

# Chapter 6

## Vibration-Induced Immobility in Coleopteran Insects



Takuma Takanashi and Wataru Kojima

**Abstract** Many insects demonstrate immobility, such as death feigning (tonic immobility) and freeze responses in the context of interactions within and between species. Immobility is induced by environmental information, including substrate vibrations generated by predators or conspecifics. In this chapter, we review immobility induced by vibrations in the order Coleoptera. Tonic immobility and freeze responses are observed in 18 coleopteran families, particularly in characteristic postures during tonic immobility with extended or flexed legs. Chordotonal sensory organs located in the legs play important roles for detecting vibrations and triggering tonic immobility. Vibration-induced immobility has various functions, e.g., defense from predators, and interactions within the species. As individual case studies, behavioral mechanisms for immobility related to vibrations have been described in the orders Cerambycidae, Nitidulidae, and Scarabaeidae. Adults of a longicorn beetle *Monochamus alternatus* (Cerambycidae) detect vibrations on their host plant via leg chordotonal organs. They show freeze or startle responses to vibrations, presumably for conspecific and predator recognition. Larvae of a group living beetle *Trypoxylus dichotomus* (Scarabaeidae) show freeze responses to vibrations produced by both conspecific pupae and mole predators in the soil. Vibrational interactions and freeze responses among larvae and predators in Scarabaeidae also shed light on the evolution of deceptive communication in *T. dichotomus*.

**Keywords** Vibration · Tonic immobility · Freezing · Chordotonal organ · Predator · Cerambycidae · Scarabaeidae

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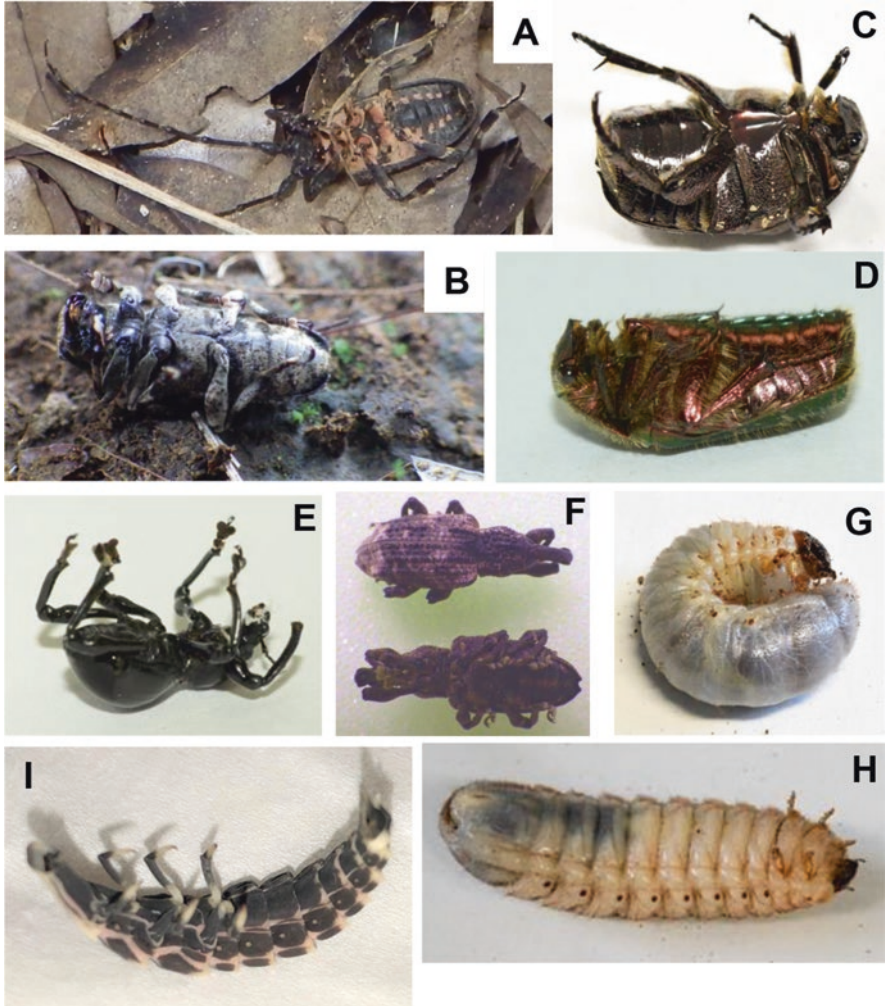
## 6.1 Introduction

### 6.1.1 *Vibration-Induced Immobility*

Vibrations transmitted through substrates are one of the essential channels that insects use to detect environmental information (Greenfield 2002; Hill 2008). Insects exhibit various behaviors in response to mechanical stimuli such as vibrations (Greenfield 2002; Hill 2008; Takanashi et al. 2019). In many insects, immobility is induced by mechanical stimuli. Immobility includes two reactions: tonic immobility and freezing (Chap. 1). Tonic immobility (TI) is also called as death feigning or thanatosis. Humphreys and Ruxton (2018) define TI as motionless posture by a prey individual triggered by physical contact or very close proximity of a predator. Fabre (1900) reported for the first time that tenebrionid beetles demonstrate TI with a range of several tens of minutes. In coleopterans and other insects, the typical posture during TI consists of either legs extended irregularly or flexed (Fig. 6.1). On the other hand, freezing is a kind of startle response, which is a short-latency, abrupt movement induced by mechanical or other stimuli (Friedel 1999). For instance, a male cricket demonstrates a “silencing reaction” during sound production in response to vibrations (Dambach 1989). In coleopterans and other insects, cessation of walking and other movement in response to stimuli is classified as freezing (Kojima et al. 2012b; Tsubaki et al. 2014; Takanashi et al. 2016). In Chap. 1, freezing is used only in the context of predator–prey interactions from an ecological point of view. In this chapter, however, freezing is also described in the context of social communication. To discriminate the two, “freeze response” is used in this chapter in the context of predator–prey interactions and social communication.

