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Prepulse inhibition of the startle reaction in the locust *Locusta migratoria* (Insecta: Orthoptera: Acridoidea)

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Abstract. A fast startle reaction of unrestrained sitting locusts (*Locusta migratoria*) can be elicited by sound pulses of steep rise time above 80 dB. The reaction consists of a fast jerky movement of legs and body with a mean latency of 35 ms and graded amplitude. The fast startle reaction did not result in any positional change; this was in contrast to acoustically induced escape reactions of flying Orthoptera. The startle reaction could be inhibited by pure tone stimuli of much lower intensity (60 dB) presented 160 ms before the startle-eliciting noise. This type of reflex modification is a striking convergence to the well-known prepulse inhibition of the mammalian startle response where it has been used to assess sensory thresholds. In the locust, prepulses between 3 and 20 kHz suppressed the startle reaction completely, with thresholds in the locust's hearing range as known from tympanal nerve recordings. No inhibition could be observed at prepulse frequencies of 40 kHz, although this frequency lies within the locust's hearing range. The presence of prepulse inhibition in an invertebrate preparation shows that it is not restricted to vertebrates.

Key words: Startle – Prepulse inhibition – Reflex modification – Auditory threshold – Grasshoppers

Introduction

Species-specific startle reactions of unexpected sensory stimuli are common throughout the animal kingdom. A great variety of reaction types from simple withdrawal in Protozoa to rather complex escape manoeuvres have been subsumed under this category (Eaton 1984). In insects such as mantids, green lacewings, crickets and bushcrickets, startle reactions of flying animals occur in response to ultrasound (Hoy et al. 1989; Libersat and Hoy 1991), and are interpreted as bat avoidance behaviour. This paper illustrates a startle reaction in sitting grasshoppers which does not involve any displacement of the animal and can be suppressed by preceding tones below startle threshold. This phenomenon is known as prepulse inhibition and so far has been reported only in vertebrates. In rats, for example, a brief presentation of a sub-threshold burst of white noise inhibits the subsequent startle response (Hoffmann and Searle 1965).

Prepulses may lie around sensory thresholds as determined by other psychophysical methods. In fact, the first evidence of the frog's hearing capacity was provided by the elegant experiments of Yerkes (1905) who inhibited the mechanically elicited leg withdrawal reflex by acoustical prepulses. This was an early demonstration that reflex modification is a valuable tool for the assessment of sensory thresholds even across sensory modalities. Meanwhile, prepulse inhibition has become a standard method to determine sensory thresholds in intact animals (Hoffmann 1984) and an important experimental paradigm especially in psychopharmacology (Cassella and Davis 1986). However, it was mainly applied to mammalian subjects and remained the domain of physiological psychologists. This paper investigates the potential of prepulse inhibition as a tool for the assessment of sensory thresholds in Orthoptera and possibly other invertebrates.

Materials and methods

Movement detection. Animals climbed up the rod in the centre of the test drum and usually settled quietly between 1 and 2 mm below the perspex lid (Fig. 1). They were illuminated from above by a 6-V DC microscope lamp generating a light spot of 4 cm diameter and 1000 lx light intensity. A reflex foil (high gain, 3M & Nordic GmbH) of 3×3 mm^2 was attached to the animal's forehead and reflected the incoming light to a photodarlington via a lens and a half-transmittant mirror. Light intensity as measured by the photodarlington was proportional to the reflecting area depending on the angle between reflex foil and the direction of incoming light. Thereby, small angular displacements of the animal's long axis produced voltage changes at the photodarlington. They were measured directly with an oscilloscope (Digital storage scope HM 208, Hameg) at AC-mode. The experiment was monitored by closed-circuit television. By using an image splitter, oscil-

