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ANTAGONIZING EFFECT OF ULTRAVIOLET AND VISIBLE LIGHT ON THE ERG FROM THE OCELLUS OF *SPIROCODON SALTATRIX* (COELENTERATA: HYDROZOA)

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Many anthomedusan jellyfish swim when ambient illumination is interrupted (Passano, Mackie & De Ceccatty, 1967; Ohtsu & Yoshida, 1973; Anderson & Mackie, 1977). This shadow response has been attributed to the ocelli, which are located at the margin of the bell. However, in some anthomedusae, it has been demonstrated that the motor neurones that innervate the swimming musculature are, themselves, directly photosensitive (Anderson & Mackie, 1977; Ohtsu, 1983). One species which possesses both classes of photoreceptor is *Spirocodon* (Ohtsu, 1983). In this animal, near ultraviolet light (u.v.) hyperpolarizes the swimming neurones and inhibits swimming. This effect is tonic, lasting long after the cessation of u.v. irradiation. However, this after-inhibition can be disinhibited by irradiation with visible light (u.v.-vis antagonism). To investigate the role of these two photoreceptor types in the behaviour of *Spirocodon*, the electroretinogram (ERG) of the ocelli was measured. The results described here are basically similar to those obtained from *Sarsia* ocelli (Weber, 1982), the only coelenterate photoreceptors investigated to date, but there are some differences.

In *Spirocodon*, the margin of the bell, where the ocelli are found, is slowly mobile, and could not be completely immobilized by mechanical restraint during recording. To overcome this, floating glass microelectrodes with tip diameters of 1–2 μm (Ohtsu, 1980) were used. Even with this method, however, gradual displacement of the electrode tip due to faint movement within the ocellus prohibited longterm recordings of the type necessary for the production of spectral sensitivity curves. The typical preparation consisted of a portion of the margin containing the ocelli, some of the tentacles, exumbrellar epithelium and mesogloea. The ocelli from freshly collected specimens could not be penetrated with either rigid or floating microelectrodes. However, when the animals were kept for a few days in captivity, without feeding, the tissues softened sufficiently to allow successful penetration. In spite of this starved condition, the animals showed basically normal light responses and electrical activities (Ohtsu & Yoshida, 1973; Ohtsu, 1980). A silver plate positioned under the ocellus was used as the indifferent electrode. Light was supplied by a grating type Xenon arc monochromator (350–600 nm). Recorded signals were amplified and displayed by conventional methods.

Key words: ERG, anthomedusa, ultraviolet light.

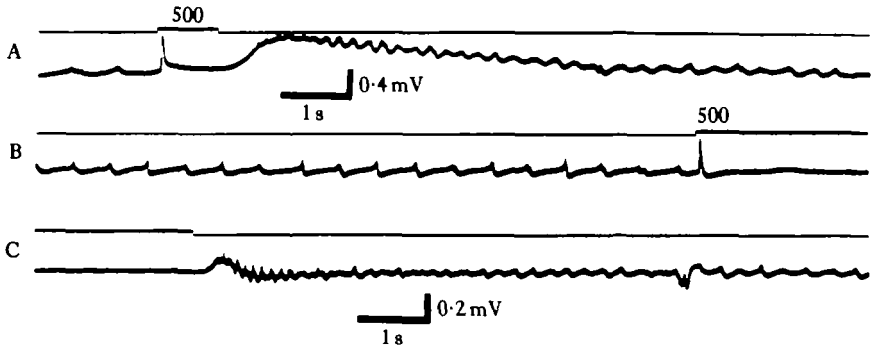

Fig. 1. The effect of intense monochromatic visible light (wavelength 500 nm) on the ERG from an ocellus of *Spirocodon*. (A) A d.c. coupled recording. Note the long lasting positive-going phase and the associated spikes and oscillations following light-off. (B, C) A continuous a.c. coupled recording. Here, small spikes and oscillations were prominent in the dark prior to illumination. The ERGs shown here are unusually large. Upper traces – light monitor; lower traces – ERG. Light energy, 18·2 mW cm^{-2}, but since the light was delivered obliquely at an angle of 60°–70°, the effective energy will have been reduced by the screening pigment of the eye cup.

The ocellus of *Spirocodon* is cup-shaped, and microvilli from the photoreceptors and surrounding pigment cells occupy the centre of this cup (Toh, Yoshida & Tateda, 1979). When the microelectrode tip appears to be in the centre of the cup, spontaneous oscillations are usually recorded in the dark (Fig. 1). Small, spike-like events are often observed at the peak of these oscillations. Irradiation with 500 nm light (vis-stimulation) produced a transient, positive-going deflection which was followed by a small hump (not clear in Fig. 1). This in turn gave way to a prolonged oscillation-free phase. Light-off produced a very obvious, positive-going potential on which were superimposed very pronounced oscillations and spike-like events. These gradually subsided and the potential decreased to the normal dark level. At the onset of u.v. irradiation, the same series of events occurred (Fig. 2A) but, in contrast, at light-off, the positive-going potential and the oscillation did not occur. Instead, the potential remained constant (Fig. 2B, C). If visible light were then applied (Fig. 2C), the usual light-on effect was almost absent. When the visible light was terminated, however, the oscillations dramatically recovered (vis-disinhibition) (Fig. 2D). With a second exposure to visible light, the usual transient depolarization was recorded (Fig. 2E). In this record, this latter transient response was somewhat smaller than normal (Fig. 2F), and even with prolonged dark recovery, became only slightly larger. However, this can probably be attributed to displacement of the electrode tip due to gradual movement of the tissue rather than a change in overall sensitivity.

