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STUDIORUM PROGRESSUS

Oscillographic Analysis of Equilibrium Receptors in Crustacea[1]

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Statocysts occur in all major metazoan phyla. Their presence in the hydromedusae qualify them in a real sense as the first organ to appear in the animal kingdom. Yet the precise functions subserved by statocysts are still uncertain.

Anatomically there exist significant analogies between invertebrate statocysts and the otolith organs of vertebrates. The description of an ectodermal sac, fluid-filled and lined by hairs supporting a relatively dense mass, can be applied to both structures. The differences, however, are fundamental. In the crustacean a single distal process of a presumed primary sensory neuron penetrates an articulated chitinous exoskeletal hair; whereas the vertebrate neuromast or equivalent cell is believed to be itself receptive, the afferent neuron thus innervating a secondary or true sense cell[4].

Physiological investigation has thus far been confined primarily to ablation experiments and has demonstrated a role in posture and locomotion. Delage[5] was perhaps among the first to suggest an equilibratory function for statocysts but believed they also functioned in audition. Following the classic iron filing experiment of Kreidl[6], the role of the crustacean statocyst in geo-orientation became well established. Subsequent work by Clark[7], and Prentiss[8] further emphasized the dominance of this modality and indicated that previously reported responses to sound were most likely mediated through tactile receptors external to the statocyst.

Since the need for exact knowledge of the adequate stimuli, the possible differentiation of receptor types and the quantitative performance of equilibrium receptors of lower animals has been enunciated[9] in order to place in perspective the vertebrate organ analyzed especially by Lowenstein, we have undertaken an investigation of various favorable invertebrates by the method of recording nerve impulses. Progress on this first study may be summarized at this time.

The results reported here were obtained mainly on the spiny lobster *Panulirus interruptus* (Randall) with some experiments on a large spider crab, *Loxorhynchus grandis* Stimpson. In each animal a statocyst is located in the basal segment of the antennules. The organ represents an invagination of the dorsal antennular wall and consists of a chitinous sac approximately 3 by 2 by 1 mm in the lobster and about twice these dimensions in the crab. An aperture to the outside remains open in the lobster but is closed in the crab. The lining of the sac includes hairs of various forms and sizes, rather generally distributed in the lobster, fewer and restricted to a fraction of the lining in the crab. Liths of external origin (probably sand grains) occur mainly in loose masses in the lobster; some may be cemented to the hairs. In crabs the liths are few and presumably secreted[1] and in most positions apparently none of the hairs will have liths resting on them. The statocyst nerve can be followed from the organ to the brain and is easily separated throughout its course from the antennular nerve; in a lobster of 800 grams this distance is 17 mm. It consists of fewer than 200 fibers ranging from less than 5 to 110 micra in diameter.

The anterior region of the cephalothorax has been used as an isolated preparation, rigidly mounted in an electrode holder which enabled both electrodes and preparation to be moved as a whole. The nerve, or a small bundle teased from it, was lifted into the air and placed across silver wire electrodes.

Continuous discharge of impulses, typically from 50–500 microvolts in spike amplitude (i.e. smallest:largest spikes = 1:10) is observed in many fibers with the preparation oriented in any position. Individual fibers are generally aperiodic and fire less than ten times per second. Some units appear only upon stimulation and are therefore not spontaneous in a given position.

Angular or linear displacement results in an alteration of spontaneous background activity. In multifiber preparations a marked increase in activity usually occurs. However, in some individual units (fibers) and small bundles, an increase in "spontaneous" activity can be seen in response to movement in one direction, whereas movement about the same axis in the opposite direction results in decreased activity. Similar differences are sometimes observed in response to movement in different planes or axes. In general the response was greater the more rapid the acceleration; but response did not faithfully follow acceleration nor reverse with deceleration. The threshold was below 10°/sec/sec with the organ in the axis of rotation.

Individual units in the lobster, identified by spike form, have been observed to maintain for several minutes an altered (nonadapting) level of spontaneous activity in different positions of the preparation. About the longitudinal axis of the animal, these units may be silent for large fractions of 360 degrees then become active at intermediate non-adapting frequencies within a quadrant on each side of the position eliciting maximum response. The units attain a rather low maximum frequency (*ca.* 20 per second) at which level they are still arhythmic. This may be the mechanism responsible for the classical postural reflexes but we would emphasize that, in our experiences, the majority of units are sensitive only to movement. Certain of the static units also respond to angular motion.

