Chapter 7
Tonic Immobility in a Cricket: Behavioral Characteristics, Neural Substrate, and Functional Significance

Hiroshi Nishino and Masaki Sakai

Abstract The field cricket (*Gryllus bimaculatu*s), a model organism for neurobiological studies, shows tonic immobility (TI) upon restraint of its legs and maintains the restrained posture for several minutes. All bodily movements including abdominal ventilations are inhibited during TI. Catalepsy, in which the animal maintains a new posture forcibly given by an experimenter, is observed in all appendages. Due to the cataleptic nature, the cricket can assume any posture. Ablations of sense organs revealed that exteroceptors such as short trichoid sensilla on the pronotum and campaniform sensilla on the legs were necessary for the flexed-leg posture, and chordotonal organs that detect the tibial movement/position were critical for the induction of TI. Cooling of the brain led to immediate termination of TI, suggesting that immobility of the entire body is maintained by continuous activity of descending neurons originating from the brain. In the natural habitat, TI occurs during escape in which the cricket creates self-imposed restraint by crawling into a small opening made by pebbles or plants, supporting the view that TI is functional for dazzling predators that primarily use vision for prey detection.

Keywords Cricket · *Gryllus bimaculatus* · Tonic immobility · Catalepsy · Chordotonal organ · Command-like neuron · Functional significance

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7.1 Introduction

Many insects show an immobility reaction when they are attacked or restrained by predators. This reaction has been called death-feigning, thanatosis, or animal hypnosis. We call it tonic immobility (TI) here according to the recommendation in Chap. 1.

Representative insects showing TI are insects in the order Coleoptera, Hemiptera, and Phasmatodea. Studies on TI in these insects and some spiders were all published in the early 1900s (Fabre 1910; Robertson 1904; Rabaud 1919; Holmes 1906; Mangold 1920; Bleich 1928; Steiniger 1936). In those studies, characteristics and mechanisms of TI were investigated by using various stimuli and ablation of the nervous system. Since then, there has been no systematic study on TI in insects except for some studies in stick insects. Therefore, TI in insects is summarized on the basis of the above reports.

TI was induced in beetles in the order Coleopteran (Fabre 1910; Mangold 1920; Bleich 1928) by rolling them on the palm of the hand or dropping them onto a table. The beetle assumed an immobile posture on its back for several minutes to 1 h. TI was not easily interrupted by disturbing stimuli but was terminated by some kinds of mechanical stimulation to particular parts of the body such as contact to the mouth or legs (Fabre 1910). There were considerable differences in features of TI among species.

On the other hand, water stick insects in the order Hemiptera (Holmes 1906) and stick insects in the order Phasmatodea (Steiniger 1936; Godden 1972; Bässler 1983) are mostly standstill in a cryptic manner. During the daytime, the former waits for prey underwater, while the latter hides from predators in trees. Although such immobility is not induced by a predator's attack but occurs spontaneously or due to environmental stimuli such as sunlight, it has been traditionally classified as thanatosis (=TI) and their cryptic mimicry is therefore included in TI. TI is also induced by mechanical stimulation. In water stick insects, TI occurred when the slender body was held or stroked with fingers or dropped on a table. TI continued for several minutes to several hours and was terminated by a light stimulus. On the other hand, in stick insects, TI is induced by light with a latency of 5–15 min and continues as long as the light is on. TI, induced by mechanical stimulation, is relatively short and the insect becomes habituated after several trails. As in beetles, TI is not easily interrupted by mechanical stimulation but is terminated by contact to the abdominal tip (Bässler 1983).

As for the mechanism of TI, insects in the three groups mentioned above share two physiological properties: one is that they showed an increase in muscle tonus and inhibition of righting reflex during TI so that they were unable to maintain their normal postures, and the other is that TI was abolished when the head ganglia (especially the brain) were removed from the body. This was strengthened by the fact that the posture in the posterior half of the body became loosened when the connectives were transected between the prothorax and the mesothorax (Bässler 1983). These findings suggested that TI is not a passive state but a state actively controlled by the head ganglia.

Apart from insects, some spiders showed TI in response to a vibratory stimulus such as shaking the web or tapping the box containing them (Robertson 1904). The occurrence and manner of TI were different among three species in line with their different behavioral properties. Such differences were due to the different controls by the brain.

As mentioned above, characteristics and mechanisms of TI in insects were studied almost a century ago. However, electrophysiological techniques have been used only in stick insects (Godden 1972; Godden 1974; Bässler 1983; Driesang and Büschges 1993). The mechanism of light-induced TI was studied at a neural level, and the results provided an important clue for understanding the mechanism of TI in stick insects (Chap. 9). However, the mechanism of TI induced by mechanical stimulation remains unknown.

Are there any other insects that are suitable for neuroethological study of TI? It is known that TI occurred in orthopteran insects such as locusts (Rabaud 1919; Faisal and Matheson 2001) and grasshoppers (Miriyala et al. 2013) and in crickets in the family Gryllidae such as the species *Nemobius sylvestris* and *Liogryllus campestris* (Rabaud 1919). We found that the field cricket *Gryllus bimaculatus* showed distinct TI by mechanical stimulation. This species has a suitable size of the nervous system for electrophysiology and has been one of the model animals for neuroethology (Huber et al. 1989). Thus, we conducted experiments on *Gryllus bimaculatus* to elucidate the neural mechanism of induction and maintenance of TI. In this chapter, we first describe the behavioral characteristics of TI in the cricket and then we show the neural basis of TI and propose its functional significance.

7.2 Time Course of TI

TI in the cricket is induced by simple methods in laboratory conditions. TI with all legs fully flexed is induced by gently pressing both sides of the pronotum and prothoracic legs for 3–5 s with the thumb and forefinger, upon which the cricket enters TI with all legs flexed (Fig. 7.1a, Nishino Lab 1 2018a). This immobility is defined as flexed-leg TI (Nishino et al. 1999). The appearance of flexed-leg TI in the cricket resembles in some species of coleopteran insects (Bleich 1928; van de Kamp et al. 2015). Occasionally, the provoked crickets resisted the restraints instead of assuming leg flexion but somehow entered a state of immobility with all knee joints opened while struggling, which is referred to as "weak TI" as described later.

