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Insect Auditory System: From Nervous System Mechanisms to Practical Applications

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Abstract: Insect hearing is very sensitive, and its auditory neurons can achieve precise sound localization in a complex sound environment. The auditory receptor of insects is a special part of the skin of their body wall, which can sense pressure changes, air or water vibration, and convert this external stimulus into the corresponding nerve impulse transmitted to the cerebral cortex to generate the corresponding sensation. The auditory system of insects shows certain conservative and directional evolution characteristics, and the adaptive evolution of their hearing helps study the biological evolution model of neuroscience. The combination of multidisciplinary knowledge and technical means is helpful for the study of neural mechanisms and the comparison between different groups of auditory systems in insects, as well as the origin-evolutionary relationship. This review summarizes the research progress of insect hearing from the aspects of neural mechanism and evolution of the auditory system, which not only contributes to the study of the biological mechanism of brain processing complex signals, but also promotes the development of bionics and engineering. This paper finds that insect auditory receptors are a class of organs that have specific effects on sound waves. The hearing of insects is particularly sensitive and plays an important role in avoiding predators, intraspecific communication and finding mates.

Keywords: Insect, Auditory sense, Neural mechanism, Evolution

1. Introduction

Insect neurons can achieve precise sound localization in complex acoustic environments, a feat that not only intrigues researchers but also challenges typical assumptions about the relationship between neural complexity and functional ability. Despite their keen sense of hearing, insects do not have ears like mammals. Insects sense pressure changes, vibrations of air or water through receptors. The receptor is a specialized part of the skin on the insect's body wall that senses the internal and external stimuli of the body and converts them into corresponding nerve impulses. This nerve impulse is then transmitted to the cerebral cortex through the sensory nerve conduction pathway and the central nervous system to produce the corresponding sensation. Since most insects have one or more sensory organs capable of detecting changes in pressure, air or water vibrations, they are not only able to hear sounds, but are also very sensitive to sound vibrations.

The auditory organs of insects consist of three main types: auditory hairs, Johnston's (JO) organ, and tympanal organs. Auditory hairs have a simple structure with little specialization, typically connected by a single nerve cell to a hair socket. They are primarily distributed on the body surface, particularly on the antennae, palps, and cerci, where they exhibit high sensitivity. In addition to

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detecting mechanical stimuli, auditory hairs can detect low-frequency sound waves and airflow pressure, functionally resembling tactile receptors. JO's organ is a structurally complex chordotonal organ composed of multiple scolopidia. Tympanal organs, specialized for sophisticated auditory functions, are widespread in sound-producing insects. These highly specialized structures can detect both near-field and far-field sounds. A typical tympanic organ consists of three components: a tympanic membrane, an air sac or trachea supporting the membrane, and scolopidia located on the inner surface of the tympanic membrane. Specifically, the auditory organs of the Grylloidea are situated at the base of the tibia of the front legs and are paired structures. These structures consist of a layer of epidermal membrane, known as the tympanum, which is connected to the tracheal air sac and the chordal organ. The tibial organs of the Grylloidea are classified as a more advanced type, comprising three distinct components: the subgenual organ, the intermediate organ, and the acoustic ridge. The intermediate organ and the acoustic ridge constitute the primary components of the tympanal organ, whereas the tympanal organ is solely present in the tibial organ of the front legs. The intermediate organ and the acoustic ridge function as auditory receptors. The intermediate organ can be further subdivided into the proximal intermediate organ and the distal intermediate organ based on the direction of the dendrites of the peg sensilla. The intermediate organ and the acoustic ridge are covered with a membrane.

The neural mechanisms in the insects' hearing systems show an amazing variety and adaptability. This makes the insects detect and localize the important information with a high degree. For example, the parasite Ochracea increases the 2-microsecond interaural temporal variation into a 50-microsecond one by tympanal coupling, which can be represented as a 300-microsecond one at the end [1]. Besides, the ability of the parasitoid fly to resolve time differences in the nanosecond range with a head width of only 0.5 mm illustrates a synergy between complicated auditory organ architecture and neural processing.

The study of insect auditory systems is not only biological, but also provides important information for a number of different fields. It provides the best possible way to study how basic brain networks process complicated signals, which in turn causes the evolutionary trajectories of acoustic communication for behavioral ecology, and encourages developments in biomimetics and engineering, which is a perfect example of neuroscience. The interaction between the morphology of the auditory organ, the physics of sound transmission, and the processing of neural circuits are all important parts of acoustic communication that are important for sound localization. The auditory organs of these animals exhibit a variety of shapes and functions. In addition, the ability of insects to effectively identify sound sources contributes to the development of practical applications. For example, small acoustic sensors inspired by insect hearing could be used in robotic navigation and hearing aid technology [2].

