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Directional Sensitivity of the Japanese Scallop *Mizuhopecten yessoensis* and Swift Scallop *Chlamys swifti* to Water-Borne Vibrations

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Abstract—Behavioral experiments were conducted on two bivalve species—the Japanese scallop *Mizuhopecten yessoensis* and the Swift scallop *Chlamys swifti*—to elucidate the role of their abdominal sense organ (ASO) in directional sensitivity to water-borne vibrations. The thresholds were determined at 140 Hz. Both species displayed the highest sensitivity to vibrations, the source of which was placed above the animal (opposite to the left valve), rostro-dorsally to its vertical axis. Removal of the ASO led to loss of directional sensitivity and a considerable increase in the sound reaction threshold. Both species were sensitive to modulated ultrasonic vibrations in the range of 30–1000 Hz. This is proposed to be caused by modulated ultrasound effects, provoking weak oscillations of the shell valves at a modulation frequency.

Key words: behavior, mollusks, directional sensitivity, mechanoreception, abdominal sense organ.

Pectinids, one of the most active bivalve groups, are capable of avoiding predators using jet propulsion. Their active behavior is essentially the result of highly developed sensory systems. Their visual system includes numerous eyes situated at the mantle periphery. The tactile system features numerous large, middle-, and small-sized tentacles of the mantle edge. The chemical sense is provided by the osphradium, and the sense of balance is produced by statocysts, which are situated in the cerebral ganglion. In addition, pectinids have a peculiar organ of hearing, the abdominal sense organ (ASO), which is highly sensitive to water-borne vibrations [5, 24]. The presence of such a specialized organ draws a distinction between bivalves and the other mollusks.

The ASO was first described by German researchers at the end of the nineteenth century (Eisig, 1887, cited in [16, 20, 21]). Later on, it was studied by light [11, 22] and electron microscopy [3, 4, 6, 7, 13, 16]. The ASO is the biggest of the known mechanosensory organs. In some species, it is up to 5 mm long and 2 mm thick. Its sensory epithelium includes some 4 million receptor cells, some 90% of its overall cell number. These cells have a single long (>200 µm) cilium.

To date, the ASO has been found in members of 19 bivalve families of the subclasses Pteriomorpha and Palaeoheterodonta [12]. The ASO is a paired organ. However, in mollusks resting on the lateral side, such as Pectinidae and Ostreidae, only the right ASO is present.

Interestingly, bivalve mollusks lacking the ASO possess organs structurally similar to it. Thus, in Tellinidae, this is the cruciform sense organ; in Nuculidae, Stempell's organ. Some authors believe these organs also serve to perceive water-borne vibrations [10, 14, 18]. Thus, bivalves, as opposed to gastropods and cephalopods, evolved specialized mechanosensory organs, functionally analogous to the acoustico-lateral system of the vertebrates.

It is known that in higher vertebrates, acoustico-lateral receptors are involved in the acoustic system of con- and interspecific communication, also including effector systems of acoustic signal production. Bivalves seem to lack the effector system. Their mechanosensory systems are only capable of detecting mechanical water-borne vibrations. This study pursues the goal to elucidate the possibility of such detection in two pectinid species and the role of the ASO in this process.

MATERIALS AND METHODS

Adult Japanese (shell height of 12–15 cm) and Swift scallops (shell height of 6–10 cm) were collected in Peter the Great Bay from June to August. Immediately after collection, the mollusks were divided into three groups, each of 5 animals. The first group was left intact (control 1). In mollusks of the second group, a portion of the mantle fold below the ASO was removed (control 2). In animals of the third group, the ASO was removed. After the operation, the mollusks were kept in the sea in