A single bout of TI in the cricket comprises three phases: (1) induction phase, (2) maintenance phase, and (3) termination phase (Fig. 7.1b; Nishino and Sakai 1996; Nishino et al. 1999). Bodily movements monitored with a photo-coupler placed beside the abdomen (P, Fig. 7.1a) during flexed-leg TI indicated that the induction phase always entails a brief struggle upon restraint (Fig. 7.1b). The struggle stops immediately after all knee joints reach fully flexed positions (Fig. 7.1b; Nishino Lab 1 2018a). The onset of the maintenance phase is often indicated by cessation of
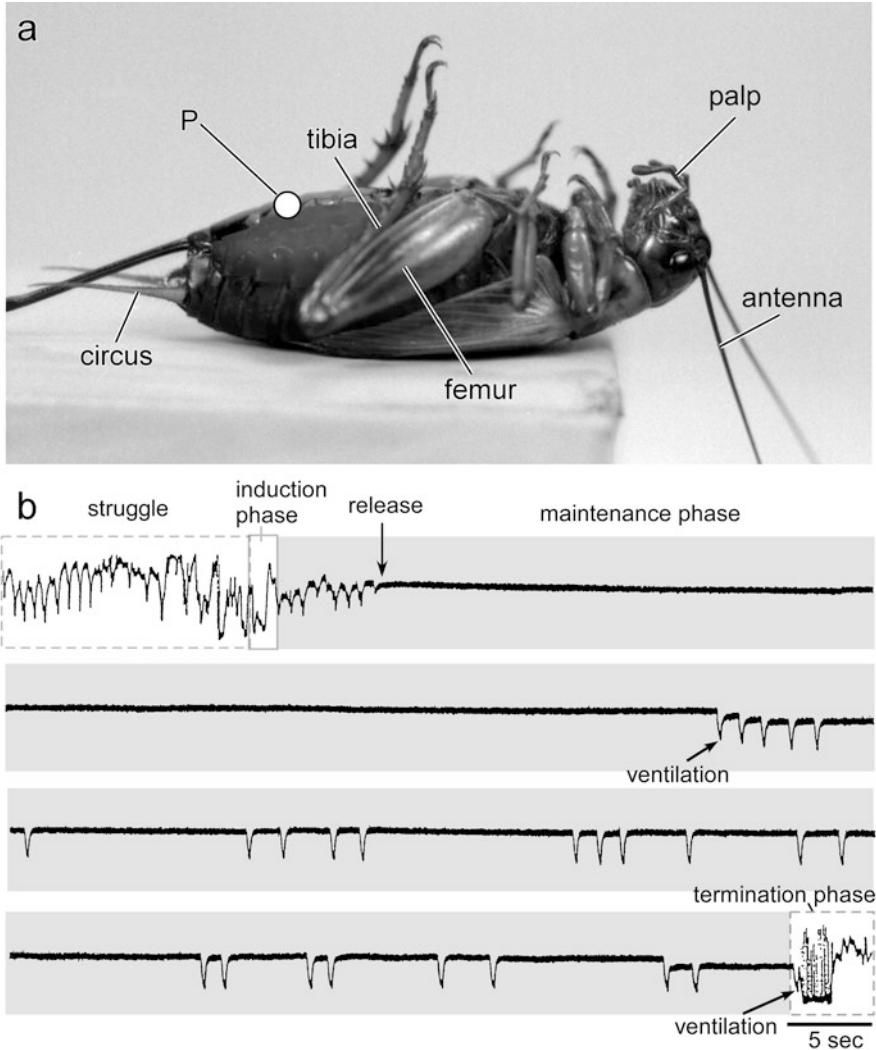
Fig. 7.1 Flexed-leg TI induced experimentally and its time course. (**a**) A cricket in TI showing a rigid posture with all knee joints fully flexed and the antennae and palpi extended in parallel. (**b**) A typical example of the time course of TI in which abdominal movements were monitored by a pair of photodiodes (P). During the induction phase, a brief struggle occurred under a restrained condition. During the maintenance phase, ventilatory movements stopped upon release of gentle pressure applied by fingers and recommenced 1 min after the release, and then ventilations became frequent. During the termination phase, a righting behavior occurred abruptly

ventilation movements in the abdomen, resulting in complete immobility of the entire body (Fig. 7.1b; Nishino Lab 1 2018a). Both antennae are straight and aligned in parallel with the rostral surface of the head (Fig. 7.1a). The palpi and legs are flexed (Fig. 7.1a). The hindlegs are pressed to the abdomen with the femurs directed

downward (Fig. 7.1a). The head is raised from the substrate, the abdomen is contracted, and the cerci are crossed. All of these features are indications that the entire body is tonically tensed. Postural adjustment including a righting reflex is inhibited during TI. Usually, abdominal ventilations occur more frequently as time passes (Fig. 7.1b), suggesting that the motor inhibition is progressively weakened toward the end of TI. Regardless of sex, the mean duration of the maintenance phase was 259 s (Table 7.1).

Recovery from the TI, which is expressed as a righting behavior for flexed-leg TI, occurs abruptly, often concurrent with a single ventilation movement in the abdomen (Fig. 7.1b). Immediately after righting behavior, the cricket showed environment searching behavior by vigorous palpation and antennation (Nishino Lab 1 2019a). When the cricket was disturbed, it tended to run very fast, suggesting the presence of a post-inhibitory rebound in the central nervous system.

7.3 Strong TI and Weak TI

The posture of flexed-leg TI varied from individual to individual and from trial to trial in the same individual (Nishino and Sakai 1996). We classified TI into two types (strong TI and weak TI) based on its appearance. In strong TI, all of the appendages including the legs and palpi were strongly flexed (Fig. 7.2a). The hindlegs were tightly pressed to the abdomen. Both antennae were straight and aligned parallel with the rostral surface of the head, which was raised from the substrate. When the body and appendages were touched with fingers, they were stiff and resistive. On the other hand, in the weak TI, the legs and palpi were flexed intermediately, the abdomen was less contracted, the head was raised only slightly, and the antennae were in different positions (Fig. 7.2b).

