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Preliminary evaluation of underwater sound detection by the cephalopod statocyst using a forced oscillation model

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Abstract: To understand the mechanism of the peripheral auditory system of the cephalopod statocyst, the frequency dependence of particle motion sensitivity in cephalopods was estimated using a physical model of the sensory system, which was assumed to be forced oscillation. Reported perception thresholds of *Sepia officinalis*, *Octopus vulgaris*, and *O. ocellatus* fit the model well at low frequencies, whereas at frequencies above 150 Hz, the empirically measured threshold increased more steeply than the predicted increment. These results indicate that the frequency response of the perception threshold of cephalopods to particle motion can be primarily understood using the forced oscillation model, while unknown factor(s) play a role in the higher frequency range. Cephalopods are thought to be sensitive to low-frequency particle motion rather than high-frequency motion. The evolutionary function of cephalopod acoustical perception is not clear; however, the data suggest that they recognize the low-frequency particle motion that may be generated by prey, predators, and conspecifics.

Keywords: Cephalopod, Hearing, Particle motion, Physical model, Statocyst

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1. INTRODUCTION

Although the myth that cephalopods are deaf was disproved at the end of the 20th century [1–3], the biological significance of cephalopod "hearing" is still unclear. Sound waves consist of particle motion and sound pressure. Since aquatic animals require a gas-filled chamber to convert sound pressure into displacement [4–6], fish with a swim bladder can detect sound pressure, while cephalopods would not have this detection ability [3]. Aquatic animals also detect particle motion using epidermal hair cells (e.g., the lateral lines of fish and the epidermal hair cells of cephalopods) and an inertial motion detector (e.g., the inner ear of fish and the statocyst of cephalopods) [7]. The working distance of the epidermal hair cells for detecting particle motion is restricted to about one body length, whereas an inertial motion detector would allow an animal to receive acoustic information from a distant source [7].

Since the detection of propagating stimuli emitted from a distant source is essential for active animals, such as cephalopods, the function of the inertial motion detector is thought to be very important for perceiving particle motion.

Recently, an empirical study using a behavioral approach showed that the cephalopod statocyst could detect particle motion [8]. This finding was then confirmed by an electrophysiological approach [9]. The cephalopod statocyst is an inertial motion detector in which a calcareous statolith is attached to the sensory hair cells (macular hair cells). When an animal moves, inertia causes the dense statolith to remain in position, bending the sensory hair cells. Consequently, the cephalopod statocyst should detect particle motion [8].

The perception thresholds of five cephalopod statocysts for particle motion have been reported [3,8,9]. The perception thresholds of these five species were low at low frequencies and high at high frequencies. This raises the question of whether cephalopods are sensitive only to low-frequency particle motion. For the purpose of under-

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standing the mechanism of their peripheral auditory system, we estimated the frequency dependence of particle motion sensitivity in the cephalopod statocyst by applying a simple physical model to the auditory system.

In this study, we first validated the physical model by comparing it with reported perception thresholds. We then discuss the postulated properties of particle motion perception in the cephalopod statocyst.

2. MODELING

The fish otolith organ has been modeled as a simple harmonic oscillator, and the movements of the otolith have been modeled as forced oscillation [10–14]. The fish inner ear and cephalopod statocyst share common basic structures: they are mass-loaded inertial motion detectors that contain a dense otolith or statolith attached to sensory hair cells [15,16]. On the basis of these similarities, the movement of the statolith could also be modeled as forced oscillation [8].

According to the forced oscillation model, the displacement of the mass-loaded sensory hair cells is governed by the following differential equation [10–13]:

$$m_e \frac{d^2x}{dt^2} + b\frac{dx}{dt} + kx = -m_d a \cos \omega t \qquad (1)$$

where x is the displacement of the macula hair cells from their equilibrium position, m_e is the effective mass of the statolith and the entrained endolymph, b is the viscous drag force per unit velocity incurred by the moving mass, k is the restoring force per unit displacement due to the stiffness of the macula hair cells, m_d is the driven mass of the statolith less the endolymph it displaces, $a \cos \omega t$ is the acceleration imparted to the animal as a result of external motion, and $-m_d a \cos \omega t$ is the inertial force driving the statolith.