Lightly tapping the table supporting the preparation elicits discrete bursts of activity in the lobster. Some units are highly sensitive to this type of vibration whereas others, active in the background discharge, are not stimulated by the same mechanical shock. Remark-

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ably enough the crab is almost insensitive to such stimuli, and therefore may prove of value in clarifying the conditions essential for vibration perception. Disturbances conducted through the air had no effect upon the spontaneous activity; hand claps, speech, and tuning forks of frequencies ranging from 128 to 320 cycles per second and placed within 5 mm of the aperture in *Panulirus* elicited no response. Similarly, no effect was observed in response to vibration conducted through water in which the statocyst was submerged; tapping a metal rod placed in the water 5 mm from the statocyst aperture, and tuning forks (128 to 320 cycles per second) placed against the wall of the glass container were equally ineffective. A paddle held close to the organ and driven by a phonograph recording head at 7 to 1000 cycles per second had no effect except in the narrow range of 70 to 120 cycles per second at very high intensity (such that vibrations could be felt by the finger in the water). The literature contains various behavioral indications of water-borne sound reception such as the response to tapping aquaria and even to the "stridulation" of the antennae in this species of lobster[1]. If this organ is involved at all in this type of response, it cannot be said on our evidence to be responsive to or adapted in any way for sound detection and even the response to vibration of the solid substratum or of the animal is not apparently more sensitive than that of hairs on the legs.

Maintained increase in temperature increases the frequency of small spikes in the spontaneous discharge by a small amount; Q_{10} between 16 and 23°C is approximately 1·7. Large spikes are much more affected by temperature (Q_{10} approximately 4·5), representing therefore a non-adapting temperature sensitivity higher than that of the non-adapting fraction of the response in the ampullae of LORENZINI in the ray[2], but lower than that of temperature receptors in the mammalian tongue[3]. There is not, however, an initial highly sensitive adapting fraction. These and the remaining experiments have been done thus far only on *Panulirus*.

A variety of discrete receptor types can be demonstrated within the statocyst. However, it is of fundamental interest that at least some of these are inconstant, changing for example from side-up responding, side-down not responding to the reverse during an experiment. This may possibly be due to shifting in position of liths. To the extent to which this is true the specificity of receptors is unavailable to the central nervous system and represents a curious point in the evolution of reception.

Units other than those spontaneously active also respond to adequate stimuli. Conversely, certain of the spontaneously active fibers fail to increase in frequency during movement or vibration stimuli effective for most units.

The details of the innervation of the statocyst in this species have so far not been described and a possibility existed that the responses observed may have originated partially in other regions of the antennule. Various controls were therefore performed. In preparations with an intact antennule, movement or touching the antennular flagellae had no effect when recording from the statocyst nerve alone. In order to determine whether proprioceptors in the basal antennular joint were primarily responsible for the observed response, the basal segment as well as the cephalothoracic portion of the preparation were rigidly clamped, thereby immobilizing the joint. Typical responses to movement and tapping were still obtained under these conditions. One or two small twigs are seen to join the statocyst nerve in the region of the joint and the possibility remains that fibers from proprioceptors in this area may be present in the main statocyst nerve.

When water at 7°C is injected into the organ through the slightly enlarged natural aperture the spontaneous activity ceases and within 15 to 30 seconds the response to previously effective stimuli is decreased or lost. Water injected at 23°C rapidly restores both spontaneous and response activity, and discrete bursts of impulses were elicited by each injection. Blotting out the water in the sac nearly eliminated response to movement and vibration, quite reversibly.

By slightly enlarging the natural aperture in the lobster, water could be injected into the organ thereby flushing out most of the sand particles. This greatly reduced sensitivity to adequate stimuli, though not the continual background discharge. Iron filings 200–300 micra in diameter can be introduced into the organ through theopening. A hand magnet moved up to 25 mm from the organ results in discrete bursts of nerve impulses resembling responses to adequate stimuli. Under a dissecting microscope some iron particles near the aperture could be seen to move as the magnet approached and it is assumed that iron particles were moving sensory hairs within the statocyst.

Crushing the nerve between the statocyst and the recording electrodes eliminated all spontaneous activity as well as the response to movement and vibration.

Thus far it appears that the invertebrate statocyst approaches, and in certain respects may exceed, the functional plasticity exhibited by the non-acoustic vertebrate labyrinth[1]. It is apparently not usefully sensitive to sound. Based on the morphological similarity to the arthropod organ, it is intriguing to speculate on the possibility that receptor types in the first animal sense organ, the coelenterate statocyst, may parallel to a large extent those of the vertebrate labyrinth.

Zusammenfassung

Die Statozystennerven zweier Krustazeenarten zeigen Spontanaktivität. Einzelne Elemente sind unperiodisch und reagieren auf Lageänderung mit Frequenzab- oder -zunahmen. In einzelnen Elementen kann man eine spezifische Erregbarkeit für Richtung, Fläche, statische Stellung nachweisen. In der Languste (aber fast gar nicht bei der Krabbe) gibt es manche Elemente, die auf Vibration des Körpers oder des Substratums, aber nicht auf wassergetragene Störungen von mässiger Stärke reagieren. Verschiedene Temperaturempfindlichkeiten, eine gewisse Labilität, Magnetismuserregbarkeit nach dem Einsatz von Eisenspänen (Kreidl) und mehrere Kontrollen sind beschrieben.

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