### 6.1.2 *Vibration-Induced Immobility and Communication*

Subsequent to discoveries of vibrational sexual communications in hemipteran insects (Ichikawa and Ishii 1974), vibrations have also been found to play essential roles in the context of predator–prey interactions and other social communications among insects (Greenfield 2002; Hill 2008; Takanashi et al. 2019). Indeed, vibrations induce TI and freeze response in beetles (Acheampong and Mitchell 1997; Kojima et al. 2012b; Tsubaki et al. 2014; Kiyotake et al. 2014; Takanashi et al. 2016; Kishi and Takanashi 2019a), fruit flies (Fabre et al. 2012; Mazzoni et al. 2013), and honeybees (Michelsen et al. 1986; Kirchner 1993; Nieh 1993). For instance, *Drosophila melanogaster* uses both vibration and sound signals for sexual communication. Male vibration signals generated by shivering induce a freeze response in females to accept copulation (Fabre et al. 2012; Mazzoni et al. 2013). As another example, worker honeybees of *Apis mellifera* produce a vibrational “stop signal” during the waggle dance to freeze other workers and leave the nest (Michelsen et al. 1986; Kirchner 1993; Nieh 1993).



**Fig. 6.1** Different postures displayed in tonic immobility in Coleoptera. Adults of (a, b) Cerambycidae, (c, d) Scarabaeidae, and (e, f) Curculionidae are shown. Adults of (a) *Moechotypa diphyis*, (c) *Protaetia brevitarsis brevitarsis*, and (e) *Pachyrhynchus infernalis* exhibit extended legs. Adults of (b) *Mesosa (Aplocnemia) longipennis*, (d) *Cetonia pilifera*, and (f) *Dyscerus perforates* exhibit flexed legs. Larvae of (g) *Trypoxylus dichotomus* (Scarabaeidae), (h) *Dicronorhina derbyana* (Scarabaeidae), and (i) *Pyrocoelia atripennis* (Lampyridae) are shown. (a) was adapted from a photo published by Takanashi and Nishino (2021)

## 6.2 TI and Freeze Responses in Coleoptera

### 6.2.1 Survey of TI and Freeze Responses

Coleoptera is the largest insect order, and includes numerous species exhibiting TI and freeze responses (Table 6.1, Fig. 6.1). Based on the findings of Bleich (1928) and others, we surveyed 49 genera from 18 families exhibiting TI with different postures and freeze responses to vibrations (Table 6.1), alternatively called thanatosis or death feigning in the literature (e.g., Bleich 1928; Crowson 1981). Acheampong and Mitchell (1997) also classified the freeze response to vibrations as quiescence. TI occurs in adults and larvae of 18 families, whereas freeze responses occur in only five of those families. Adults exhibit TI postures with two different leg positions, either legs extended irregularly or legs flexed regularly (Bleich 1928; Crowson 1981). Even within same families, both of these postures are adopted. Six families are known to exhibit extended postures (Brentidae, Silphidae, Carabidae, Histeridae, Geotrupidae, and Anobiidae), five families exhibit flexed postures (Nitidulidae, Elateridae, Coccinellidae, Byrrhidae, and Dermestidae), and six other families exhibit extended and flexed postures dependent on individual species (Cerambycidae, Tenebrionidae, Scarabaeidae, Chrysomelidae, Curculionidae, and Lucanidae).

### 6.2.2 TI and Other Behavior in Coleopteran Adults

In the family Cerambycidae (Table 6.1), *Moechotypa diphysis* exhibits a TI posture with femoro-tibial joints in extended positions at various angles and extended antennae after dropping from a host tree (Takanashi and Nishino 2021; Fig. 6.1a). On the other hand, *Mesosa (Aplocnemis) longipennis* demonstrates a flexed posture after dropping from a tree (Fig. 6.1b). In the Scarabaeidae and Curculionidae families, extended postures are observed in *Protaetia brevitarsis* and *Pachyrhynchus infernalis* (Fig. 6.1c, e), whereas flexed postures are observed in *Cetonia pilifera* and *Dyscerus perforatus* (Fig. 6.1d, f). In Curculionidae, adults of *Eusepes postfasciatus* and *Erodiscus proximus* make stridulatory sounds during TI with flexed postures (Tatsuta and Kumano 2015; Gaiger and Vanin 2006) (Table 6.1). *Erodiscus proximus* produces sounds from the elythro-femoral stridulatory organ for 15 s during TI lasting 60 s or more (Gaiger and Vanin 2006). This sound, in conjunction with TI, might play roles in defense from predators. In the family Chrysomelidae, Caprinera (1976) observed different proportions of TI, stridulation, and other behaviors between *Crioceris asparagi* and *C. duodecimpunctata*. *Crioceris asparagi* frequently exhibits dropping and/or TI with flexed postures and stridulation, whereas *C. duodecimpunctata* take flight and stridulate easily with infrequent TI. These observations suggested that both TI and sound production can serve as multiple defenses against predators. Also, chemical defense by the exocrine gland secretion,

**Table 6.1** Tonic immobility (TI) and freeze responses in Coleoptera. TI in adults with legs extended or flexed, TI in larvae, and freeze responses in adults and larvae in response to vibrations are shown