The durations of TI were measured. The duration of strong TI was significantly longer (264 ± 150 s) than that (92 ± 61 s) of weak TI. Both durations were longer than that (66 ± 55 s) in a quiescent state as a control that spontaneously occurred between searching movements (Nishino and Sakai 1996). The ventilation rate was

Table 7.1 Comparison of parameters in different immobile states induced by different methods

Immobile state	Leg flexion (degree)	Respiration rate (min)	Duration (s)	Auditory response (%)
Flexed-leg TI	2 ± 3	1 ± 2	259 ± 62	9.9
Extended-leg TI	61 ± 27[a]	2 ± 5	241 ± 63	10.0
TI in a natural habitat	/	3 ± 6	216 ± 96	/
Quiescence				
Extended-leg	66 ± 37[a]	3 ± 8	16 ± 32[a]	20.5[a]
Flexed-leg	0 ± 1[a]	9 ± 4[a]	368 ± 241	70.0[a]

[a]Presence of statistical significance with respect to the TI test group (Student's T-test). Thirty trials were conducted for each group of 10 crickets. /, not measured
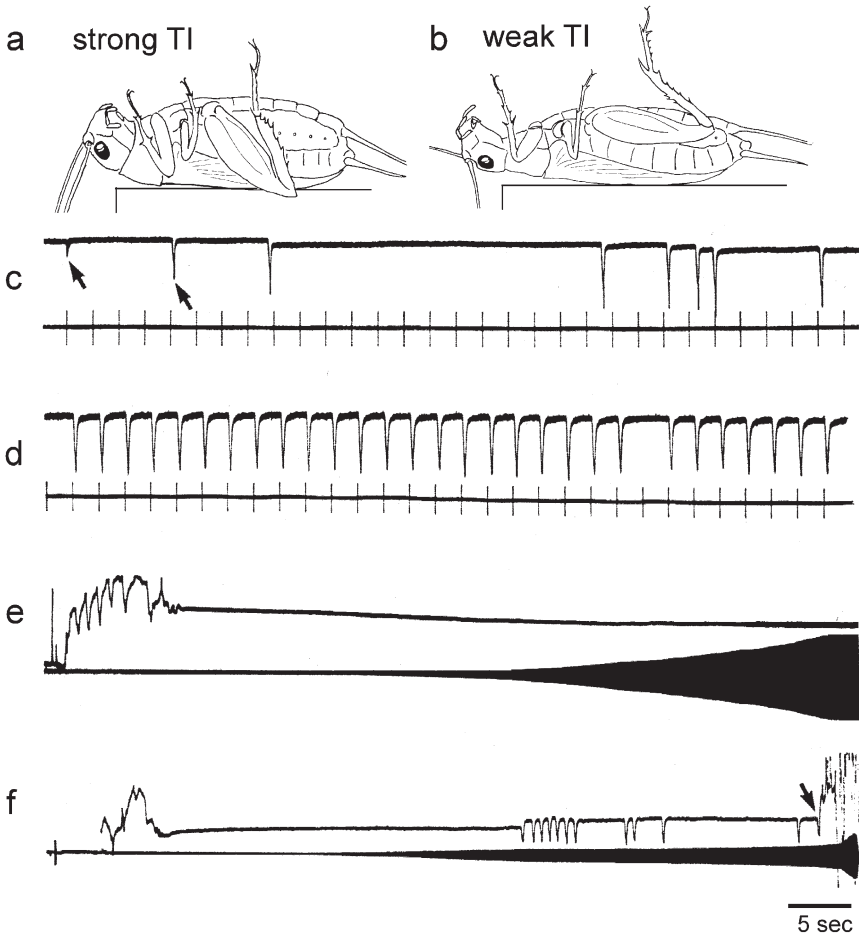
Fig. 7.2 Sensory responsiveness in strong TI and weak TI. (**a**) and (**b**) show strong TI and weak TI, respectively. In (**a**), the cricket is stiffened with all appendages rigidly flexed, while in (**b**), it shows weaker flexion in all body parts. In C ~ F, the upper trace shows abdominal ventilatory movements and the lower trace shows sound stimulation. (**c**) and (**d**) show abdominal ventilatory reactions to a series of sound pulses at 95 dB. The reaction is sporadic during strong TI and the amplitudes of the first two responses were smaller of the beginning of a bout (arrows, **c**), whereas ventilatory reactions occur at almost every stimulation during weak TI (**d**). In strong TI (**e**), the cricket remained immobile without ventilation when the sound intensity was gradually increased up to 103 dB at maximum. In weak TI (**f**), a ventilatory response first appeared at approximately 90 dB and then righting response took place at 98 dB (arrow)

lower in strong TI (1 ± 2 min^{-1}) than in weak TI (5 ± 4 min^{-1}). On the other hand, heart pulsation rate was higher in strong TI (105 ± 7 min^{-1}) than in weak TI (75 ± 8 min^{-1}) although heart pulsation rate in weak TI was still significantly higher than that (59 ± 8 min^{-1}) in the quiescent state (Nishino and Sakai 1996). Whether the increment of heart pulsation rate during TI reflects the struggle before the start of TI or represents the energy consumption for maintaining a low rate of

ventilations remains to be clarified. It is noteworthy that crickets exhibiting strong TI ran away more quickly than did those exhibiting a weak posture when disturbed.

7.4 Responsiveness to Sensory Stimuli During TI

In order to examine sensory responsiveness, various stimuli were applied to the cricket during the maintenance phase of TI. For auditory stimulation, a series of sound pulses elicited abdominal ventilations only sporadically in crickets exhibiting strong TI with initial responses (arrows) being weaker than the following responses (Fig. 7.2c). Some ventilations were not stimulus-coupled (Fig. 7.2c). In contrast, crickets in weak TI reacted with abdominal ventilations at nearly one-to-one correspondence to the sound pulse stimulation (Fig. 7.2d). With continuous sound stimulation, crickets in strong TI remained immobile in response to the stimulation even at the maximum intensity of 103 dB (Fig. 7.2e). In contrast, in weak TI, a bout of ventilations appeared at around 90 dB and righting behavior took place at 98 dB (arrow, Fig. 7.2f).

