



Update article

Auditory neuroscience in fruit flies

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ABSTRACT

Since the first analysis of the *Drosophila* courtship song more than 50 years ago, the molecular and neural mechanisms underlying the acoustic communication between fruit flies has been studied extensively. The results of recent studies utilizing a wide array of genetic tools provide novel insights into the anatomic and functional characteristics of the auditory and other mechanosensory systems in the fruit fly. Johnston's hearing organ, the antennal ear of the fruit fly, serves as a complex sensor not only for near-field sound but also for gravity and wind. These auditory and non-auditory signals travel in parallel from the fly ear to the brain, feeding into neural pathways similar to the auditory and vestibular pathways of the human brain. This review discusses these recent findings and outlines auditory neuroscience in flies.

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1. Introduction

Hearing is an important sensory modality for animal communication as well as for predator avoidance. The tympanic membrane in human ears detects sound energy as changes in air pressure. Insects, another spectacularly successful group of animals on earth, have also developed specialized hearing organs. Compared with vertebrate ears, which all share the same basic structural organization and location, insects have an amazing diversity of auditory sensory organs, from single “hairs” to complex tympanal ears (Yager, 1999; Yack, 2004; Vater and Kössl, 2011). Tympanal ears are found in various insect orders, such as in Orthoptera, Lepidoptera, Hemiptera, Diptera, Dictyoptera, Coleoptera, and Neuroptera (Yager, 1999; Yack, 2004). These ears occur on a variety of different body regions, including the mouthparts, wings, thorax, and abdomen (Yager, 1999). Singing insects, e.g., crickets, katydids, and cicadas, have sophisticated tympanal ears, which are capable of detecting “far-field sounds” at distances up to kilometers (Yager, 1999). Tympanal ears in Lepidoptera have evolved several times;

they are ultrasound-sensitive and detect echolocating bats (Miller and Surlykke, 2001).

On the other hand, honeybees, fruit flies, mosquitoes, and midges detect sound with an antennal ear, so-called Johnston's organ (JO). JO is located in the second segment of the antennae and detects “near-field sounds” close to the source (Yack, 2004). With this antennal ear, male and female mosquitoes detect the flight tone of their potential mates (e.g., Roth, 1948; Wishart and Riordan, 1959; Gibson and Russell, 2006; Warren et al., 2009), honeybees detect acoustic components of the waggle dance (Dreller and Kirchner, 1993), and fruit flies detect species-specific courtship songs (Tauber and Eberl, 2003).

Compared to the complicated communication sounds of mammals and birds, the relatively simple acoustic communication via the JO serves as an excellent model system for analyzing the neuronal and molecular mechanisms essential for auditory processing. In particular, the auditory system of the fruit fly *Drosophila melanogaster* has attracted considerable attention in the field of auditory neuroscience because many properties of the hearing system of flies parallel those in the vertebrate auditory system. The *Drosophila* auditory organ and vertebrate hair cells are both specified by atonal family genes (Jarman et al., 1993; Bermingham et al., 1999), and the introduction of a transgene for the mouse atonal homolog Math1 into *Drosophila* partially rescues *ato* mutant phenotypes (Ben-Arie et al., 2000). Genes such as *spalt*, *Distal-less*, and *crinkled*, whose mammalian homologs are linked to various human deafness syndromes (Weil et al., 1995; Kohlhase et al., 1998; Tackels-Horne et al., 2001), are also required for ear formation in the fruit fly (Dong et al., 2002, 2003; Todi et al., 2005). Fly ears

Abbreviations: JO, Johnston's organ; UAS, upstream activation sequence; AMMC, antennal mechanosensory and motor center; VLP, ventrolateral protocerebrum; GFP, green fluorescent protein; eYFP, enhanced yellow fluorescent protein; eCFP, enhanced cyan fluorescent protein.

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have both genetic and functional parallels with vertebrate ears; key characteristics of the cochlear amplifier, a positive mechanical feedback system within the ear that actively increases sound sensitivity, are found in the antennal ear of the fly and mosquito (Göpfert et al., 1999; Göpfert and Robert, 2003). Moreover, the structure of central projections from the fly ear to the brain is similar to that of its mammalian counterparts (Kamikouchi et al., 2009), suggesting that the design principle that governs auditory processing is also shared. Beginning with a brief description of the fruit fly ear, this update article discusses recent findings related to the anatomy and function of the neural circuit from the fly ear to the brain. Additional information on the auditory system in fruit flies, including the molecular mechanisms, signal transduction, mechanics of the antennal ear, and auditory communication, can be found in Caldwell and Eberl (2002), Tauber and Eberl (2003), Göpfert and Robert (2007), Kernan (2007), and Nadrowski et al. (2011).