Family	Species	Tonic immobility	Freeze responses	References
Cerambycidae	<i>Moechotypa diphysis</i>	Adult extended	Adult	Takanashi and Nishino (2021)
	<i>Mesosa (Aplocnemina) longipennis</i>	Adult flexed	–	Takanashi pers.com
	<i>Hippopsis lemniscata</i>	Adult flexed	–	Bleich (1928)
	<i>Monochamus alternatus</i>	None	Adult	Takanashi et al. (2016)
	<i>Paraglenea fortunei</i>	None	Adult	Tsubaki et al. (2014)
	<i>Eburia ulkei</i>	Adult extended	–	Chemsak and Linsley (1970)
Scarabaeidae	<i>Trypoxylus dichotomus</i>	Larvae	Larvae	Kojima et al. (2012a, b)
	<i>Protaetia</i> spp. ( <i>P. orientalis</i> , <i>P. cuprea</i> , <i>P. brevitarsis brevitarsis</i> )	Adult extended, larvae	Larvae	Kojima et al. (2012a), pers.com, Bleich (1928)
	<i>Dicronorhina derbyana</i>	Larvae	Larvae	Kojima et al. (2012a)
	<i>Cetonia pilifera</i>	Adult flexed, larvae	–	Kojima pers.com
	<i>Taeniodera nigricollis</i>	Adult flexed	–	Kojima pers.com
	<i>Anomala albopilosa</i>	–	Larvae	Kojima et al. (2012a)
	<i>Phyllopertha horticola</i>	Adult extended	–	Bleich (1928)
	<i>Apogonia</i> sp.	Adult flexed	–	Kojima pers.com
	<i>Holotrichia kiotonensis</i>	Adult extended	–	Kojima pers.com
	<i>Onthophagus</i> sp.	Adult flexed	–	Kojima pers.com
Tenebrionidae	<i>Tribolium castaneum</i>	Adult flexed <sup>a</sup> , larvae	–	Kiyotake et al. (2014)
	<i>Blaps mortisaga</i>	Adult extended	–	Bleich (1928)
	<i>Zophobas atratus</i>	Adult extended	–	Nishino pers.com
Nitidulidae	<i>Phenolia (Lasiodites) picta</i>	Adult flexed <sup>a</sup> , larvae	–	Kishi and Takanashi (2019a, b)
Curculionidae	<i>Eusepes postfasciatus</i>	Adult flexed <sup>b</sup>	–	Tatsuta and Kumano (2015)
	<i>Trigonopterus vandekampi</i>	Adult flexed	–	de Kamp et al. (2014)
	<i>Erodiscus proximus</i>	Adult flexed <sup>b</sup>	–	Gaiger and Vanin (2006)

(continued)

**Table 6.1** (continued)

Family	Species	Tonic immobility	Freeze responses	References
	<i>Dyscerus perforatus</i>	Adult flexed	–	Ichikawa et al. (1987)
	<i>Lixus</i> sp.	Adult extended		Kojima pers.com
	<i>Pachyrrhynchus infernalis</i>	Adult extended		Kojima pers.com
Chrysomelidae	<i>Callosobruchus maculatus</i>	Adult flexed	–	Ohno and Miyatake (2007)
	<i>Crioceris</i> spp. ( <i>C. asparagi</i> and <i>C. duodecimpunctata</i> )	Adult flexed <sup>b</sup>	–	Caprineria (1976)
	<i>Leptinotarsa decemlineata</i>	–	Adult	Acheampong and Mitchell (1997), Metspalu et al. (2002)
	<i>Phaedon brassicae</i>	Adult flexed, larvae	–	Matsubara and Sugiura (2018)
	<i>Zabrotes subfasciatus</i>	Adult flexed	–	Cardoso and Mendonça (2019)
	<i>Galeruca tanacetii</i>	Adult extended	–	Bleich (1928)
Brentidae	<i>Cylas formicarius</i>	Adult extended	–	Miyatake (2001), Kuriwada et al. (2009)
Elateridae	<i>Agriotes</i> spp. ( <i>A. lineatus</i> , <i>A. obscurus</i> , <i>A. sordidus</i> , and <i>A. ustulatus</i> )	Larvae	–	Ritter et al. (2016)
	<i>Selatosomus aeneus</i>	Adult flexed	–	Bleich (1928)
Lucanidae	<i>Lucanus cervus</i>	Adult extended	–	Bleich (1928)
	<i>Dorcus rectus</i>	Adult flexed	–	Kojima pers.com
Coccinellidae	<i>Epilachna varivestis</i>	Adult flexed	–	Happ and Eisner (1961)
	<i>Coccinella septempunctata</i>	Adult flexed	–	Bleich (1928)
Silphidae	<i>Silpha obscura</i>	Adult extended, larvae	–	Bleich (1928)
	<i>Phospuga atrata</i>	Adult extended, larvae	–	Bleich (1928)
	<i>Nicrophorus quadripunctatus</i>	Adult extended	–	Kojima pers.com
Lampyridae	<i>Pyrocoelia</i> spp. ( <i>P. fumosa</i> , <i>P. atripennis</i> )	Larvae	–	Ohba (2007), Kojima pers.com
Carabidae	<i>Broscus cephalotes</i>	Adult extended	–	Bleich (1928)

(continued)

**Table 6.1** (continued)

Family	Species	Tonic immobility	Freeze responses	References
Histeridae	<i>Hister quadrinotatus</i>	Adult extended	–	Bleich (1928)
Geotrupidae	<i>Geotrupes silvaticus</i>	Adult extended	–	Bleich (1928)
Byrrhidae	<i>Byrrhus pilula</i>	Adult flexed	–	Bleich (1928)
Dermestidae	<i>Dermestes lardarius</i>	Adult flexed, larvae	–	Bleich (1928)
Anobiidae	<i>Anobium striatum</i>	Adult extended	–	Bleich (1928)

<sup>a</sup>Vibration-induced TI.

<sup>b</sup>TI with stridulation.

so-called reflex bleeding, during TI has been observed in Chrysomelidae, Coccinellidae, and Lampyridae (Happ and Eisner 1961; Caprineria 1976; Ohba 2007).

It has been assumed that the flexed and extended postures could play roles in defense against predators, but there is no direct evidence for defense with regard to the postures in Coleoptera. In the pygmy grasshopper *Criotettix japonicus*, extended posture with the hind legs, pronotum, and lateral spines is crucial to avoid being swallowed by frog predators (Honma et al. 2006). Thus, coleopteran extended postures may function as a defense against large predators. A flexed posture could make insects more difficult for bird and insect predators to hold or pick up, compared to postures with extended legs. Apart from the posture, Miyatake and his colleagues elegantly revealed that the length of TI in *T. castaneum* adults (Tenebrionidae) played an important role in defense against jumping spider predators *Hasarius adansonii* (Miyatake et al. 2004, Chap. 8). As these spiders attack and eat only active beetles, immobile beetles are able to avoid predation. Induction and arousal of TI in *T. castaneum* are triggered by 33–60 Hz vibrations (Table 6.1) (Kiyotake et al. 2014; Miyatake et al. 2019), which are supposed to be generated by approaching predators. Future studies are necessary to address the adaptive significance of TI with different postures across the order Coleoptera.