For mechanical stimulation, gentle contact to the body often elicited a ventilation movement but did not affect the maintenance of TI. No response occurred during gentle stroking of the antenna or cercus in strong TI. In the case of the resting state, the cricket instantly responded to contact stimulation to a cercus; that is, the cricket brushed off the stimulus with its hindleg. In the weak posture, stroking an antenna occasionally elicited oscillatory movements of antenna and stroking a cercus induced small leg movement or righting response. On the other hand, TI was terminated by prodding the cricket with a needle regardless of the type of TI (Nishino Lab 1 2020).

Visual stimuli such as intense cold-light illuminating compound eyes were not effective in either strong or weak TI.

The results revealed that responsiveness to sensory stimulation is generally decreased during TI compared with that during the resting state. The sensory responsiveness in strong TI is lower than that in weak TI, as shown in different depths of TI of stick insects (Bässler 1983).

7.5 Emergence of Catalepsy

An index characterizing TI in the cricket was the emergence of "catalepsy" (Fig. 7.3). Catalepsy is defined as "maintaining a new posture forcibly given by an experimenter" (Godden 1974; Bässler 1983; Driesang and Büschges 1993: see Chaps. 2, 8 and 9). During TI, catalepsy is observed in any appendages including the legs, antennae, and palpi. Catalepsy is phenomenally explained by resistance reflex (stretch reflex in vertebrates, Pflüger and Sillar 2013) and its rapid decay in skeletal muscles (Bässler 1983). For example, resistance reflex in the flexor tibiae
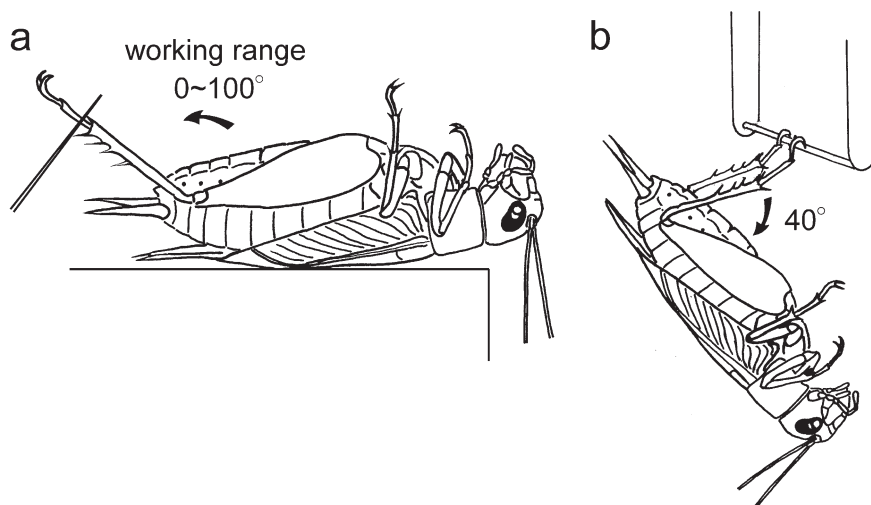
Fig. 7.3 Induction of catalepsy. (**a**) Catalepsy during lying. It was induced by displacing the metathoracic tibia to an arbitrary position. Catalepsy in an intact cricket occurs at any knee joint angle from 0° to ca. 100°. (**b**) Catalepsy during hanging. The cricket continued to be immobile with knee joints opened (ca. 40°) by the body weight

muscle occurs even when the tibia is slightly extended, and the reflex is therefore important for an animal to maintain the initial posture against mechanical perturbations (Field and Burrows 1982). Two types of catalepsy tests in crickets were feasible, though care was needed not to disturb the cricket during TI.

Catalepsy During Lying The metathoracic tibia was forcibly extended to an arbitrary position from full flexion (= 0°) to an extended position with a needle (Fig. 7.3a), held for ca. 3 s, then released to test the degree of imposed catalepsy (Nishino Lab 1 2019b). The experimenter initially felt resistance during displacement of the tibia because of the resistance reflex in the flexor tibiae muscle, but the reflex soon ceased while holding the tibia at the extended position. In the intact cricket, this test caused the F-T joint to be maintained at any angle up to ca. 100° (Fig. 7.3a). When the tibia was extended beyond this limit (maximum extension = 160°), it returned quickly to an angle of around 100°. The range of 0–100° is exactly the working range of the flexor tibiae muscle but not that of the extensor tibiae muscle, suggesting that only flexor muscles contribute to the emergence of catalepsy (Nishino et al. 1999).

Catalepsy During Hanging The cricket was hung by the tarsal claws of the metathoracic legs on a horizontal wire. The body weight caused the knee joints to open from 0° to 40–50°, which was maintained until recovery (Fig. 7.3b; Nishino Lab 1 2019c). This treatment allowed measurement of the strength of the resistance reflex in the flexor tibiae muscle (particularly in slow motor units) during the tonic exten-

sion stimulus. In this case, continual resistance reflex occurred to counter the continuous extension by the weight.

Another important feature that underlies the catalepsy is muscle rigidity. To maintain a given posture, skeletal muscles need to retain not only plasticity but also sufficient rigidity so that the knee joint is under complete immobilization. Emerging catalepsy explains why various animals including crickets maintain varied and sometimes even peculiar postures passively taken during TI.

7.6   Survey of Sense Organs Involved in Induction of TI

To facilitate an understanding of the neural substrate underlying the induction and maintenance of TI, we here introduce results of dysfunctioning of sensory elements. Insects are equipped with two types of mechanoreceptors in the body and appendages: exteroceptors and internal proprioceptors. Typically, the exteroceptors have short to long cuticular protrusions housing one mechanosensory neuron (Keil 1997). These receptors are functionally equivalent to nociceptors embedded in the skin of vertebrates (Abbracchio and Reggiani 2013). The primary internal proprioceptors are chordotonal organs distributed extensively in appendages and body segments that measure the position and movement of their own segments and vibrations via a chord-like cuticular apodeme (Field and Matheson 1998). There are various sizes and forms of chordotonal organs (Field and Matheson 1998), as exemplified by subgenual organs and tympanal organs specialized for detecting substrate vibration and airborne sound, respectively (Yack 2004; Nishino et al. 2019).

