



The neurobiological basis of orientation in insects: insights from the silkmoth mating dance

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Counterturning is a common movement pattern during orientation behavior in insects. Once male moths sense sex pheromones and then lose the input, they demonstrate zigzag movements, alternating between left and right turns, to increase the probability to contact with the pheromone plume. We summarize the anatomy and function of the neural circuit involved in pheromone orientation in the silkmoth. A neural circuit, the lateral accessory lobe (LAL), serves a role as the circuit module for zigzag movements and controls this operation using a flip-flop neural switch. Circuit design of the LAL is well conserved across species. We hypothesize that this zigzag module is utilized in a wide range of insect behavior. We introduce two examples of the potential use: orientation flight and the waggle dance in bees.

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Introduction

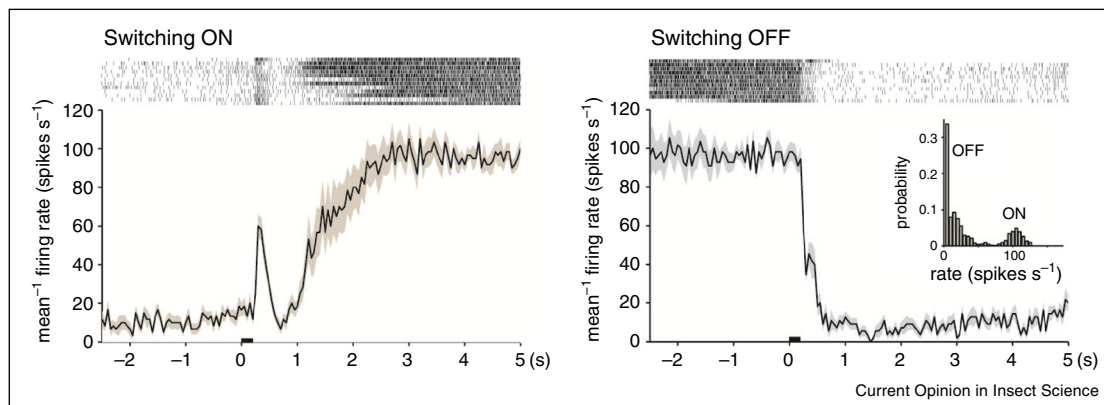
Orientation is the ability of animals to relate the position and movement of their bodies to spatial cues [1]. Animals often show characteristic locomotor patterns, which can be considered as motor components of active sensing strategies. Cues obtained by self-motion are used to extract relevant sensory features [2]. The zigzag movement, which is the successive counterturning toward the left and then right side, is one of the characteristic movements in orientation behavior. This movement increases the probability to contact the sensory cue [3]. This tactic has been well studied using the moth pheromone communication system [4,5^{*}]. Male moths react to species-specific sex pheromones emitted by conspecific females and show zigzag movements during the orientation behavior. This zigzag movement pattern for olfactory

navigation has also been reported in other insects: housefly [6], fruitfly [7], mosquito [8], and cockroach [9]. In moths, a brain region called the lateral accessory lobe (LAL) plays a crucial role in orientation behavior toward the odor source. In this article, we first summarize anatomical and physiological results on the LAL in the silkmoth and other insects. Because the LAL is present in all insects, we hypothesize that the same neuronal mechanism is also utilized in other insects. We will introduce two examples: orientation flight and the waggle dance in bees.

