HABITUATION OF THE ULTRASOUND-INDUCED ACOUSTIC STARTLE RESPONSE IN FLYING CRICKETS

By MICHAEL L. MAY* AND RONALD R. HOY†

Section of Neurobiology and Behavior, S. G. Mudd Hall, Cornell University, Ithaca, NY 14853, USA

Summary

The ultrasound-induced negative phonotactic response of tethered, flying Australian field crickets habituates to repeated stimuli. Using the magnitude of the metathoracic leg's swing during a series of ultrasonic stimuli as a measure of habituation, we show that: (1) the response declines exponentially; (2) the response recovers spontaneously; (3) repeated trials produce more rapid and stronger habituation; (4) successive stimuli presented more rapidly produce more rapid and stronger habituation; (5) a weaker stimulus intensity produces more rapid and stronger habituation; (6) the habituation shows stimulus generalization (i.e. the response is similar for different ultrasonic frequencies); (7) a novel stimulus produces dishabituation; and (8) the effect of the dishabituating stimulus habituates after repeated trials. These findings place habituation of cricket negative phonotaxis in the context described for habituation in mammals.

Introduction

Organisms at all phylogenetic levels exhibit behavioral responses that decrease in magnitude in response to a repetitive stimulus (Humphrey, 1930). Even *Hydra* show a decremental response to repeated probing (Rushforth, 1965). Many studies describe these patterns of behavior as habituation. However, specific methodology defines habituation more precisely than as a simple decremental response to a series of stimuli. Thompson and Spencer (1966) formulated a list of criteria for habituation that included nine points. Therefore, studies should assess habituation through this structured paradigm.

In most animals that show an acoustic startle response, habituation is in accordance with the criteria of Thompson and Spencer (Davis and File, 1984). Australian field crickets (*Teleogryllus oceanicus*) display an ultrasound-induced acoustic startle response (Hoy *et al.* 1989). When tethered, flying crickets hear an

* Present address: PO Box 141, Etna, NY 13062, USA.
† To whom reprint requests should be addressed.

ultrasonic stimulus, they steer away from the source of the sound by invoking a host of kinematic and aerodynamic changes (Moiseff *et al.* 1978; May *et al.* 1988; May and Hoy, 1990*a,b*). This occurs in response to even a single suprathreshold pulse of ultrasound. However, as well as being an acoustic startle response, which may simply involve a nondirectional jump or jerk, this negative phonotactic response also appears to be a directional, complicated escape behavior. Moiseff *et al.* (1978) postulated that this response may be a bat-avoidance behavior.

If negative phonotaxis by a cricket is a predator-avoidance response, this behavior might not be expected to habituate. According to Thompson *et al.* (1973), responses to danger signs (e.g. predators) do not habituate. Shalter (1984) claimed that only two examples provided evidence of prey habituating to predators hunting in a natural environment. In the first example, caterpillars habituated to stimuli from a predaceous bug (Arnold, 1971). The second example showed that royal terns habituate to stimuli from laughing gulls (Buckley and Buckley, 1972). Although habituating to predators may be rare, and neither of these examples used auditory stimuli, many years of observation indicate that ultrasound-induced negative phonotaxis by crickets does indeed habituate during a series of stimuli.

To describe habituation of negative phonotaxis in crickets, we measured the magnitude of the ultrasound-induced metathoracic leg kick (May and Hoy, 1990*b*) throughout a series of stimuli. We show that this habituation satisfies eight of Thompson and Spencer's (1966) nine criteria.

Materials and methods

We used adult female crickets, *Teleogryllus oceanicus* (W. Cade and D. Otte, personal communication), 1–4 weeks after the adult molt. We tested only females for two reasons (1) to conform to precedents set for this species (Moiseff *et al.* 1978); and (2) because females, whose forewings are softer than the male's, are easier to tether. These crickets came from our laboratory colony developed from Hawaiian specimens collected about 4 years ago. We maintained the crickets at a high density and on a reversed light cycle. Using the crickets during the first few hours of their subjective night increased their flight performance.

To stabilize the crickets for tethered flight, we used a small amount of dental wax to attach a wire tether on the dorsal surface at the intersection of the thorax and the first abdominal segment. To maximize visualization of the metathoracic leg, we removed the cricket's hindwings under cold anesthesia. Crickets have been shown to maintain robust flight behavior and ultrasound avoidance even with the hindwings removed (May and Hoy, 1990*a,b*). The tether held the crickets upright in a wind stream which we adjusted to $2.1 \, \mathrm{m \, s^{-1}}$, the average tethered flight speed for crickets (May *et al.* 1988), by using a digital anemometer (Omega model HH 30).