Equation (1) is usually written in the form

$$\frac{d^2x}{dt^2} + \gamma\frac{dx}{dt} + \omega_o^2 x = -na \cos \omega t, \qquad (2)$$

where $\gamma = b/m_e$, $\omega_o^2 = k/m_e$, and $n = m_d/m_e$. The eigenfrequency of oscillation in the absence of damping ($\gamma = 0$) is ω_o.

Equation (2) was solved in terms of $a \cos \omega t$, the acceleration imparted to the animal:

$$a\cos(\omega t - \delta) = -x \frac{[(\omega_o/\omega - \omega/\omega_o)^2 + (\gamma/\omega_o)^2]^{\frac{1}{2}} \cdot \omega_o^2}{(\omega_o/\omega) \cdot n}, \qquad (3)$$

where δ is the phase angle by which the displacement lags behind the inertial force, and ω is the angular frequency of particle motion imparted to the animal.

According to Eq. (3), the minimum acceleration necessary to stimulate the sensory system (i.e., the acceleration

threshold for particle motion) can be estimated by assigning the minimum displacement of the macular hair cells to be stimulated (i.e., the displacement threshold of macular hair cells) to x, the proper values to the other constants (ω_o, γ, and n), and the frequency of the stimulus to ω. In estimating the acceleration threshold, we assigned 1 to $\cos(\omega t - \delta)$ to consider the maximum acceleration and multiplied the right side by -1 to make it an absolute value.

Because there are no available data on the physical properties of the cephalopod statocyst, we assumed a statolith density of $3\,\text{g/cm}^3$ and that the damping was critical ($\gamma = 2\omega_o$), on the basis of measurements of the physical properties of the flatfish inner ear [10]. We also assumed an endolymph density of $1\,\text{g/cm}^3$. Consequently, n in Eq. (3) is calculated using Eq. (4) and equals 0.33.

$$n = \frac{m_s(1 - 1/\rho_s)}{m_s(1 + \rho_e)} \qquad (4)$$

Here, m_s is the mass of the statolith, ρ_s is the density of the statolith, and ρ_e is the density of the endolymph.

On the basis of the above assumptions, we substituted $\gamma = 2\omega_o$ and $n = 0.33$ into Eq. (3) to estimate the acceleration threshold of the statocyst:

$$a_{\min} = x_{\min} \frac{[(\omega_o/\omega - \omega/\omega_o)^2 + (2\omega_o/\omega_o)^2]^{\frac{1}{2}} \cdot \omega_o^2}{(\omega_o/\omega) \cdot 0.33}, \qquad (5)$$

where $a_{\min}$ is the acceleration threshold for particle motion and $x_{\min}$ is the displacement threshold of macular hair cells.

We used Eq. (5) as the model formula. In this study, the response variable was $a_{\min}$, the acceleration threshold for particle motion, and the empirically controlled variable was ω, the frequency of particle motion. Two unknown constants, the displacement threshold of macula hair cells ($x_{\min}$) and the eigenfrequency (ω_o), affect the characteristics of the frequency response of the acceleration threshold for particle motion ($a_{\min}$). $x_{\min}$ governs the absolute value of $a_{\min}$ because $a_{\min}$ is proportional to $x_{\min}$. This is natural to interpret since the threshold of the inertial motion detector will be in proportion to the physiological displacement threshold of its sensory hair cells. The other parameter ω_o affects the frequency responses of $a_{\min}$. The macula hair cell cannot follow the particle motion when the projected frequency is higher than ω_o. The smaller driven mass or larger stiffness of the hair cells increase ω_o because ω_o is equal to $(k/m_e)^{1/2}$ (Eq. (2)).

According to this model, displacement of the hair cells (x in Eq. (1)) will be in proportion to acceleration imparted to the animal ($a \cos \omega t$ in Eq. (1)) at low frequencies, to velocity at intermediate frequencies around ω_o, and to displacement at high frequencies [13]. Consequently, $a_{\min}$ will be stable at low frequencies, double every octave at intermediate frequencies around ω_o, and quadruple every

octave at high frequencies [13,17]. This means that the statocyst system would only be sensitive to low-frequency particle motion when the forced oscillation model is the appropriate proxy of the perception threshold of cephalopods.