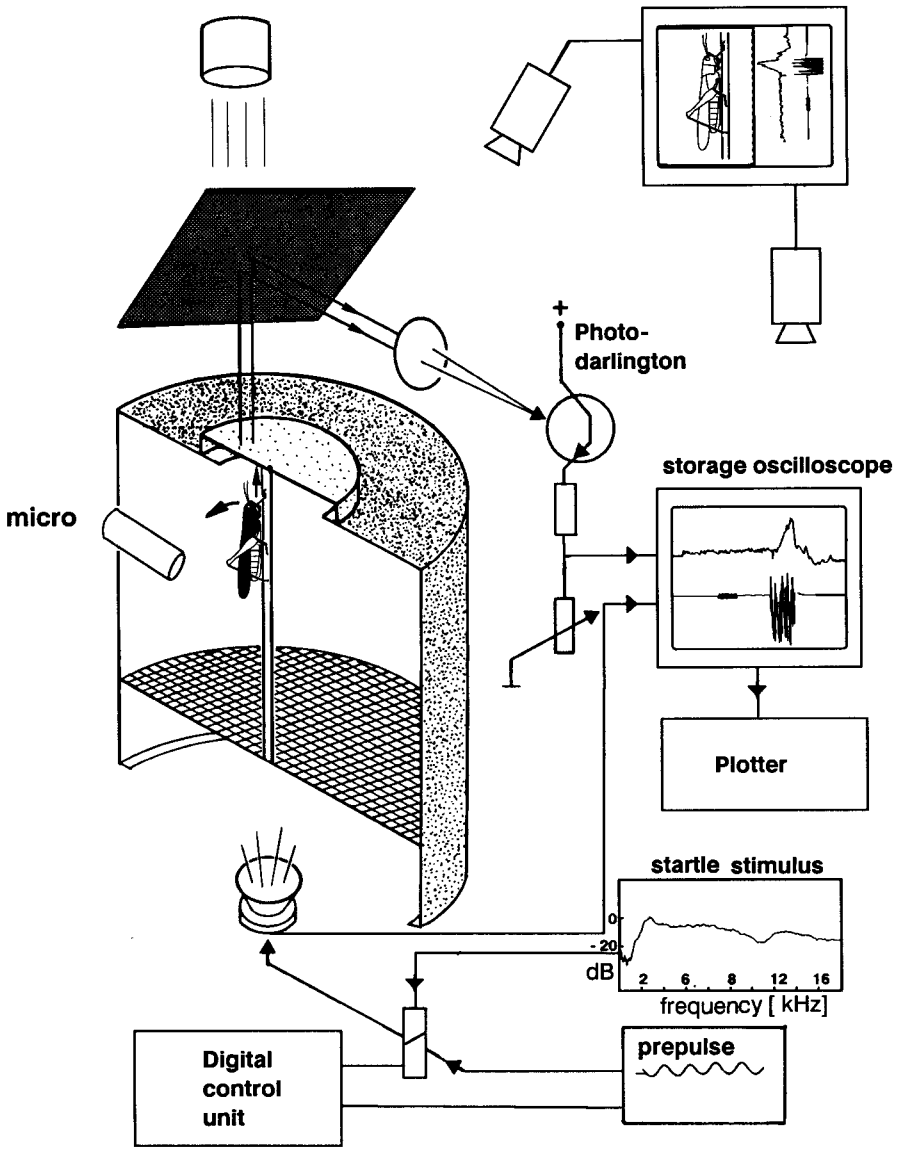

Fig. 1. Apparatus for eliciting and monitoring the startle reaction and schematic sketch of opto-electronic recording circuitry and acoustic stimulation. The animal was free to move around a rod attached to a perspex disc. The reflex foil attached to the animal's forehead reflected incoming light to a photodarlington via a semi-transmittant mirror. White noise startle stimuli and prepulses of adjustable frequency, amplitude and envelope were fed into a loudspeaker via a relay. The power spectrum of the startle stimulus was measured at the site of the tympanal organ and analyzed by a spectrum analyzer (Spectro 2000, MEDAV). Intervals between prepulse and startle stimulus could be varied by electronic delay units. Loudspeaker voltage and animal reaction were registered by a digital storage oscilloscope and plotted after each stimulation. A TV camera allowed video-taping of the animal, together with oscilloscope traces, to correlate animal movements with the output from the opto-electronic movement detector. Note that the microphone (*micro*) was only used for monitoring sound intensity, while calibration was done after the experiment. For further details, see text

loscope traces were stored on a videorecorder together with the animal's image. The whole set-up was calibrated by attaching the reflex foil to a loudspeaker membrane and measuring its angular deflection by the projection of a laser beam. Within a frequency range between 0.2 and 1000 Hz, an opto-electronically measured voltage of 1 mV corresponded to an angular displacement of 0.1° which was far below the observer's detection capacity of a startle reaction on the video screen. Resolution could easily be increased by enlarging the image of the reflex foil on the photodarlington. The projection scale was chosen in such a way that signals were independent of the animal's position around the rod. Any other transducer system such as a commercial phonographic cartridge or a ballistic chamber used for the registration of vertebrate startle behaviour would have been suitable, but the opto-electronic method was chosen because it directly revealed the main component of the locust's startle: the change of the animal's position relative to the rod.