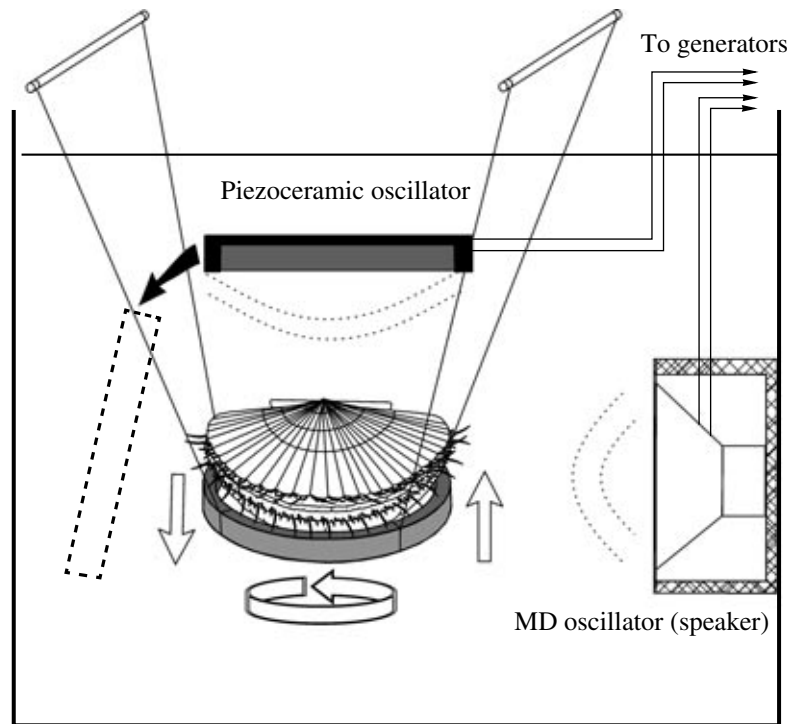


Fig. 1. Scheme of the experimental setup. See the Materials and Methods section for details.

a cage at a depth of about 2 m for 3–6 days. Immediately before the experiments, they were kept in aquaria with running aerated water at 14–17°C.

Experiments were conducted in running-water aquaria 60 × 40 × 40 cm in size without aeration at 14–17°C. Mollusks were placed with either the left or right valve down onto a platform, a rubber ring 13 cm in diameter (Fig. 1). The platform was fixed using thin threads at approximately half the water column. This allowed one to easily change the position of the scallop relative to oscillators by rotating the platform up to 360° around the vertical axis and tilting it up to 45°. The oscillators were placed 6 cm from the shell edge.

Oscillators of two types were used. The first one, of our original design, was based on a 0.5-Wt dynamic speaker, placed into a hermetic plastic box with a thin (1 mm) front wall. This stationary oscillator was attached to the walls or bottom of the aquarium opposite to the platform. The second oscillator was a piezoceramic in the shape of a disk 150 mm in diameter and 15 mm thick. It was attached to a hinged rod and could be moved around the platform.

The oscillators were fed from two pairs of sinusoid generators, GZ-112/1 and ZG-34. In experiments with the stationary oscillator, the modulation frequency was 140 Hz and the time of amplitude increase was 25 ms. The piezoceramic oscillator was tuned to generate amplitude-modulated ultrasonic vibrations with a carrier frequency of 40 kHz. In most of the experiments,

the modulation frequency was 150 Hz and the modulation depth was about 100%.

For the threshold sensitivity to be determined, a scallop was subject to a series of 5 2-s impulses at a 2-min interval. The impulse intensity provoking a minimal visible reaction of the animal to three impulses of each five was assumed to be the threshold intensity. In each experiment, 3–4 threshold intensity estimations were performed for each animal.

For valve oscillation parameters to be measured, an originally designed measurement scheme was used (Fig. 2). An instrument capacitor, one of whose plates was connected to the valve by means of a thin rod, was used as a sensor. A shift in the valve resulted in a change in the distance between the coatings and, therefore, in the condenser's capacity. This, in turn, led to a proportional change in the test oscillator's frequency. Mixing the signals of the test oscillator and the reference generator resulted in beatings at a frequency equal to the difference between the generators' frequencies. After low-pass filtering, the signal was sent to a frequency discriminator and rectifier. The output signal was proportional to the shift amplitude of the plate of the instrument capacitor.