3. METHODS

3.1. Datasets

To validate the forced oscillation model, we used the reported perception thresholds for particle motion for *Sepia officinalis*, *Octopus vulgaris* [3], and *Octopus ocellatus* [8], which is currently classified in the genus *Amphioctopus* [18]. We could not use the data of Hu *et al.* [9] for this examination for two reasons: first, the data were reported as means and errors only, not as individual thresholds, and second, the perception thresholds were presented as sound pressure, not as particle motion, an adequate stimulus for cephalopods [3].

3.2. Model Fit

We compared the reported empirical perception thresholds and calculated theoretical threshold (Eq. (5)) according to the frequency. First, we estimated the unknown constants, and then we calculated the theoretical thresholds using the least-squares method for each species. If the empirical and theoretical thresholds are identical, the least square is zero and the function of the regression line of the empirical and theoretical thresholds will be $y = x$. Therefore, we used the function $y = \alpha x$ for the linear regression, and the fit between the empirical and theoretical thresholds was determined by the coefficient α, which was predicted to be about 1. The consistency of the model was also examined using an estimated constant. One of the unknown constants, the displacement threshold of a macula hair cell (x_{min}), was measured experimentally to be about 0.9 μm for *Octopus bimaculoides* [19]. The estimated displacement threshold of macula hair cells was compared with the measured value (0.9 μm). The other unknown constant, the eigenfrequency (ω_o), was not used to examine the model fit because it has never been reported for any species.

4. RESULTS

4.1. Sepia Officinalis

For the linear regression between the empirical and theoretical thresholds, coefficient α was 1.0 and the coefficient of determination (R^2) was 0.84 (Fig. 1). The empirical and theoretical thresholds were almost equal for *S. officinalis*. The displacement threshold of macula hair cells (x_{min}) was estimated to be 1.1 μm, which is very close to the empirical value of 0.9 μm [19]. The estimated eigenfrequency (ω_o) was 6 Hz. The forced oscillation model explained the perception threshold of the *S. officinalis* statocyst well.

4.2. Octopus Vulgaris

For the linear regression between the empirical and theoretical thresholds, coefficient α was 1.0 and the coefficient of determination (R^2) was 0.89 (Fig. 1); the empirical and theoretical thresholds were also almost equal. The estimated displacement threshold of macula hair cells (x_{min}) was 0.4 μm, which is somewhat close to the empirical value of 0.9 μm [19]. The estimated eigenfrequency (ω_o) was 5 Hz. The forced oscillation model also explained the perception threshold of the *O. vulgaris* statocyst well.

4.3. Octopus Ocellatus

For the linear regression between the empirical and theoretical thresholds, coefficient α was 12.6, which was far from 1 (Fig. 1). This means that the theoretical thresholds were very different from the empirical ones. Moreover, the estimated displacement threshold of macula hair cells (x_{min}) was 0.3×10^{-3} μm, which is much smaller than the measured value of 0.9 μm [19]. The estimated eigenfrequency (ω_o) was 3×10^{-5} Hz. The forced oscillation model cannot explain the perception threshold of the *O. ocellatus* statocyst.

5. DISCUSSION

5.1. Model Fit

The forced oscillation model explained the acceleration thresholds for particle motion well in *S. officinalis* and *O. vulgaris*. Therefore, we assume that the forced oscillation model can basically explain the acceleration threshold of cephalopod statocyst.

