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THE VIBRATIONAL STARTLE RESPONSE OF THE DESERT LOCUST *SCHISTOCERCA GREGARIA*

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Summary

Substratum vibrations elicit a fast startle response in unrestrained quiescent desert locusts (*Schistocerca gregaria*). The response is graded with stimulus intensity and consists of a small, rapid but conspicuous movement of the legs and body, but it does not result in any positional change of the animal. With stimuli just above threshold, it begins with a fast twitch of the hindlegs generated by movements of the coxa–trochanter and femur–tibia joints. With increasing stimulus intensity, a rapid movement of all legs may follow, resulting in an up–down movement of the whole body.

The magnitude of both the hindleg movement and electromyographic recordings from hindleg extensor and flexor tibiae muscles increases with stimulus amplitude and reaches a plateau at vibration accelerations above 20 m s^{-2} (peak-to-peak). Hindleg extensor and flexor tibiae muscles in unrestrained animals are co-activated with a mean latency of 30 ms. Behavioural thresholds are as low as 0.47 m s^{-2} (peak-to-peak) at frequencies below 100 Hz but rise steeply above 200 Hz. The response habituates rapidly, and inter-stimulus intervals of 2 min or more are necessary to evoke maximal reactions.

Intracellular recordings in fixed (upside-down) locusts also revealed co-activation of both flexor and extensor motor neurones with latencies of approximately 25 ms. This shows that the neuronal network underlying the startle movement is functional in a restrained preparation and can therefore be studied in great detail at the level of identified neurones.

Key words: startle reaction, vibration reception, leg movement, motor neurone, co-activation, locust, *Schistocerca gregaria*.

Introduction

A startle response is a short-latency, abrupt, fast movement elicited by a sudden, unexpected stimulus, which is often alarming, and the response is therefore of high survival value. Startle reactions have been found in all animal groups examined and are thought to be evolutionarily ancient (Bullock, 1984). A fast evasive movement is often included, which may be mediated by rapidly conducting giant neurones (e.g. annelid worms, Bullock, 1945; Drewes et al., 1978; cockroach, Westin et al., 1977; Camhi, 1980; crayfish, Wine and Krasne, 1972; Wine, 1984; teleost fish, Eaton et al., 1977). Although some startle reactions may result in a translation movement of the whole body, many involve only parts of the body with no overall translation of the animal (Bullock, 1984). The most prominent startle response observed in mammals, the acoustic startle response (Davis, 1984; Koch and Schnitzler, 1997), belongs in this latter category.

Both the stereotypic motor sequence and the short latency of startle responses indicate that relatively simple neuronal circuits containing only a few central synapses mediate most startle reactions. Nevertheless, the neuronal networks of startle responses have proved to be of great value in explaining the properties of more complex motor control systems (Ritzmann and Eaton, 1997). The neuronal mechanisms underlying the fast startle reaction of teleost fish (C-start) and the acoustic startle response of rodents are amongst the most completely understood neuronal circuits in vertebrates (e.g. Eaton and Hackett, 1984; Ritzmann and Eaton, 1997; Koch and Schnitzler, 1997). Similarly, in invertebrates, the study of escape responses and their neuronal substrates have contributed greatly to our understanding of the neuronal principles underlying motor control and behaviour (e.g. Hoy et al., 1989; Comer and Dowd, 1993; Hoy, 1993; Ritzmann, 1993). Startle reactions therefore continue to serve as important animal models that are instrumental in the quest for an understanding of the neuronal control of behaviour in both vertebrates and invertebrates.

I describe a fast startle reaction in the desert locust *Schistocerca gregaria* elicited by small-amplitude, low-frequency substratum vibrations. The response involves a brief rapid movement of the legs and the body, without any positional change of the animal. The flexed hindlegs of the resting locust perform a conspicuous movement that may function as a preparatory activation or positioning for an escape jump or defensive kick. Some of the results have been presented in abstract form (Friedel, 1998).

Materials and methods

Stimuli and behavioural threshold

Locusts (*Schistocerca gregaria* Forskål) were taken from our crowded laboratory colony and placed on a platform (12 cm in diameter) mounted on an electrodynamic vibrator (V101, Ling Dynamic Systems). A locust was allowed to move freely on the platform, which was encased in a cylindrical Perspex tube 25 cm high. The eyes of the locusts were covered with typist's white correction fluid both to prevent any possible influence of visual inputs on the responses of the animals and to reduce their general activity. An experimental animal was placed on the platform at least 30 min prior to an experiment to allow it to explore the test arena and to settle down. All experiments were carried out at room temperature (23–28 °C).

The experimental stimuli were either produced using a function generator (Farnell) driven by tone bursts from a pulse generator (Master 8) or computer-generated using LabVIEW software (National Instruments) and played out through an AD/DA card (NI-DAQ AD, National Instruments). Tone bursts 100–750 ms in duration and carrier frequencies within the range 10–1000 Hz were used. Changes in the stimulus duration above 100 ms had no obvious effect on the startle response. Shorter stimuli were not tested systematically. In habituation experiments, a series of 20 vibration bursts of 250 ms duration was presented at intervals of 500 ms. The vibration stimuli were monitored with an accelerometer (Brüel & Kjær type 4369 or type 4393 V) mounted in the centre of the platform. The accelerometer signal was amplified using a charge amplifier (Brüel & Kjær type 2635). Thus, the amplitude of the vibrational stimulus could be controlled precisely.