2. How the fruit-fly ear works

Males of many *Drosophila* species produce a courtship song to attract females (Shorey, 1962). The fruit fly (*D. melanogaster*) uses antennae to detect this courtship sound (Fig. 1A). The branched

arista at the tip of the antenna captures the particle velocity component of a sound wave from nearby sources and vibrates together with the club-shaped antennal third segment (funiculus) (Göpfert and Robert, 2001). This antennal receiver, the arista coupled with the funiculus, plays a crucial role in detecting the courtship song of flies, as ablation of this receiver eliminates their behavioral response to the song (Kamikouchi et al., 2009). The vibration of the receiver along the longitudinal axis of the funiculus (Fig. 1A) is then detected by sensory units in JO, the auditory organ of fruit flies located at the second antennal segment (pedicel). Each sensory unit, called a scolopidium, typically contains a cap cell, a scolopale cell, a ligament cell, and two or three JO neurons (Fig. 1B). JO of the fruit fly comprises approximately 200 scolopidia (Caldwell and Eberl, 2002). JO neurons in each scolopidium, approximately 480 per JO, are bipolar neurons that act as stretch receptors and translate the receiver's vibrations into neural activity (Kamikouchi et al., 2006; Eberl and Boekhoff-Falk, 2007; Nadrowski et al., 2011). Moreover, JO neurons actively modulate receiver mechanics to amplify sound-evoked vibrations of the antennal receiver (Göpfert and Robert, 2003). This active amplification, as betrayed by the mechanics of the antennal receiver, is linked to a transducer-based process (Nadrowski et al., 2008) and is suggested to mediate the

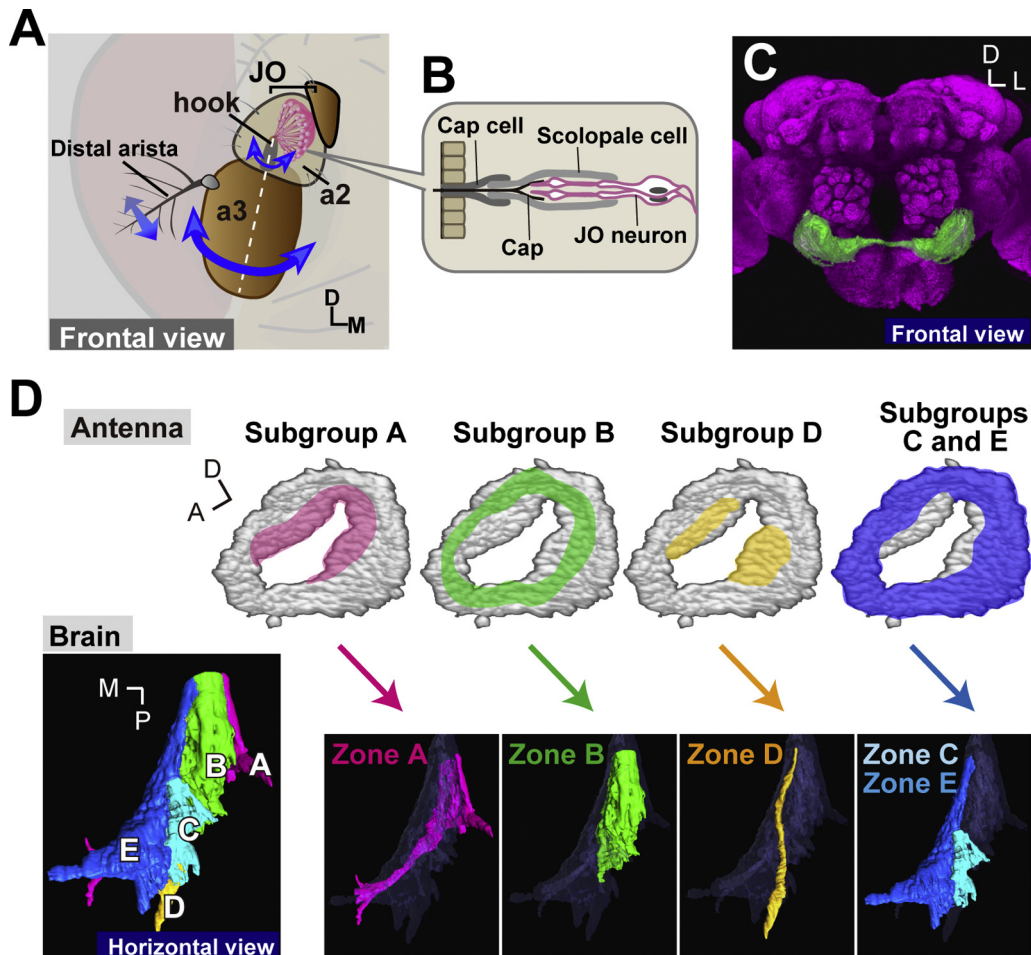


Fig. 1. Anatomy of the hearing system in fruit flies. (A) Frontal view of the antennal ear. JO is located within the second segment of the antenna (a2). Vibrations of the third segment of the antenna (a3) are picked up and translated into neural activities by JO neurons, housed in ~200 scolopidia. Arrows indicate the oscillating movement of the receiver. The white broken line indicates a longitudinal axis of the funiculus. (B) A sensory unit in the fly ear. (C) The AMMC, the primary center for JO neurons. Green fluorescent protein (GFP), expressed in JO neurons using the GAL4/UAS system, visualizes the AMMC (green). The brain was counterstained with a neuropil marker, nc82 antibody (magenta). (D) *Top*: Distribution of cell bodies for JO neurons in the antenna. Lateral views of the somata array for neural subgroups are shown. *Bottom*: The five zones in the AMMC. The target of JO neurons in the brain comprises five spatially segregated zones, zones A to E, each of which receives bundles of axons that gradually branch out from the main axon bundle of JO neurons. Because specific strains for either of the C and E neuron subgroups have not been identified, the somata locations of the C and E neurons are mapped together (*Top right*). A, anterior; P, posterior; D, dorsal; M, medial; L, lateral (modified from Kamikouchi et al., 2009) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

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