



Post-molting development of wind-elicited escape behavior in the cricket



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ABSTRACT

Arthropods including insects grow through several developmental stages by molting. The abrupt changes in their body size and morphology accompanying the molting are responsible for the developmental changes in behavior. While in holometabolous insects, larval behaviors are transformed into adult-specific behaviors with drastic changes in nervous system during the pupal stage, hemimetabolous insects preserve most innate behaviors whole life long, which allow us to trace the maturation process of preserved behaviors after the changes in body. Wind-elicited escape behavior is one of these behaviors and mediated by cercal system, which is a mechanosensory organ equipped by all stages of nymph in orthopteran insects like crickets. However, the maturation process of the escape behavior after the molt is unclear. In this study, we examined time-series of changes in the wind-elicited escape behavior just after the imaginal molt in the cricket. The locomotor activities are developed over the elapsed time, and matured 24 h after the molt. In contrast, a stimulus-angle dependency of moving direction was unchanged over time, meaning that the cercal sensory system detecting airflow direction was workable immediately after the molt, independent from the behavioral maturation. The post-molting development of the wind-elicited behavior was considered to result not simply from maturation of the exoskeleton or musculature because the escape response to heat-shock stimulus did not change after the molt. No effect of a temporal immobilization after the imaginal molt on the maturation of the wind-elicited behavior also implies that the maturation may be innately programmed without experience of locomotion.

1. Introduction

During postembryonic development, the body structure of animals matures and subsequent behaviors are modified to adapt to the body changes. The developmental changes in the body and behavior accompanied by the reorganization of the nervous system have been reported in various animal species, including vertebrates and invertebrates (Easter, 1983). Unlike vertebrates, arthropods such as insects and crustaceans develop over “molt” to shed the exoskeleton. At around the specific timing of molt, the body size or structure of arthropods changes abruptly. This drastic changes in body structure and nervous system have been well studied in holometabolous insects such as hawk moth (Levine and Truman, 1985; Weeks, 1999) and fruit fly (Grueber et al., 2005; Tissot and Stocker, 2000). These changes are the basis for behavioral transformations from larval behaviors such as crawling, feeding, and ecdysis, to adult behaviors such as walking, flying, mating, and egg-laying (Consoulas et al., 2000).

The maturation process of adult-specific behaviors after the imaginal molt such as sexual maturation and change in their circadian rhythm has been also studied in hemimetabolous insects (Tomioaka and

Chiba, 1982). In contrast to the holometabolous insects, basic body structure, neurons, and behaviors of the hemimetabolous insects are preserved from all stages of nymph to adult whereas their sensory and motor organs develop over the molting (Boyan, 1983; Chambille and Rospars, 1985; Libersat, 2005; Sbrenna, 1971). However, it remains unknown when and how the behaviors preserved throughout post-embryonic developmental stages mature following the changes in body structure and nervous system at the molt. Comparing the maturation process between the adult-specific and life-preserved behaviors will gain a better understanding of biological basis in post-molting development in insects.

Escape behavior, which has been studied as a universal innate behavior in animals for survival (Domenici et al., 2011a,b), is one of the behaviors preserved throughout development in hemimetabolous insects. Some hemimetabolous insects including crickets and cockroaches exhibit a wind-elicited escape behavior that is mediated by a cercal system, which detects air currents as a sign of an approaching predator and triggers escape behavior (Baba and Shimozaawa, 1997; Casas and Dangles, 2010). The length and number of mechanosensory hairs on the cerci increase throughout the developmental stages (Chiba et al., 1992;

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Dangles et al., 2006), altering the response threshold to airflow velocity (Kämper, 1992; Kanou et al., 1988). These developmental changes of the cercal receptors are accompanied with the rearrangement of synapse connections of the cercal sensory neuron onto giant interneurons (GIs) (Chiba et al., 1988). However, the post-molting maturation process in the wind-elicited escape behavior is still unknown. In cockroaches, the latency of wind-elicited escape behavior reported increase over 30 days after the imaginal molt (Libersat et al., 2004), but it is unrevealed how the escape behavior was matured immediately after the molt.

In this study, to clarify the maturation process of wind-elicited escape behavior, we examined short-term changes in various locomotor parameters in the escape behavior just after the imaginal molt in the cricket. The response probability, reaction time, and moving speed and distance were matured 24 hours after the imaginal molt. Because the wind-elicited escape behavior of the crickets is well controlled directional behavior (Oe and Ogawa, 2013), we also focused on the elapsed-time dependency of the directional control in the escape behavior. In addition to investigating these parameters, we examined whether feedback signals of self-generated air current during spontaneous walking are required for post-molting maturation of the wind-elicited escape behavior. Although recovery of the directional control impaired by unilateral ablation of the cercus (Kanou et al., 1999; Vardi and Camhi, 1982a,b) requires the feedback signals during spontaneous walking (Kanou et al., 2002), our results indicated that the self-generated stimuli did not require the post-molting maturation of the escape behavior.