After-inhibition occurred with wavelengths of up to 400 nm but the effect was weaker than at shorter wavelengths. Similarly, dis-inhibition occurred with wavelengths from 450 to 600 nm but the effect became weaker at long wavelengths.

As indicated earlier, movement of the preparation prevented accurate quantitative measurement of these responses. However, in experiments using equal quanta of low-intensity light, the amplitudes of the transient ERG response were largest with stimuli in the blue-green range, smaller around 400 nm and, with shorter wavelengths yet, became larger, suggesting that there is a second near-u.v. sensitivity. In this respect these responses are different from those measured from *Sarsia* (Weber, 1982). T

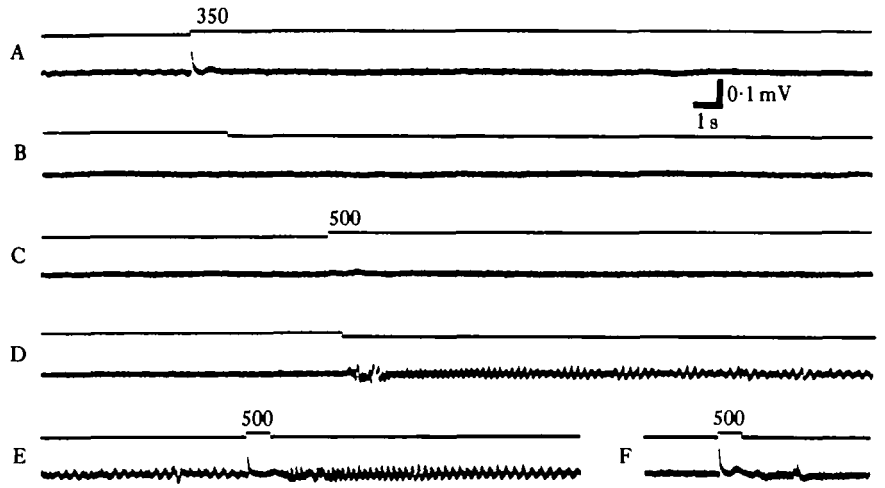

Fig. 2. u.v.-Inhibition, u.v.-after-inhibition and vis-dis-inhibition of the oscillations. (A) to (E) are continuous recordings. (F) is presented as a control response to 500 nm light and was recorded prior to (A). This preparation produced fewer oscillations than usual, and the spikes are masked by noise. Note that almost no ERG was induced by 500 nm light during the u.v.-after-inhibition (C) and it recovers only after vis-adaptation (E). Light energy: 14·6 mW cm^{-2} at 350 nm and 18·2 mW cm^{-2} at 500 nm.

transient responses that accompany changes in illumination (Figs 1, 2) probably originated in the photoreceptor cells of the ocelli, as suggested for *Sarsia* (Weber, 1982). However, it is possible that the oscillation and spikes may be the result of synaptic interactions between ocellar photoreceptors and other neurones, by way of feedback synapses such as those described ultrastructurally by Toh *et al.* (1979).

In *Spirocodon*, as in other hydromedusae, swimming is controlled by the inner nerve ring (Ohtsu & Yoshida, 1973) which is separated from the ocellar region by a large intervening space, the radial streaks (Ohtsu & Yoshida, 1973). In view of the distances involved, it is reasonable to assume that activity from the ocelli was transmitted to the swimming neurones through spikes rather than slow potentials and that the spikes that are superimposed on the slow potentials here may instead be action potentials in the photoreceptor neurones or post-synaptic cells.

The phenomena of u.v.-inhibition, u.v.-after-inhibition and vis-dis-inhibition, as observed in these records, are very similar to those found in the giant motor neurones of the nerve ring (Ohtsu, 1983) that control swimming. However, in ocellar-free preparations of these neurones, vis-excitation alone, without prior u.v.-irradiation, produced neither inhibition nor off-excitation. This implies that the light-off response in this animal originates directly in the ocelli as has been reported for *Polyorchis* (Anderson & Mackie, 1977). These signals must come by way of the light-off induced spikes and oscillations, since the spikes and oscillations are inhibited during vis-irradiation. During this period of inhibition, the giant motor neurones will receive no excitation inputs from the ocelli. The animal continues to swim, however, because of the inherent spontaneity of these neurones (Anderson, 1979). During u.v.-irradiation the neurones are directly inhibited (Ohtsu, 1983), as are the oscillations and spikes in ERG.

The function of the u.v.-vis antagonism is not known. However, when the animals swim up to the surface of the sea, they are exposed to strong u.v. light which immediately inhibits their ocellar activities. This type of inhibition, together with that of the giant motor neurones, might cause the animals to sink down and thus secure them from deleterious u.v. light (see Ohtsu, 1983).

It is not clear, from the records described here, whether the intracellular responses of the photoreceptors are depolarizing or hyperpolarizing. The phenomenon of u.v.-after-inhibition is best interpreted as being the result of a prolonged hyperpolarization or depolarization similar to that reported for a variety of invertebrate photoreceptors, where the thermally stable, interconvertible pigments rhodopsin and metarhodopsin are present (Nolte & Brown, 1972; Minke, Hochstein & Hillman, 1973; Minke, Wu & Pak, 1975; Cornwall & Gorman, 1982). The similar events in *Spirocodon* may reflect the presence of two similar thermally stable photopigments in this species.

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