The behavioural threshold of the startle reaction was determined by delivering a test stimulus to the locust that had assumed its resting position. The occurrence of a startle movement was judged by eye. After an interval of at least 2 min, the next test stimulus was delivered. The amplitude of successive stimuli was either raised until a startle response occurred or lowered until the startle response could no longer be elicited. The amplitude at which a startle response appeared or disappeared, respectively, was scored as the behavioural threshold for a given frequency (precision 0.01–0.05 $m\,s^{-2}$ peak-to-peak). Both procedures yielded similar results with inter-stimulus intervals of 2 min or longer. Once the threshold had been determined for a certain frequency, the threshold was determined in the same way for the next frequency. The sequence of stimulus frequencies from 10 to 1000 Hz tested in a particular locust was randomised.

Movement analysis

To analyse the sequence of leg and body movements in detail, startle responses of unrestrained locusts on the platform were videotaped while electromyograms from the hindlegs were recorded simultaneously. Movements of the locust were videotaped from a lateral view using a CCD camera with an adjustable shutter speed (JVC TK-C1380E). The oscilloscope display of the stimulus and the muscle recordings were videotaped simultaneously using a Sony Video Hi8 Handycam. Both video images were combined using a multi-viewer (FOR-A MV-40PS) and mixed with a timer signal (FOR-A VTG-33). The combined signals were recorded at 25 frames s^{-1} in VHS format for subsequent frame-by-frame analysis. The muscle recordings and the vibration stimuli were recorded simultaneously on a DAT tape recorder (Biologic DTR 1801). A precise matching of the single video frames of the movement with the recording from the DAT tape was possible using the video image of the oscilloscope display of trigger pulses, stimuli and muscle recordings. Particular sequences were captured on computer using a video capture card (miroVideo DC30plus). To reveal the trajectories of the movements involved, the positions of the legs, body and antennae were plotted from individual frames. The amplitude of the movement of a hindleg was determined and used as a measure of the magnitude of the startle response.

Electrophysiology

Pairs of steel wire electrodes (50 μm in diameter) insulated but for their tips were implanted into the leg muscles for electromyographic recordings. Recordings were made from the flexor and/or extensor muscle of one or two hindlegs simultaneously. These signals were analysed off-line using either a CED 1401 interface and Spike 2 software or a NI-DAQ-AD card and LabVIEW software running on a PC.

Intracellular recordings from the somata of flexor and extensor motor neurones were made in a fixed preparation using conventional glass microelectrodes and recording techniques. The locust was fixed in Plasticine ventral side uppermost, and a hole was cut into the sternum to expose the meso- and metathoracic ganglia. The sheath of the metathoracic ganglion was treated with protease (Sigma, type XIV) to facilitate penetration of the electrodes. The fast extensor tibiae motor neurone (FETi) was identified by antidromic action potentials evoked by a pair of wire electrodes implanted in the extensor tibiae muscle and used to stimulate electrically the synaptic endings of the motor neurone. Flexor motor neurones were recognised by the position of the soma recordings and by the occurrence of a monosynaptic excitatory postsynaptic potential (EPSP) following an action potential of FETi. The vibration stimulus was delivered *via* the platform to both hindlegs simultaneously. The platform was lowered until the tarsi of the hindlegs rested on its underside. The femoro-tibial joints were flexed in the same way as when the locust was in its natural resting position.

Results

The startle movement

In a resting locust, all the legs are used for support. The forelegs are held forward at an angle of approximately 45 ° relative to the horizontal long axis of the body, and the middle legs are held backwards at a similar angle. The hindlegs are held alongside the body with the femoro-tibial joints almost fully flexed. In this position, the dorsal edge of the tibia is usually at an angle of 10–15 ° relative to the horizontal long

axis of the body. The body is often lowered, but the ventral thorax and abdomen do not touch the substratum.

The startle response elicited by substratum vibrations consisted of a brief and rapid movement of the legs and body. It typically started with a conspicuous jerking or cocking-like movement of the hindlegs followed by an up–down movement of the whole body. Movements of the coxal and femoral joints generated hindleg jerking. The distal ends of the femora of the flexed hindlegs described a small yet conspicuous up–down movement, during which both the flexor and extensor tibiae muscles were co-activated (Fig. 1). At levels of stimulation close to threshold, the hindleg jerking movement was the only visible movement. The amplitude of this hindleg movement increased with stimulus amplitude in a graded fashion until it reached a plateau value. Movement amplitudes were up to 5 mm, covering a vertical angle of 5–20 ° relative to the long axis of the body. In response to stronger stimuli (several times the threshold value, Fig. 1), an up–down movement of the whole body involving the action of the fore- and middle legs followed the hindleg movement. The movement of the fore- and middle legs also involved both the coxal and femoral joints. The body was lifted by up to 1.5–2 mm. The tarsi were not repositioned during this movement, and no translation of the animal occurred. Small movements of the antennae and pedipalps or other mouthparts sometimes occurred. In this study, I concentrated on movements of the hindlegs to quantify the startle response.