However, the acceleration threshold of *O. ocellatus* could not be explained by this model. One of the possible reasons is the difference in the experimental designs. *S. officinalis* and *O. vulgaris* were stimulated by an acoustical tube that vibrated the water mass via two walls vibrating in the same phase [3]. On the other hand, *O. ocellatus* was stimulated by airborne sound [8]. As another possibility, the threshold cutoff around 150 Hz may be the reason why the perception threshold of *O. ocellatus* could not be explained by the forced oscillation model. According to the forced oscillation model, the perception threshold for particle acceleration will be stable at low frequencies, double every octave at intermediate frequencies, and quadruple every octave at high frequencies [13,17]. The perception threshold of *O. ocellatus* is almost stable at frequencies below 150 Hz, which is consistent with the forced oscillation model. However, the perception threshold increases much more steeply at high frequencies than does the predicted increment, indicating that unknown factor(s) may increase the perception threshold above 150 Hz. In the previous study, the mechanics of the otolith organ of goldfish was analyzed using a model that includes the action of the sensory hair cells attached through a
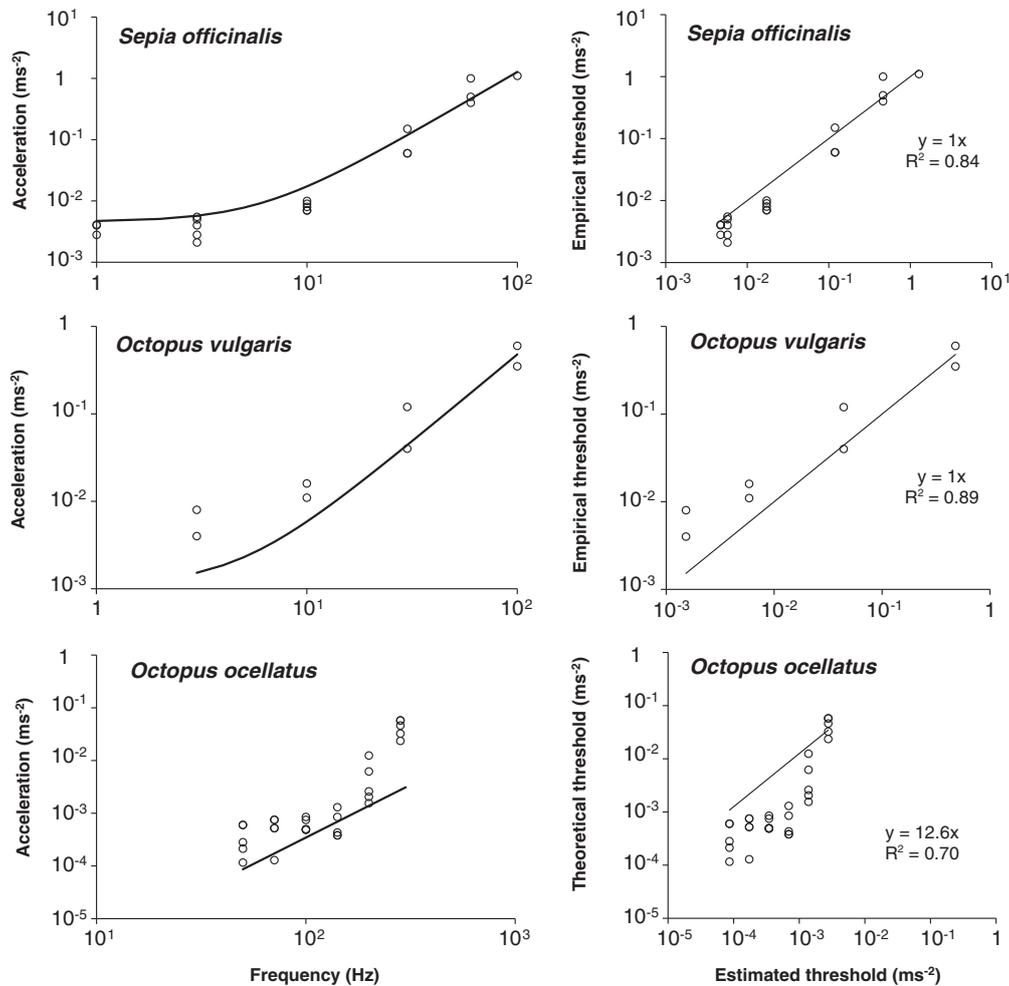
Fig. 1 Comparison of empirical thresholds and theoretical thresholds estimated using the forced oscillation model. The figures on the left indicate the empirical thresholds (open circles) and the best-fit line. Those on the right indicate the results of linear regression analysis.

membrane to the inertial mass [20]. Additional modeling of these hair cells could help us to understand the perception threshold of *O. ocellatus* above 150 Hz. On the other hand, the perception threshold are determined by several processes (e.g., stimulus, peripheral perception system, and central nervous system), but this model can explain the properties of only the peripheral perception system. It is also possible that the unknown factor(s) might be related with a perception process other than the peripheral perception system. Although unknown factor(s) possibly raise the threshold at high frequency, we concluded that the forced oscillation model would primarily explain the perception threshold of the cephalopod statocyst.

