



## Review

## Auditory system of fruit flies



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## ARTICLE INFO

## Article history:

Received 9 September 2015

Received in revised form

12 October 2015

Accepted 30 October 2015

Available online 10 November 2015

## Keywords:

Courtship song

Johnston's organ

Antennal ear

Auditory neural circuits

Brain

## ABSTRACT

The fruit fly, *Drosophila melanogaster*, is an invaluable model for auditory research. Advantages of using the fruit fly include its stereotyped behavior in response to a particular sound, and the availability of molecular-genetic tools to manipulate gene expression and cellular activity. Although the receiver type in fruit flies differs from that in mammals, the auditory systems of mammals and fruit flies are strikingly similar with regard to the level of development, transduction mechanism, mechanical amplification, and central projections. These similarities strongly support the use of the fruit fly to study the general principles of acoustic information processing. In this review, we introduce acoustic communication and discuss recent advances in our understanding on hearing in fruit flies.

*This article is part of a Special Issue entitled <Annual Reviews 2016>.*

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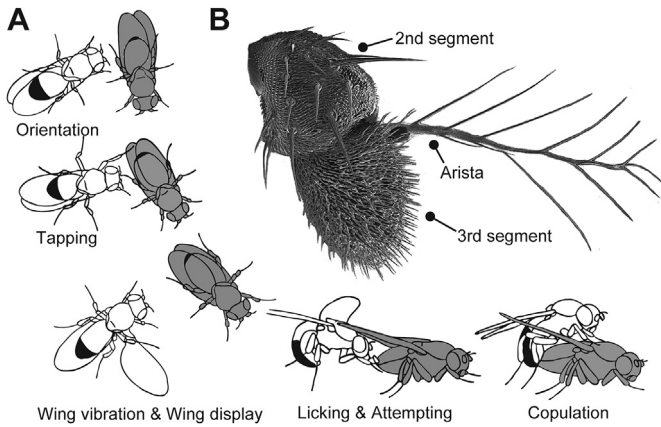
## 1. Introduction

The courtship of *Drosophila melanogaster* males is fascinating, involving a series of stereotyped behaviors, each of which requires processing and integration of multiple sensory stimuli, and decision-making (Billeter et al., 2006) (Fig. 1A). During the courtship ritual, the male produces a species-specific courtship song for a female by vibrating his wings (Shorey, 1962; Ewing and Bennet-Clark, 1968). The song is received with the antennal ear (Fig. 1B), whose structure and response properties exhibit no detectable differences between males and females. Intriguingly, many

*Drosophilid* species have their own courtship song characterized by a unique temporal pattern (Ewing and Bennet-Clark, 1968; Cowling and Burnet, 1981). For example, the songs of *D. melanogaster* and its sister species *D. simulans* have two components, the sine song and the pulse song. In the pulse song, the interval between pulses (interpulse interval, IPI) is species-specific; those of *D. melanogaster* is ~35 ms and that of *D. simulans* is ~50 ms (Moulin et al., 2004). The species-specific pattern of songs, such as the IPI, is widely considered to be important for reproductive isolation in *Drosophilid* flies. This hypothesis is supported, at least in some species such as *D. melanogaster*, by observations of an increased mating rate with playback of artificial courtship songs (Bennet-Clark and Ewing, 1969; Ritchie et al., 1999). The auditory system of *Drosophila* thus provides a useful model for understanding how species-specific

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**Fig. 1.** Mating behavior and the antenna of *Drosophila melanogaster*. (A) Behavioral elements in a courtship sequence of *D. melanogaster*. Males and females are indicated as white and gray colors, respectively. (B) Antennal ear of *D. melanogaster*.

sounds are represented and appreciated in the brain.

A prominent feature of *D. melanogaster* as a model in neuroscience is that in principle all cells and neurons are genetically identifiable and manipulable at the single-cell level. Thousands of fly strains, each of which expresses transcriptional activators such as GAL4, LexA, and QF in distinct subsets of cell populations (Venken et al., 2011), are readily available from nonprofit stock centers (e.g., Bloomington Stock Center, Kyoto Stock Center, and Vienna *Drosophila* Resource Center). By crossing these flies with marker, reporter, or effector strains, any gene of interest can be expressed in specific cell populations. Moreover, the activity of these genes can be turned on and off at will by shifting the temperature or feeding a chemical compound to control the time window of gene expression. This feature provides a great advantage for investigating the general mechanism of sensory processing at the level of molecules, cells, and neural circuits (Simpson, 2009; Kazama, 2014).