This review summarizes the progress of research on the hearing of insects from two aspects: the neural mechanism of the auditory system and the evolution and adaptation. It can be concluded that elucidating the neural mechanisms underlying insect hearing will support practical applications in neuroscience, ecology and engineering.

2. Neural mechanisms of insect auditory systems

Insect auditory genes including the Atonal (Ato) gene, Spalt (Sal) gene, Touch insensitive larvae B (TilB), No mechanoreceptor potential (Nomp), and Smetana (Smet), among others. Of particular evolutionary significance, the Ato gene stands out as one of the most highly conserved genes encoding the basic helix-loop-helix (bHLH) transcription factors. Specifically, these molecular components are crucial for neural transformation and the determination of neural phenotypic traits. Notably, the Ato gene demonstrates dual functionality through its expression patterns - not only in the central nervous system but also in the peripheral nervous system of fruit flies. In this context, it

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acts as a proneural gene essential for the development of both chordotonal organs (vibration sensors) and olfactory receptor neuron subunits.

The Sal gene family members encode nuclear C2H2 zinc finger proteins that operate as transcriptional regulators. Interestingly, Drosophila melanogaster possesses two adjacent Sal genes - Sal and Spalt-related (Salr) - that exhibit both shared regulatory mechanisms and distinct independent functions. This genomic arrangement results in considerable functional redundancy between the two genes.

When examining auditory dysfunction mechanisms, studies reveal that TilB and Smet gene mutants primarily affect ciliary axoneme structures, ultimately leading to hearing impairment phenotypes in fruit flies. More precisely, TilB gene mutants show complete absence of sound-evoked antennal nerve action potentials, indicating its fundamental role in auditory signal transduction. Similarly, the Nomp gene cluster (located on the second chromosome) demonstrates critical functions in mechanosensation. The Nomp gene is located on the second chromosome, and its gene mutants show a reduction or disappearance of mechanoreceptor action potentials on the thoracic dipteran bristles. Commonly studied Nomp genes include NompA, NompB, NompC, etc.

The neural mechanism of the insect auditory system, characterized by simplicity and efficiency, has become an ideal model for the study of acoustic signal processing. Insects can complete the entire process from sound perception to behavioral decision making through the coordinated action of peripheral and central neurons. For example, studies on the katydid Mecopoda elongata have shown that its auditory system has selective mechanisms under natural noise conditions [3]. Certain interneurons of the elongate katydid showed increased sensitivity to frequencies at 2 kHz and remained responsive at signal-to-noise ratios as low as -21 dB. Meanwhile, another set of interneurons use stimulus-specific adaptation (SSA) to filter out masked signals, thus showing high sensitivity only to the 2 kHz band. This selective mechanism of the insect facilitates the detection of valid information in its noisy natural environment.

In addition, cricket ON1 neurons have a long response latency to 4.5 kHz call frequencies, but are sensitive to ultrasound via monosynapses [4]. High frequency signals (e.g. ultrasound) directly excite ON1 via a monosynaptic pathway, whereas low frequency call signals involve a multisynaptic delay pathway. In addition, cricket auditory neurons can adjust their frequency response through input-driven adaptation, which enhances sensitivity to novel signals by modulating receptor responses to repeated stimuli.

Drosophila females innervate the mating process by integrating excitatory inputs from vpoEN auditory neurons and inhibitory signals from pC1 neurons that encode the mating state [5]. The vpoDN neurons receive acoustic signals directly from courting males and decide whether or not to mate based on the reproductive state of the female, which is regulated by pC1 activity. In addition, 44 interneurons in the Drosophila brain are used to innervate primary auditory centers, forming frequency-selective and amplifying pathways through projection neurons that connect multiple brain regions. These neurons distribute auditory information to visual and olfactory regions by establishing localized interneurons and projection neurons in frequency-specific pathways within the brain. Adult fruit flies can narrow the auditory tuning bandwidth to 120-160 Hz by upregulating the expression level of the GABA(A) receptor Rdl in pC1 neurons [6]. This results in the selective reception of pulsed song signals. Furthermore, studies have shown that insect organs can achieve selective reception of sound frequencies through calcium ion-dependent potassium channels [7]. Multidisciplinary techniques can enhance researchers' understanding of the neural mechanisms of insect hearing. For example, optogenetic and electrophysiological methods have shown that the transient receptor potential (TRP) channel family plays a central role in mechanoelectric conversion, with TRPV responsible for basic transduction and TRPN involved in signal amplification [8]. The vibrations of the waggle dance in the acoustic system of the honeybee are caused by interactions

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between neurons such as DL-Int-1 and DL-Int-2, whose excitation depends mainly on inhibitory connectivity [9]. It's remarkable that the male Anopheles mosquito (Anopheles spp.) has about 16,000 auditory neurons in its organs. These neurons control the dynamic frequency tuning (precision of plus or minus 2 Hz) through central feedback.

