Chapter 14
Cercal System-Mediated Antipredator Behaviors

Yoshichika Baba and Hiroto Ogawa

Abstract In crickets, the cercal system is a mechanosensory system in which the receptor organ is a pair of antenna-like appendages called cerci located at the rear of the abdomen and covered with mechanosensory hairs, similar to the bristles on a bottlebrush. This system mediates the detection, localization, and identification of air currents surrounding the animal. Owing to the easy accessibility of the nervous system and advantages in physiological techniques, the cercal system of the cricket has been used as a model system for investigations of development, mechanoreceptor biomechanics, neural maps, and neural coding over the past few decades. In contrast, the behavioral significance of this system is still poorly understood. In early studies, the cercal system was regarded to be a simple system for triggering an escape reflex against an approaching predator. However, recent studies suggest that it is a more complex "generalist" system involved in various behaviors. In this chapter, we review studies on the cercal system from a neuroethological point of view and discuss the future direction of neuroethological research on this system.

Keywords Cercal system • Wind-sensitive organ • Identified interneurons • Antipredator behavior • Escape response • Mechanosensory receptors

14.1 Introduction

Most researchers of neuroethology (the study of animal behavior and its underlying control by the nervous system) have studied behaviors that show clear stimulus–response causalities, because they are likely to be driven by reliable neural circuits. An escape behavior in arthropods is one such behavior because it is reliably elicited by a key stimulus, and the input–output relationships in this behavior are clear. For

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example, escapes by crayfish elicited by water flow are driven by specific neurons (e.g., Reichert and Wine 1983). The running escape behavior of the cockroach is driven by a few identified giant interneurons (GIs), which are activated by air currents (e.g., Camhi 1980). Both behaviors are simple, repeatable responses, and relatively few identifiable neurons are involved in the initiation of the behavior. These key-triggering neurons are often called command neurons or are said to be part of a command system.

Studies on wind-evoked escape behavior in insects began in the 1970s. The cercal system was shown in early studies to be important for the oriented escape response (Hoyle 1958; Camhi 1980; Boyan et al. 1986). Briefly, the information pathway mediated by the cercal system is as follows: the cerci are mechanoreceptive organs comprising a pair of antenna-like appendages at the rear of the abdomen. Large numbers of mechanoreceptors distributed on the cerci detect the air current surrounding the animal. The receptor (hair) neurons extend their afferent axons to the terminal abdominal ganglion (TAG) and have synaptic contacts with interneurons. The projection interneurons receive signals from the sensory afferents and send the processed information to higher interneurons in the rostral central nerve system (CNS), including thoracic and cephalic ganglia. The leg movement for escape running is orchestrated by motor outputs produced by the interneuron network within the CNS. Many of the findings relating to the pathway come from studies of the escape behavior of cockroaches, pioneered by Roeder (1948) and more recently by Camhi and colleagues (e.g., Camhi et al. 1978; Camhi and Tom 1978), Ritzmann and colleagues (e.g., Ritzmann and Pollack 1986, 1990), and Comer and colleagues (e.g., Comer and Dowd 1987). Other researchers have carried out comparative studies using other insects, such as crickets (e.g., Edwards and Palka 1974; Matsumoto and Murphey 1977; reviewed in Jacobs et al. 2008), locusts (reviewed in Boyan and Ball 1990), and mantis (Boyan and Ball 1986).

Primary neural circuits for the cricket cercal system are located within the TAG, which is relatively easy to access. Because of this technical advantage, in terms of the electrophysiology and neuronal histology, this system has been used as one of the most suitable model systems for various fields of neuroscience. Therefore, many studies have been carried out on cercal system development and neural rearrangement (e.g., Murphey 1985; Kämper and Murphey 1987; Chiba et al. 1992), receptor biomechanics (e.g., Shimozawa and Kanou 1984a, b; Kumagai et al. 1998; Shimozawa et al. 1998; Magal et al. 2006; Cummins et al. 2007; Dangles et al. 2008), and interneuron networks (e.g., Bodnar 1993; Baba et al. 2001). Studies by Miller and colleagues on the cricket cercal system provided significant insights into neural coding (e.g., Theunissen and Miller 1991; Crook et al. 2002; Dimitrova et al. 2002; Aldworth et al. 2005, 2011) and neural maps (e.g., Troyer et al. 1994; Jacobs and Theunissen 1996; Paydar et al. 1999). Jacobs et al. (2008) provide a review of their recent studies focused on neural coding at the interface between the mechanosensory afferents and primary interneurons. Recent imaging studies mentioned in Chap. 18 have also demonstrated dendritic integration of the identified interneuron (Ogawa et al. 2004, 2008) and spatiotemporal representation of the stimulus by afferents (Ogawa et al. 2006).

