

behavioural evidence indicating that information from the feet and the eyes is important in releasing and coordinating the paddling behaviour^{1-3,5}, I surmise that the neostriatal area in question links the forementioned circuit, specifically the neighbouring nucleus basalis, with both a cutaneous³⁵ and a visual sensory projection³⁶ that exist within the overlying hyperstriatum. That the hyperstriatum projects to, among other structures, the neostriatum has actually been shown anatomically³⁷.

Zusammenfassung. Zwei artspezifische Verhaltensabläufe, die Silbermöwen (*Larus argentatus*) bei der Futteraufnahme und Futteraufnahme zeigen, wurden durch elektrische Reizung begrenzter Bezirke des rostralen Vorderhirns experimentell hervorgerufen. Diese Befunde stützen

vergleichend-anatomische Schlussfolgerungen über die funktionelle Rolle des rostralen Vorderhirns bei Vögeln.

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³⁸ The work was supported by grants from the United States Air Force, the Science Research Council and the Royal Society to Professor N. TINBERGEN and myself. It was partially carried out at the Department of Zoology, Oxford. The assistance of Dr. G. THOMPSON and Mr. A. JACKSON is gratefully acknowledged.

Modification of Ionic Membrane Currents of Ranvier Nodes by UV-Radiation Under Voltage Clamp Conditions

There are several reports concerning the effects of UV-radiation on the threshold of excitation and the properties of the action potential of peripheral nerve¹⁻³ or axons^{4,5}. But, to our knowledge, UV-radiation effects on axonal or nodal membranes have not yet been studied under voltage clamp conditions. LIEBERMAN⁶ measured changes of the characteristics of membrane excitability due to UV-irradiation in single motor axons of the crab. He suggested a specific action of UV-radiation of 285 nm on the sodium system on a basis which according to himself⁶ needs confirmation by direct measurement of the sodium and potassium currents before, during and after irradiation. Our approach meets this prerogative and permits a determination of the quantitative relation between dose or dose rate and the radiation effect.

Our measurements were done on single Ranvier nodes of motor nerve fibres from *Rana esculenta* with the voltage clamp technique developed by NONNER⁷, using the dissection technique described by one of us⁸. Irradiation was performed by a high-pressure stabilized mercury arc

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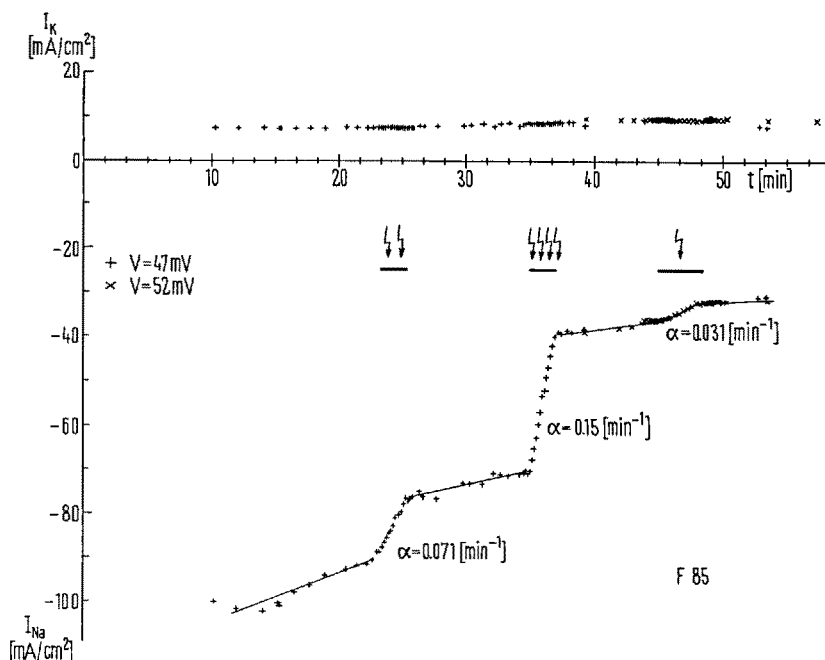


Fig. 1. Change of the maximum sodium inward current and of the potassium current at depolarizing voltage clamp steps of 47 mV and 52 mV respectively with time. Periods of irradiation are indicated by arrow symbols. Temperature was 16.4°C. Fibre 85. For further details see text.

(Quarzlampengesellschaft Hanau: St 75) combined with a Leitz-monochromator and surface-aluminized mirror optics. All measurements reported here were made at a wavelength of 280 nm with a dose rate ranging from about 80 to 1200 erg/mm² sec. The size of the irradiation field was 0.1 mm by 0.5 mm.