At very large stimulus amplitudes, the animals sometimes started to walk immediately after showing a startle response, but only very few jumps were elicited. If a vibratory stimulus was presented to an active animal that was, for example, grooming or walking, a distinct freeze reaction was observed. This reaction was elicited only at thresholds higher than the startle response (i.e. above 2 m s^{-2} at 60 Hz).

In some experiments, a brass rod was mounted on the vibrator and the locust was allowed to rest in its preferred vertical position. In this situation, a similar startle movement with comparable thresholds was observed when the rod was vibrated. In this case, the leg movements resulted in a movement of the body away from and back towards the rod.

Thresholds and latency

Behavioural threshold curves were determined in 17 locusts (Fig. 2). Mean thresholds were as low as 1.66 m s^{-2} (peak-to-peak) at frequencies below 100 Hz, rising steeply above 200 Hz

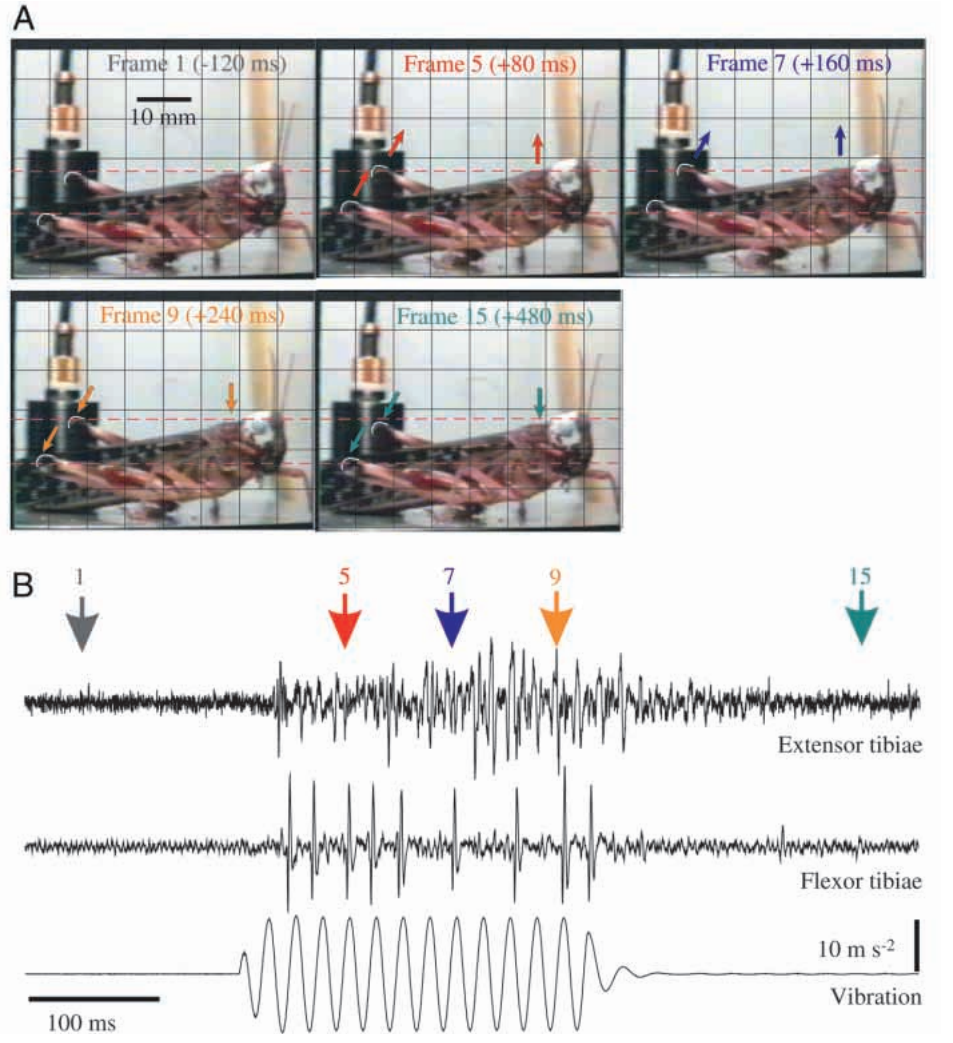

Fig. 1. The vibrational startle response. (A) Single frames from a video sequence. Frame number and time relative to the start of the stimulus are indicated. (B) Electromyographic recordings of the activity of the hindleg flexor and extensor tibiae muscle in the same animal during this startle reaction. Coloured arrows and numbers indicate the time of the corresponding video frame in A. Vibration stimulus parameters: 55 Hz, 20 m s^{-2} (peak-to-peak), 250 ms duration.