Acoustic stimuli. Acoustic stimuli were presented via a high frequency piezo-loudspeaker (PHT-25, Becker) placed 35 cm below the animal (Fig. 1). Startle reactions were elicited by white noise pulses of 150 ms duration and 1 ms rising time, covering a frequency range of 2–40 kHz. The frequency spectrum of the noise pulse deviated from ideal white noise according to the transfer function of the piezo-loudspeaker (Fig. 1, inset); for the sake of simplicity, this noise pulse is henceforth classified as "white noise". Prepulses were generated by a custom-made acoustic stimulator. They consisted of pure sine waves between 3 and 40 kHz, 120 ms length and were smoothed by an envelope of 2 ms rise time. The interval between prepulse and startle stimulus could be adjusted by digital delay units. To avoid amplifier noise during interstimulus intervals, the loudspeaker was switched off via a relay. Acoustic stimuli were monitored near the animal with a 1/2″ condenser microphone (Brüel and Kjaer, type 4133). Loudspeaker voltage was recorded by the storage oscilloscope, together with the positional information, and plotted after each experiment. Acoustic conditions were not ideal, as the rod and the perspex lid, as well as the animal's appendages, modify sound levels by diffraction, reflection and absorption. Leg position alone may affect incoming sound levels by several dB (Adam 1983). Therefore, for each frequency loudspeaker voltage and actual sound levels at the tympanum were calibrated after the experiments. To measure incoming sound at the site of the tympanal organ, a 1/8″ microphone (Brüel & Kjaer, type 4138, giving all sound levels relative to 2×10^{-5} N·m^{-2}) was mounted into a freshly killed locust at the site of the tympanal organ.

The whole apparatus was housed inside a wooden box of 1 m^3, lined with 7 cm foam wedge plates (Illsonic), which reduced reflections and incoming sound (sound intensities from 250 to 20 kHz were below 20 dB).

Animals. Ninety-eight adult male *Locusta migratoria* L. from the Institute's laboratory culture were tested. Animals were kept under continuous light in crowded conditions (gregarious phase) and fed ad lib.

Procedure. Animals were transferred to the rod in a vial; they usually climbed up to the top of the rod and sat there quietly after several minutes exploratory unrest. Animals which did not come to a rest after 20 min were removed. A preliminary series of startle stimuli of between 85 and 100 dB was presented to determine the sound intensity necessary to elicit a small startle reaction between 0.4 and 1°; a constant stimulus intensity was maintained throughout the experiment. Series of startle stimuli preceded by prepulses alternating with unpreceded test stimuli were presented at an interstimulus interval around 5 min. The prepulse intensity necessary for a complete suppression of the startle reaction was determined by an up-down technique (Levitt 1971). Series were terminated when animals became restless, turned down and left the rod, or when unpreceded stimuli failed to elicit any startle reaction due to habituation. To avoid eventual effects from long-term habituation these animals were not used again. Habituation was less likely with longer interstimulus intervals; an average of 5 min proved to be a good compromise between duration of the experiment and the disturbing effects of habituation.

Results

The startle reaction

Resting locusts react to sound bursts of high intensity and steep rise time with a fast, jerky contraction of legs and several trunk muscles. This startle reaction begins with an up-down movement of the hindlegs, combined with a slight outward turning of the coxae. The subsequent bending of middle and front legs results in an approach of the animal's body to the rod, sometimes followed by an immediate return to the original position. The sequential order described here corresponds to the different reaction types in response to increasing intensities. At lower intensities, only hindleg jerks are observed, while increasing intensities produce a "body startle" brought about by the middle and front legs and the muscles of the neck, thorax and abdomen. In essence, the main component of the movement is a tilt about the abdominal end, resulting in a change of the angle between the animal's long axis and the rod. As the reflex foil on the animal's head moved by the same angle, the recording via the photodarlington gave a direct measure of the startle response. Startle magnitudes between 1 and 20 mV correspond to angular deflections between 0.1 and 2° with typical rise times of 20 ms. This corresponds to angular velocities up to $100° \cdot s^{-1}$ and accelerations in the order of 20 ms^{-2}.

All animals tested showed the startle reaction, but startle amplitude, latency and habituation varied between individuals. The startle response could be elicited by pure frequencies and broad-band noise pulses. A systematic investigation of the properties and frequency response of the startle response itself is beyond the scope