### 6.2.3 TI and Freeze Responses in Coleopteran Larvae

To our knowledge, larvae in eight families (Tenebrionidae, Scarabaeidae, Nitidulidae, Chrysomelidae, Elateridae, Silphidae, Lampyridae, and Dermestidae) are more likely to exhibit postures with extended legs during TI (Table 6.1; Fig. 6.1g–i). For instance, larvae of *Pyrocoelia atripennis* (Lampyridae) display lengthy TI, with extended legs and a ventrally curved abdomen in response to physical contact (Ohba 2007). Scarabaeid larvae show unique postures during TI; for example, larvae of *Protaetia orientalis* and *Cetonia pilifera* roll up their body, as



with some woodlice and millipedes, while those of *Dicronorhina derbyana* and *Pseudotorynorrhina japonica* stretch out their body (Fig. 6.1h). The posture of some Dynastinae (e.g., *Trypoxylus dichotomus*) is U-shaped (Fig. 6.1g), intermediate between the “roll up” type and “stretch” postures. Despite this diversity, the insects’ body is always hardened during TI (Kojima, personal communication). Although deterring effects against predators have not been determined, the hardened integument may be less vulnerable to attack from predators. We will describe in more detail in further sections the freeze response to vibrations in Scarabaeidae, Cerambycidae, and Nitidulidae.

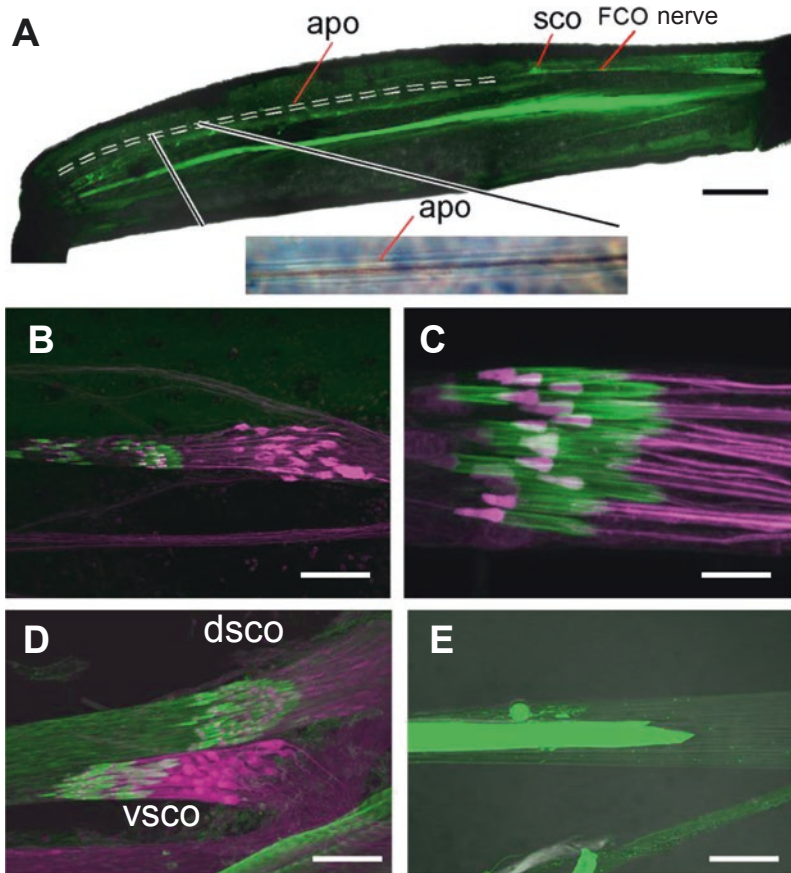
## 6.3 Vibration Sense Organs

### 6.3.1 Chordotonal Organs

Chordotonal organs, which are located in the legs and other body parts of insects (Nishino and Sakai 1997; Field and Matheson 1998), are internal mechanoreceptors that can detect vibrations via the legs and positions of leg joints. There are two different major chordotonal organs found in all six legs: the femoral chordotonal organs in the femur, and subgenual organs in the tibia (Field and Matheson 1998). Characteristically, coleopteran insects possess only the femoral chordotonal organ (Schneider 1950; Nishino et al. 2016; Takanashi et al. 2016). There are other minor chordotonal organs, including a tibio-tarsal chordotonal organ and a tarso-pretarsal chordotonal organ, each with small numbers of sensory neurons (Takanashi et al. 2016). The femoral chordotonal organs of the cerambycid species *Monochamus alternatus* consist of the scoloparium, including sensory neurons, and a chord-like cuticular apodeme, which is connected to sensory neurons and the joint pivot of the tibia (Takanashi et al. 2016) (Fig. 6.2a). Sensory neurons possess stretch-sensitive mechanosensory channels localized in the sensory cilia of the dendrite (Field and Matheson 1998), which is inserted into the scolopale cap (Field and Matheson 1998; Takanashi et al. 2016). Each pair of sensory neurons may be bifunctional, able to detect vibrations as well as mediate proprioceptive feedback (Takanashi et al. 2016; Takanashi and Nishino 2021), such as resistance reflex in the leg muscles (Field and Burrows 1982; Sauer and Stein 1999).