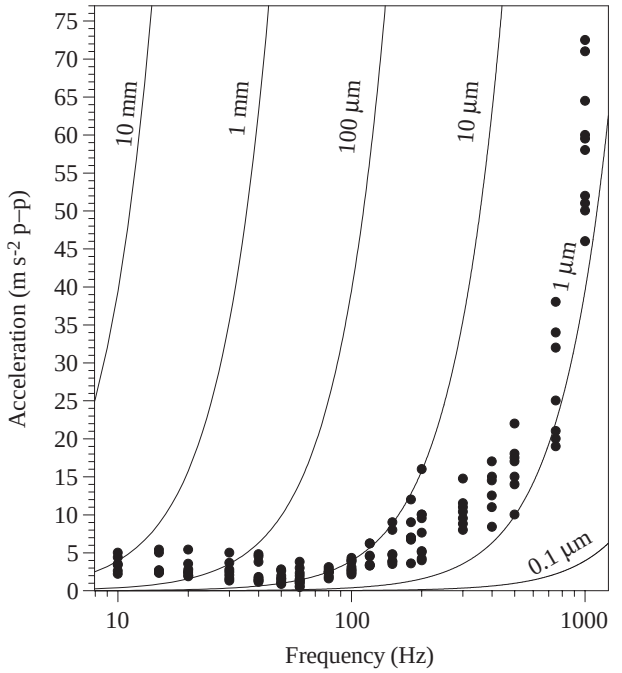

Fig. 2. Behavioural threshold curve of the vibration-elicited startle response. Each filled circle represents the peak-to-peak (p–p) acceleration at the behavioural threshold of an individual animal measured for the given frequency (6–10 locusts for each frequency). An indication of the peak-to-peak displacement is given by the iso-displacement lines. *N*=17 locusts.

(Fig. 2). The lowest acceleration threshold of 0.47 m s^{-2} (peak-to-peak) was found at 60 Hz, corresponding to a displacement of the substratum of 3.3 µm (peak-to-peak). At low frequencies, the acceleration thresholds of all locusts were nearly uniform, indicating that, at lower frequencies, the locusts responded to the acceleration component of the vibration. At higher frequencies, the threshold curve increased following the iso-displacement lines.

In videotaped sequences, the startle response started within one frame (40 ms) of the start of a vibratory stimulus. A more accurate measurement of the latency was, therefore, obtained by making recordings from hindleg muscles using stimuli in the best frequency range for the behaviour pattern. Measured in this way, the latency of the startle response to a 250 ms burst of a 60–65 Hz vibration was 30 ms in both the extensor and flexor tibiae muscle (extensor 29.8±5.6 ms; flexor 29.9±5.1 ms; *t*-test, not significant). Thus, the two antagonistic muscles moving the femoro-tibial joint were co-activated during the vibrational startle response. Above threshold, the latency of the response did not change over a broad range of amplitudes (up to 40 m s^{-2}).

Hindleg muscle activity

Both tibial muscles in the hindleg responded in a phase-related manner to the individual cycles of the vibration stimulus burst (Figs 1B, 3). The spikes in muscle recordings were identified and pooled for the phase histograms so that the responses of single units were not analysed separately. Nevertheless, a pronounced phase-related response of the muscle spikes to stimulus frequencies up to 120 Hz occurred. At frequencies above 200 Hz, phase-locking was not observed. Whereas the muscle response to low frequencies lasted as long or sometimes longer than the stimulus burst, the muscle response to higher frequencies was