The central question for deciphering triggering mechanisms of TI is which sense organ detects physical restraint of the legs, inasmuch as TI in the cricket is commonly induced by restraint of the legs. In fact, amputation of the legs prevented crickets from entering TI; more legs ablated lead to more difficulty in entering TI (Nishino and Sakai 1996), indicating that the total amount of sensory input from legs is related to inductivity of TI. Amputation of three hemilateral legs resulted in reduced inductivity of TI, similar to results when all six legs were amputated, suggesting that bilateral restraint of legs is important for induction of TI (Nishino and Sakai 1996).

Ablation of various exteroceptors on the body surface revealed that sense organs sensitive to deformation of the exoskeleton, such as campaniform sensilla on prothoracic legs (Fig. 7.4a) and short trichoid sensilla numerously distributed on the pronotum (Fig. 7.4b, c, d), participate in the leg flexion reflex (Nishino and Sakai 1996). However, extended-leg TI still occurred in animals with these exteroceptors eliminated, suggesting that exteroceptors mediate flexion reflex but are not critical for triggering TI. In contrast, ablation of the internal proprioceptors, femoral chordotonal organs (FCOs), in all six legs (see Fig. 7.4a for the location) somehow mimicked the results of ablation of the entire leg, preventing the induction of TI.
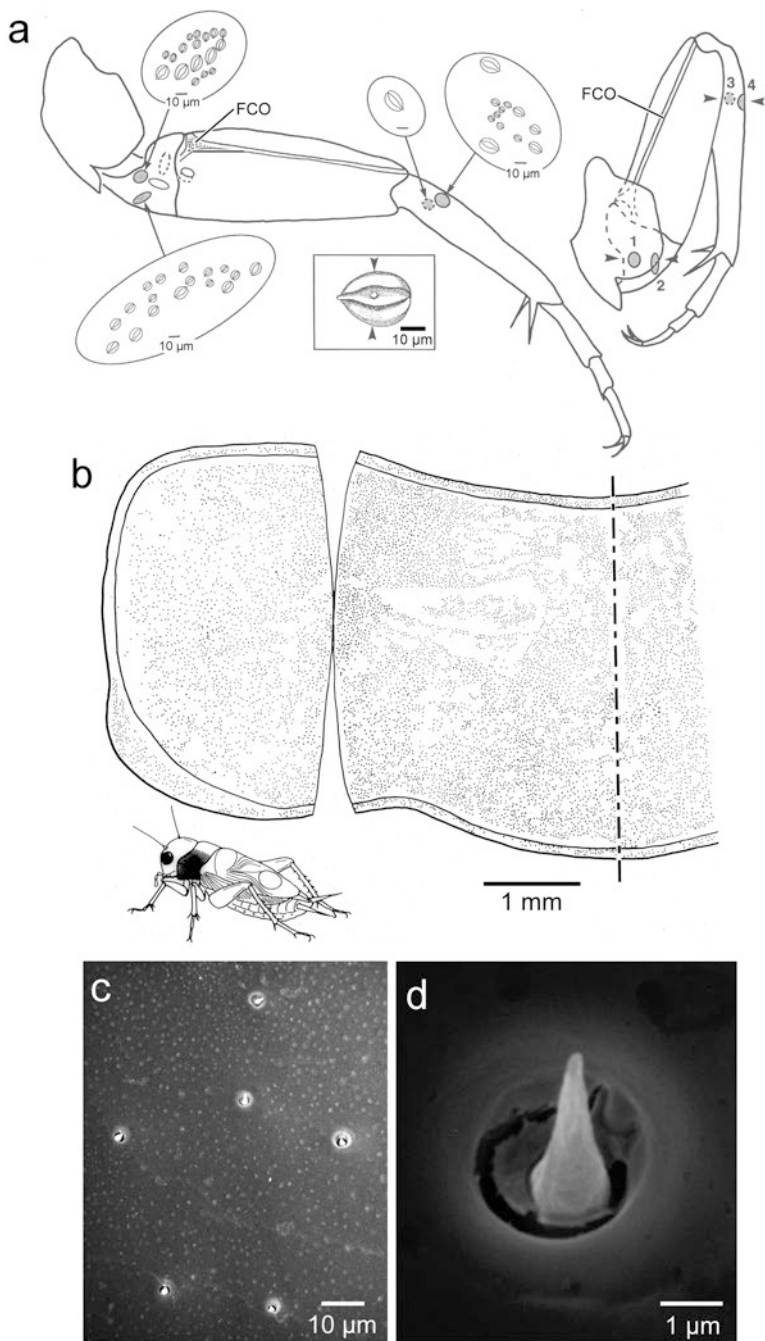
Fig. 7.4 Mechanoreceptors that elicit leg flexion reflex in the prothoracic leg and the pronotum. (**a**) Groups of campaniform sensilla indicated by gray (individual sensilla magnified in circles in

7.7 Contribution of the Central Nervous System to TI

In order to evaluate the contribution of the central nervous system to maintenance of an immobile state, cooling of the brain was performed during TI by placing a small piece of dry ice on the frontal cuticle of the head. Crickets showed ventilatory movements as soon as cooling started. Such an early ventilation response can be taken as an indication of the commencement of neural inactivation because a similar effect was observed immediately after the connective cut between the brain and subesophageal ganglion. The latency of the ventilatory response was 5 ± 3 s (n = 10), which was much shorter than the latency of 150 ± 95 s in the control (non-cooled) animals. The duration of TI was 6 ± 3 s (n = 10), which was also much shorter than the duration of 288 ± 150 s in the control animals. Separate experiments (see Materials and methods in Nishino and Sakai 1996) indicated that the brain temperature was lowered to about 11 °C at 5 s after the start of cooling, while it was 16 °C on the surface of the suboesophageal ganglion after 1 min. Synaptic transmission or spike conduction in neurons of the head ganglia was not severely interrupted until the head temperature was lowered below about 10 °C. These findings indicated that the effect of head cooling on termination of TI is caused by inactivation of the brain and suggested that the brain is crucial for the cricket to maintain TI.