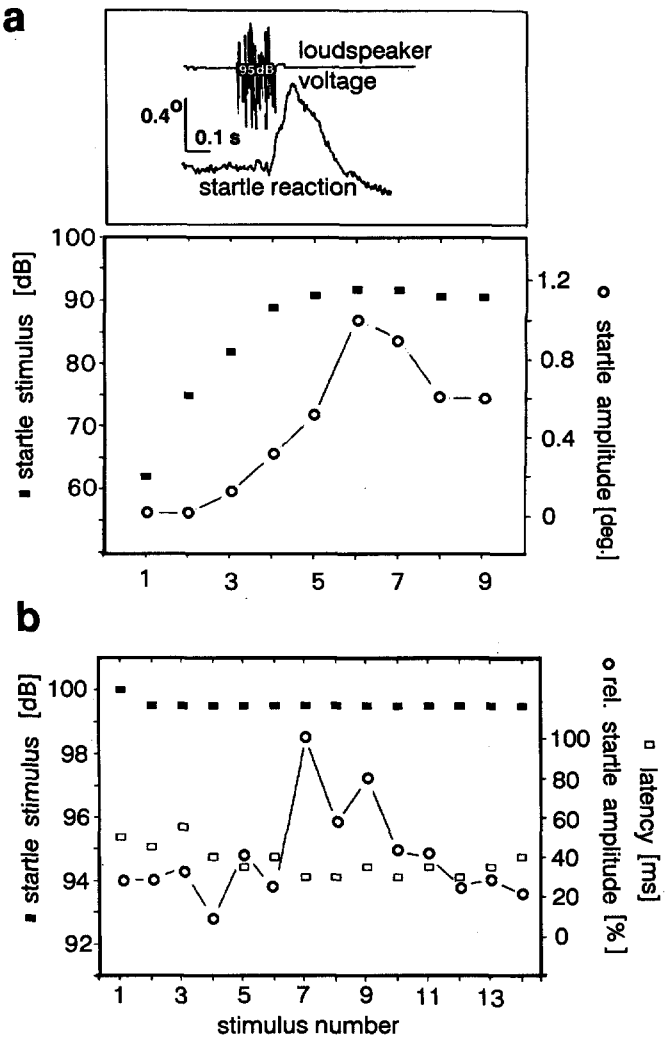

Fig. 2a, b. Variation of startle reactions within stimulus series of white noise pulses with an interstimulus interval of 5 min: **a** original registration of body startle reaction elicited by a white noise sound pulse of 95 dB and variation of startle amplitude (○) within a series of progressively increasing stimuli (■). Startle amplitude is defined as maximal displacement (for the registration example, a body axis displacement of 0.6° and a rise time of $16° \cdot s^{-1}$). The first measurable body startle reaction was observed at the third stimulus at 82 dB, corresponding to a threshold between 77 and 82 dB. Startle amplitude increased with stimulus intensity and dropped after repetition of a 92 dB stimulus. The experiment was terminated by the animal leaving the rod; **b** repetition of a constant white noise pulse (■) of 99.5 dB evoked startle reactions of considerable variation, with a maximum of 2.8° at stimulus 7. Startle amplitudes are expressed in per cent of this maximal reaction. Latency (□) varies much less

of this paper and will be the subject of forthcoming investigations (K. Riede, unpublished observations). For the investigation of prepulse inhibition it was necessary to elicit a series of startle reactions of fairly constant amplitude. "White noise" sound pulses proved to be best because startle thresholds were several dB below pure tones and habituation less likely. Last, but not least, the energy of the white noise startle stimulus is distributed on the different receptor groups according to their frequency characteristics, so that the actual sound ener-

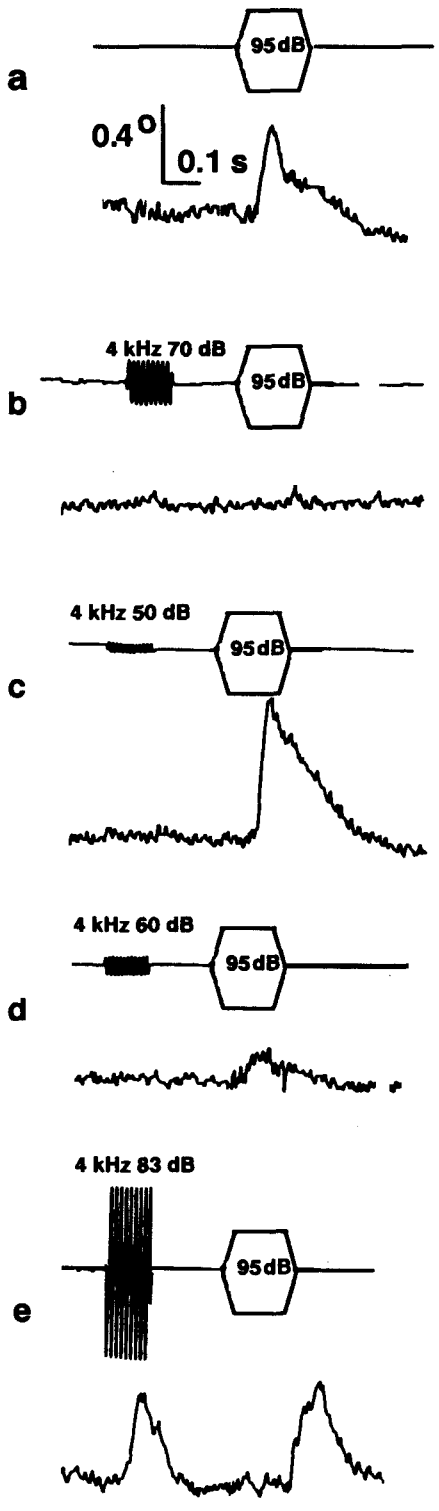

Fig. 3a–e. Original recordings of startle reactions and their inhibition by prepulses from a series of consecutive stimuli (interstimulus interval: 5 min). *Upper traces*: loudspeaker voltage and corresponding sound intensity; the white noise startle stimulus remains constant and is symbolized by a *box*. *Lower traces*: voltage induced by opto-electronically measured body startle reactions (cf. Fig. 2): **a** fast body startle reaction of 40 ms latency and 0.47° amplitude; **b** a prepulse of 4 kHz and 70 dB which terminated 160 ms before the onset of the startle stimulus inhibited the startle reaction; **c** a consecutive startle stimulus preceded by a prepulse of only 50 dB provoked again a strong startle reaction; **d** a 4 kHz prepulse of 60 dB led to a considerable reduction of startle amplitude and rise time; **e** a prepulse of increased intensity elicited a startle reaction without inhibiting the reaction to the second white noise pulse; amplitudes of both reactions were of comparable size, but the latency of the second reaction was prolonged with respect to the first (150 ms vs. 40 ms)

gy for each receptor group is lower compared to pure frequency stimuli of equal intensity. Therefore, possible deafening effects by the startle stimulus are less likely.