In early studies, it was assumed that the cercal system in crickets would be involved in a similar escape response to that seen in cockroaches. However, recent studies have suggested that it is a considerable oversimplification to class this system as an “escape system.” Rather, the cercal system should be thought of as functioning as a low-frequency, near-field extension of the auditory system of the animal (Jacobs et al. 2008). From a neuroethological point of view, it might be that the cercal-mediated escape behavior in crickets is more complicated than that in the cockroach. For example, there are four types of mechanoreceptors in the cercus of crickets: filiform hairs, bristle hairs, clavate hairs, and campaniform sensilla. Briefly, filiform hairs detect air currents, bristle hairs detect tactile sensation, clavate hairs detect gravity, and campaniform sensilla detect distortions of the cuticle on the cercus. These receptors make contributions to important behaviors; for example, bristle hairs are involved in mating behavior (Sakai and Ootsubo 1988; Shell and Killian 2000); filiform hairs drive defense behavior (Gnatzy and Heußlein 1986; Gnatzy and Kämper 1990) as well as escape behavior (Kanou et al. 1999); and clavate hairs contribute to postural maintenance (Horn and Bischof 1983; Horn and Föller 1985). Other than postural maintenance, these behaviors are all competitive behaviors. The neural pathways for the processing of information sent by the four types of cercal signal are likely to interact in the CNS. In addition, even when focusing on air-current information, crickets have at least four options against an approaching predator: to (1) jump escape, (2) run or walk escape, (3) defend, or (4) freeze (see below). Such complexity makes it difficult to elucidate the neural system of cercal-related antipredator behaviors in crickets.

In this chapter, we review the cercal-mediated antipredator behaviors of crickets and the underlying cercal sensors and neural systems in the CNS. To elucidate the complete neural circuits driving antipredator behavior would result in significant insights into information coding and decision-making in real neural networks. Most of the data reviewed here come from two cricket species, the house cricket, *Acheta domesticus*, and a field cricket, *Gryllus bimaculatus*, with a few from the wood cricket, *Nemobius sylvestris*. However, the differences among the species are not considered in depth here.

14.2 Cercal-Related Antipredator Behaviors

Crickets use their cerci to detect the air current generated by predators and take various actions to survive. According to previous reports, such actions include a jump escape, run escape, walk escape, turn, headstand, stillstand, abdominal lift, kick, antennal swing, withdrawal, cercal cleaning, or no response (Dumpert and Gnatzy 1977; Stabel et al. 1985; Gnatzy and Heißlein 1986; Gras and Hörner 1992; Tauber and Camhi 1995; Baba and Shimozawa 1997; Kanou et al. 1999; Dangles et al. 2006a, 2007; Oe and Ogawa 2013; Table 14.1). In a recent review, Casas and Dangles (2010) described how the air current detected by the cerci can elicit at least 14 distinct responses, including evasion, flight, offensive reactions, scanning,

Table 14.1 Cercal-related antipredator behaviors in the cricket

Type of behavior	Condition, sex, age, and species	Air-current stimulus	References
Kick	Thorax fixed, female, 4–5 day adult, *G. bimaculatus*	$d = 9$ mm $f = 20$ mm $v = 1.9$–3.75 m/s	Dumpert and Gnatzy (1977)
Run	Tethered walking, both sexes, adult, *A. domesticus*	$d = 8$ mm Both sides $v = 0.5$–1.5 m/s	Stabel et al. (1985)
No reaction, jumping, head stand, stillstand, kick	Free moving, both sexes, nymphs and adult, *A. domesticus*	Air current generated by hunting wasp	Gnatzy and Heußlein (1986)
Run	Tethered on treadmill, both sexes, adult, *G. bimaculatus*	$d = 2$ mm $f = 6$ mm Both sides $v = 0.2$–2 m/s	Gras and Hörner (1992)
Jump, turn, turn + jump	Free moving, both sexes, adult, *G. bimaculatus*	$w = 2 \times 25$ cm^2 $f = 20$ mm All directions $v = 2.3$ m/s	Tauber and Camhi (1995)
Jump, run, walk, turn, withdrawal, abdominal lift, kick, cercal cleaning, antennal swing, freeze	Free moving in arena, male, adult (3–30 days), *G. bimaculatus*	$d = 1$ mm $f = 20$ mm Above 2 cm from cerci $v = 38$–770 cm/s	Baba and Shimozawa (1997)
Any movements, but no observe kick, head stand, cercal cleaning	Free moving in arena, female, adult (>1 week), *G. bimaculatus*	$d = 10$ mm $f = 20$ mm All directions $v = 10$–390 cm/s	Kanou et al. (1999)
Run, jump	Free moving in arena, *N. sylvestris*	Air current generated by spider or piston movement	Dangles et al. (2006a, 2007)
Run + turn	Free moving in area, tethered on treadmill, male, adult, *G. bimaculatus*	$d = 15$ mm $f = 75$ mm All directions $v = \sim 1$ m/s (measured at cerci)	Oe and Ogawa (2013)

d/w diameter or width of nozzle, f distance from nozzle to animal, v velocity of air current

freezing, and various reactions during male stridulation. In addition, the response can depend on the behavioral state of the animal as well as on the context of the environment. We classify these responses into four strategies: the escape strategy (jump run and walk escape), the defense strategy (headstand, stillstand, abdominal lift, and kick), the alert strategy (turn, antennal swing, withdrawal, and cercal cleaning), and the freeze strategy (no response). All strategies except for the alert