To measure the movement of the metathoracic leg, we used a cadmium sulfide photocell (Radio Shack no. 276–1657). The edges of the photocell's surface were

masked with tape such that only a triangular area remained exposed. We positioned the photocell just below the distal end of the femur of the left metathoracic leg such that one corner of the exposed triangle was slightly medial to the leg's lateral edge. A fiber-optic light source, projected from above, cast the leg's shadow on the photocell. When the cricket moved its leg laterally, some of the photocell's surface was in the leg's shadow. Because of the triangular receptive area on the photocell, increasing lateral movement by the leg produced increasing shadow. Using this technique, the photocell produced a d.c. signal that was linearly related to the magnitude of the leg's lateral movement up to 6 mm (data not shown). However, all magnitudes are given in relative units. All experiments were recorded on analog tape (Vetter model 420) for off-line analysis.

To stimulate a negative phonotactic response, and thus a leg swing, we synthesized ultrasonic pulses. A custom-built trapezoid wave shaper modified the output of a sine-wave generator (Brüel & Kjaer model 3011) which was then temporally adjusted (A.M.P.I. Master-8). We attenuated (Hewlett-Packard 350D) and amplified (Nikko NA-790) the stimulus, which was delivered through a piezoelectric speaker located in the cricket's horizontal plane and 90° to the right of the cricket's longitudinal axis. A second stimulus, created as above, delivered pulses to a second speaker placed on the cricket's left. Using a sound level meter (Brüel & Kjaer 2209) fitted with a 1/4 inch microphone (Brüel & Kjaer 4135), we calibrated the intensities, which are given in decibels (dB) relative to 20 μPa (dB SPL). Using a real-time spectrum analyzer (Nicolet 444A), we examined the spectral properties of the stimulus and found that all harmonics were at least 40 dB less intense than the carrier frequency. The carrier frequency of the stimulus pulse was a pure tone.

All experiments utilized pulse trains. Trains are defined by the pulse duration, the interpulse interval (IPI) and the intensity. In all cases, the pulse duration was 50 ms and the rise/fall time for the pulse was 5 ms. The IPI was defined as the time from the onset of one pulse to the onset of the next pulse. Intensities are given relative to threshold, which was defined as the lowest intensity that elicited movement of the metathoracic leg in 50% of the trials. For the 50 crickets tested, the average threshold was 75.2±0.8 dB (mean±S.E.M.).

We designed the following experiments to assess habituation of the ultrasound-induced swing by the metathoracic leg. In particular, the tests examine the principles of habituation as outlined by Thompson and Spencer (1966). We tested 50 crickets, in five groups of ten each.

In experiments on the first group of ten crickets, we used an IPI of 750 ms for twenty pulses with a carrier frequency of 20 kHz delivered at 10 dB over threshold. All of these pulses came from the right speaker and induced abduction (i.e. a swing) of the cricket's left metathoracic leg. Between pulses number ten and eleven, we delivered a single 50 ms pulse at a carrier frequency of 20 kHz, also at 10 dB over threshold, from the left speaker as a potential dishabituating stimulus.

In the second group of animals, ten crickets received eleven pulses with a carrier frequency of 20 kHz from the right and an IPI of 750 ms. Between the tenth and

eleventh pulse, we delivered one 50 ms pulse of 20 kHz and an IPI of 750 ms from the left. All stimuli were 10 dB over threshold. Each cricket was tested with three trials separated by 5 min to examine the effect of repeated trials.

For the third group of crickets, we used an IPI of 500 ms and a carrier frequency of 20 kHz. Ten crickets received ten pulses at 10 dB over threshold from the right. At the end of the series of pulses, we waited 10 min and then gave a single 50 ms pulse at 20 kHz, still from the right, and at 10 dB over threshold to assess recovery.

To examine the effect of stimulus intensity, we stimulated the fourth group of ten crickets with pulses at 20 dB over threshold. Again the IPI was 500 ms for ten pulses given at a carrier frequency of 20 kHz. All of these pulses came from the right speaker.

To assess the possibility of stimulus generalization (i.e. similar responses to different, but both ultrasonic, frequencies), we used a carrier frequency of 40 kHz for the fifth group of crickets. Using an IPI of 500 ms for ten pulses from the right speaker given at 10 dB over threshold, we tested ten crickets.

All values for the amplitude of the leg's swing were normalized. Thus, for each series of pulses, we considered the first response to be the standard or 100 %. All responses that followed were treated as a percentage of the initial response. All values are given in the text and figures as the mean±S.E.M. for the ten crickets tested and our statistical methods are according to Sokal and Rohlf (1981).