Prior to each experiment, the intensity of the sound impulse was measured throughout the aquarium volume using a piezoceramic ball hydrophone 30 mm in diameter. This paper presents measurements only for the area occupied by the valve edges closest to an oscillator. The data on the sound signal intensity and valve

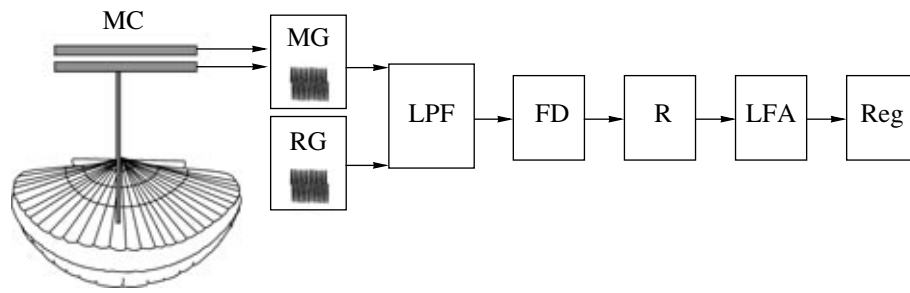


Fig. 2. Flowchart of the sound-elicited valve oscillation registration setup. MC—measuring condenser; MG and RG—measuring and reference generators, respectively; LPF—low-pass filter; FD—frequency discriminator; R—rectifier; LFA—low-frequency amplifier; Reg—register.

oscillation amplitude are presented in terms of the output signals of the hydrophone and capacity sensor.

The experiments were conducted at night. To prevent visual stimulus effects on the experimental results, the platform with an animal was only illuminated.

RESULTS

In both scallop species studied, the ASO is situated in the mantle cavity right to the anus, along the fold of the right mantle, to which it is attached by a thin (some 2 mm thick) band of tissue (Fig. 3). In the site of band attachment, at the top of the tonic adductor muscle, the fold is about 8 mm high and gradually decreases to disappear at approximately the center of the unattached zone between the adductor muscle and the mantle edge. Situated at the middle of the fold, the ASO is about 5 mm above the mantle surface. It is covered with long sensory cilia, appearing as an opalescent halo. Under a stereomicroscope, the sensory epithelium is observed to lie asymmetrically to the long axis of the organ. Most of the epithelium surface is oriented upward and rostro-caudally (Fig. 3). When the mantle fold surface is touched close to the ASO, the tissue band contracts. As a result, the ASO is pressed against the fold and turns about 30° around its long axis so that the sensory epithelium is almost completely directed rostro-caudally.

The ASO is innervated with two branches of the posterior mantle nerve. The nerve originates from the visceral ganglion. Both branches arrive at the ASO from the side of the adductor muscle. Thus, a removal of a portion of the tissue band and mantle fold right to the ASO (control operation) does not injure these nerves. Furthermore, in the site of operation, no large nerve trunks are situated. Therefore, a denervation of vast portions of the mantle edge is excluded.

Approximately 30 min after their placement on the platform, the scallops displayed a particular behavior, opening the valves at about 10°, extending large tentacles to their maximum length, and turning the mantle velum normally to the shell plane so that a small slit appeared between the velum edges, making the mantle interior observable.

Preliminary experiments showed that the scallop reaction to vibrations in the sound range depended on the sound frequency and intensity and was more pronounced when modulated stimuli were used. Weak stimuli elicited a light contraction of the mantle velum edge. As the stimulus intensity grew, both long and short tentacles began to contract, followed by a slow shell closure (rapid shell closure was observed occasionally). In this study, a positive reaction to a stimulus was assumed if a weak contraction of the mantle velum edge was observed.

Since the ASO is situated asymmetrically to the shell and internals, one could expect that the sensitivity will depend on the direction of sound propagation. Indeed, the reaction threshold depended on the shell orientation relative to the oscillator. In control groups, when the stimulus propagation area was limited by the shell plane, the sensitivity was maximum when an oscillator was placed opposite to the shell anterior (Fig. 4a). In this case, the reaction threshold was half as great as that under stimulation from the opposite side.

When stimulus propagation was limited to various directions within the vertical plane, the threshold was minimum when an oscillator was placed above the left (upper) valve (Fig. 4b). The maximum sensitivity was observed when an oscillator was placed 45° rostrally to the vertical plane.