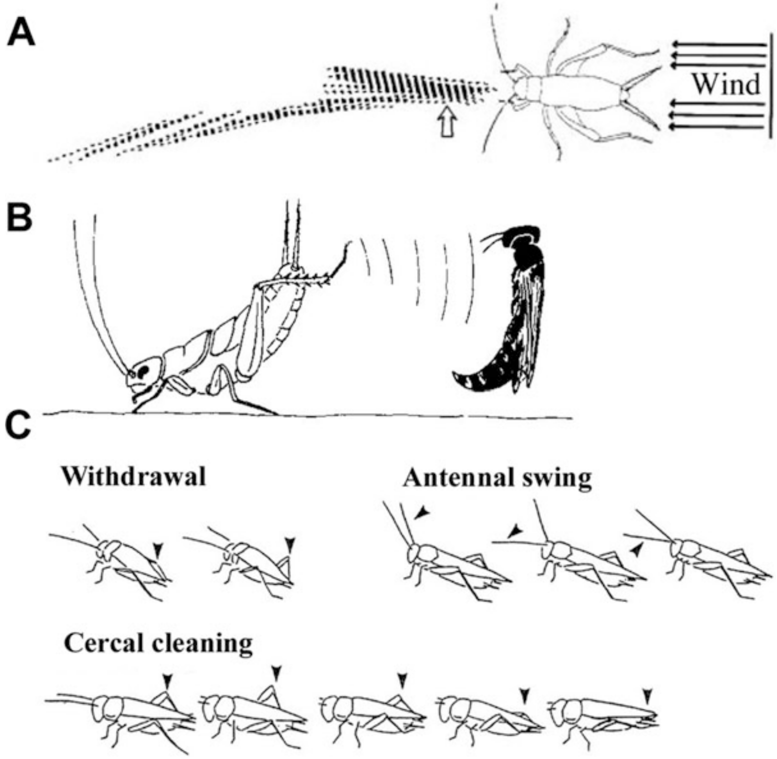

Fig. 14.1 Cercal-related behaviors. (**a**) Jump escape. *Black arrows* show the air current and the *white arrow* shows the jump point. *Dashed lines* represent the long axis of the cricket at 4-ms intervals. (**b**) Defense behavior (stillstand). A cricket lifts its abdomen and hind legs up against a wasp. (**c**) Alert behaviors. *Arrowheads* show the movement of antenna or legs (Reproduced, with permission, as follows: (**a**) from Fig. 3b in Tauber and Camhi (1995); (**b**) from Fig. 1 in Gnatzy and Heußlein (1986); and (**c**) from Fig. 2 in Baba and Shimozawa (1997))

strategy compete against each other. Here, we focus on the three strategies elicited in response to natural and potential predators, as well as artificial air currents.

The first natural predator investigated was a sphecid wasp, *Liris niger*. When *A. domesticus* individuals were attacked by the wasps, they adopted three survival strategies, escape (jump), defense (headstand, stillstand, and kicking; Fig. 14.1b shows kicking), and freeze (Gnatzy and Heißlein 1986). Headstand referred to a behavior in which the crickets suddenly raised their abdomen from a resting position (we also assumed that “stillstand” involved more abdominal lift compared with “headstand”; the “abdominal lift” behavior involved both “headstand” and “stillstand”; thus, we use “abdominal lift” hereafter). These actions were triggered before tactile contact occurred and after the wasp had approached within a radius of 1–3 cm, as measured from the rear end of the abdomen of the cricket. The running speed of the wasp was approximately 20–50 cm/s (Gnatzy and Heißlein 1986; Ganzy and Kämper 1990). The second natural predator investigated was the wolf spider, *Pardosa spp*. The spider attacked *N. sylvestris* only when the cricket came within 2–7 cm, whereupon the spider launched its attack at a median distance of 4.5 cm. In response, the crickets adopted an escape strategy, using a jump or walk escape (Dangles et al. 2007). Typical escape behavior comprised an initial 90° pivot followed by a jump escape, which was observed in more than half of the crickets tested. Escape performances were higher in juvenile than older instars (Dangles et al. 2007). On average, crickets escaped after the spider came within 1.4 cm. Attack velocities by spiders ranged from 2 to 41 cm/s (Dangles et al. 2006a).

Some researchers have observed the behavior of small mammals when hunting crickets (Ivanco et al. 1996; Munz et al. 2010). Baba et al. (2009) reported that *G. bimaculatus* would respond to an approaching mouse, with most crickets choosing the escape strategy (walk and run escape) and some choosing the alert (turn, antennal pointing), defense (abdominal lift, kick), or freeze strategies. However, crickets did not show a jump escape before a mouse had come into contact with the body of the cricket. Velocities of approaching mice to crickets ranged from 2.8 to 617 mm/s. Crickets standing in an arena (40 cm in diameter) began to move when mice entered a circle that was 20 cm in diameter, with the center being the tip of abdomen of the cricket. The mean distance was 83.8 mm for escape, 93.6 mm for alert, and 67.4 mm for defense behaviors. The average velocities of the approaching mice driving the escape and defense posture were 150 mm/s and 177.2 mm/s, respectively. When the freeze strategy was employed and the crickets were touched by a mouse, they started a run and jump escape (Baba, unpublished data). The study about “tongue hunting” of frogs provides additional insights into how the cercal system detects the approaching predator. The mean velocity of air currents generated by the tongues of toads hunting cockroaches was 2 cm/s measured at the location of the prey (Camhi et al. 1978).