In *M. alternatus*, there are 37 scolopale rods in the prothoracic FCO, and therefore there are an estimated 74 sensory neurons (Takanashi et al. 2016; Takanashi and Nishino 2021) (Fig. 6.2b, c). In *M. diphysis*, the estimated number of sensory neurons is 82 (Takanashi and Nishino 2021), indicating that both cerambycid species have similar structures. The number of sensory neurons is mostly identical among pro-, meso-, and metathoracic FCOs (Takanashi et al. 2016). Both species also have a single scoloparium; however, a tenebrionid species *Zophobas atratus* has two ventral and dorsal scoloparia with and an apodeme (Nishino et al. 2016) (Fig. 6.2d, e). The number of scolopale rods in ventral and dorsal scoloparia of the





**Fig. 6.2** Femoral chordotonal organs in *Monochamus alternatus* and *Zophobas atratus*. (a) Prothoracic femoral chordotonal organs (FCOs) of *M. alternatus*. The scoloparium (sco), including sensory neurons, is connected to a cuticular apodeme (apo). (b–e) Sensory neurons (magenta) and scolopale rods (green) in (b, c) the prothoracic FCO of *M. alternatus* and (d) mesothoracic FCO of *Z. atratus* are shown by differential fluorescent labeling. (d) The mesothoracic FCO is divided into the ventral scoloparium (vsco) and dorsal scoloparium (dsco). (e) A cuticular apodeme (green) of *Z. atratus* is shown. Adapted from photos published by Takanashi and Nishino (2021) and Nishino et al. (2016). Scale bars = 500  $\mu\text{m}$  in a; 50  $\mu\text{m}$  in b, d, e; 10  $\mu\text{m}$  in c

mesothoracic FCO (Nishino et al. 2016) is approximately 150; therefore, there are an estimated 300 sensory neurons (Fig. 6.2d). Because there are distinct differences of subdivision in scoloparium and the number of sensory neurons in FCOs between cerambycid species and tenebrionid species, FCOs are assumed to be diversified functionally between these species.

Central projections of FCO axons are revealed by bilateral labeling of FCO nerves in the legs, which enter the medio-ventral and the lateral association centers in *M. alternatus* (Takanashi and Nishino 2021). The medio-ventral association

center, specialized for vibratory/auditory processing, is conserved among different insect orders (Boyan 1993; Pflüger et al. 1981; Newland 1991). The lateral association center, located laterally from the medio-ventral association center, is the motor association neuropil (Pflüger et al. 1981, 1988; Mücke and Lakes-Harlan 1995).

### 6.3.2 *Mechanosensilla and Chordotonal Organs*

Insects possess other mechanoreceptors, such as external campaniform sensilla and hair (trichoid) sensilla, which are touch receptors for detecting low-frequency vibrations or strain on cuticular surfaces (Keil 1997; Field and Matheson 1998), although the vibrational sensitivities of the sensilla are lower than those of chordotonal organs (Kühne 1982; Ai et al. 2010). In pupae of *Z. atratus*, many campaniform and hair sensilla distributed in various body parts play roles in the detection of forces by physical contact, in order to induce the defensive behavior of pupal rotation (Kurauchi et al. 2011).

Bleich (1928) reported that the main receptors involved in TI seemed to be located in the thorax, particularly in the meso- and metathorax in several coleopteran species. In the cricket *Glyptus bimaculatus*, prothoracic femoral chordotonal organs were involved in triggering both the flexion reflex and TI, whereas hair sensilla on the prothorax and campaniform sensilla in the legs were involved in the elicitation of the flexion reflex alone (Nishino and Sakai 1996; Nishino et al. 1999). Considering the positions and functions of the femoral chordotonal organs and the mechanosensilla in coleopterans (Nishino and Sakai 1996), the femoral chordotonal organs are assumed to be mainly involved with TI. Additionally, mechanosensilla on the thorax and legs are also assumed to be involved with coleopteran TI.

## 6.4 Freeze Responses and TI in Cerambycidae

Adults and larvae of longicorn beetles (Cerambycidae) feed on tree bark or other plant tissues, thereby damaging the plants (Wang 2017). Various behaviors, such as freeze responses and walking, are induced by vibrations in adults of *M. alternatus*, *M. diphysis*, and *P. fortunei* (Takanashi et al. 2016, 2019; Takanashi and Nishino 2021; Tsubaki et al. 2014). These three species are distributed mainly in Asia, including Japan (Kobayashi et al. 1984; Ohbayashi and Niisato 2007; Kosaka 2011). *Monochamus alternatus* is the vector of a plant disease caused by the pine wilt nematode *Bursaphelenchus xylophilus* (Kobayashi et al. 1984; Yazaki et al. 2018), *Moechotypa diphysis* is an invasive pest of Shiitake mushroom (*Lentinula edodes*) bed logs from oak trees (Ohbayashi and Niisato 2007; Kosaka 2011), and *Paraglenea fortunei* feed on ramie and other plants (Ohbayashi and Niisato 2007; Tsubaki et al. 2014).

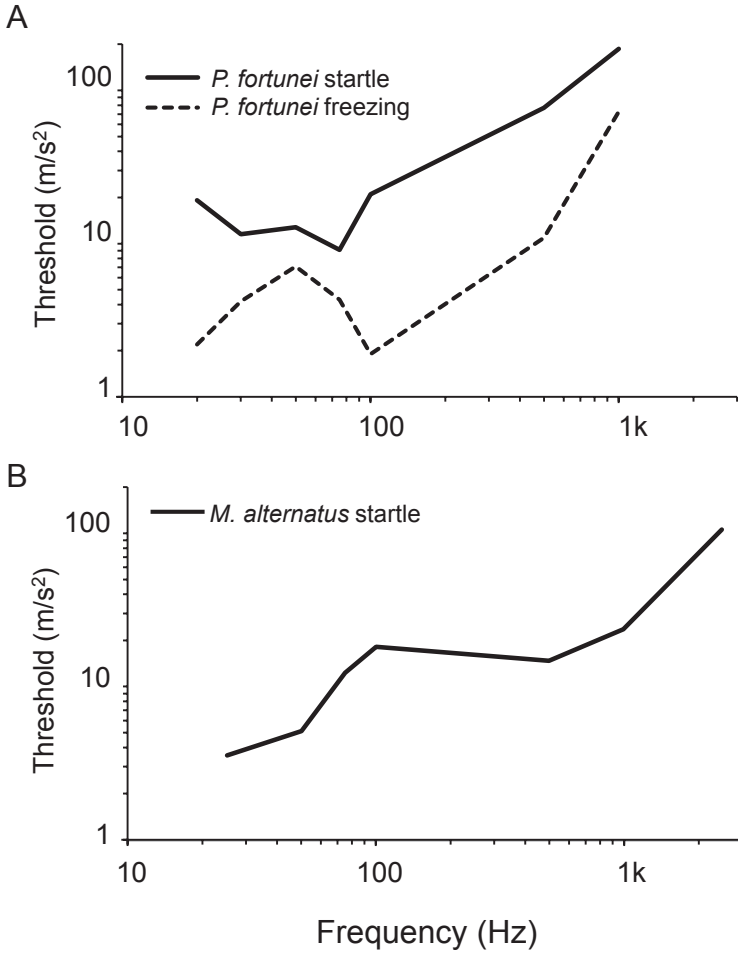
Adults of *M. alternatus* show various behavioral responses to vibrations. Walking adults show freeze responses to vibrations of 100 Hz and 1 kHz. Takanashi et al. (2016) confirmed that FCOs detect vibrations because of behavioral experiments described below. After the scoloparia attached to the apodemes were removed, adults with altered FCOs in all six legs did not freeze in response to 100 Hz or 1 kHz vibrations while walking. In contrast, freeze responses were frequently induced in intact and sham-operated beetles. In this way, the FCO involvement in the freeze response has been identified in a coleopteran species.

