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Motor responses obtained by stimulation of the peduncle lobe of *Sepia officinalis* in chronic experiments

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The perfecting of a technique using a stimulating electrode chronically implanted in the central nervous system of the cuttlefish allows us to establish the precise function of the different lobes of the nervous system, which is very complex for an invertebrate. We have already described the motor and behavioural responses obtained by stimulating the optic lobe[2]. We have carried on this study by observing the motor responses induced by stimulation by chronic implantation of a stimulating electrode in the peduncle lobe, a small structure close to the optic lobe.

The experiments were performed either with 50–100 g animals bred in the laboratory of Luc-sur-Mer or with 200–1500 g individuals caught in summer by local fishermen.

The peduncle lobe is a very small oblong structure lying horizontally and dorsally on the optic tracts. In an adult cuttlefish this lobe is about 2 mm long and 1 mm wide. The histological structure of this lobe has been studied especially by Messenger[4], Hobbs and Young[3], Messenger and Woodhams[6], Young[8] and by Woodhams[7]. The photographs (Figs. 1 and 2) illustrate the situation of this lobe.

It receives a great number of afferents. Among the sensory ones, most come from the eye and the statocyst. The efferents of this lobe go principally to the ipsilateral optic lobe, to the contralateral peduncle lobe and to the basal lobes.

The operating procedure has already been presented in a previous study[2]. The stimulating electrode is a bipolar coaxial electrode with a very limited field of stimulation. The exact site of implantation of the electrode end can only be determined a posteriori; after the experiment a slight electrocoagulation is performed (1 mA for 20 sec) and the site can easily be detected on sections made with a cryostat.

After the operation, the animal is placed in a tank containing fresh circulating seawater. It generally recovers after 5 min.

Stimulating the basal zone and the dorsally situated 'spine' of the peduncle lobe produces similar responses. No differences seem to appear between the responses when the electrode has a cortical or a neuropilar position. Stimulation at threshold strength produces several simultaneous motor responses: increased frequency of fin beat, dar-

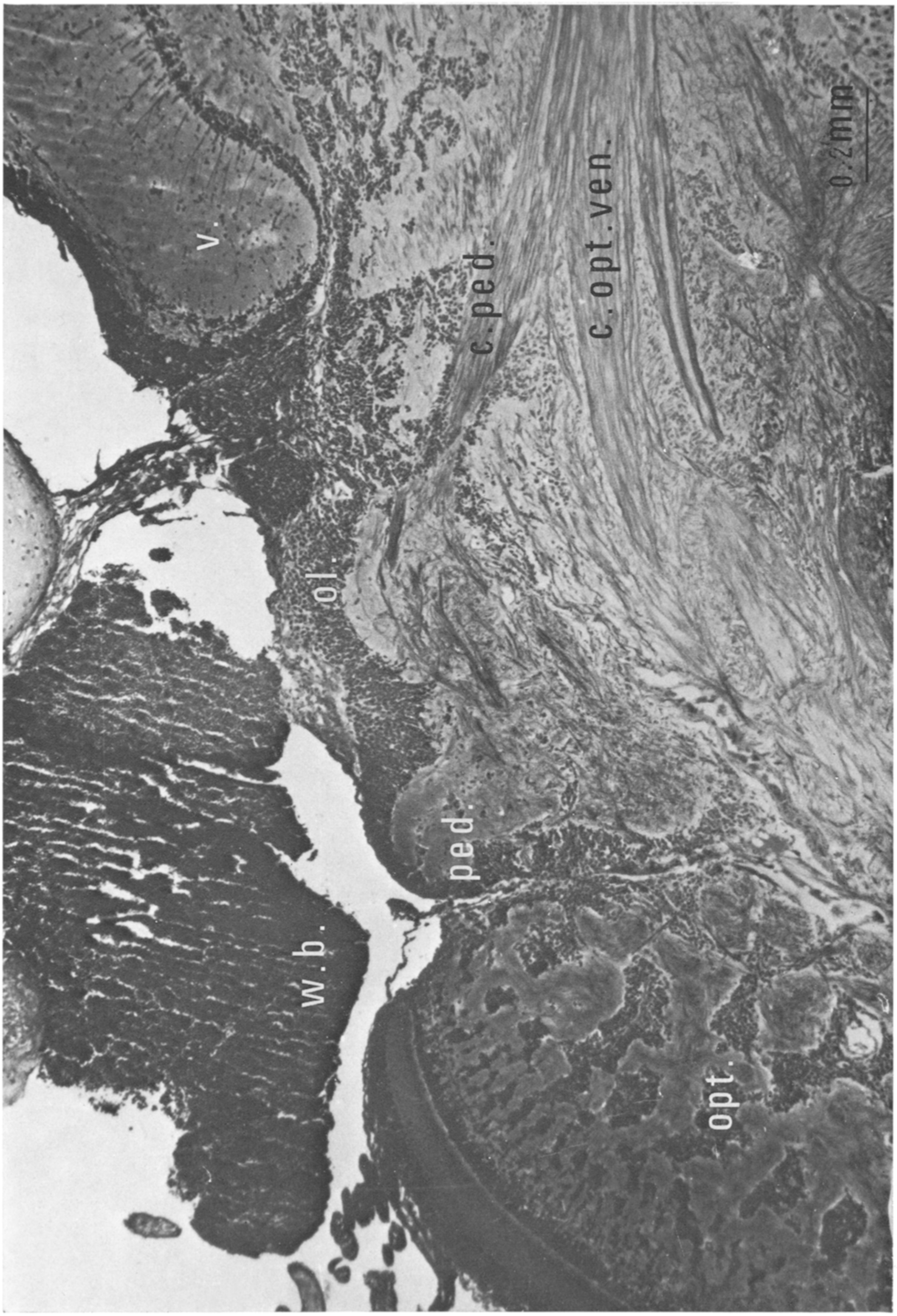

Fig. 1. Transverse section through the brain at the level of the ventral optic and peduncle commissures (Cajal silver stain). Abbreviations: c.opt.ven., ventral optic commissure; c.ped., peduncle lobe commissure; ol., olfactory lobe; opt., optic lobe; ped., peduncle lobe; v., vertical lobe; w.b., white body.