In contrast to natural predator studies, three studies addressed the behavior of crickets in response to an artificial air-current stimulus. In the first report, the wind stimulus was produced by a motor that depressed a plastic sheet, which closed off one end of a wind tunnel. This end of the tunnel, which was rectangular in cross section, measured 25 × 30 cm^2. An air puff was expelled from the opposite, open end of the tunnel, which was a slit 2 cm high and 25 cm wide (Tauber and Camhi 1995). In this experiment, *G. bimaculatus* adopted an escape strategy against the air puff (duration approximately 200 ms, peak velocity 2.3 m/s). The observed behaviors were classified into three categories: turn response, jump response (Fig. 14.1a), and a turn + jump response. In the second report, air current was delivered with a nozzle (10 mm in inner diameter) placed 18 cm away from the cricket (Kanou et al. 1999). The air-current velocities were 0.1, 0.9, 1.5, 3.0, and 3.9 m/s and stimulus duration was 70 ms. In this study, neither defensive behavior nor cercal cleaning were observed. More than half (56 %) of crickets responded to the stimulus of 3.9 m/s velocity. At the stimulus velocities of 1.5 and 3.0 m/s, most escapes were triggered in the opposite direction to the stimulus (Kanou et al. 1999). In the third report, a fine nozzle (1 mm in diameter) was used for stimulus delivery, and the air-current velocity ranged from 38 to 770 cm/s (Baba and Shimozawa 1997). Stimulation was applied 2 cm above the cerci and stimulus duration was 2 s. In this study, the crickets exhibited various responses, which were classified into 11 types: walk, run, jump, turn, antennal swing, withdrawal, cercal cleaning, kick, abdominal lift, leg lift, and freeze. Antennal swing occurred simultaneously with 60 % of the kicks, 63 % of the walks, 70 % of the runs, 75 % of the leg lifts, 80 % of abdominal lifts, 87 % of cercal cleanings, and 90 % of withdrawal behaviors (Baba and Shimozawa 1997; Fig. 14.1c).

When taken together, these results show that crickets have at least three strategies for reacting to a stimulus: escape, defense, and freeze (we assume that the alert strategy is not a final action but is performed to collect more information or to prepare a final action). The escape strategy has two sub-strategies: jump escape or walk and run escape. Tauber and Camhi (1995) highlighted the advantages of the jump escape, explosive or rapidly accelerating quality, and the use of movement in three dimensions, thus incorporating an additional degree of freedom for the running escape. By contrast, the freeze strategy has not received much attention, although it might be an important survival strategy. Major predators of crickets, which include amphibians, reptiles, spiders, and insects, are known to prey mainly upon moving objects mainly. Mice, which we used in a preliminary study of crickets' escape behavior, and mammals tended to aim more at a moving cricket more than one that was in a frozen state (Baba unpublished data). These facts suggest that a freeze strategy must be one of the rational actions of some crickets that have less strong motor abilities. For example, the period of running and its velocity in the escape behavior of the crickets were not as long or as fast as recorded for cockroaches (Gras et al. 1994). Furthermore, Nishino and Sakai (1996) reported that *G. bimaculatus* showed thanatosis and discussed that it could have a role for predator avoidance. Thus, more focus is required on the freeze strategy as an important antipredator behavior in the crickets.

It is likely that there is a robust relationship between input (stimulus) and output (response) in cercal-mediated behavior in response to the small range of stimuli. For example, wide strong airflow applied by the wind tunnel drove a jump escape, whereas a small puff applied from an air nozzle drove a run and walk escape. A smaller (1 mm diameter) or vertical stimulation elicited the defense strategy in addition to other responses. When we studied the cercal system using artificial stimulation, only the stimulus intensity could be controlled. However, it is likely that vertical angle or flow diameter of the air-current stimulus would also affect behavior. Thus, when discussing the behavioral function of the cercal system, we must include specific stimulus parameters.

14.3 Cercal Mechanoreceptors

Crickets use filiform hairs to detect air currents. The filiform hairs are comprised of a rod-type hair, which is movable, and a socket (Murphey 1985). The base of the hair is elliptical and is inserted into a collar of flexible cuticle in the socket (Keil and Steinbrecht 1984). The directional movement axis of each hair is determined by the orientation of a hinge-like structure in the socket. A single receptor neuron innervating each hair at the socket generates action potentials as the hair moves (Edwards and Palka 1974). The amplitude of the response of each sensory receptor cell to any air-current stimulus depends upon the velocity and direction of the air current, and the directional tuning curves of the receptor afferents are well described by cosine functions (Landolfa and Jacobs 1995; Landolfa and Miller 1995). The hair length affects the response properties and thresholds. Longer hairs, which are more flexible and respond to low-frequency air currents with low thresholds, could code wind velocity. In contrast, shorter hairs are stiffer and respond only to high frequencies. Given that their thresholds depend on stimulus frequencies, these hairs would code wind acceleration (Shimozawa and Kanou 1984a, b). The threshold range is 0.03–300 mm/s, with an absolute sensitivity of approximately 0.03 mm/s (Shimozawa and Kanou 1984a, b). Most receptor neurons were saturated by an air current of 3–60 cm/s, and their maximum firing rate was approximately 400 spikes/s (Landolfa and Miller 1995). Conductance velocities of sensory afferents were approximately 1–2 m/s in *G. bimaculatus* (Baba, unpublished data) and 1.87 m/s in *A. domesticus* (Mulder-Rosi et al. 2010). The cercal length is approximately 10 mm. Given that the filiform hairs are distributed over a cercus about 10 mm long, the afferent spikes of the sensory neurons would vary in arrival time from 5 to 10 ms, assuming the conduction velocities of the afferent spikes are constant. Recently, it was reported that small variations in spike-propagation velocities between afferent axons enables the cercal system to function as a “delay line” (Mulder-Roshi et al. 2010).

