INTERACTION BETWEEN HAIR CELLS IN THE STATOCYST OF Helix lucorum

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An electrophysiological study of interactions between hair cells within the statocyst of Helix lucorum was undertaken by intracellular and extracellular recording. Analysis of the results led to the following conclusions. First, some hair cells, subtending on angle on the arc of the statocyst sphere of not more than 90°, were electrically connected; electrical synapses, moreover, possessed polar properties; the coefficient of coupling in one direction was about 10 times greater than the other. Second, some connections between hair cells which subtended an angle of not more than 90° were mixed electrochemical in character. The excitatory chemical component in this case was directed in a direction opposite to effective electrical conduction. Third, inhibitory connections were observed between statocyst receptors: monosynaptic chemical (subtending an angle of about 180°, evidently, between the hair cells) and polysynaptic weak inhibitory interactions (subtending an angle in this case of not less than 90-100° between the test neurons). Fourth, all types of connection between hair cells were observed in CNS preparations with the vestibular nerve divided close to the cerebral ganglion. This means that zones of synaptic contacts between these receptors are located not in the CNS, but close to the statocyst.

INTRODUCTION

Investigations [4, 7, 8] on statocyst hair cells of the nudibranchiate mollusk Hermisenda crassicornis have shown the existence of electrical, electrochemical (with electrical excitatory and chemical inhibitory components) and inhibitory chemical interactions between receptors of the same and different statocysts. Electrical interactions were of the usual monosynaptic nature, and every action potential in the presynaptic cell evoked a separate PSP in the postsynaptic cell [4, 7]. However, the character of the inhibitory chemical interactions makes it doubtful whether these connections between the statocyst receptors were monosynaptic. In response to a high-frequency burst of action potentials, evoked by a current passed through the recording electrode in one hair cell of the statocyst (adequate stimulation never evoked discharges of this frequency [5, 7] a long-latency (40 msec) response developed in the other hair cell in the form of weak hyperpolarization and cessation of the spike discharge [4, 7]. These inhibitory interactions, in which every action potential in the presynaptic neurons would be accompanied by the appearance of an IPSP in the postsynaptic neuron, have never been found either between hair cells within statocysts or between hair cells and other CNS neurons of the mollusk Hermisenda [3, 4, 7]. The explanation of this fact was that the zone of synaptic contacts in hair cells of the nudibranchiate mollusk, which is located in the CNS [7], is very far removed from the receptor bodies, and the separate inhibitory waves arising in this region decay on their path from synapse to neuron soma. Meanwhile, in other investigations by the same workers [5, 6], IPSPs whose appearance was not disturbed by the long distance between the zone of synaptic contacts and the receptor bodies, were described in the spontaneous activity of the hair cells of Hermisenda, contradicting data on the character of inhibitory interactions in the hair cells of this mollusk.

The present investigation, conducted on hair cells of statocysts of the snail Helix lucorum was undertaken in order to resolve this contradiction, by studying interaction between hair cells on statocysts isolated from CNS influences, which is not possible with the mollusk Hermisenda. The zone of synaptic contacts (inhibitory at least [1]) in statocyst receptors of H. lucorum does not lie in the CNS, as in the mollusk Hermisenda, but near the bodies of the hair cells. This means that interaction between mechanoreceptors can be studied on statocyst preparations isolated from the CNS (by division of the vestibular nerve), and this makes interpretation of the results easier.


0090-2977/85/1702-0161$09.50 © 1985 Plenum Publishing Corporation
Fig. 1. Interaction between two electrically coupled hair cells of the same statocyst in a preparation with divided vestibular nerve. Spontaneous activity of one hair cell (bottom line) is pacemaker for the other (top line) cell (a); hyperpolarization of one receptor evokes a shift of membrane potential in the other cell (b, c); coefficient of coupling 0.27 (for b) and 0.028 for c). Spike on top line in a is truncated.

The aim of this investigation was to study interactions between hair cells of the organs of balance of *H. lucorum* and to discover the functional importance of connections of each type for the reception of adequate information by the statocyst.

**METHOD**

Experiments were carried out on 35 preparations of the CNS of the snail *Helix lucorum*, whose membranes above the statocysts, lying between the pedal and pleural ganglia, were removed mechanically. The isolated circumesophageal ring was placed in a special bath with continuously flowing Ringer's solution for cold-blooded animals. The experiments were carried out at room temperature. In some cases the vestibular nerve, connecting the statocyst with the CNS, was divided close to the cerebral ganglion. The order of treating the preparation with papain (to facilitate passage of the electrodes through the thin connective-tissue membranes surrounding the statocyst after mechanical removal of the coarse membranes), characteristics of the microelectrodes, and instruments recording the currents passed through the recording electrodes, were the same as in the writer's previous investigation [1].

To study interactions between hair cells, simultaneous intracellular recording of activity of two to four receptors of the upper hemisphere of the statocyst by independent microelectrodes was used (receptors of the lower hemisphere were almost inaccessible for investigation by intracellular methods, because the lower half of the statocyst sinks into the pedal ganglion and is surrounded by its neurons). With high amplification of the signal recorded through any intracellular microelectrode, besides activity of the hair cell in which this electrode actually lay, it was found that extracellular spike activity could be recorded from several other hair cells nearby, and possibly from all the hair cells of the statocyst. The amplitude of spikes recorded extracellularly in this way depended on the distance from the recording electrode and did not exceed 1.5 mV. Incidentally, the pattern of extracellular spike activity obtained by means of amplification of the signal derived by the microelectrode located in one receptor coincided with that observed when the electrode was positioned for extracellular recording in the statolymph of the statocyst.

To produce reversible inhibition of activity of the chemical synapses CoCl₂ (10 mM) in Ringer's solution was used; it was applied to the CNS for 25-35 min, after which the preparation was washed for 1 h or more with physiological saline at the rate of 1 ml/min.