In addition to *M. alternatus*, freeze responses to vibrations are also observed in *P. fortunei* and *M. diphysis* (Table 6.1). Startle responses are found in all three species, as well as in the house longhorn beetle *Hylotrupes bajulus* (Breidbach 1986; Tsubaki et al. 2014; Takanashi et al. 2016). A startle response—that is, small movement of the legs and antennae—is induced by vibrations when resting in quiescence, distinct from immobility. Behavioral thresholds of these responses have been determined in *P. fortunei* and *M. alternatus* (Tsubaki et al. 2014; Takanashi et al. 2016). Briefly, behavioral responses in quiescence were observed on a flat steel plate attached to a vibration exciter. The amplitude of the stimulus was gradually increased, and the threshold was defined as the least acceleration necessary to evoke a response at frequencies of 20–1 kHz. In freeze responses, *P. fortunei* showed high sensitivity to frequencies of 20–500 Hz, with response thresholds of 2–10 m/s<sup>2</sup> (Fig. 6.3a). Similarly, *M. alternatus* and *P. fortunei* showed high sensitivity to these same frequencies of 20–500 Hz (Fig. 6.3a, b). The thresholds of the startle response are 2–20 m/s<sup>2</sup>, which is higher than that of the freeze response in *P. fortunei*. In contrast, the desert locust *Schistocerca gregaria* exhibits startle responses with a threshold of 0.23 m/s<sup>2</sup> (zero-to-peak) at 60 Hz, which is lower than the threshold of 1.0 m/s<sup>2</sup> in the freeze response (Friedel 1999).

Cerambycid adults can show behavioral responses to vibrations generated by approaching conspecifics or predators. In *P. fortunei*, vibrations from approaching individuals on host plant leaves were recorded (Tsubaki et al. 2014). Vibrations generated by a walking individual were 2 m/s<sup>2</sup> at <30 Hz, and those generated by a landing individual were 9 m/s<sup>2</sup> at <30 Hz. These values were high enough to induce freeze responses in *P. fortunei*, indicating that this species can recognize approaching conspecifics according to characteristic vibrational frequencies and accelerations, presumably without sexual recognition (Tsubaki et al. 2014).

In addition to conspecifics, cerambycid adults can recognize approaching predators with higher vibrational accelerations (Tsubaki et al. 2014; Takanashi et al. 2019). Subsequent to startle responses, adults show behavior triggered by vibrations or other sensory information. Indeed, *M. alternatus* begins walking in response to vibrations at 100 Hz, which allows the adult to avoid predators or orientate to conspecifics (Takanashi et al. 2016, 2019).

*Moechotypa diphysis* is more sensitive to vibrations than *M. alternatus* and *P. fortunei*, as the thresholds of startle responses were shown to be 1 m/s<sup>2</sup> at 100 Hz in *M. diphysis* (Takanashi and Nishino 2021). In the field, *M. diphysis* and *M. (A.) longipennis* likely drop from a host tree, the so-called drop-off reflex (Crowson 1981), and subsequently exhibit TI on the ground (Takanashi and Nishino 2021).



**Fig. 6.3** Thresholds of behavioral responses to vibrations in (a) *Paraglenea fortunei* and (b) *Monochamus alternatus*. Startle responses (solid lines) in both species and a freeze response in *P. fortunei* (dashed line) are indicated. Modified from Takanashi et al. (2019)

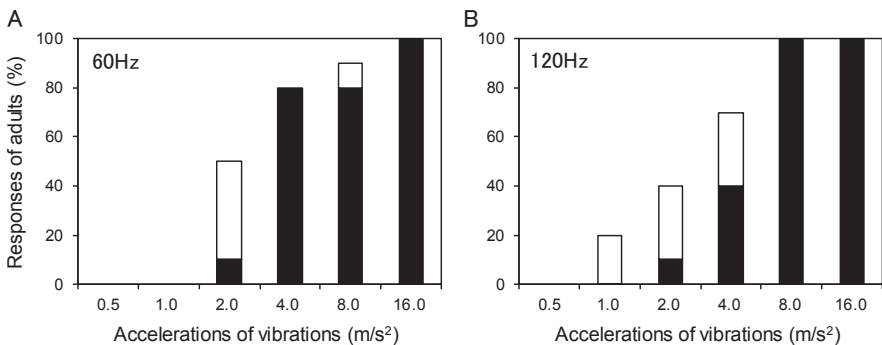
(Fig. 6.1). In contrast, *M. alternatus* and *P. fortunei* do not show TI (Takanashi personal communications). *Monochamus alternatus* rarely drops from the host tree, and *P. fortunei* is likely to drop from the host and/or take flight following disturbance (Takanashi personal communications). Thus, high sensitivities of startle responses to vibrations may explain why cerambycid species exhibiting TI drop easily from the host, like *M. diphyis* and *M. (A.) longipennis*. Dropping, in conjunction with TI, is widespread among many insects, including beetles (Crowson 1981; Humphreys and Ruxton 2019; Caprineria 1976; Miyatake et al. 2004; Ohno and Miyatake 2007; Honma et al. 2015; Matsubara and Sugiura 2018; Kishi and

Takanashi 2019a); however, the mechanism of dropping by virtue of TI has not yet been clarified in coleopteran insects.

