und 1 Endung unbestimmter Art.

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¹⁰ G. L. KIDD and J. KUČERA, *Experientia*, in press (1969).

¹¹ C. CÖERS, in *Symposium on Muscle Receptors* (Hong Kong University Press, Hong Kong 1962).

¹² C. CÖERS and J. DURAND, *Archs. Biol., Liège* 67, 685 (1956).

¹³ D. BARKER, in *Myotactic, Kinesthetic and Vestibular Mechanisms* (J. and A. Churchill Ltd., London 1967), p. 3.

¹⁴ G. STEG, *Acta physiol. scand.* 61, Suppl. 225 (1964).

¹⁵ M. N. ADAL and D. BARKER, *J. Physiol.* 177, 288 (1965).

¹⁶ Medical Research Council Junior fellow.

On the Possible Existence of Muscarinic Cholinoreceptors on the Postsynaptic Membrane of the Frog Muscle

It is known that cholinoreceptors of the postsynaptic membrane of skeletal muscle of vertebrates have all the pharmacological characteristics of nicotinic receptors. However, these muscles are markedly affected by some muscarinomimetics, and the effect of ACh may be blocked by muscarinolytics, for example by atropine (AS)¹. The question arises whether there are differences in the specificity of cholinoreceptors of the skeletal muscle or whether all cholinergic substances act on identical cholinoreceptors of the postsynaptic membrane.

The ability of AS to shift the point of reversal (E_r) of the endplate potential towards the Na equilibrium potential^{2,3} and to change its shape¹ could be explained if it were possible to establish that receptors with muscarinic properties were present among the receptors of the postsynaptic membrane. It could be supposed that one

type of receptor is connected with Na and the other with the K permeability of the postsynaptic membrane. AS blockage of the 'K cholinoreceptors' would then change the relationship $\Delta gNa/\Delta gK$ and cause a shift in E_r . It could be assumed that the shape of the normal endplate potential results from the effect of ACh on both types of receptor. In the presence of AS, only the effect on the nicotinic receptors would remain and the shape of the endplate potential would be altered.

In order to confirm this assumption, the dose-response curves for butyrylcholine (BCh), a nicotinomimetic drug,

¹ R. BERÁNEK and F. VYSKOČIL, *J. Physiol.* 195, 493 (1968).

² T. V. POTAPOVA, *Biofizika* (Russ.), in press (1968).

³ L. G. MAGAZANIK, F. VYSKOČIL, *Experientia*, in press.