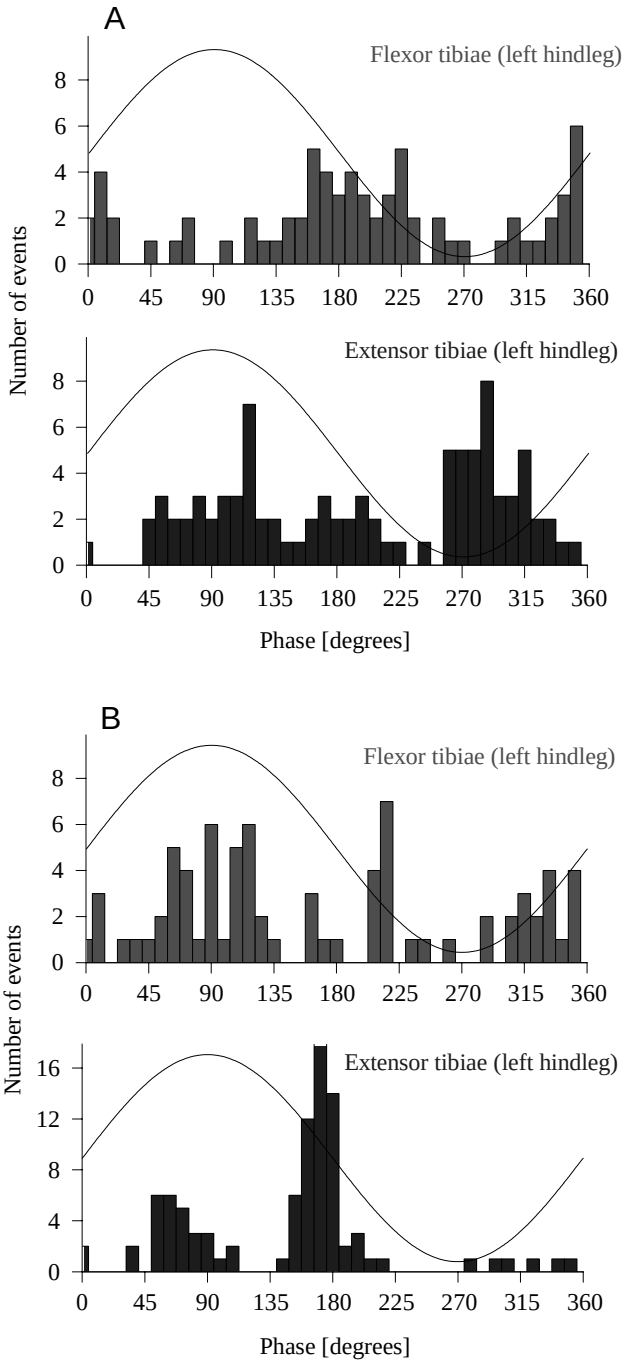

Fig. 3. Phase relationship between the spikes of the extensor and flexor tibiae muscles and the individual cycles of the vibration stimulus during the startle response. (A) Phase-related responses of the flexor and extensor muscle spikes of the left hindleg to 68 cycles (4×250 ms vibration stimuli at 60 Hz). (B) Phase-related responses in a different trial (68 cycles, 4×250 ms vibration stimuli at 60 Hz) in the same animal. The animal had moved between the trials, and the phase relationships of the muscle responses have changed.

often shorter and contained fewer spikes. The exact phase of the muscle responses relative to the individual cycles of the vibration burst was variable and often changed between trials in the same locust. Furthermore, the relationship between the response phases in the two muscles was variable. In the same animal, the antagonistic muscles fired out of phase by approximately 90 ° in one trial, but in a subsequent trial their phase relationship changed (cf. Fig. 3A,B). This variability occurred in different trials, between which the locust may have moved or changed its position slightly. The phase of the muscle activity relative to the stimulus cycle always remained constant in trials when the locust remained completely stationary.

The startle reaction is graded both in the movement of the distal tip of the femur and in the spike activity of flexor and extensor tibiae muscles (Fig. 4). The magnitude of the response increased with stimulus amplitude and reached a plateau at vibration accelerations greater than 20 m s^{-2}, thus spanning a range of two orders of magnitude from its lowest threshold of 0.47 m s^{-2} at 60 Hz.

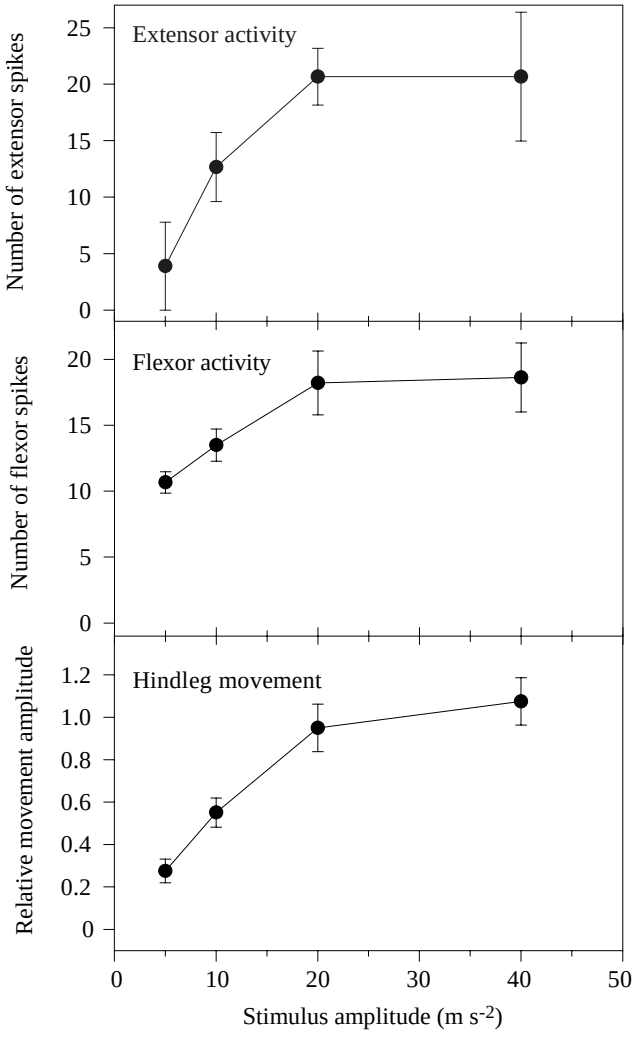

Fig. 4. The graded nature of the vibrational startle response. The number of extensor and flexor tibiae muscle spikes (per 250 ms) increases and saturates with increasing stimulus amplitude in parallel with an increase in the amplitude of the movement of the tip of the femur. The number of motor spikes is therefore a good indicator of the response magnitude. Vibration stimulus parameters: 60 Hz, 250 ms duration. Values are means ± S.D., *N*=4 locusts.