Removing the ASO resulted in a considerable decrease in sound sensitivity (Fig. 5). Thus, under stimulation from the left valve side, in animals with the ASO removed the reaction threshold was 62 ± 10.5 times as high as in intact animals ($n = 18$). The control operation had no apparent effect on sound sensitivity ($n = 16$). Removing the ASO also resulted in the loss of directional sensitivity. In animals with the ASO removed, the reaction thresholds to stimuli propagating in different directions did not differ significantly (Fig. 6). However, the threshold decreased somewhat when under stimulation from the hinge side. These data imply that the ASO plays a considerable role in general and in the directional sensitivity of the Japanese scallop to water-borne vibrations.

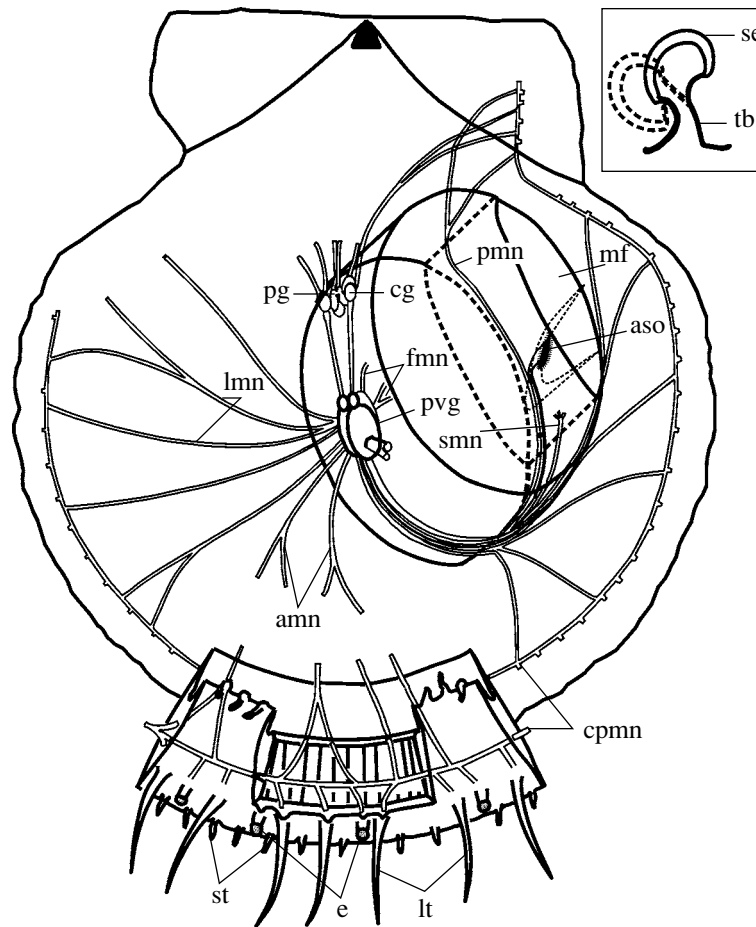


Fig. 3. Scheme of the CNS and mantle edge and ASO innervation in the Japanese scallop *Mizuhopecten yessoensis*. In the lower part of the figure, a detailed scheme of mantle edge innervation is given. The corner insertion presents a cross-section of the ASO and its possible shift under tissue band contraction. aso—abdominal sense organ; fmn and smn—fast and slow motor nerves, respectively; lt—large tentacles; e—eyes; pmn, lmn, and amn—posterior, lateral, and anterior mantle nerves, respectively; mf—mantle fold; st—small tentacles; pvg—parieto-visceral ganglion; pg—pedal ganglion; se—sensory epithelium; tb—tissue band; cg—cerebral ganglion; cpmn—circumpallial mantle nerve (after [23], modified).