The auditory receptors of crickets and katydids are sensitive to both sound and vibration. Studies have shown that the Nanchung-inactive ion channel may be a key auditory transactivation pathway in grasshoppers. The lever system of the katydid ear is similar to that of mammals, and the concentration of ions in the ear fluid correlates with the frequency of courtship songs. Insects can recognize mating songs through the simple nervous system. The diversity of JO-A and JO-B neurons in Drosophila auditory neurons connecting escape and song pathways favors the reception of specific audio signals [10].

The cricket's neck system is a network of mechanosensory fibre on the abdomen that detect near-field air motion and low-frequency signals [11]. These fibres convert mechanical vibrations into electrical signals, which are then processed using a delay line method. This method uses the time difference in signal propagation to distinguish directional signals, effectively filtering out background noise and increasing sensitivity to moderate airflow. This remarkable ability allows crickets to detect predators or mates in their immediate environment. The neural basis of directional localization, as elucidated by the brain's integrated circuitry, involves not only mechanical gain but also binaural signal comparison and temporal coding. Female crickets mimic the signal strength of a large male cricket's call by responding to a single sound pulse. In insects, antennae are important sensory organs used to detect chemical signals in the environment, touch, and airflow. Antenna motor neurons are neurons that control the movement of the antennae. Insects can adjust signal strength and wind sensitivity through physical displacement based on antenna motor neurons [12].

3. Adaptation and evolution of auditory environments in insects

Behaviorally, fruit flies modify song preferences based on prior acoustic experience, relying on integration centers to process external stimuli and internal states. This interplay of nature and nurture, revealed by single-cell transcriptomics and connectomics, underscores the experience-dependent plasticity of auditory systems. JO neurons and AMMC-B1 neurons of D. melanogaster and D. simulans are highly conserved in morphology and neurotransmitter composition [13]. Drosophila melanogaster has a stronger capacity to amplify 200-400 Hz signals. This difference may have led to interspecific mating isolation.

Environmental stress can cause insect hearing to rapidly adapt to the environment. The parasitic fly Ormia adapts its hearing and behavior to the rapid diversification of host cricket calls, preferring novel calls with specific spectral characteristics [14]. This suggests that predation pressure can drive host-parasite coevolution through selective preferences. Grasshopper auditory receptors encode sound by temperature compensation, maintaining a Q10 emission rate of about 1.5 through intrinsic cellular processes [15]. This dynamic ionic conductance balance ensures stable signal encoding under temperature fluctuations. Phylogenetic analyses suggest that insects may retain an ancient sensor-based amplification mechanism, while the evolution of mammalian Prestin may be involved in the loss of NompC.

It is imperative to examine the role of AN2 neurons in mediating ultrasound-evoked escape behaviors and testing for burst firing with sensitivity adjusted to predation pressure [16]. AN2 neurons utilize high-frequency bursts to relay ultrasonic information, inducing avoidance responses through precise modulation of predator signals. Monaural locusts modulate auditory pathways via collateral sprouting, forming new connections within 20 days of nerve damage, and demonstrating repair capacity in regeneration and plasticity, which in turn modifies auditory pathways through collateral

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sprouting [17]. These studies demonstrate that insect auditory systems employ gene regulation, mechanical innovation, and neural plasticity to adapt to ecological demands.

4. Conclusion

Insect auditory receptors are a class of organs that have specific effects on sound waves. The hearing of insects is particularly sensitive and plays an important role in avoiding predators, intraspecific communication and finding mates. With the development of multidisciplinary fields and the improvement of detection technology, people's research on the auditory system of insects is in-depth. In addition, many achievements have been made in the bionic study of insect hearing. Compared with vertebrate auditory organs, insect auditory organs are much simpler, so it is easier to model and study, and can provide a reference for the study of more complex auditory systems. For example, male antennae specialize in listening to female mosquitoes' characteristics of the development of passive acoustic direction finder, imitation of animal sense system of bugs, imitation of insect hearing structure, "anti-sonar" device.

The number of neurons used by insects to process auditory information is much smaller than that of mammals, and the insect auditory apparatus is easy to dissect and obtain, so it is often used as an animal model to study the occurrence and evolution of hearing. This review summarizes in two key areas: neural mechanisms, orientation and signal processing and the remarkable capabilities of the insect auditory system.

The purpose is to provide more powerful support for people to study the evolution of the hearing organs and nervous system and provide theoretical guidance for practical applications. At present, the ontogeny and phylogeny of the insect auditory system, as well as the comparison among different taxa and the origin-evolution relationship still need to be further studied. The differences and relationships between the different types of auditory receptors present in insects need to be further explored. In the future, it is very necessary to conduct comprehensive research on the insect auditory system from different levels by combining multidisciplinary knowledge and technical means.

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