## 6.5 TI in Nitidulidae

Sap beetles of *Phenolia (Lasiodites)* (Nitidulidae) consist of many species native across the Eastern Hemisphere (Kirejtshuk and Kvamme 2002), while *P. (L.) picta* is distributed in Asia and Australia (Kishi and Takanashi 2019b). Both adults and larvae feed on fallen rotten fruits, such as the Japanese apricot *Prunus mume* (Kishi and Takanashi 2019b).

Vibrations have been shown to induce TI, startle responses, or other behavioral responses in the adults and larvae of the sap beetle *P. (L.) picta* (Kishi and Takanashi 2019a, b). In adults at standstill, TI and startle responses are induced by 60 and 120 Hz vibrations with different accelerations from 1 to 16 m/s<sup>2</sup> (Fig. 6.4) (Kishi and Takanashi 2019b). These beetles display TI in a position with fixed legs, normally lasting for several seconds (Kishi and Takanashi 2019b). At 60 and 120 Hz, the startle responses are induced by accelerations of 1–8 m/s<sup>2</sup>, whereas TI is induced by accelerations of 2–16 m/s<sup>2</sup> (Fig. 6.4). This indicates that the thresholds of startle responses are lower than those of TI, with a range of 1–2 m/s<sup>2</sup>. Furthermore, different intervals from 1 to 9 s of pulsed vibrations with 1-s durations at 120 Hz and 8 m/s<sup>2</sup> affect TI and startle responses during walking, compared with control stimuli of continuous vibrations or without vibrations (Kishi and Takanashi 2019b). Long intervals of 9 s induced the highest proportion of TI and startle responses per pulsed vibration (50%) among the different intervals tested. A negative relationship was observed between the numbers of TI and startle responses and walking durations.



**Fig. 6.4** Percentages of adults of *Phenolia (Lasiodite) picta* that responded to different accelerations of pulsed vibrations at (a) 60 Hz and (b) 120 Hz. Open and closed sections of vertical bar represent the startle response and tonic immobility, respectively. Reproduced from Kishi and Takanashi (2019b)

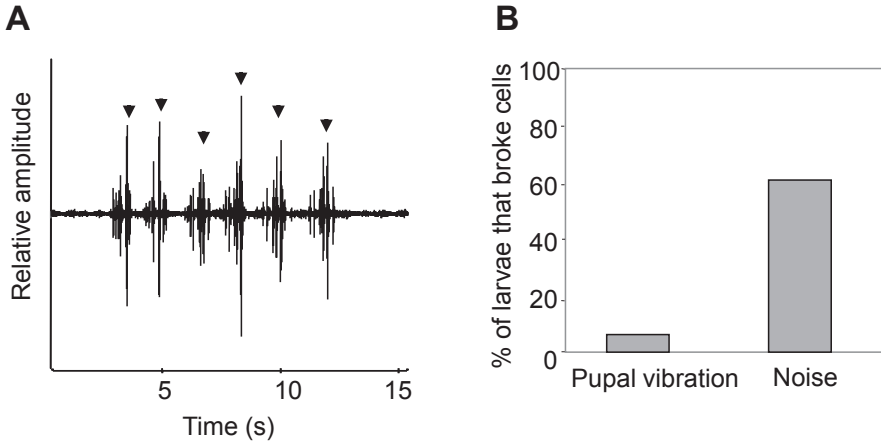
Short intervals of vibrations decreased the induction of TI and startle responses, presumably due to habituation (Kishi and Takanashi 2019b).

In larvae of *P. (L.) picta*, TI presents with a ventrally curling abdomen within several seconds following stimulation by physical contact or dropping to the ground (Kishi and Takanashi 2019a). An escape behavior of quick crawling is also observed after stimulation. This escape behavior was observed when the larvae were presented with various vibrations through the fruit of a sliced banana (Kishi and Takanashi 2019a). At 120 Hz and  $\geq 8$  m/s<sup>2</sup>, pulsed vibrations of 1-s duration at intervals from 1 to 29 s induced this behavior in 40–50% of larvae within 30 min. Vibration-induced TI was not investigated, as it could not be observed within the tested fruit (Kishi and Takanashi 2019a). Vibrations caused by predators can induce a range of defensive behaviors, including TI, startle responses, and escape responses in both the adults and larvae of *P. (L.) picta*.

## 6.6 Freeze Responses in Scarabaeidae

### 6.6.1 Pupal Vibratory Signals and Larval Freeze Responses

Freezing of insects typically functions as a method of resistance against predators. However, freeze responses also occur in conspecific interactions, such as in larvae of *T. dichotomus* (Coleoptera, Scarabaeidae, Dynastinae). *Trypoxylus dichotomus* is native to east Asia, including Japan. This beetle has a relatively large body; the maximum mass of the larval form can reach 35 g. Larvae live in accumulated dead leaves, and are often found in composts for agricultural use, where they feed on decaying organic matter (Kojima et al. 2014). More than one hundred larvae are sometimes found within a few square meters of humus. This clumped distribution is formed via the following two mechanisms: first, female adults lay eggs at intervals of a few centimeters, and the larvae therefore hatch in close proximity to each other; second, larvae are attracted to carbon dioxide (CO<sub>2</sub>) emitted by neighboring larvae (Kojima 2015a). Although the preference for CO<sub>2</sub> is probably an adaptation to locate fermented food rather than to form colonies, this habit results in a clumped distribution. Larvae build their own pupal cells in early summer by compacting a mixture of fecal pellets and humus. The pupal cells are oval (7–8 cm along the major axis, 3–4 cm along the minor axis) and built vertically underground at the same site where the larvae matured. The timing of building pupal cells is not completely synchronized, with 5–10 days of lag between the fastest and slowest larvae within microhabitats (Kojima 2015b). Larvae do not cannibalize pupae, but they do actively move in the humus (ca. 30 cm/h). Considering the high larval density within microhabitats, frequent encounters of larvae with other pupal cells are likely common. Pupal cells are fragile, and therefore at high risk of being accidentally damaged by neighboring larvae.