Figure 1 shows an example of the change with time of the maximum sodium inward current and of the potassium current at depolarizing steps of 47 mV and 52 mV respectively. Periods of irradiation are indicated by horizontal bars, the number of the arrow symbols is proportional to the dose rate (1 symbol standing for a dose rate of about 80 erg/mm² sec). The maximum sodium current decreases rapidly during irradiation at a wavelength of 280 nm, whereas the potassium current is practically not affected. The decrease of sodium current can be described by a function of the type

$$I = I_0 \cdot \exp(-\alpha t) - \beta t \quad (1)$$

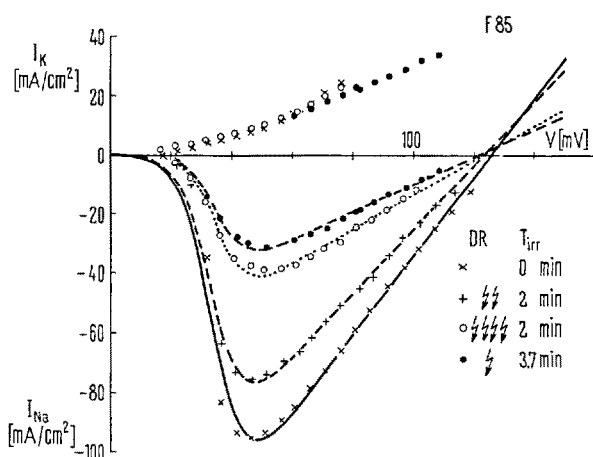


Fig. 2. Current-voltage relation for the sodium and the potassium currents before and after irradiation. Dose rate (DR) and duration of irradiation (T_{irr}) as in Figure 1. Fibre 85.

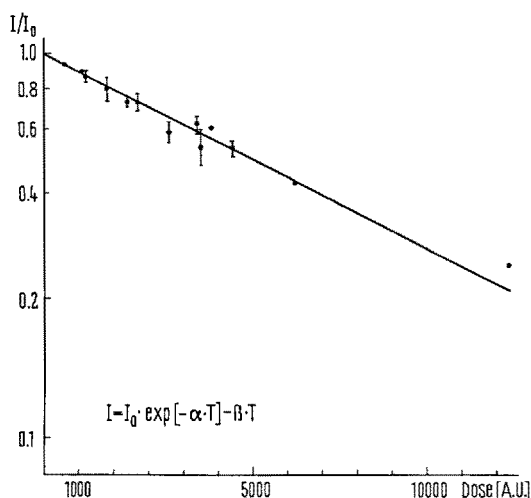


Fig. 3. Dose effect curve: Decrease of the maximum sodium inward current by UV-irradiation. Analysis of 48 irradiations of 16 different Ranvier nodes. Dose given in arbitrary units ranging from about 1400 to 22000 erg/mm².

where α represents the rate of decrease of the maximum sodium inward current I starting from an initial value of I_0 , and β takes into account the normal decrease of the activity of the fibre during an experiment, which for a first approximation is assumed to be linear. As can be seen from Figure 1, the rate constant α is directly proportional to the dose rate.

Figure 2 shows the relation of the sodium and potassium currents to membrane potential. Again, the rapid decrease of sodium current due to irradiation can be seen, but there is no significant change in potassium currents. Several experiments showed a decrease of potassium currents of about 20% (including normal run down), especially at high depolarizing voltages, when the sodium inward current was lowered simultaneously to more than $1/5$ of its initial value. If there is an effect of UV-radiation, it must be small, and we were not yet able to differentiate it from the normal run down of the fibre. No marked changes of leak conductance can be observed. The equilibrium potential for sodium remains constant, the resting potential is not lowered by more than 10% (including the run down of the fibre). The UV-effect is clearly limited to the periods of irradiation as can be seen by comparison of sodium currents before and after irradiation in Figure 1.

In accordance with the results just described, current clamp experiments reveal a high sensitivity of the rate of rise of the action potential. An 'initial enhancement of activity' by irradiation as described by others, e.g.⁴, was never observed under these conditions.

The blocking of sodium pathways is an irreversible effect. Figure 3 shows the dose effect curve: $(I + \beta t)/I_0$ is plotted in a semilogarithmic scale against the irradiation dose. The figure summarizes the results of 48 irradiations of 16 different Ranvier nodes. The straight line obtained indicates that the probability of blocking a sodium pathway by UV-radiation is proportional to the number of remaining functional pathways at any instant. In terms of the hit-theory the blocking of a sodium pathway is a one-hit-event. Our present results thus confirm the sensitivity of the sodium pathways of the nodal membrane to UV-radiation in the region of $\lambda = 280$ nm. The potassium pathways are not, or very little, affected. Measurements with other wavelengths are under way.

Zusammenfassung. Die Wirkung ultravioletter Strahlung von 280 nm Wellenlänge auf die Ionenströme der Membran des Ranvierschen Schnürringes wurde im «voltage clamp»-Verfahren gemessen. Die «Kanäle» für Natrium werden im Sinne eines Ein-Treffer-Ereignisses blockiert. Die daraus resultierende Herabsetzung des maximalen Natrium-Einstromes ist eine Exponentialfunktion der Bestrahlungsdosis. Der Kaliumstrom wird bei dieser Wellenlänge nur wenig beeinflusst.

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⁹ Supported by Deutsche Forschungsgemeinschaft, Sonderforschungsbereich 38 'Membranforschung'.