Neural circuits for pheromone orientation in the silkmoth

Pheromone-triggered orientation behavior in the silkmoth *Bombyx mori* has long been a model system for pheromone research [10,11]. The presence of sex pheromone alone is sufficient to trigger full sexual behavior in the silkmoth. After a brief exposure to pheromones, moths immediately start a surge in movement. In the pheromone plume, moths show the surge frequently, resulting in zigzag upwind walking. They often show straight-line trajectory, which depends on the plume structure [12]. After the loss of the plume contact, moths repeated clockwise and counterclockwise turning [13]. The pheromone is received at the receptor neurons on the antennae and the information is conveyed to the brain [14]. The antennal lobe, which is the primary olfactory center, extracts information about the plume structure at different temporal scales [15,16]. Projection neurons, which are second order olfactory neurons, receive input from glomeruli and convey information to the higher order center, a specific area in the inferior lateral protocerebrum [17] where the terminals are segregated from those of non-pheromonal glomeruli. The information is then transmitted to the LAL via the superior medial protocerebrum [17,18^{*}]. The neurons with similar morphology are reported in *Drosophila* [18^{*},19^{**}], suggesting a common circuit design. The LAL has been identified as the area involved in controlling motor function for pheromone orientation [20]. Recording from the neck connective has identified a group of axons exhibiting state-dependent neural activity that correlates with turning behavior [21]. Descending neurons exhibiting the flip-flop neural unit (named after the toggle flip-flop in electronics) have dendritic innervation specific to the LAL [20]. They show rapid state-transition and the identical sensory stimulation toggle the firing state [18^{*}] (Figure 1). Because this neuronal activity correlates with the head angle, which in turn correlates with the

Figure 1



Bistability in the activity of the LAL descending neuron. Spike timing and mean firing rate changes in response to sex pheromone stimulation (black bar, 200 ms) are shown. Data are presented as the mean \pm S.E.M. *Inset*, bistability of flip-flop descending neurons modulated by pheromone stimulation (bin size 5 Hz). Modified from Namiki *et al.*, 2014 [18*].

turning direction, the flip-flop signal is thought to underlie the locomotion occurring during pheromone-triggered orientation behavior [21]. The high correlation between the kinematics of wing motion (particularly wing retraction) [22], and the pattern of zigzag walking, suggests that the motor programs underlying pheromone modulated flight and walking may receive similar synaptic input from the flip-flop descending neurons projecting to the ventral nervous system [23]. This assumption is further supported by the observation that the flip-flop neural signal is present in a breed of *B. mori*, which is able to fly (Kanzaki, unpublished observation). Neurons with a similar morphology to the flip-flop descending neurons have been identified in flying moth species [24]. In addition, descending neurons innervating the LAL, have some functions on walking control in other insects [25,26*].

Organization of motor control in the insect brain

The central complex (CX) is a group of 4 distinct neuropils including the fan-shaped body (central body upper division), ellipsoid body (central body lower division), protocerebral bridge, and noduli. They are thought to be the higher order center for locomotor control [27,28*] and show functional similarity to the basal ganglia in vertebrates [29]. Most of the innervating interneurons do not show an obvious response to sex pheromone [18*], suggesting that the contribution of the CX to pheromone-triggered behavior is relatively small in the silkworm, although this region is probably relevant to a sort of adaptability [30]. As we describe in later sections, zigzag motion in other species (Table 1), such as object recognition or spatial processing, may require functioning of the CX. No descending output from the CX has thus far been reported in insects [20,31,32], indicating that

intermediate layers, including at least the LAL, are present between the CX and the thoracic motor center.

To explore the organization of the information pathway from the CX to the descending output, we summarize the neuroanatomy of the circuits surrounding the CX (Figure 2). The most prominent feature is that the LAL is densely connected with the CX [33] (Figure 2, green). In addition, there are connections between the left and right sides of the LAL, some of which show GABA-like immunoreactivity [34] (Figure 2, blue). Back-filling from the cut end of the neck connective reveals a population of descending neurons innervating the LAL (Figure 2, thin red). This pathway conveys locomotor commands from the CX to the thoracic motor center [20,35], although the total number of descending outputs is low.

The majority of descending neurons originate from the posterior-ventral part of the brain [20,31,36,37*], the area called the posterior slope (Figure 2, thick red). The lobula plate conveys optic flow information, which is crucial for flight control [38,39], and supplies substantial input to the posterior slope (Figure 2, thick yellow). Dorsal descending neurons originating from the posterior slope project to the dorsal neuropils of the thoracic ganglia, where flight-related circuits are present [36]. Hence, the dorsal descending pathway is thought to be crucial for insect locomotion [40]. The posterior slope is a candidate area for mediation of the CX locomotor command; however, the direct connection with the CX is weak. Although neurons connecting the posterior slope and CX have been reported [41], the pathway is likely to be rather sparse. Also, no dense connection is observed between the posterior slope and the CX when dye is injected into

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