The number of filiform hairs on a cercus varies depending on species, instar stages, and probably the growth environment. Each cercus is covered with 300–750 filiform hairs in adult *A. domesticus* (Edward and Palka 1974; Palka and Olberg 1977; Jacobs et al. 2008; Miller et al. 2011; Chiba et al. 1992), 400–500 in adult *G. bimaculatus* (Shimozawa and Kanou 1984b), and 322 in adult *N. sylvestris* (Dangles et al. 2006b). Individual filiform hairs vary in length and diameter even on a single cercus. The approximate length of 120 hairs was 800–1,500 μm, with most of the remainder (300–400 hairs) being approximately 400 μm long in adult *A. domesticus* (Edwards and Palka 1974). In adult *G. bimaculatus*, the largest hairs were 1,500 μm long and 9 μm in diameter, and the smallest were 30 μm long and 1.5 μm in diameter (Shimozawa and Kanou 1984b). Filiform hairs can be classified approximately into two or three subtypes depending on their movable direction: transverse (T-hair), longitudinal (L-hair), or oblique (O-hair) relative to the longitudinal axis of the cercus. T-hairs occur on the dorsal and ventral surface, L-hairs on the medial and lateral surface, and O-hairs on the dorsal–lateral, ventral–lateral, and ventral–medial surfaces of the cercus (Landolfa and Jacobs 1995). Additionally, Landolfa and Jacobs (1995) reported a more detailed classification (eight types). Recently, Miller and colleagues (2011) reported the complete distribution of filiform hairs on a cercus and provided a summary of the distribution of preferred direction of each hair (Fig. 14.2c, d). The directional data showed that crickets have hairs arranged in four diagonal directional bands (Miller et al. 2011).

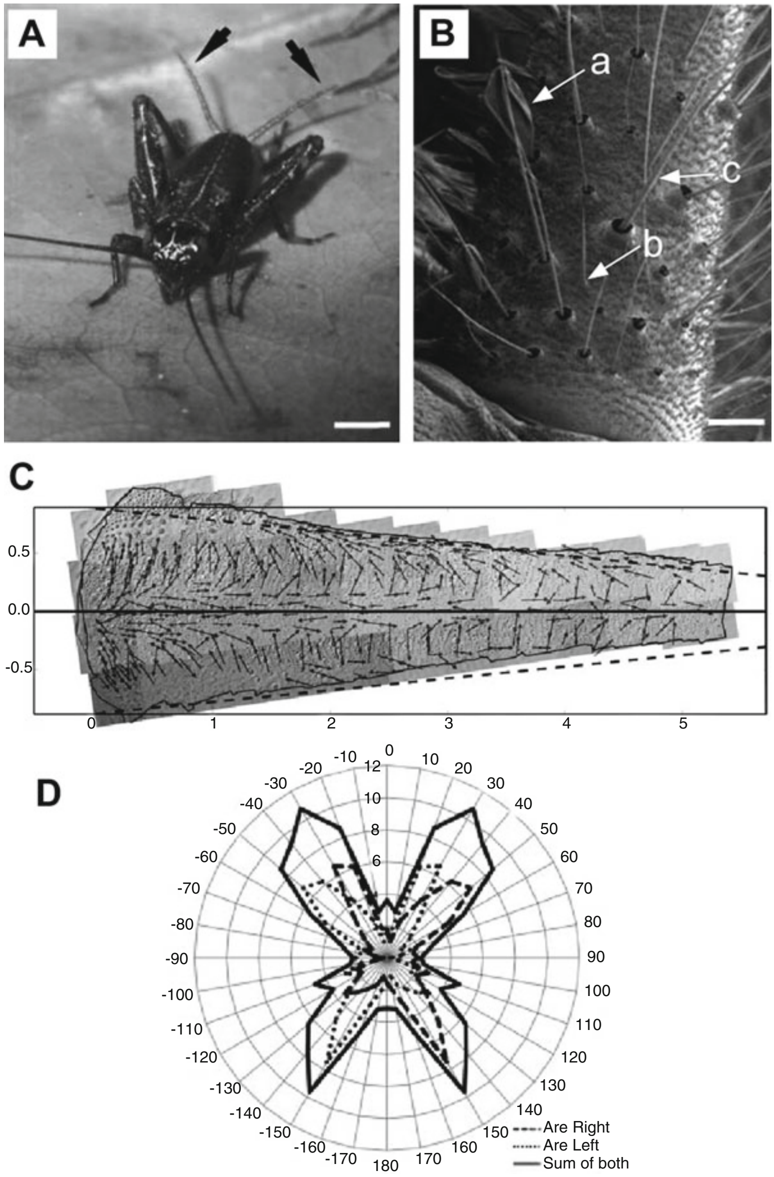

Fig. 14.2 Cercal mechanoreceptors. (**a**) A wood cricket and its cerci (*arrows*). Scale bar = 2 mm. (**b**) Scanning electron micrograph of the proximal region of the cerci. *Arrows* **a**–**c** show a clavate hair, bristle hair, and filiform hair, respectively. Scale = 100 µm. (**c**) Distribution of filiform hairs on filet preparation. *Arrows* show the excitatory direction of each hair. Vertical and horizontal units are in mm. (**d**) Number of filiform hairs in individual directions. Zero refers to the anterior direction (Reproduced, with permission, as follows: (**a**, **b**) from modified Fig. 1 in Dangles et al. (2006b); and (**c**, **d**) from modified Figs. 8a and 11d, respectively, in Miller et al. (2011))

14.4 Synaptic Connections from Receptor Afferents to Interneurons

Filiform sensory neurons project to the posterior TAG, which comprises five neuromeres (abdominal neuromere 7–11; Jacobs and Murphey 1987). The seventh to eighth neuromeres have a structure similar to unfused abdominal ganglion, which is the anterior TAG. Neuromeres 9–11 (posterior TAG) are fused and their structure modified (Baba et al. 2010). The TAG in adult *G. bimaculatus* shows sexual dimorphism, but dimorphism of the filiform sensory projection has not been observed.