Results

The magnitude of the ultrasound-induced swing of the metathoracic leg decreased during a series of stimuli. Although the magnitude of the response decreased rapidly when presented with a series of like stimuli, it was restored by a single pulse from the opposite side (Fig. 1). However, the response did not always decrease smoothly throughout the series of stimuli. This can be seen by comparing the responses to stimuli number 9 and 10 in Fig. 1. Similar variability occurs in nearly all animals subjected to habituation (Davis and File, 1984).

With an IPI of 750 ms, the response decreased to 73±5.7 % of the original response by the second stimulus (Fig. 2). By the tenth stimulus, the magnitude decreased to 31±3.3 % of the original response. Over a series of pulses, the magnitude of the response decreased along a negative exponential function (Fig. 2).

By decreasing the IPI to 500 ms, the magnitude of the response decreased even more and at a faster rate (Fig. 2) relative to an IPI of 750 ms. With an IPI of 500 ms, the response decreased to 63±7.5 % of the original response by the second stimulus. The response was only 9±1.6 % of the original response by the tenth stimulus pulse. The steeper initial slope of the exponentially fitted line for the IPI of 500 ms revealed the increased rate of habituation relative to the 750 ms IPI.

By repeated application of pulse trials, the continual decrease in response magnitude was illustrated more dramatically (Fig. 3). Furthermore, repeated pulse sessions showed habituation of the restorative action of a dishabituating
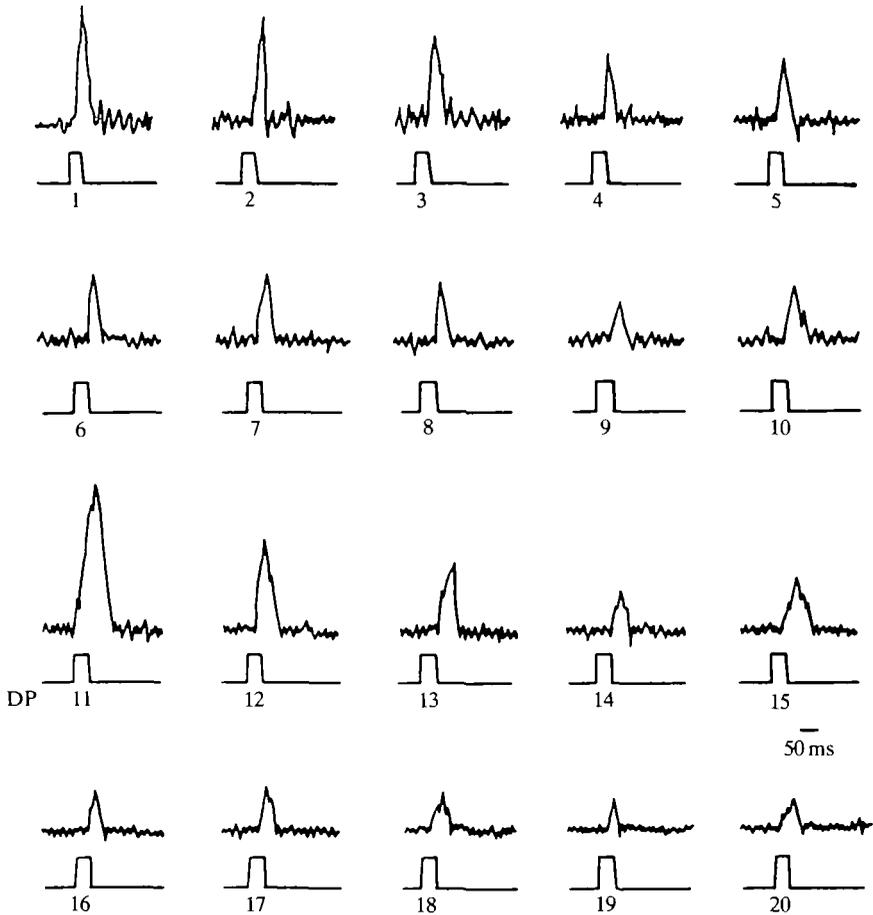
Fig. 1. Habituation and dishabituation of the ultrasound-induced swing of the metathoracic leg. The segments show the response to a series of 20 pulses, labeled 1–20, with an IPI of 750 ms, a carrier frequency of 20 kHz and an intensity of 10 dB over threshold from the right side for a single cricket. For each segment, the upper trace shows the abduction of the left metathoracic leg and the lower trace shows the stimulus. Between pulses 10 and 11, we gave a dishabituating pulse (DP), also with a 20 kHz carrier frequency and 10 dB over threshold, from the left. The temporal calibration bar applies to all traces. The magnitudes for the abduction are relative values.

pulse (Fig. 3). After one stimulus series, the 20 kHz dishabituating pulse from the contralateral side restored the response to 67±5.6% of the original response. After the second and the third series, the dishabituating stimulus only restored the response to 46±6.1% and 38±2.7%, respectively, of the original magnitude.