Figure 2a shows the startle amplitude in a stimulus series of white noise sound pulses with increasing amplitude. Above a threshold around 80 dB, reaction amplitude increases with stimulus amplitude and drops again after several repetitions of the same stimulus. The series was terminated by the animal leaving the apparatus. Startle amplitudes up to 8° could be provoked by increasing the stimulus intensity. However, stronger reactions induce restlessness. Therefore, stimuli were adjusted to produce small startle amplitudes between 0.5 and 1.2° which required white noise pulses between 82 and 105 dB, depending on the individual tested. Such series allowed up to 50 stimulations, with the animal maintaining its fixed position.

Figure 2b shows a typical example of the variation of startle response amplitude and latency within a series of constant white noise stimuli of 99.5 dB. Although there is considerable fluctuation of amplitude, the reaction did not disappear and the series was terminated by the animal leaving the rod.

Latency varied much less and probably was not correlated with startle amplitude. Latencies of startle reactions fell into two classes: short latencies below 60 ms (mean $= 35 \pm 23$ ms, $n = 75$, range 5–60 ms), and longer latencies between 100 and 150 ms. Long latency reactions were frequently observed in restless animals or at the beginning of a stimulus series. They were often followed by a position change. Because the signals induced by such body displacements were much higher than the startle amplitude, no reliable measurements of startle amplitude and prepulse inhibition could be made with these animals. Out of 98 tested males, 42 showed series of fast latency startle long enough to investigate prepulse inhibition (Figs. 2b, 4).

Prepulse inhibition

A fast body startle reaction (Fig. 3a) could be inhibited completely by an acoustic prepulse of 120 ms length and a frequency between 3 and 20 kHz presented 160 ms before the startle-eliciting white noise (Fig. 3b). The inhibitory effect was completely reversible: when prepulse intensity was reduced below a certain threshold (50 dB) the startle reaction recovered (Fig. 3c). Having increased the prepulse's intensity to 60 dB, startle was suppressed again. However, inhibition was not complete and a small reaction of reduced amplitude but unchanged latency was still detectable. In this series, the 60-dB prepulse was classified as efficient and the 50-dB prepulse as inefficient.

Startle-inhibiting prepulses exerted an influence on the subsequent startle reaction without eliciting any reaction themselves, even after repeated presentation. This means that conditioning did not occur, although the experimental procedure is similar to a conditioning paradigm. Of course, a startle reaction to the prepulse alone could be provoked by increasing its intensity above startle threshold (83 dB; Fig. 3c). Interestingly, the subsequent startle reaction was not inhibited, but showed an increase in latency.

Figure 4 illustrates the suppression of startle amplitude by a 4-kHz prepulse of constant intensity (58 dB) interspersed within a series of constant startle stimuli. Suppression was either complete or at least 70% with respect to the nearest unpreceded stimulus. Disappearance of the startle reaction at stimulus 10 was completely reversible at unpreceded stimulus 11, so that the prepulse can be considered as an on-off switch for the following startle reaction. Prepulses at 12 and 13 were not classified as efficient because amplitude reduction at stimulus number 14 could have been due to habituation. The series could be continued by increasing the startle stimulus intensity. For threshold determination, stimulus series were terminated when the first dropout of startle reaction to an unpreceded stimulus was observed. This was done to keep experimental conditions as homogeneous as possible. In most cases, however, the experimental test was terminated by the animal leaving the rod.

Table 1 reveals that the absence of startle reactions is correlated with the presentation of prepulses between 3 and 20 kHz, while prepulses of 40 kHz have no significant effect.