The vertebrate and fruit fly auditory systems are strikingly similar with regard to their transduction mechanisms within the auditory organ (Albert et al., 2007), as well as specification of sensory organ precursor cells by the proneural gene *atonal* at its developmental stage (Jarman et al., 1993; Bermingham et al., 1999). Both the vertebrate cochlea and *Drosophila* antennal ears have a positive mechanical feedback system within the ear, which actively increases the sensitivity to faint sound (Göpfert et al., 2005). Moreover, noise-induced hearing loss is observed in flies; 1-day exposure to loud noise reduces sound-evoked behavior, sound-evoked nerve potentials, and mitochondrial size in auditory sensory neurons of flies (Christie et al., 2013). Such changes in acoustically traumatized flies are comparable to those in noise-induced hearing loss in mammals (Van Heusden and Smoorenburg, 1981; Böttger and Schacht, 2013), paving the way for using flies in studies of the molecular and genetic mechanisms of hearing loss, in addition to general mechanisms of the auditory system. In this review, we discuss current knowledge on the fly's auditory system by introducing the acoustic behavior, hearing organ, transduction mechanism, and auditory neural circuits of fruit flies. Additional information on the development of auditory organs can be found in Boekhoff-Falk and Eberl (2014).

## 2. Acoustic behavior

The male courtship song, first described in *D. melanogaster*

(Shorey, 1962), has been reported for more than 110 *Drosophila* species (Hoikkala, 2005). *D. melanogaster* male typically produces a courtship sound including sine songs (pure-tone like sound of about 140-Hz frequency) and pulse songs (trains of single cycle pulses with about 35 ms IPI and 170-Hz intrapulse frequency) (Riabinina et al., 2011). A male typically alternates sine songs with pulse songs, patterned by fast modulations in visual and self-motion signals (Coen et al., 2014). Pulse songs, in particular, have attracted many researchers because flies mate more when played pulse songs with species-typical parameters (Bennet-Clark and Ewing, 1969; Ritchie et al., 1999). This observation indicates that the fruit fly is able to discriminate a particular sound from other sounds. Comparison of the mating rate with/without the courtship song is a classical way of monitoring sound-evoked behavioral changes in fruit flies (Bennet-Clark and Ewing, 1969).

Interestingly, sound-evoked behavioral changes are also observed under a single-sex group condition. Males exposed to pulse songs exhibit increased locomotor activity and begin courting each other if there are no females in the group (Eberl et al., 1997). This acoustically-induced behavior, known as chaining behavior, is not evoked by a pure tone that imitates sine songs (Yoon et al., 2013). Females, on the other hand, exhibit reduced locomotor activity when exposed to pulse songs (Crossley et al., 1995). These stereotyped behaviors, especially male chaining behavior, are widely used to analyze the behavioral output downstream of hearing (Fig. 2A). The recent development of a computer-based auto detection system for chaining behavior accelerated high-throughput analysis (Yoon et al., 2013). This detection system, termed ChalN (Chain Index Numerator), scans a movie file and counts the number of flies forming chains on a frame-by-frame basis (Fig. 2B). ChalN can be used to compare chaining behaviors across *Drosophila* species and is thus a useful tool for exploring the mechanism of species-specific tuning of the auditory system. A comparison of the behavioral outputs downstream of various artificial songs in *D. melanogaster* and its sister species *D. simulans* revealed that both species exhibit dramatic selective increases in chaining behavior when exposed to specific auditory cues that correspond to the species-typical pulse songs (Yoon et al., 2013) (Fig. 2C).

## 3. Hearing organ: antennal ear

As sound has a dual nature, pressure and particle velocity, animals that rely on sound have developed either a pressure receiver or a movement receiver to detect acoustic signals (Ewing, 1989). While the majority of vertebrates and many insect groups (e.g., crickets, grasshoppers, and cicadas) possess a tympanic membrane that moves in response to air pressure fluctuations, some insect groups, such as honeybees, mosquitoes, midges, and fruit flies, use an antennal receiver that tracks the oscillation of air particles (Yack, 2004; Nadrowski et al., 2011). Because the air particle velocity increases more rapidly than pressure when a sound source is approached, the use of particle velocity-sensitive movement receivers is advantageous for close-range communication.

The fruit fly uses antennae to detect particle velocity as near-field sound (Fig. 1B). The arista, a feather-like structure sticking out from the third antennal segment, serves as the sound receiver and vibrates back and forth in response to particle velocity. Movement of the arista is mechanically coupled with the third antennal segment. The basal part of the third antennal segment is called the hook, a structure that articulates the antennal third segment to the second antennal segment. The hook rotates forward and backward as the arista vibrates (Albert and Göpfert, 2015).

Johnston's organ (JO), the largest chordotonal organ in fruit flies, detects sound, gravity, and wind (Kamikouchi et al., 2009; Yorozu

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