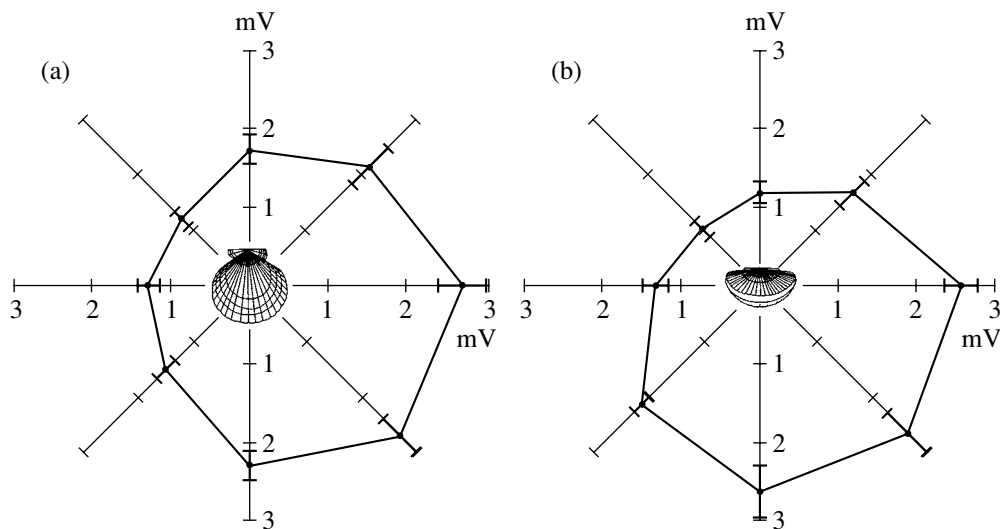


Fig. 4. Diagram of directional sensitivity of intact Japanese scallops to sound stimuli propagating in various directions within the (a) horizontal and (b) vertical planes. Axes represent sound thresholds as measured with a hydrophone in the place of the location of the animal. Numbers represent standard deviations. In all, five and four animals were used to obtain the data presented in (a) and (b), respectively.

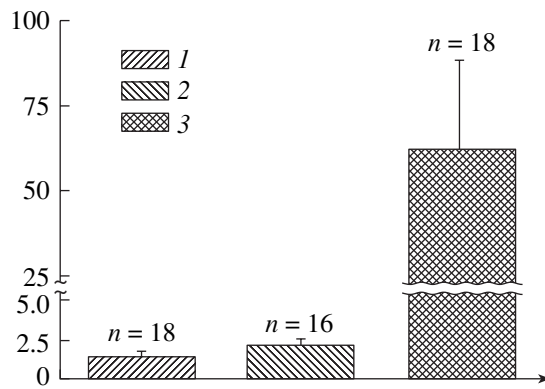


Fig. 5. Behavioral response thresholds of Japanese scallops to sound stimuli approaching the animal from the left (upper) side. 1—intact animals ($n = 5$); 2—mollusks subject to the control operation ($n = 4$); 3—mollusks with the ASO removed ($n = 6$). The ordinate represents sound thresholds as measured with a hydrophone in the location of the animal. Numbers present standard deviations.

Amplitude modulation of the stimuli resulted in a marked decrease in the reaction threshold both in intact animals and in ones with the ASO removed. Thus, in control animals, 30-Hz modulation of standard (140 Hz) signals decreased the threshold 2.4 ± 0.6 times ($n = 12$), and in animals with the ASO removed, it decreased the threshold 3.2 ± 1.1 times ($n = 12$).

In the Japanese scallop, the left and right valves differ in shape (the former is flat, and the latter, convex). This might be a reason for the difference in sensitivity to signals approaching the animal from the left and right sides. To check this suggestion, we studied directional sensitivity in the Swift scallop. In this species, the shell valves are almost the same in shape and the

location of the ASO relative to the internals is similar to that in the Japanese scallop. The diagrams of directional sensitivity in the two species proved generally similar (Fig. 7) suggesting that valve geometry probably has no effect on the directional sensitivity of the pectinids to sound stimuli.

The species studied proved also to be sensitive to ultrasonic stimulation, which provided an additional opportunity to elucidate the role of shells in the perception of water-borne vibrations. They displayed a distinct reaction to turning an ultrasonic signal on and off, but did not respond to a gradual change in the sound intensity. Amplitude-modulated stimuli at a modulation frequency of 30–1000 Hz and carrier frequency of 20–50 kHz also provoked a distinct reaction.