Thresholds of prepulse efficiency

It is evident from Fig. 3c, d that prepulses exert their inhibitory properties only above a certain intensity. To

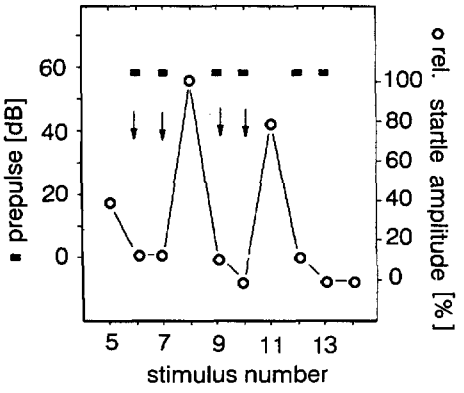

Fig. 4. Prepulses of 4 kHz and 58 dB (■) reproducibly led to reduction of the startle response (○) in a series of constant startle stimuli (interstimulus interval 5 min, white noise pulses of 93 dB). The recovery of startle at unpreceded stimulus 11 shows that prepulse inhibition is reversible which allows to classify prepulses from stimuli 6 to 9 as efficient (marked by *arrows*). Startle did not recover at stimulus 14, which means that reductions at stimuli 12 and 13 could be due to habituation and the respective prepulses cannot be classified as efficient

Table 1. Frequency of complete dropout of startle reactions to stimuli preceded by prepulses compared with unpreceded ones

	No prepulse	Prepulse 3–20 kHz	Prepulse 40 kHz
No startle	2.4%	23.3%	5%
Startle	98.6%	76.7%	95%
n	207	348	90

Stimulations from all 40 series are pooled; series length varied between 11 and 68 stimuli. Prepulses of frequencies between 3 and 20 kHz are summarized, but prepulses of 40 kHz are treated separately. Arranging data into 2×2 contingency tables and calculating chi-square values shows a highly significant ($\chi^2 = 43.38$; $P < 0.0005$) increase of dropouts due to prepulses between 3–20 kHz, while dropout frequency with 40 kHz prepulses does not differ significantly from the "no prepulse" condition. Note that all prepulses are summarized, regardless of their intensity, and that only complete suppression (Fig. 3b) is classified as "no startle"

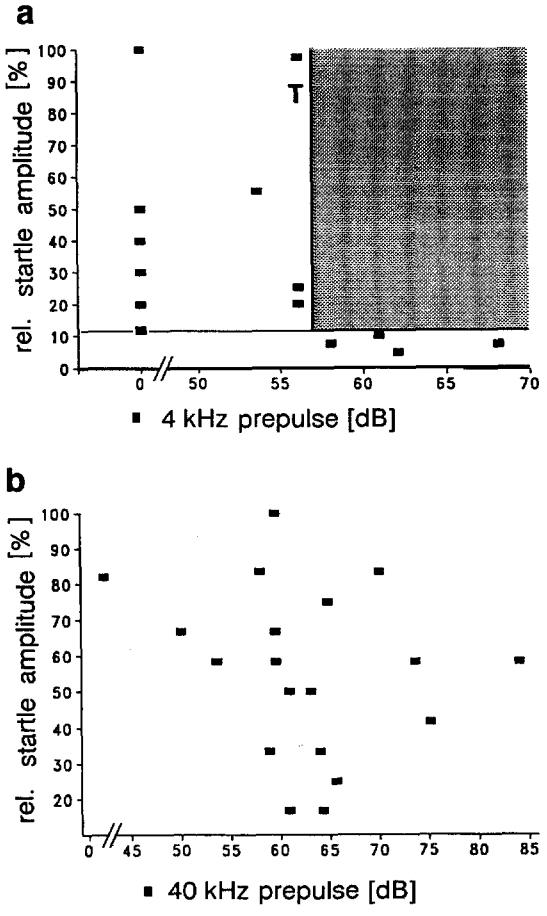

Fig. 5a, b. Influence of prepulse intensity on a following startle reaction (■) within one stimulus series (constant white noise pulses, interstimulus interval 5 min): **a** prepulses of 4 kHz above 57 dB (threshold intensity *T*) suppressed startle reactions to less than 10% of maximal startle amplitude. The sharp transition and the absence of reactions in the hatched area illustrates the all-or-nothing character of the threshold criterion; **b** at prepulse frequencies of 40 kHz, no correlation could be observed between prepulse and following startle reactions which were unaffected in spite of high prepulse intensities

find this threshold the intensity of prepulses was varied according to an up-down technique (Levitt 1971). To differentiate reductions by a prepulse from the considerable fluctuations in a series of unpreceded startle stimuli (Fig. 2b), a rigorous criterion for prepulse efficiency had to be applied: the prepulse must induce complete suppression or a massive reduction of 70% with respect to the former and subsequent unpreceded startle reaction. With average startle amplitudes of 0.7°, a reduction of 70% signifies startle reactions of only 0.2° (Fig. 3d) and are at the resolution limit of the recording apparatus.

To illustrate this threshold criterion, Fig. 5 gives an example of the relation between prepulse intensity and startle amplitude within a single stimulus series. This response function is extremely steep: any prepulse above a threshold of 58 dB reduced the following startle below 10%. The population of inefficient prepulses to the left of the threshold line (T) can clearly be differentiated from the efficient prepulses to the right. For prepulses between 3 and 20 kHz such a threshold could be found, while prepulses of 40 kHz (Fig. 5b) proved to be inefficient throughout the intensity range.