Habituation

The startle response to repetitive stimulation habituated (Fig. 5). A series of 20 vibration bursts of 250 ms duration at 60 Hz was presented to resting locusts at inter-burst intervals of

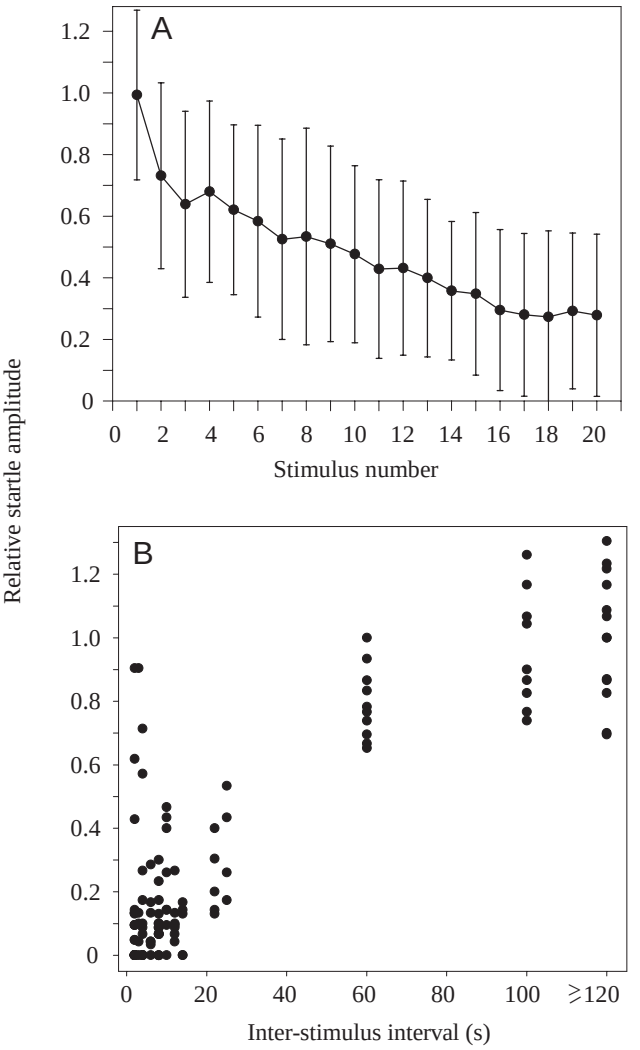

Fig. 5. Habituation of the vibrational startle response. (A) The response magnitude decreases significantly (ANOVA, $F_{19,580}$=13.69, P<0.0001) during a series of 20 vibration stimuli presented at intervals of 500 ms. The relative startle magnitude is derived from the number of flexor or extensor tibiae motor spikes. Values are means ± S.D., *N*=5 locusts. Four animals were tested six times with the series of 20 vibration stimuli, and one animal was tested five times with the series of 20 vibration stimuli. (B) Stimulus intervals of 2 min or more were necessary to elicit consistently a maximal startle response (extensor spikes) with a single vibration stimulus. The relative startle magnitude is derived from the number of extensor tibiae motor spikes. Vibration stimulus parameters in A and B: 60 Hz, 20 m s^{-2} (peak-to-peak), 250 ms duration.

500 ms (Fig. 5A). The response magnitude, derived from the number of extensor tibiae motor spikes, decreased to 27.8 % of the initial value, but the response latency did not change significantly (Spearman rank correlation, r=0.25; analysis of variance, F=0.619, P<0.885, not significant). No changes were observed in the motor sequence of the startle response during habituation.

In experiments with single vibration bursts of 250 ms duration at 60 Hz, the startle magnitude, derived from the number of extensor tibiae motor spikes, increased with increasing inter-stimulus interval (Fig. 5B). At stimulus intervals below 20 s, the response magnitude was on average less than 20 % of the full response. Inter-stimulus intervals of 2 min or more were necessary to elicit repeatedly a full response.

Motor neurones in the restrained preparation

In the restrained (upside-down) locust preparation, intracellular recordings showed that the same vibratory stimuli that elicited a startle response in the freely moving animal also activated flexor and extensor tibiae motor neurones (Fig. 6). Both were depolarised with a latency of approximately 25 ms, and their synaptic potentials appeared to be phase-locked to the individual cycles of the stimulus (Fig. 6B). As expected in a restrained preparation, the intracellular recordings are at a much lower response level than the electromyograms of the free-ranging animal. The stimulus sometimes evoked action potentials. The latencies, co-activation of the antagonists and phase-related occurrence of synaptic potentials suggest that the vibratory stimulus elicits similar responses in both restrained and freely moving animals. The neuronal networks underlying the hindleg movements involved in this vibrational startle response are therefore functional in the restrained preparation.