**Fig. 6.5** Vibratory interactions between pupae and larvae in *Trypoxylus dichotomus*. (a) An oscillogram of vibration produced by a pupa. Six pulses generated through pupal rotating behavior are indicated by arrows. (b) Percentage of larvae that broke an artificial pupal cell when pupal vibrations or background noise were played near the artificial pupal cell. Reproduced from Kojima et al. (2012a)

Kojima et al. (2012a) found that pupae and prepupae of *T. dichotomus* rotated their abdomen 3–7 times in succession when conspecific larvae approached their pupal cells (<5 cm). This rotating behavior is likely induced by vibrations emitted “unintentionally” by the burrowing larvae. When pupae (or prepupae) rotate their abdomen, vibration is produced, consisting of several pulses with 1.3 s inter-pulse interval and a low-frequency range, below 500 Hz (Fig. 6.5a). According to synchronous recordings of this vibration and the rotating movement of pupae via high-speed video, the pulses are produced when pupae beat the dorsal side of their prothorax against the inner wall of the pupal cells. The interval between each two successive pulses is equivalent to the time required for pupae to complete a rotation inside their pupal cells (Fig. 6.5a).

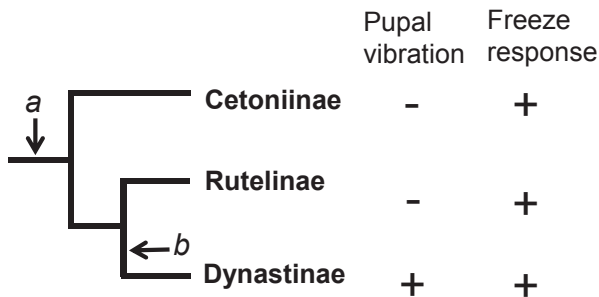
To test deterring effects of the pupal vibrations to burrowing conspecific larvae, pupal vibrations were artificially induced near vacant artificial pupal cells (Kojima et al. 2012a). The percentage of damaged pupal cells was remarkably decreased when pupal vibrations were played, compared to when a negative control background noise was played instead (6% vs 60%) (Fig. 6.5b). Monitoring of vibrations associated with larval movement revealed that nearby larvae stopped moving immediately after pupal vibratory signals were played (Kojima et al. 2012b). This suggests that these larvae showed a freeze response, which was prolonged for 3 to 22 min. Thus, pupae produce vibrations to protect themselves from larval disturbance by arresting the movement of conspecific larvae. However, whether the body of the larvae in the freeze response is hardened, as occurs in larvae in TI (Fig. 6.1g), is unknown, since the larval response to pupal signals was characterized by vibrations caused by larval movement in soil, prohibiting visual observation.



### 6.6.2 Evolution of Freeze Responses

Why do *T. dichotomus* larvae respond to conspecific pupal vibrations? Considering that freeze responses generally play a role in predation avoidance in insects (Takanashi et al. 2019; Chap. 1), the larval response to pupal signals may have originated from an anti-predator adaptation. The predominant predators of *T. dichotomus* larvae in Japan are moles *Mogera* spp. Moles emit vibrations during burrowing in the soil or foraging. Kojima et al. (2012c) provided *T. dichotomus* larvae with mole vibrations, and found that the larvae exhibited freeze responses similar to those following conspecific pupal vibrations. The response to mole vibrations might enhance larvae survival given that various fossorial mammals locate prey using vibrations associated with their activity (Narins et al. 1997; Hill 2009). Kojima et al. (2012c) also found that mole vibrations and *T. dichotomus* pupal vibrations were similar in that both predominantly contain low-frequency components (mostly below 500 Hz) and successions of pulses at intervals of a few seconds. These results imply that pupal vibrations function to mimic vibrations from predators including moles, eliciting larval freeze responses.

To assess the evolutionary process of pupae-larvae communication in *T. dichotomus*, Kojima et al. (2012b) provided the vibrations of *T. dichotomus* to larvae of other scarab species in different subfamilies of Scarabaeidae, including *Protaetia orientalis* (Cetoniinae), *Dicronorhina derbyana* (Cetoniinae), and *Anomala albopilosa* (Rutelinae), whose pupae do not produce vibrations. These three species were found to exhibit similar freeze responses as *T. dichotomus* larvae. The presence of a freeze response instinct in these three subfamilies (Dynastinae, Rutelinae, and Cetoniinae) suggests that the freeze responses to certain types of vibration are not unique to *T. dichotomus*, but have been conserved across scarabaeid beetles, presumably due to the fitness advantage in predator avoidance (Fig. 6.6). Pupae of



**Fig. 6.6** Phylogenetic relationships among Cetoniinae, Rutelinae, and Dynastinae. As larval freeze responses to vibrations have been observed in all three subfamilies, it was likely present in the common ancestor indicated by **a**. Pupal vibration was found in only Dynastinae, suggesting that pupal vibration has been acquired in the ancestor of Dynastinae indicated by **b**. Reproduced from Kojima et al. (2012b)

*T. dichotomus* likely exploit this anti-predatory response for the protection of their own pupal cells.

If pupae of *T. dichotomus* manipulate larval behavior with deceptive signaling, the larvae may incur a fitness cost through restrictions in their own behavior. This may lead to the counter-selection of larvae that can identify and disregard these deceptive signals (Ruxton and Schaefer 2011); however, larvae do not distinguish pupal signals from signals associated with predators. Additional playback experiments using synthetic vibrations indicate that *T. dichotomus* larvae show stereotypic freeze responses upon perceiving low-frequency vibrations with various temporal patterns (Kojima 2013). The counter-adaptation of larvae may be hindered because the patterns of predator vibrations vary with environmental factors, and larvae risk being attacked by predators in cases of misidentification. In addition, kin selection may favor a larval response to pupal signals. If larvae can avoid breaking the pupal cells of siblings, the cost imposed by pupae is partly offset; however, relatedness of larvae within microhabitats is unknown. The deceptive communication in *T. dichotomus* sheds a new light on the functions of freeze responses in insects.

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