2. Material and method

2.1. Animals

Laboratory-bred adult male crickets (*Gryllus bimaculatus*) immediately after the imaginal molt were used throughout experiments. They were reared under 12–12 h light/dark conditions at a constant temperature of 27 °C. All experiments were conducted during the light phase at room temperature.

2.2. Behavioral experiment

Cricket movement was monitored using a high-speed digital camera (CH130EX, Shodensha, Osaka, Japan) installed above the experimental arena ($\phi = 260$ mm). Crickets were manually marked with two white spots on the dorsal surface of the head and thorax, of which size were enough large to detect the moving of crickets. The cricket was placed at the center of the arena within an inverted beaker ($\phi = 50$ mm) covered with aluminum foil. After the beaker was carefully lifted up, an air current stimulus was immediately applied to the cricket standing still. To measure the response probability for each individual, 10 trials were performed at each time-point after-mentioned. The interval between trials in a given test session was > 1 min. Based on the video data (1 pixel = 0.21 mm²; frame size, 640 × 480 pixels; shutter speed, 1 ms; sampling rate, 120 frames/s = 8.3 ms; total recording duration, 1660 ms), the two markers detected as the centers of painted spots on the animal were automatically traced, and locomotion parameters could be measured using motion analyzing software (Move-tr/2D, Library, Tokyo, Japan). To examine the time series of the change in wind-elicited escape behavior after the imaginal molt, we measured wind-elicited behavior for the same individuals repeatedly in different temporal sessions performed 0.5, 1.5, 3, 6, 24, 72, and 168 h after the molt (Fig. 1A). The escape behavior of animals 1 week (168 h) after the molt was considered to be completely matured. All crickets were isolated within a plastic container (138 mm × 220 mm × 135 mm) and had free access to food and water throughout the experiment.

2.3. Stimulation

An air current stimulus was administered to a stationary cricket using a short puff of nitrogen gas from a plastic nozzle ($\phi = 15$ mm) connected to a pneumatic picopump (PV820, World Precision Instruments, Sarasota, FL, USA). The velocity of the air current measured at the center of the arena was 0.6 m/s, and the stimulus duration was 200 ms. One air current nozzle was installed on the inside wall of the arena to be positioned on the same horizontal plane as the animal. Although crickets were always positioned at the center of the experimental arena by using a beaker, the stimulus angle against crickets was varied across the trials because crickets were oriented randomly when the beaker was lifted up.

A heat-shock stimulus was applied to a stationary cricket by touching the posterior surface of the abdomen with a heating pen (DENSTAR-110, Compact Plus Co., Bangkoknoi, Bangkok, Thailand). The tip of the heating pen was touched right side of the posterior-lateral surface of cricket's abdomen in all trials. The temperature of the tip of the heating pen was set to 100 °C throughout the experiment. For the heat-shock experiment, a different group of crickets from the airflow stimulating experiments were used.

2.4. Behavioral analysis

Locomotion parameters, including reaction time, moving distance, maximum translational velocity, moving direction, and turn angle were measured from video data. Like the previous study using a treadmill system (Fukutomi et al., 2015), if the maximum translational velocity was greater than 50 mm/s, we considered that the cricket responded to the air current (Fig. 1C). Throughout the experiments, we analyzed cricket movement during the initial response (Oe and Ogawa, 2013), of which the duration was defined as the period between the start and finish of the first trot (Fig. 1B). The start of the response was defined as the point at which the translational velocity became more than 10 mm/s during the period of 250 ms after stimulus onset, because the stimulus duration was 200 ms (Fig. 1C). The finish was defined as the point at which the velocity was less than 10 mm/s, following local maxima.

Behavioral responses were categorized as “jump”, “running”, and “no response” based on the leg movements during the behavior. If all six legs were off from the ground simultaneously, the response was defined as “jump”. If any legs touched the ground during the moving, we defined that as “running”. From this criterion, “running” included both forward and withdrawal movements.

The response probability for each individual was calculated from the number of responses categorized into running or jump in 10 trials. The reaction time was measured as a delay between the stimulus onset and the start of the initial response, from which the mean value of the travel time of the air current was subtracted. The travel time was about 15 ms, which was measured as a delay in GIs' spikes that was extracellularly-recorded ($N = 3$ animals) at the center of the arena used for the behavioral experiment. The moving distance of the initial response and maximum translational velocity were calculated from tracing the thoracic marker. The moving direction was measured as the angle between the cricket's body axis at the response onset and a line connecting the start and finish points of the initial response (Fig. 3A). The turn angle was measured as the angle made by the body axes at the start and finish points (Fig. 4A). If the cricket ran outside of the field of view (116.7 mm × 87.5 mm) during the initial response, we measured only the response probability, reaction time, and moving direction. In this case, the position where the cricket was out of frame was defined as the finish point. The definitions of the moving direction and turn angle followed those used for treadmill experiments in our previous studies (Fukutomi et al., 2015; Oe and Ogawa, 2013).

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