Fig. 2. Transverse section of the peduncle lobe, detail (Cajal silver stain). Abbreviations: bz., basal zone of the peduncle lobe; ol., olfactory lobe; opt., optic lobe; sp., spine or dorsal zone of the peduncle lobe.

kening of the whole animal and dilatation of the ipsilateral pupil. With stimulation above threshold or with longer excitation and ipsilateral swinging movement of the animal can sometimes be seen.

More numerous undulatory movements are observed in the ipsilateral fin as well as in the contralateral fin. This motor response is always induced. It can be seen first in the anterior area of the fin and spreads on towards the back. Usually, the animal remains 'hovering' for a while, its funnel being in sagittal position. The duration of this phase may vary and it is often followed by slight movements (forwards, backwards, lateral etc.). This motor response of the fins is maintained throughout stimulation, the animal quickly resuming its resting state after stimulation has ceased. The optimum stimulation conditions are as follow: frequency of trains, 30–40 cycles/sec; duration of pulses, 2–3 msec. Only trains longer than 250 msec can induce clear responses. The complete refractory period ot this reaction is almost 5 sec.

The animal turns darker as the stimulation proceeds. Clearly, the muscle fibres of the brown chromatophores are excited. This reaction is obtained only by long-lasting trains (at least 1000 msec), and it disappears progressively after stimulation has ceased.

The pupil dilatation, although frequent, is not constant, however, and this motor response occurs only in the ipsilateral pupil. The extent pupil dilatation increases with the duration of the train (at least 1000 msec). The pupil gradually resumes its normal state after stimulation has ceased.

The threshold of excitation for these 3 types of responses is much lower (0.06–0.08 mA) and much more uniform than in the optic lobe[2]. As with the optic lobe, stimulation at low frequency (1 cycle/sec) or by short pulses (less than 1 msec) will produce no motor response.

The ipsilateral swinging movement was only seen occasionally (5 times out of 34 experiments) and then always at higher thresholds than in the previous responses with trains of at least 2000 msec. The animal stays still, but at the same time turns towards the ipsilateral side. The ipsilateral fin is stretched and nearly motionless; in the contralateral fin, however, very important movements appear, which seem to maintain this position. This reaction is coupled with an ipsilateral pupil dilatation and by a considerable colour darkening of the whole animal.

We can first compare these results to those obtained previously on the optic lobe[2]. The following table (Table I) illustrates the principal motor responses obtained by stimulation of these two lobes. It can be noticed that the two lobes have a common action on the ipsilateral pupil, on colour changes and on the movements of the fins. The responses obtained with the peduncle lobe do not seem to be as well organized as those produced by the stimulation of the optic lobe. However, the motor response induced on the fins may involve various changes of position which appear after a period of 'positioning', during which the animal lies motionless in spite of conspicuous fin movements. This implies a very precise coordination of these movements, and it must be remembered that the cuttlefish, like some fishes, is perfectly able to maintain itself 'hovering' with active movements of its fins.

These results must now be compared to those obtained by Boycott[1], who studied the motor responses produced by stimulation of the central nervous system of the cuttle-

TABLE I

Comparative table of the results: optic lobe and peduncle lobe

	Reactions of the whole animal	*Effectors*
Optic lobe	ipsilateral rotation movement	ipsilateral pupil chromatophores fins funnel
	alarm reaction	Pupils collar muscles mantle chromatophores fins
Peduncle lobe	positioning various movements	ipsilateral pupil chromatophores fins

fish by a monopolar electrode in acute experiments. Boycott[1] reports that stimulating peduncle lobe produces expansion of its chromatophores. Messenger[4] resumes the study on octopus with the same stimulation technique. His principal results are as follows: general darkening of the animal, various general motor responses (walking, swimming, ipsilateral turning movements etc.). These results agree with those obtained in the present study. Bilateral removal of the peduncle lobes performed by the same author[5] shows a disturbance of motor coordination (position, walking etc.), though this disappears after 4–6 days.

Our results must also be compared with recent anatomical studies[3,6–8]. These authors, considering the histological structure of the peduncle 'spine', which strongly recalls that of a cerebellar lamella, of sensory inputs (eye, statocyst) and the numerous connections of the peduncle lobes with the other motor centres, suggested that it could play a physiological part which can be compared to that of the cerebellum of vertebrates. Our results, and especially the fin motor response, which is absolutely constant, seem to support this hypothesis. In fact, the structure responsible for the motor programs involved in the activity of the fins might be situated in the palliovisceral complex (fin lobes[1]). Depending on sensory information, the peduncle lobe might thus control directly or indirectly (by basal lobes) the activity of the fin lobes. The peduncle lobe, because of its anatomical position, is included in combined circuits made up of the optic lobes, peduncle lobes and basal lobes. To further understand its physiological significance it will therefore be necessary to analyze in detail the motor responses caused by stimulation of the basal lobes, as it has been recently suggested[8].

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