These results are somewhat unexpected, as in previous electrophysiological studies the maximum frequency that elicited a bioelectrical ASO response was 1500 Hz [5, 8]. The upper vibration perception threshold of mechanoreceptors of the mantle edge was even lower [6, 19]. From this, it is logical to propose that modulated ultrasonic signals are transformed into low-frequency oscillations by some of the molluskan structures, most probably, by the shell.

To check this proposal, we examined modulated ultrasound-elicited oscillations of valves. Such an examination is virtually not possible using well-conditioned animals, as touching the valve with a sensor ending results in a rapid shell closure and loss of contact between the valve and the sensor. For these reasons, in these experiments, we used animals kept for a long time under poor conditions (nonrunning water, insufficient aeration, water temperatures above 20°C), which resulted in an increase in the reaction threshold 2–3 times above the norm. Indeed, during ultrasonic

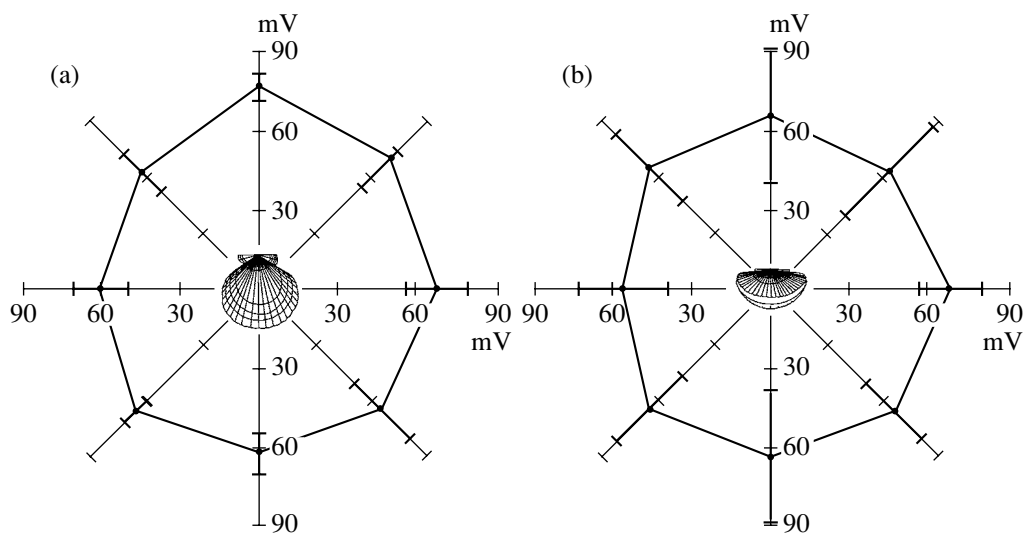


Fig. 6. Diagram of directional sensitivity of Japanese scallops with the ASO removed to sound stimuli propagating in various directions within the (a) horizontal and (b) vertical planes. All designations are as in Fig. 4. In all, four animals were used to obtain the data presented.