In *A. domesticus*, the 1500 sensory afferents synapse with a group of approximately 30 local interneurons and approximately 10 pairs of identified ascending interneurons. The putative neurotransmitter of the cercal-to-interneuron synapses is acetylcholine (Meyler and Reddy 1985; Yono and Aonuma 2008). Jacobs and colleagues demonstrated that the sensory afferents of filiform sensilla terminate in an orderly array, which is not related to their location on the cercus but to directional sensitivity in the horizontal plane (Jacobs and Theunissen 1996; Paydar et al. 1999). The functional afferent map was constructed from anatomical data of central projections and physiological response properties of mechanosensory afferents (Jacobs and Teunissen 1996) and visualized by calcium-imaging experiments (Ogawa et al. 2006). The topography of mechanosensory afferents based on their response property is very interesting to note because we have assumed that the projection of mechanosensory afferents is generally organized to reconstruct their topography within the CNS like a mammalian somatosensory system, but the afferent map in the cercal system is based on physiological relationships. Furthermore, the observation that postsynaptic neurons targeted by cercal afferents were changed by partial ablation of the afferents suggests synaptic rearrangement adjusting to the development of filiform hairs in each molt (Chiba et al. 1992).

14.5 Interneurons

Dendrites or neurites of ascending and local interneurons are arborized within the projection area of the filiform sensory neurons. At least eight (in *G. bimaculatus*) to ten (in *A. domesticus*) pairs of ascending interneurons have been identified as giant interneurons (GIs) owing to their relatively large-diameter axons, which enable rapid conduction of action potentials. The axons of the GIs run through the ventral nerve cord contralateral to the somata (hereafter, we used ipsilateral or contralateral to the somata position). In *G. bimaculatus*, it was confirmed that eight pairs of GIs project their axons to motor centers in the thorax and integrative centers in the brain. The GIs are named on the basis of the location of somata in the TAG, such as GI 7-1, 8-1, 9-1, 9-1b, 9-2, 9-3, 10-2, and 10-3 (Fig. 14.3b). The first number represents the soma location of the abdominal neuromere, and the second number