It is known that the head ganglia play an important role in maintenance of TI in insects. In the water stick insect, death-feigning did not continue for more than several seconds after the brain had been removed (Holmes 1906). The removal of the brain abolished twig mimesis in the stick insect because locomotor activity was increased (Godden 1972). Our results in crickets are consistent with those in other insects for the role of the brain in maintenance of TI (see Introduction). It was reported that there is a command interneuron in the hemi-connective originating from head ganglia in the crayfish (named statue fiber) that evokes a sudden cessation of ongoing movements during electrical stimulation (Bowerman and Larimer 1974). A pair of command neurons that evoke cessation of ongoing movements by optogenetic activation have been identified recently in fruit flies (Zacarias et al. 2018). Command-like neurons playing a similar role in movement inhibition may be present in the cricket. In our preliminary study (Nishino and Sakai 1991), it was found that some descending interneurons from the head ganglia were discharging throughout the period of TI, while many others ceased to discharge, supporting the view that the brain in the cricket may contain command-like fibers responsible for induction and maintenence of TI, as in other arthropods.

Fig. 7.4 (continued) the left figure) were more effective for eliciting the flexion reflex than were those indicated by white, presumably because the former groups are mechanically compressed when prothoracic legs are pressed laterally (arrowheads in the right figure). One representative campaniform sensillum is illustrated in the rectangle, indicating the direction of the force that was effective for stimulating the sensillum. The location of the femoral chordotonal organ (FCO) is also indicated in **a**. (**b**) Each dot in B represents a single trichoid sensillum in the left half of the pronotum (inset). (**c**) and (**d**) show low-power and high-power photos of trichoid sensilla and a single sensillum taken by a scanning electron microscope

7.8   TI that Occurs in Natural Settings

TI can be induced in more natural situations in which the ventral side of the thorax and abdomen was in contact with the substrate (Nishino and Sakai 1996). Under experimental conditions, TI occurs in conjunction with fleeing when disturbed or urged by an experimenter: a physical restraint when the cricket attempts to crawl into a small tunnel made on the substrate makes the cricket immobilize (Fig. 7.5a; Nishino Lab 1 2018b). The legs were immobilized at extended positions as restrained between the substrate and the ceiling (61° ± 27°, n = 30), thus designated as extended-leg TI (Fig. 7.4b). The duration of TI, ventilation rate, and responsiveness to sensory stimulation are similar to those in flexed-leg TI, suggesting that both states are basically identical (Table 7.1). When the extended-leg TI was terminated, the cricket raised its body with the palpi and antennae moving and began to walk slowly with searching movements (Nishino Lab 1 2018b). When the imposed leg restraint was insufficient due to a large space on the substrate, the cricket never entered TI and walked out from the tunnel. These results indicated that TI in the cricket always entails a self-generated restraint resulting from the flexion reflex or struggling in a narrow space. An adequate stimulus to elicit TI in crickets is therefore restraint of the legs, and a minimum pressure not to permit resistive leg movements appears to be effective for smoothly guiding the cricket into TI.

In the natural habitat, we observed that TI indeed occurred when the cricket (*G. bimaculatus* in Okinawa Islands of Japan) attempted to hide by crawling into a small opening made by pebbles or roots of plants (Fig. 7.5c). This is supposed to occur by the same mechanism as that in the extended-leg TI. The sudden stopping by the cricket is probably effective for dazzling the eyes of predators (Chap. 1; Channel Wani 2020).

7.9   Differences in TIs and Escape Reactions in Related Species

Variations in inductivity and duration of TI were observed in four species of field crickets. *G. bimaculatus* and the genus *Teleogryllus* species, which are phylogenetically close (Chintauan-Marquier et al. 2016) and have similar body sizes. However, *G. bimaculatus* prefers to inhabit a gravel-rich field, whereas *T. emma* inhabits a grass field. *G. bimaculatus*, which has shorter legs and rarely jumps, rushed into a small opening between pebbles and was immobilized for a while when urged by experimenters (Fig. 7.6a). In contrast, *T. emma* and *T. occipitalis*, both having longer legs relative to their body size, ran fast in combination with jumps when disturbed (Fig. 7.6b). *T. infernalis*, another *Teleogryllus* species tends to live in a gravel-rich field as does *G. bimaculatus*. However, *T. infernalis* stops only briefly upon restraint in a narrow space and tries to crawl deeper to search for a safer place. Since *T. infernalis* is more agile than *G. bimaculatus,* finding safe places might be
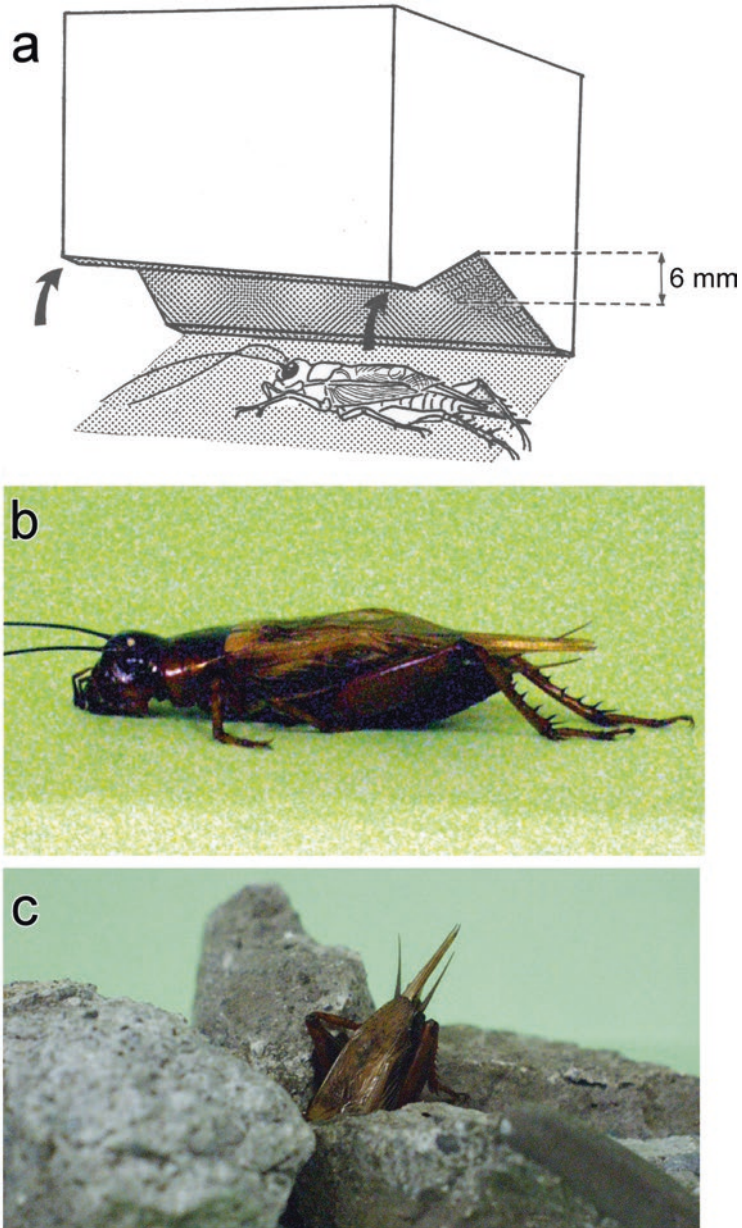
Fig. 7.5 TIs in natural settings. (**a**) TI occurred when the cricket crawled into a small tunnel made by a manipulator base and the substrate. Note that the posture in TI is maintained even after removal of the manipulator base. (**b**) A picture of the cricket taken in **a**. (**c**) TI occurred in a space between pebbles