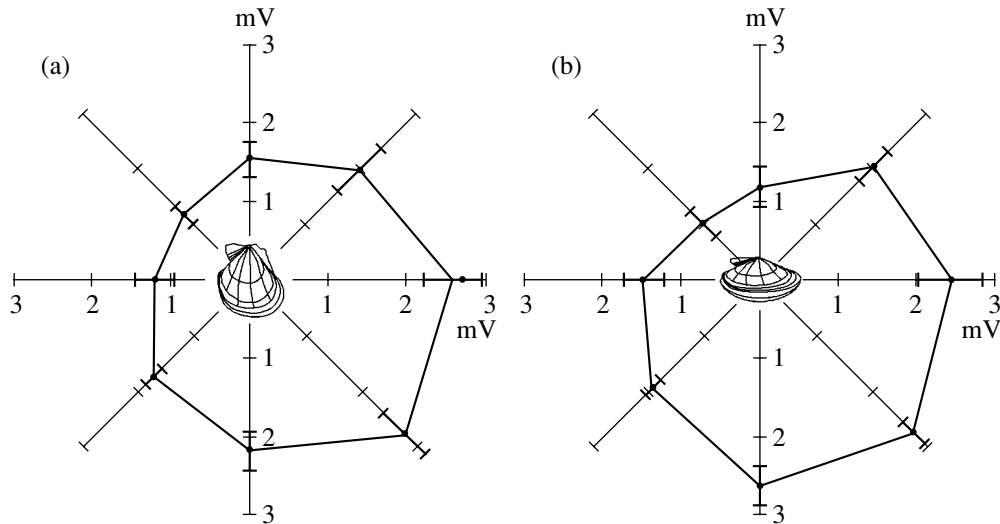


Fig. 7. Diagram of directional sensitivity of intact Swift scallops to sound stimuli propagating in various directions within the (a) horizontal and (b) vertical planes. Axes represent sound thresholds as measured with a hydrophone in the location of the animal. Numbers represent standard deviations. In all, three animals were used to obtain the data presented.

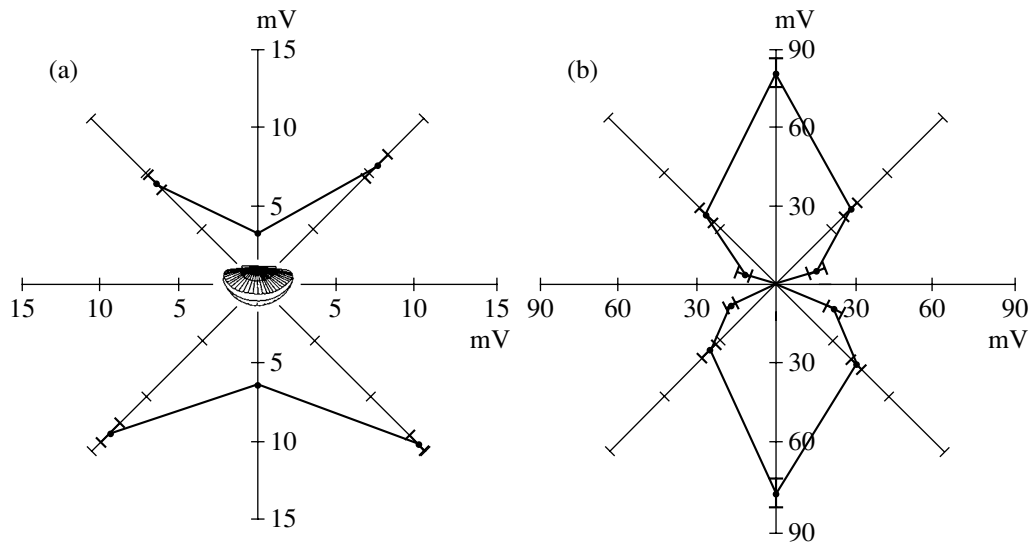


Fig. 8. Diagram of directional sensitivity of intact Japanese scallops (a) to modulated ultrasonic stimulation and (b) to valve oscillation at stimulus propagation in various directions within the vertical plane. Axes represent sound thresholds as measured with a hydrophone (a) in the location of the animal and (b) valve oscillation amplitude as measured by the capacitance sensor.

stimulation, the valves oscillated at a low frequency, equal to that of the modulation. The amplitude of the modulated ultrasound-elicited valve oscillations was maximum when the oscillator and valve planes were parallelized decreasing to zero as the angle between two planes approached 90° (Fig. 8a).

The directional sensitivity of the Japanese scallop to modulated ultrasonic stimulation differed considerably from that to low-frequency stimulation (Fig. 8b). A behavioral response was only detected at a lateral stimulation (with an oscillator placed opposite to one of the valves). As in experiments with 140-Hz stimulation, the

sensitivity was higher when an oscillator was placed opposite to the left valve. Stimuli propagating in the rostro-caudal and dorso-ventral directions elicited no detectable response.

DISCUSSION

Sound wave propagation in a water medium is accompanied by pressure change and particle movement. Water vertebrates, as opposed to invertebrates, can perceive wave-induced pressure changes owing to the closed air-filled cavities present in their bodies. A

pressure change makes these cavities vibrate. As their compressibility is far higher than that of the water and surrounding tissues, their vibration results in a particle shift with an amplitude greater than that of the original sound wave [15]. This shift is detected by specialized hair mechanoreceptor cells.