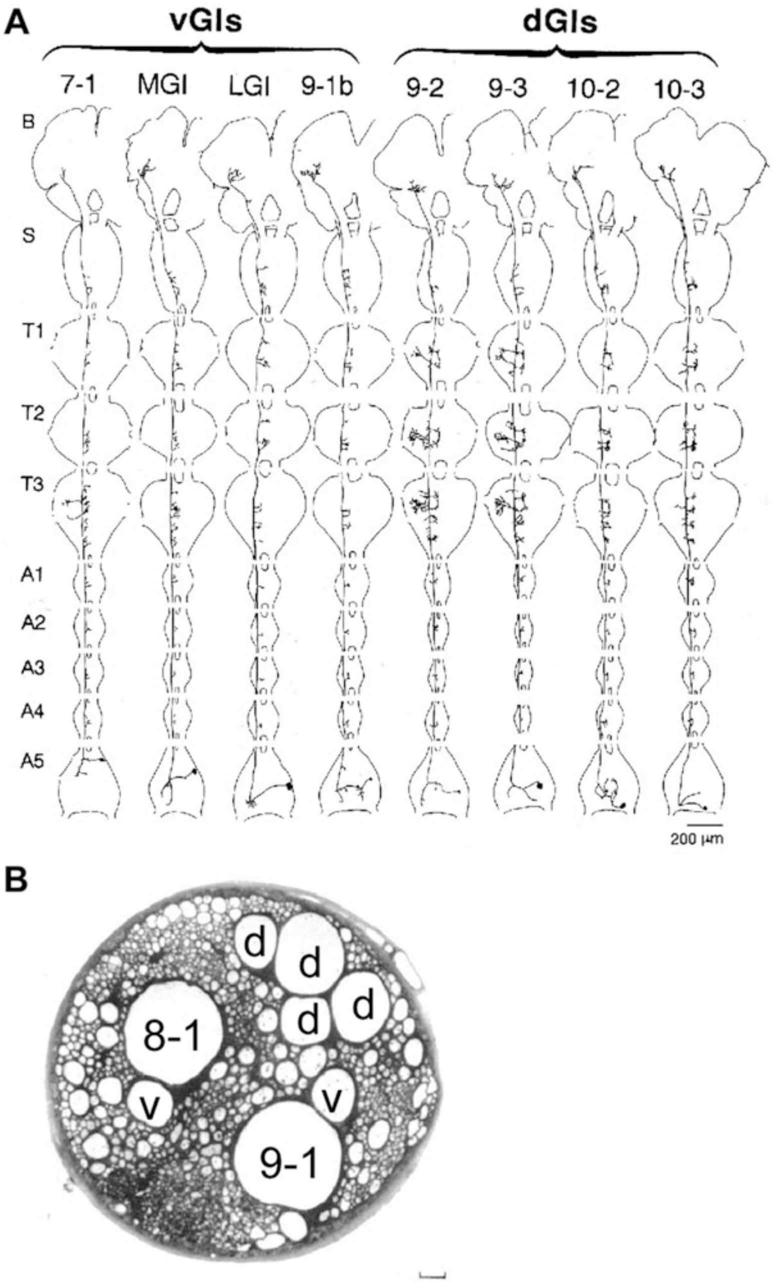

Fig. 14.3 (**a**) Morphology of eight types of giant interneuron (GIs). GIs 7-1, 8-1, 9-1, and 9-1b are ventral GIs (vGIs) and the others are dorsal GIs (dGIs). (**b**) Cross section of ventral nerve cord. The axons labeled 8-1, 9-1, and v are delivered by vGIs. The axons labeled with d are delivered by dGIs. Scale bar = 10 μm (Reproduced, with permission, as follows: (**a**) from Fig. 1 in Hirota et al. (1993) and (**b**) from modified Fig. 6 in Edwards and Palka (1974))

represents the identified number. These are classified into two groups depending on the position of the axons within the ventral nerve cord. The GIs 7-1, 8-1, 9-1, and 9-1b are classified as ventral GIs (vGIs) owing to the middle or ventral position of their axons. The other GIs with axons located at the dorsal side of the ventral nerve cord are classified as dorsal GIs (dGIs). In the wood cricket, eight GIs have also been identified, although these were named differently to the system described above (Insausti et al. 2011). Here, we use the conventional names for GIs in *G. bimaculatus* and *A. domesticus*. In *G. bimaculatus*, eight pairs of GIs project their axons to all segmental ganglia, including thoracic and cephalic ganglia (Fig. 14.3a; Hirota et al. 1993). The axonal projection within thoracic ganglia differed in its branching pattern between dGIs and vGIs. The dGIs arborize medial and lateral branches, whereas the vGIs, except for GI 7-1, have only medial branches. Depolarizing current injection into dGIs elicited neural activities in the thoracic nerve branch and occasionally induced leg movements, such as walking, whereas the activation of vGIs elicited no activity (Gras and Kohstall 1998; Hirota et al. 1993). Directional sensitivity of ascending interneurons, including GIs, would mediate some directional control of the cercal-mediated response.

The response properties, including directional and frequency sensitivity to sinusoidal sounds or air puffs, threshold, and input source of the filiform hairs, have been well studied in the GIs. Integrative studies have described that the directional sensitivity of GIs is primarily based on the location of GI's dendritic arbor within the functional afferent map mentioned above (Jacobs and Theunissen 2000; Ogawa et al. 2008). Most electrophysiological data were recorded from decapitated animals. Recording sites of the intracellular electrode varied between studies, such as axons within the ventral nerve cord, cell body, or dendrite within the TAG. An in vivo calcium-imaging technique has been used to examine dendritic excitability (Ogawa et al. 2000, 2002a, b) and synaptic integration of directional information in GIs (Ogawa et al. 2004, 2008). Furthermore, whole-cell clamp recording of cultured GIs has demonstrated voltage-activated Na^+, K^+, and Ca^{2+} currents (Kloppenburg and Hörner 1998). The Ca^{2+} accumulation in dendrites of GIs modulated wind sensitivity via synaptic depression (Ogawa et al. 2001). Below, we describe the distinct response properties of individual GIs and other interneurons.

GI 8-1, also called the medial giant interneuron (MGI), and GI 9-1, also called the lateral giant interneuron (LGI), have been well studied because they have the largest and second largest axons, respectively, and the responses are easy to record intracellularly. The T-hairs contralateral to the somata of the GIs provide the strongest excitatory input to GI 8-1 and 9-1. The ipsilateral T-hairs inhibit GI 8-1 (Matsumoto and Murphey 1977), and the ipsilateral T-hairs and contralateral L-hairs inhibit GI 9-1. The inhibition reduced the number of outgoing spikes from a level elicited by excitation alone, and it did so in proportion to the level of wind responsiveness displayed in GI 8-1 (Baba et al. 2001). The Gl 8-1 displayed the highest sensitivity to the air currents from a contralateral-rear direction (Kanou 1996). The GIs 8-1 and 9-1 received their main excitatory inputs from rather short cercal hairs but not from the conspicuously long filiform sensory hairs (Kanou and Shimozawa 1984). A simple model of the directional sensitivity of the interneurons based on their monosynaptic inputs from the cercal sensory neurons can account for the major features of the directional sensitivity of the interneurons (Bacon and Murphey 1984; Shephard and Murphey 1986). Laser ablation of GI 8-1 diminished control of the turn angle and decreased locomotion distance in the initial walking response to air-puff stimuli, suggesting that GI 8-1 is involved in turn-angle control and maintenance of wind-elicited walking behavior (Oe and Ogawa 2013).