Action spectrum of prepulse inhibition

With the above criterion, a well-defined prepulse threshold could be determined for each stimulus series and each prepulse frequency between 3 and 20 kHz, thus giving the action spectrum of prepulse efficiency (Fig. 6). Thresholds for various frequencies determined within one series are connected by lines; startle-eliciting prepulses are symbolized by *s* and lie at least 20 dB above efficient prepulses.

In spite of considerable variation it can be stated that the mean efficient prepulse is around 60 dB with a flat action spectrum between 3 and 20 kHz. This covers the sensitivity range of low-frequency tympanal receptor cells [group a–c: Michelsen (1971)] but does not include the high-frequency d-cells.

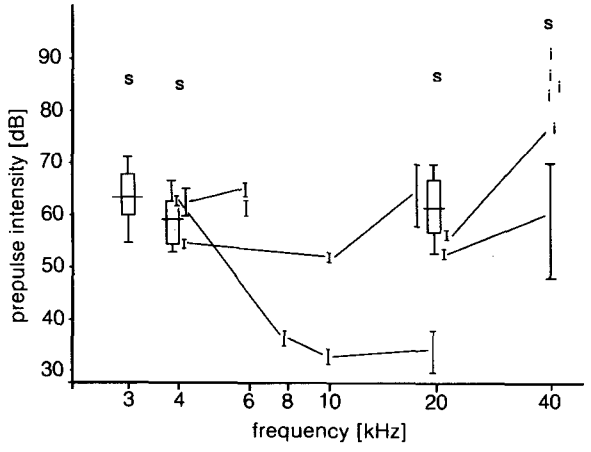

Fig. 6. Action spectrum of prepulse inhibition. For 40 animals, a threshold was determined after a series of prepulses of varying intensity (cf. Fig. 5). Means of ten animals each are summarized by box-and-whisker representation (whisker represents range, box contains 75% of values). *Single bars* represent results from one individual; *lower margin*: loudest inefficient prepulse, *upper margin*: faintest efficient prepulse. Thresholds for varying frequencies determined within one series are connected by *lines*. Startle reactions elicited by prepulses alone are symbolized by *s*. At 40 kHz, most prepulses were inefficient (*i*), despite intensities close to startle threshold (*s*)

Discussion

Startle reactions and escape behaviour

For invertebrates, the startle response is defined in a broad sense and includes several types of escape manoeuvres from bat evasion of crickets (Hoy et al. 1989) to the locust jump (Pearson and O'Shea 1984). The startle reaction of sitting locusts described here belongs to the type of "good startle responses" which "... fail to translate the body" (Bullock 1984, p. 4). Like the rat's startle, the amplitude of the locust's startle is graded and can become very small. Together with the cricket's variable abdominal deflection (Hoy et al. 1989), this is further evidence that insect startle is not necessarily an all-or-nothing response which was claimed to be a fundamental difference from mammalian startle (Davis 1984). The occurrence of prepulse inhibition in the locust is an additional striking analogy to the vertebrate startle.

With a mean latency of 35 ms the locust's startle reaction is among the fastest in insects and lies in the range of other short latency reflexes like the optically elicited leg reflex in flies (Kirschfeld and Vogt 1985). In some individuals, slower startle reactions with long latencies around 100 ms were observed which lie in the range of avoidance manoeuvres of flying locusts [80 ms latency of abdominal deflection; Baader (1991)] and frequently initiated a displacement of the sitting animal. Therefore, slower startle reactions could be interpreted as an indicator of a "flight mood" in sitting, but restless animals. However, flight initiation was never observed. Busnel et al. (1959) discovered a phonokinetic reaction in freely suspended *Locusta migratoria* and defined it as a "non-oriented motoric reaction, usually of great amplitude and provoked by sounds of high intensity". Threshold and latency of this reaction were determined electrophysiologically in the metathoracic ganglion by Busnel and Burkhardt (1961); they coincide with the flat frequency characteristics and high threshold of the fast startle reaction (Fig. 6).

Although startle behaviour is certainly related to escape reactions, possibly as a preparatory reaction, the fast startle reaction neither results in displacement nor does it facilitate optically elicited jumps (Riede 1990). The observed hindleg movements do not result in the typical "cocking" position necessary for the jump (Pearson and O'Shea 1984). Therefore, the above experiments do not reveal the biological significance of this behaviour.

Determination of auditory threshold by prepulse inhibition

The all-or-nothing character of startle suppression by prepulses above a certain intensity (Fig. 5) served as a clear threshold criterion which allowed determination of the action spectrum in Fig. 6. Between 3 and 20 kHz this flat action spectrum lies within the sensitivity range determined behaviourally for grasshopper phonotaxis (von Helversen 1984). This is in good agreement with findings in both rats and guinea pigs that prepulse thresholds lie in the range of sensory thresholds as determined by traditional psychophysical techniques (Hoffmann 1984). Compared with electrophysiological data, prepulse thresholds coincide with those of central auditory neurons. In the protocerebrum, various broadband neurons as well as high and low frequency elements can be found (Adam and Schwartzkopff 1967; Adam 1969). A remarkable correspondence exists between their central elements b and c (op cit, Abb. 2, sensitivity around 60 dB) and the prepulse action spectrum (Fig. 6). Even the sensitive animal showing prepulse inhibition around 35 dB fits nicely with Adam and Schwartzkopff's broadband neuron going down to 35 dB (op cit, Abb. 2, curve a). These neurons could be candidates for the neuronal substrate mediating prepulse inhibition.