5.2. Comparison with Fish Inner Ear

The system for detecting particle motion in the cephalopod statocyst might be similar to that in the fish inner ear because these receptors share a common structure. Flatfish lack a swim bladder, which acts as a pressure-displacement converter. Like cephalopods, they are only able to detect particle motion and are not affected by sound

pressure [21]. It was reported that the forced oscillation could explain the lowest threshold of the flatfish inner ear for particle motion, but it was difficult to explain the perception thresholds at relatively high frequencies [21]. The perception thresholds of flatfish increased steeply at about 200 Hz, just like that of *O. ocellatus* [8], whereas the acceleration thresholds for particle motion were essentially stable below 200 Hz (Fig. 2). The similar trends in the perception thresholds of *O. ocellatus* and flatfish, which increase steeply at 150–200 Hz, suggest that the mechanisms of these threshold cutoffs could be common to cephalopods and fish. Future research should focus on the mechanism that elevates their perception thresholds at high frequencies.

Although frequency responses of *O. ocellatus* and flatfish are similar, the minimum threshold is much greater in *O. ocellatus*. According to the forced oscillation model, the minimum acceleration threshold (a_{min}) is in proportion to the displacement threshold of macular hair cells (x_{min}) (Eq. (5)). The reported displacement threshold of sensory hair cells in cephalopods is of 10^{-7} m order [19], while that in fish is of 10^{-9} m order [22]. It is in agreement that the
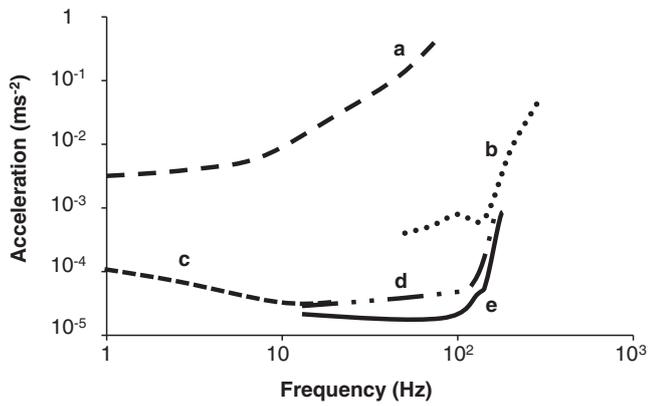
Fig. 2 Acceleration thresholds of cephalopods and flat-fish. a, *Sepia officinalis* [3]; b, *Octopus ocellatus* [8]; c, plaice [21]; d, plaice [5]; e, dab [5].

Fig. 3 Acceleration thresholds of *Sepia officinalis* predicted using the forced oscillation model. Open circles indicate empirical thresholds. a, the predicted threshold based on the estimated constants; b, the predicted threshold when the eigenfrequency is 100 Hz; c, the predicted threshold when the displacement threshold of macula hair cells is 1/100 of the estimated value.

perception threshold of *O. ocellatus* is dozens of times greater than those of flatfish.
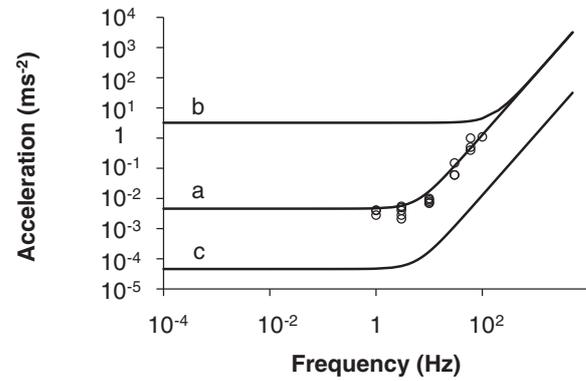
5.3. Threshold Prediction

By using the forced oscillation model, we predicted the perception threshold of *S. officinalis* at frequencies lower and higher than those previously examined [3] (Fig. 3(a)). The statocyst of *S. officinalis* should be sensitive only to low-frequency particle motion.