The GIs 10-2 and GI 10-3 show spontaneous activity and are highly sensitive (the lowest threshold was 0.03 mm/s or less). The long filiform hairs connect to them (Shimozawa and Kanou 1984b). GIs 10-2 and 10-3 are similar in terms of their synaptic inputs, which include excitatory synaptic input from ipsilateral L-hairs and contralateral T-hairs and inhibitory input from contralateral L-hairs and ipsilateral T-hairs (Levine and Murphey 1980). These interneurons are tuned broadly to the direction and velocity of bulk airflow movements and project a coarse-coded image of these parameters to higher centers, which is accurate to approximately 8° (Theunissen and Miller 1991; Theunissen et al. 1996). The four GIs comprising left and right 10-2 and left and right 10-3 serve as a functional unit encoding the direction of the air current in the horizontal plane (Miller et al. 1991). Recent research has demonstrated that the GIs 10-2 and 10-3 also respond with high sensitivity to complex dynamic multidirectional features of air currents on a smaller spatial scale than the physical dimensions of the cerci (Mulder-Rosi et al. 2010), using a coding scheme that is more complex than simple linear encoding (Aldworth et al. 2011).

Relatively few studies have demonstrated the response characteristics of other GIs. Gl 9-2 is the most sensitive to air currents from contralateral-rear directions and is less sensitive to air currents from ipsilateral-front directions (Miller et al. 1991; Kanou 1996). Gl 9-3 is more sensitive to air currents from contralateral-front directions and is less sensitive to those from an ipsilateral-front direction (Miller et al. 1991; Kanou 1996). It has been suggested that GIs 9-2 and 9-3 form a second directional encoding unit sensitive to higher velocities (Miller et al. 1991). GI 7-1 responds to wind stimulation, although its dendrites do not overlap the projection area of sensory afferents (Hirota et al. 1993). GI 9-1b has spontaneous activity, with a threshold of <0.2 cm/s (Kämper 1984). The recent report that ablation of GI 9-1b delays reaction time of the wind-elicited walking implies an important role for G I9-1b in rapid initiation of that response (Oe and Ogawa 2013).

In total, 7–15 pairs of ascending interneurons, other than GIs, have been identified and also determined to respond to air particle displacement of filiform hairs (Kämper 1984; Jacobs and Murphey 1987; Baba et al. 1991). These non-giant ascending interneurons are likely to contribute to antipredator behaviors. In addition, at least 21 pairs of non-spiking local interneurons and 15 pairs of spiking local interneurons have been found in the TAG (Bodnar et al. 1991; Baba et al. 1995). If some of these local interneurons influenced the activities of GIs, it would contribute to signal processing (Bodnar 1993; Baba 2002), but further work is required to determine the mechanisms behind this effect.

14.6 Conclusion and Further Studies

Although there have been several studies on sensory neurons and interneurons in the cercal system of crickets, there is still a gap in knowledge between the neural mechanisms and their behavioral functions. Although basic neural study does not require behavioral relationships, behavioral data would enhance the relevancy of the neural data. For example, the recovery level of neural networks by rearrangement could be tested using a behavioral assay. To understand the contributions of GIs and other ascending interneurons in cercal-mediated behaviors, one should consider the following points. First, decapitated crickets have been used in most physiological studies focused on elucidating directional sensitivity, neural connection, and input source. Lower diversity in physiological responses in this preparation was useful to figure out the basic mechanism of neural coding and information processing in the receptor neurons and interneurons. However, these data are not enough to explain the variety of cercal-mediated behaviors. Second, there are very few studies using interneuron ablation experiments. Although it is known that there are eight pairs of GIs and some pairs of non-GIs and that giant ascending interneurons are assumed to contribute to antipredator behaviors, their roles are not known from a behavioral perspective. In the cockroach, ablation of GIs affected directional sensitivity in escape response (Comer 1985; Comer and Dowd 1987). Recently, it has been reported that selective ablation of GIs modified motor control depending on the stimulus direction and that the directional control in the wind-evoked walking behavior required descending signals from the brain ganglion (Oe and Ogawa 2013). The directional information conveyed by GIs is essential for giving the direction of the escape behavior. If genetic manipulation techniques are established in the crickets as mentioned in other chapters, cell-specific activation or silencing will provide direct evidence of the behavioral function of individual interneurons.

Another point to consider is stimulus intensity. According to behavioral reports, the range of velocity of approaching predators that trigger antipredator behavior is 20–500 mm/s. It is assumed that the air current that crickets detect would be slower than the approaching velocity because the air current reaching the cerci must be smaller than the movement of the predator. As mentioned above, the threshold of the sensory neurons and GIs is more than 0.03 mm/s, and the dynamic range is approximately 0.03–300 mm/s. By contrast, in behavioral analyses, artificial (air puff) stimuli of relatively higher velocities (380–7700 mm/s) than observed in natural conditions or in neural studies have been used. This gap also suggests that the cercal system should not be classified as a simple escape system but as a near-field and low-frequency auditory system (Jacobs et al. 2008). Additionally, crickets use three strategies in response to cercal stimulation, but strict directional orientation is only required for the defense strategy. Ascending interneurons including GIs would convey the information for crickets to choose the appropriate strategy in addition to the directional information for performing a particular behavior. Although the above data have shown some input–output relationships, they have not shown that these are robust. The cercal-mediated antipredator behavior is more complicated than was previously thought. Given that the nervous system of the cricket is relatively easy to access and manipulate under free moving conditions, this system is a suitable model to use to analyze the neural basis underlying flexible and situation-dependent behaviors.

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