No threshold for prepulse inhibition could be determined at 40 kHz, which indicates that in spite of tone-deafness of prepulse inhibition between 3 and 20 kHz, some frequency information is evaluated and leads to distinct categorization above 20 kHz. This is a behavioural correlate for the frequency discrimination as observed earlier by electrophysiologists (Horridge 1960). Further evidence is provided by behavioural experiments on grasshopper phonotaxis (*Chorthippus biguttulus*) which suggest different weighting of high and low frequencies (von Helversen 1990). In crickets, identified acoustical interneurons project to different areas in the brain corresponding to a low-frequency and high-frequency central pathway (Elsner and Popov 1978). For the time being it must be inferred that in contrast to the startle response, prepulse inhibition is mediated only by the low, and not by the high, frequency pathway.

Possible mechanisms of prepulse inhibition

The immediate efficacy of a prepulse after its first presentation shows that it does not involve learning and must be considered as a form of reflex modification mediated by established neural connections. In spite of numerous psychophysiological studies of prepulse inhibition of the rat's startle, the underlying mechanisms are still debated. Hoffmann and Ison (1980) give evidence for a prepulse-induced increase of startle threshold, while Pilz (1989) describes experiments which can be explained by inhibitory effects on the efferent side. As in the rat, prepulse inhibition in the locust could be mediated by modulation of either afferent or efferent pathways. However, candidates for a possible neuronal substrate mediating prepulse inhibition might be higher-order acoustical interneurons where a variety of inhibitory effects have been described (Marquart 1985). Kalmring (1975) showed that neuronal activity of locust B1-neuron [corresponding to IN 531; cf. Boyan (1991)] could be reduced by double pulses presented simultaneously or delayed, which corresponds to prepulse stimulation. In addition, auditory responsiveness was affected by other sensory modalities such as wind (Boyan 1986) or ongoing motor activities such as song (Wolf and von Helversen 1986). Therefore, for further specification of neuronal correlates of prepulse inhibition, a further behavioural dissection of the polysegmental startle reflex and experiments with prepulses of other sensory modalities, e.g. wind, are necessary.

Finally, it must be taken into consideration that inhibition takes place at the efferent side. Because various segments are involved in the polysegmental startle reflex, it should be mediated by some overall inhibitory activity of the brain. There are well-known examples for inhibitory effects of the insect's brain on simple behaviour [see Huber (1960) for the cricket's song]. Rowell (1964) demonstrated that inhibition of a reflex leg movement increased with ganglionic activity. His general principle that "... the probability of obtaining the desired response to a standard input is inversely related to the total extraneous signal which arrives simultaneously at the integrating area from other sources" (loc. cit. p. 571) probably holds also for prepulse inhibition. The difference would be that integration is not spatially, but temporarily, within the short interstimulus interval between prepulse and startle.

Biological significance of prepulse inhibition and its potential for the study of invertebrate behaviour

One may ask if prepulse inhibition is an emergent property of the locust's complex auditory system, or if it has any evolutionary significance. The remarkable convergence of prepulse inhibition in vertebrates and locusts indicates a common biological function. Its survival value could be interpreted as a suppression of unnecessary, energetically wasteful startle reactions in a noisy environment. The absence of prepulse inhibition above 20 kHz could be interpreted as an adaptation to bat avoidance, as an approaching bat always produces series of high-frequency "prepulses" which should not inhibit the escaping insect's startle reaction.

Despite our ignorance of its biological significance, the presence of prepulse inhibition in the locust, and possibly other insects, opens an additional window for the study of their sensory capacities. Up to now, psychophysical determination of sensory capacities was limited to the few insect species with a highly developed learning disposition such as bees (von Helversen 1972) or those exhibiting fixed action patterns associated with mate recognition and localisation. In the case of Orthoptera, numerous studies on duetting and phonotaxis provided detailed knowledge of their astonishing hearing capacities [e.g. von Helversen (1984) for gomphocerine grasshoppers]. However, there are numerous non-singing grasshoppers which do not show acoustic communication

(Riede 1987), not withstanding their well-developed hearing organs (Riede et al. 1990) and great interspecific similarity at the level of thoracic auditory interneurons (Ronacher 1990). Therefore, one must consider the possibility that processing of acoustical information did not evolve for mate recognition exclusively, but in the context of an acoustical startle/escape system.

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