Lacking air-filled cavities, invertebrates evolved alternative sound detection mechanisms. A sound wave propagating through the animal body encounters structures of a different density and persistence (e.g., cilia and statocyst statoconia). This results in a relative shift of these structures, detectable by mechanoreceptor cells [9]. That is, ciliary mechanoreceptors of water mollusks can only perceive one of the sound wave constituents—particle movement.

The present experiments showed that ASO removal leads to an almost two-order increase in the sound reaction threshold. This suggests that the ASO plays an important role in water-borne vibration perception. The vibration sensitivity remaining after ASO removal is apparently caused by cells with short cilia, abundant on the mantle and tentacle surfaces [6, 17]. These cells are less sensitive to mechanical stimulation than ASO sensory cells [2]. The high sensitivity of the latter is probably caused by the unique morphology of their unusually long cilia, which have thin and highly flexible tips [3, 4].

The heightened sensitivity to modulated sound stimulation found both in intact animals and in those with the ASO removed is probably because the ASO sensory cells, as well as the mantle edge mechanoreceptors, respond phasotonically to mechanical stimulation [6, 19, 24]. In such receptors, amplitude-modulated stimulation can elicit an impulse response of greater frequency and duration than nonmodulated stimulation.

The directional sensitivity presently revealed is obviously supplied by the ASO, as its removal resulted in the loss of this type of sensitivity. Directional sensitivity may depend on many factors including ASO location, sensory epithelium orientation, and shell presence. The ASO with the supportive mantle fold lies in the plane normal to the maximum sensitivity direction (Fig. 3). The major part of the ASO sensory epithelium is pointed in this direction. This may be not just by chance. It may be the ASO location and sensory epithelium orientation that determine the animal's directional sound sensitivity. According to my observations, in the burrowing bivalves *Glycymeris yessoensis* and *Scapharca broughtoni*, the ASO sensory epithelium is pointed upward, i.e., toward the direction of the approach of a potential predator.

All along this, it should be pointed out that the above peculiarities may serve other biological tasks. The observed location of the ASO makes the most of the sensory epithelium isolated from, and thus essentially unaffected by, the outgoing water flow. As the tissue band contracts, the sensory epithelium is virtually completely protected from, and thus even less affected by, the water flow (Fig. 3). This is especially important dur-

ing the movement of the animal, when the speed of water expelled from the mantle cavity increases many times.

It is more difficult to explain a heightened sensitivity to stimuli approaching the animal from the side of left valve, i.e., from above the animals' natural position. According to recent electrophysiological experiments [1], the ASO is most sensitive to stimuli propagating from its base. Some part of sound wave energy may be imparted to a valve and make it oscillate. From this, one could expect that in behavioral experiments, the sensitivity is higher when an oscillator is placed against the right valve, as it is closer to the ASO, allowing for vibration propagation directly to the ASO base.

The molluskan capability to perceive ultrasonic vibrations is itself of interest as a new phenomenon, requiring separate investigation. As was found in the electrophysiological experiments [5], the upper limit of sound frequency perceivable by ASO mechanosensory cells and mantle edge mechanoreceptors is about 1500 Hz. Thus, these structures are not capable of direct ultrasound perception. This is also supported by the absence of a behavioral response to ultrasonic stimuli propagating in various directions within the shell plane. The measurements of the valve oscillations elicited by modulated ultrasonic signals, viewed in conjunction with the data of behavioral responses, suggest that modulated ultrasonic stimuli are perceived by the receptor structure just because they elicit low-frequency valve oscillations. The presence of valves can therefore considerably widen the sound frequency range scallops can perceive in water medium.

The fact that a maximum sensitivity was detected when an oscillator was placed above, or rostro-dorsally to, the animal has a meaningful biological interpretation. The rostral, ventro-rostral, and ventro-caudal sides of the scallop are rich in sensory elements including numerous eyes and the small and large tentacles of the mantle edge. As opposed to them, the dorsal (hinge) side lacks these sensors, and the adjacent areas are relatively poor in sensory elements. Given this, the presence of additional sensory input from this side is beneficial to the animal capable of sound detection, as it warns it about a predator approaching from above.

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