more adaptive for *T. infernalis* than immobilizing in exposed places. The occurrence rates of TI in the three *Teleogryllus* species were lower and the periods of TI were shorter than those in *G. bimaculatus* (Fig. 7.6c, Yukari Konishi, unpublished data). These results suggest that TI in crickets depends on anti-predator strategies linked to their habitats.
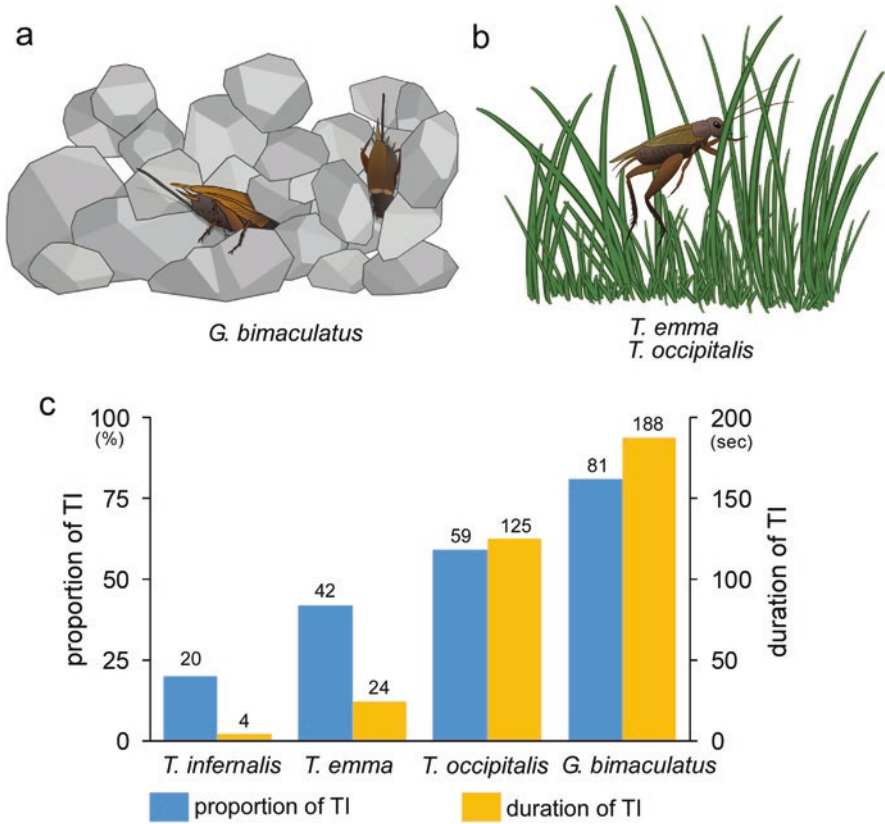

Fig. 7.6 Different escape strategies linked to habitats in four species of field crickets. (**a**) *G. bimaculatus* prefers to inhabit a gravel-rich field and tends to rush into a small opening between stones or between roots of grasses when disturbed and exhibits TI close to the entrance. *T. infernalis* inhabits a gravel-rich field and tends to crawl into small spaces to hide. (**b**) *T. emma* and *T. occipitalis* inhabit grassland and escape by jumping mixed with running. (**c**) Comparisons of the proportions of crickets showing TI and the durations of TI in the four species of crickets. Note that two species with a higher proportion of TI had longer duration of TI

7.10 Summary

TI in the cricket has the following characteristics: (1) TI is induced by physical restraint of the legs, (2) the duration of TI is several seconds to several minutes, (3) during TI, responsiveness to sensory stimulation is decreased, (4) TI is terminated spontaneously or by a mechanical disturbance, (5) catalepsy emerges during TI, (6) TI is used as one of the anti-predator strategies in conjunction with fleeing behavior. Many of these findings for TI in the cricket are similar to those for vertebrates such as birds and mammals (Ratner 1967).

Regarding the mechanisms of TI in the cricket, chordotonal organs which are internal proprioceptors are critically important for inducing TI and the brain is necessary for maintaining immobility of the whole body. In Chap. 8, concrete roles of chordotonal organs in induction and postural control of TI and motor output characterizing TI are described in more detail.