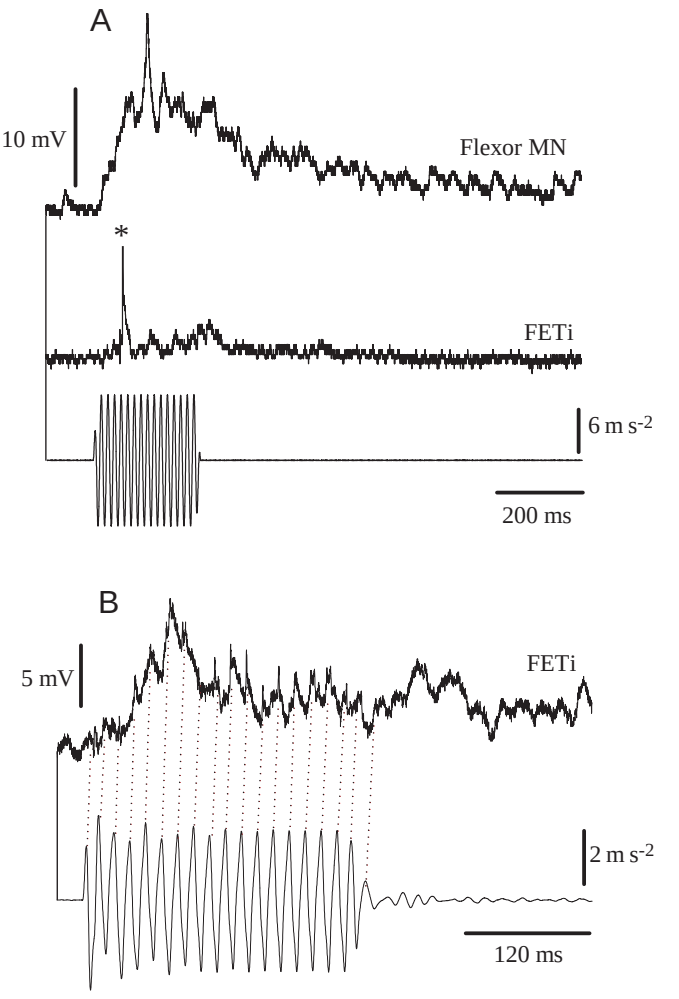

Fig. 6. Intracellular recordings in the restrained animal preparation. Responses of motor neurones to the vibration stimulus (60 Hz, 250 ms duration). (A) Response of a fast extensor tibiae motor neurone (FETi) and a flexor tibiae motor neurone (MN). The asterisk marks a truncated FETi spike. (B) Postsynaptic potentials related in phase to the stimulus waveform were regularly observed in FETi.

Discussion

In this study, I described a newly discovered startle response in the desert locust elicited by substratum vibrations. Short bursts of low-frequency substratum vibrations reliably elicit a distinct motor sequence with a short latency of 30 ms that is graded in amplitude and habituates rapidly. The vibrational startle response consists of distinct movements of the legs and body without a translatory movement of the whole locust. At frequencies below 100 Hz, acceleration thresholds are as low as 0.47 m s^{-2} (peak-to-peak) and nearly uniform, suggesting that locusts respond to the accelerational component of the vibration.

The function of the stationary vibrational startle response

Startle or escape reactions that involve an evasive translatory movement of the whole animal have been studied in some detail in a variety of invertebrates (e.g. Westin et al., 1977; Camhi, 1980; Wine, 1984; Hoy et al., 1989; May and Hoy, 1990). When resting on a vertical rod, locusts perform a distinct visual hiding response by moving away from an approaching visual stimulus (Hassenstein and Hustert, 1995). Stationary startle reactions such as the vibrational startle response, however, have received little attention in insects, although such responses are common and may indeed be considered primary reactions preceding the evasive or escape movement.

Casual observations in summer meadows show that grasshoppers and crickets stop singing or may even jump away when an observer approaches. Substratum vibrations, caused by the footsteps of the approaching observer, may provide an appropriate warning signal because the reactions occur even if the source of disturbance is not seen. In singing field crickets, the silencing reaction occurs in response to substratum vibrations with frequencies below approximately 400 Hz, whereas a delay reaction in the song pattern is elicited by higher frequencies (400 Hz to 3 kHz) (Dambach, 1989). The silencing reaction and the vibrational startle response are therefore elicited within the same frequency range and may

have similar sensory input pathways. The threshold of the cricket silencing reaction, however, is considerably lower (below 0.01 m s^{-2}). Acoustic stimuli may also elicit stationary startle reactions in locusts. Riede (1993) described a stationary acoustic startle response in locusts resting on a vertical rod and used this response to analyse the phenomenon of prepulse inhibition for the first time in an invertebrate. Although a less detailed description of the startle movement was given without electromyographic evidence or threshold analysis, this acoustic startle reaction is very similar to the vibrational startle reaction described in the present study. In general, startle reactions without an evasive movement, such as the vibrational startle response of the locust, are thought to serve a preparatory function and to result in an elevated muscle tonus and greater alertness, thus facilitating or preparing for subsequent activities such as escape movements.