The variation in the eigenfrequency (ω_o) and displacement threshold of macular hair cells (x_{min}) was considered. The alternated ω_o was arbitrarily determined as 100 Hz, and the alternated x_{min} was determined as 1/100 of the estimated value because the reported displacement threshold of sensory hair cells is of 10^{-7} m and 10^{-9} m order in cephalopod [19] and fish [22], respectively. The eigenfrequency affects the lowest perception threshold, but it does not change the threshold at levels higher than the eigenfrequency (Fig. 3(b)). This indicates that eigenfrequency variation would not contribute to the threshold decrease at high frequency. The acceleration threshold (a_{min}) is proportional to the displacement threshold of macular hair cells (Eq. (5)). A decrease in the displacement threshold of macular hair cells would decrease the acceleration threshold at all frequencies but would not change the frequency dependence. The predicted acceleration threshold at 1,000 Hz is about 2×10^4 times the lowest threshold at low frequencies in *S. officinalis* (Fig. 3) and about 4.4×10^4 times in *O. vulgaris*. The perception threshold of the statocyst of these species would be low at low frequencies and elevated at high frequencies. Therefore, we postulate that underwater sound detection by the cephalopod statocyst would be limited to low frequencies.

5.4. Biological Significance

The biological significance of underwater acoustical perception by the cephalopod statocyst is not clear.

Nevertheless, underwater acoustical cues may be important in prey–predator interactions. *Octopus ocellatus* responds to sound stimuli with respiratory suppression and retraction of the basal parts of the eyes, responses that seem to be related to defense against predation [23]. It was reported that *Sepioteuthis sepioidea* in the wild showed greater fright behavior 3 to 4 s before predatory fish in the family Carangidae were observed approaching the squid school and suggested that the squid uses a sense other than vision to detect these predatory fish [1]. The use of underwater acoustical cues produced by prey species also might be possible. The capture of *Todarodes pacificus* was reported to be enhanced in the presence of a 600 Hz pure tone combined with the sound produced by a fishing boat [24].

Toothed whales, one of the major predators of cephalopods [25], emit sonar signals with dominant frequencies above several kHz [26], but we showed that underwater sound perception by the cephalopod statocyst could be limited to low frequencies. Consequently, cephalopods may not be able to detect the biosonar emitted by toothed whales. Experimentally, intense ultrasonic clicks mimicking the sound from an echolocating toothed whale did not elicit any detectable antipredator behavior in *Loligo pealeii* [27]. On the other hand, many fishes produce low-frequency sound [28] and swimming animals cause low-frequency water disturbances. Cephalopods might be able to detect such sounds and disturbances caused by aquatic animals. We postulate that cephalopods recognize low-frequency particle motion that may be generated by prey, predators, and conspecifics.

5.5. Advantage and Possible Applications of This Model

The advantage of this model is that it provides us with the relationships between physical properties of a receptor

system and the perception threshold. For instance, this model enables us to understand how the displacement threshold of the macula hair cells ($x_{\min}$), the stiffness of hair cells (k), and the driven mass of the statocyst (m_e) affect the perception threshold of the cephalopod statocyst (see Sect. 2 for details).

Although this study is still in the preliminary stage, the forced oscillation model is potentially applicable to estimating the perception threshold of the cephalopod statocyst using the physical and physiological properties of the statocyst (e.g., the mass and density of the statolith, density of the endolymph, the restoring force, and displacement threshold of macula hair cells). For instance, this method may enable us to estimate the perception threshold of extinct species to understand the evolution of this sense, the perception threshold of small larvae to understand ontogenic development of this sense, and even the perception threshold of giant squid to understand the deep-sea ecology of cephalopods. Moreover, this model could be applicable to nonspecialist hearing other than cephalopods, because this model depends on the basic structure of the inertial motion detector, which is shared by a large number of species, including vertebrates and invertebrates.

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