References

Abbracchio MP, Reggiani AM (2013) Pain and nociception. In: Neurosciences - from molecule to behavior: a university textbook. Springer, Berlin, pp 445–459

Bässler U (1983) Neural basis of elementary behavior in stick insects, vol 10. Springer, Berlin

Bleich OE (1928) Thanatose und hypnose bei coleopteren. Z Morphol Okol Tiere 10:1–61

Bowerman R, Larimer J (1974) Command fibres in the circumoesophageal connectives of cray-fish: I. Tonic Fibres J Exp Biol 60:95–117

Chintauan-Marquier IC, Legendre F, Hugel S, Robillard T, Grandcolas P, Nel A, Zuccon D, Desutter-Grandcolas L (2016) Laying the foundations of evolutionary and systematic studies in crickets (Insecta, Orthoptera): a multilocus phylogenetic analysis. Cladistics 32:54–81

Driesang RB, Büschges A (1993) The neural basis of catalepsy in the stick insect. IV: properties of nonspiking interneurons. J Comp Physiol A 173:445–454

Fabre JH (1910) Souvenirs entomologiques. De Lagrave, Paris

Faisal AA, Matheson T (2001) Coordinated righting behaviour in locusts. J Exp Biol 204:637–648

Field L, Burrows M (1982) Reflex effects of the femoral chordotonal organ upon leg motor neurones of the locust. J Exp Biol 101:265–285

Field LH, Matheson T (1998) Chordotonal organs of insects. In: Advances in insect physiology, vol 27. Elsevier, Amsterdam, pp 1–228

Godden DH (1972) The motor innervation of the leg musculature and motor output during thanatosis in the stick insect *Carausius morosus* Br. J Comp Physiol 80:201–225

Godden DH (1974) The physiological mechanism of catalepsy in the stick insect *Carausius morosus* Br. J Comp Physiol 89:251–274

Holmes SJ (1906) Death feigning in Ranatra. J Comp Neurol 16:200–216

Huber F, Moore TE, Loher W (1989) Cricket behavior and neurobiology. Cornell University Press, Ithaca and London

Keil TA (1997) Functional morphology of insect mechanoreceptors. Microsc Res Tech 39:506–531

Mangold E (1920) Die Tierische Hypse (einschliesslich tnische, tetranische und Totestell-Reflexe, Reaktions-Akinese der Protisten). Erg Physiol 18:79–117

Miriyala A, Dutta-Gupta A, Joseph J (2013) Muscle group dependent responses to stimuli in a grasshopper model for tonic immobility. Biol Open 2:1214–1222

Nishino H, Sakai M (1991) Neural activities during thanatosis in the crickets. Zool Sci 8:1040

Nishino H, Sakai M (1996) Behaviorally significant immobile state of so-called thanatosis in the cricket *Gryllus bimaculatus* DeGeer: its characterization, sensory mechanism and function. J Comp Physiol A 179:613–624

Nishino H, Sakai M, Field LH (1999) Two antagonistic functions of neural groups of the femoral chordotonal organ underlie thanatosis in the cricket *Gryllus bimaculatus* DeGeer. J Compar Physiol A: Sens Neural Behav Physiol 185:143–155

Nishino H, Domae M, Takanashi T, Okajima T (2019) Cricket tympanal organ revisited: morphology, development and possible functions of the adult-specific chitin core beneath the anterior tympanal membrane. Cell Tissue Res 377:193–214

Pflüger HJ, Sillar K (2013) Motor control. In: Neurosciences - from molecule to behavior: a university textbook. Springer, Cham, pp 479–524

Rabaud E (1919) L'immobilisation reflexe et l'activite normale des arthropods. Bull Biol France Belg 53:421–436

Ratner S (1967) Comparative aspects of hypnosis. In: Handbook of clinical experimental hypnosis. Macmillan, New York

Robertson TB (1904) On the "sham-death" reflex in spiders. J Physiol 31:410–417

Steiniger F (1936) Die Biologie der sog. "Tierischen Hypnose". In: Ergebnisse der Biologie. Springer, Berlin, pp 348–451

van de Kamp T, Cecilia A, dos Santos Rolo T, Vagovic P, Baumbach T, Riedel A (2015) Comparative thorax morphology of death-feigning flightless cryptorhynchine weevils (Coleoptera: Curculionidae) based on 3D reconstructions. Arthropod Struct Dev 44:509–523

Yack J (2004) The structure and function of auditory chordotonal organs in insects. Micros Res Tech 63:315–337

Zacarias R, Namiki S, Card GM, Vasconcelos ML, Moita MA (2018) Speed dependent descending control of freezing behavior in *Drosophila melanogaster*. Nat Commun 9:3697

YouTube

Channel Wani (2020) Predatory behavior of a toad against filed crickets. In: YouTube. https://www.youtube.com/watch?v=KOsQ1zLBF2E <https://www.youtube.com/watch?v=KOsQ1zLBF2E>

Nishino Lab 1 (2018a) Flexed-leg TI. In: YouTube. https://www.youtube.com/watch?v=FlbCxmpU8I0 <https://www.youtube.com/watch?v=FlbCxmpU8I0>

Nishino Lab 1 (2018b) Extended-leg TI. In: YouTube. <https://www.youtube.com/watch?v=jskKf9SkowE>

Nishino Lab 1 (2019a) Awakening from TI. In: YouTube. https://www.youtube.com/watch?v=flrbXVsYMJ8 <https://www.youtube.com/watch?v=flrbXVsYMJ8>

Nishino Lab 1 (2019b) Catalepsy during lying. In: YouTube. <https://www.youtube.com/watch?v=bKhETrj6rKg>

Nishino Lab 1 (2019c) Catalepsy during hanging. In: YouTube. <https://www.youtube.com/watch?v=fEUGwFWLuGU>

Nishino Lab 1 (2020) Awakening from TI by mechanical disturbance. https://www.youtube.com/watch?v=DSzCr2AKFKs