Co-activation of hindleg muscles and jump preparation

Simultaneous activation of antagonistic muscles is a prominent feature of the hindleg movement during the vibrational startle response. Co-activation of antagonistic muscles has been described in a tactile startle response in the stick insect (Kittmann et al., 1996) and also occurs during mammalian startle responses (Davis, 1984). It therefore seems to be a common feature of many startle reactions. In the locust, co-activation of flexor and extensor tibiae muscles also occurs during the initial cocking and co-contraction phase of the jump or kick (Heitler and Burrows, 1977a; Burrows, 1996). Thus, the hindleg movement observed during the vibrational startle reaction of the locust may indeed serve as a preparation for a jump or kick. However, on the platform, jumps rarely occurred, even at very high stimulus amplitudes. This observation may indicate a fundamental difference between the stationary vibrational startle response and the initiation of the jump. The latter may need additional stimuli to be triggered or completed. Although it has been reported frequently (e.g. Pearson et al., 1980; Pearson and Robertson, 1981; Gynther and Pearson, 1986; Pearson and O'Shea, 1984) that not only visual stimuli but also acoustic, tactile or vibrational stimuli can trigger hindleg cocking and jump, this has not been quantified. Accordingly, the role of identified multimodal sensory interneurones in jump initiation remains unclear (Gynther and Pearson, 1989; Burrows, 1996). The vibrational startle response may serve as a useful paradigm to elucidate the function of these neurones in jump initiation.

Which sensory systems mediate the vibrational startle response?

The antagonistic muscles moving the hindleg tibiae characteristically responded in a phase-related manner to the individual cycles of the vibration stimulus in freely moving animals. Phase-locking also occurred in motor neurone responses. In recordings from leg sensory nerves, certain types of vibration receptors respond in a phase-locked fashion to the individual cycles of vibration stimuli that elicit the startle response (T. Friedel, personal observation). Afferents from campaniform sensilla respond to substratum vibrations in a phase-locked fashion in the low-frequency range from 15 to 200 Hz (Kühne, 1982a,b), thus matching the best frequency range of the vibrational startle response. Furthermore, the lowest thresholds of single campaniform afferents are approximately 0.1 m s^{-2} at frequencies below 100 Hz and are thus within the same range of magnitude of the behavioural thresholds found in this study (0.47 m s^{-2} peak-to-peak at 60 Hz). For these reasons, it seems likely that campaniform sensilla are involved in the mediation of the vibrational startle reaction of the locust. In contrast, afferents from the much more sensitive subgenual organ respond best to higher frequencies and do not respond in a phase-locked fashion (Schnorbus, 1971; Kühne, 1982a). This suggests that the subgenual organ may not be involved primarily in mediating the vibrational startle response. Other vibration-sensitive receptors, which could play a role in the mediation of the vibrational startle reaction, are those of the chordotonal organs of the leg joints (Kühne, 1982a; Field and Pflüger, 1989; Field and Matheson, 1998). The threshold curves of type II afferents described by Kühne (1982a), which are thought to be of chordotonal origin, follow a constant acceleration with minimum acceleration thresholds of 1 m s^{-2} in the low-frequency range. Clearly, more experiments are necessary to identify the sensory organs that mediate the vibrational startle response.

Stimulus–response relationship and habituation

The vibrational startle response can be elicited by vibrations with accelerations spanning at least two orders of magnitude, but the overall pattern of the response does not change with increasing stimulus amplitude. The response merely increases in amplitude with increasing stimulus amplitude. Furthermore, the vibrational startle response is not changed in quality or pattern during habituation, but merely reduced in amplitude. Such simple stimulus–response characteristics are also found in many other startle responses, e.g. the mammalian acoustic startle response (Koch and Schnitzler, 1997). This makes it easy to quantify reliably the effects of many modulation phenomena (e.g. habituation and dishabituation, prepulse inhibition), to study their neuronal bases and to relate these findings to other systems in order to define general principles of modulation and plasticity of behaviour.

Identified neurones in the restrained preparation

In this study, I have shown that several characteristics of the responses of FETi and flexor tibiae motor neurones to vibratory stimuli suggest that their activation relates to the startle response observed in the freely moving animal. Both extensor and flexor motor neurones were co-activated with latencies of approximately 25 ms, and postsynaptic potentials were observed that appeared to be phase-related to the individual waveform cycles of the stimulus. These observations correspond well with findings in the freely moving animal and indicate that the vibrational startle response is functional in the

restrained preparation, which is accessible for intracellular recordings.

Outlook

Simple behaviour patterns, such as startle responses, and their underlying neuronal networks have proved to be of great value in understanding the basic principles of sensory motor integration and motor control that are also applicable in more complex systems (Ritzmann and Eaton, 1997). The locust in particular is an important neurobiological model animal for which a large body of information on identified neurones and their connections is available. The local neuronal networks controlling leg movements are understood in great detail (e.g. Burrows, 1992, 1996), with the networks generating the motor output for the escape jump and kick having been described in particular detail (Heitler and Burrows, 1977a,b; Burrows, 1996). Furthermore, the sensory structures and neurones involved in the processing of substratum vibrations have been characterised in locusts (Cokl et al., 1977, 1985; Kühne, 1982a,b; Grosch et al., 1985; Bickmeyer et al., 1992). The vibrational startle response described here adds a reliable and easily quantifiable behavioural paradigm, which is functional in a restrained preparation. This means that the processing of vibratory information and the neuronal interactions underlying this behaviour can now be studied in greater detail and related to the neuronal networks for jumping and kicking on the basis of a quantified stimulus–response relationship. The vibration-elicited startle response of the desert locust and its underlying motor pattern may therefore provide further insight into the basic principles of sensory-motor integration and the neuronal control of behaviour.

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