The cricket's response recovered from habituation in as little as 10 min (Fig. 4). After the recovery period, the recovery pulse elicited a response that was 96±8.9% of the original response. Furthermore, a paired *t*-test showed that the

magnitude of the response to the original stimulus was not significantly different from the response to the recovery pulse ($t=1.15$; $P>0.10$).

A pulse series delivered at a higher intensity showed a decreased magnitude of habituation. When comparing two stimulus sessions, both using a 500 ms IPI and a 20 kHz carrier frequency, where one used an intensity of 10 dB and the other 20 dB over threshold, the louder stimulus produced less habituation (Fig. 5). With the less intense stimuli, ten pulses decreased the magnitude to $9\pm1.6\%$ of the original
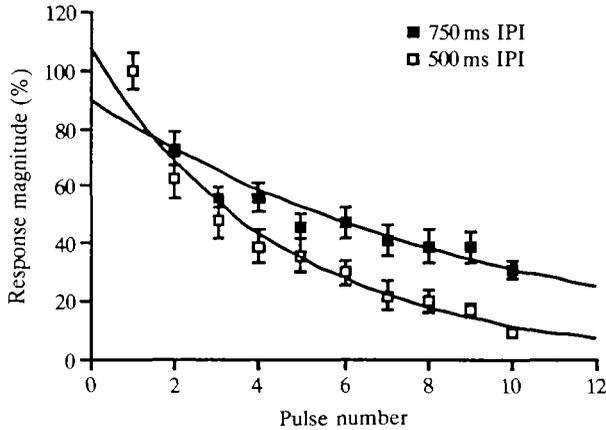

Fig. 2. The effect of decreasing interpulse interval (IPI) from 750 ms to 500 ms. The average response magnitude over a series of 10 pulses. The lines represent an exponential fit for the 750 ms IPI ($y=89.9e^{-0.09x}$; $r^2=0.90$) and the 500 ms IPI ($y=107.3e^{-0.23x}$; $r^2=0.96$). All pulses had a carrier frequency of 20 kHz and an intensity of 10 dB over threshold. Values are mean±S.E.M., $N=10$.
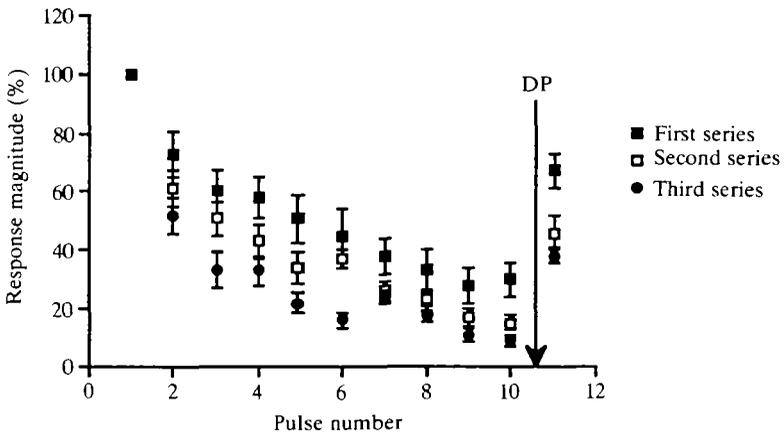

Fig. 3. The effect of a series of habituation sessions. Each of 10 crickets received 11 pulses with an IPI of 750 ms, a 20 kHz carrier frequency and an intensity 10 dB over threshold from the right side. Between pulses number 10 and 11, a dishabituating pulse (DP) of 20 kHz was given from the left at 10 dB over threshold. Each cricket received this stimulus regime three times separated by 5 min. Values are mean±S.E.M.

response. Yet with the louder stimuli, ten pulses only decreased the magnitude to 54±5.6% of the original response.

The form of the habituation, however, did not depend upon the carrier frequency of the stimuli, as long as it was ultrasonic. Comparing the results from stimuli using 20 kHz with those using 40 kHz stimuli showed the effect to be the same (Fig. 5). A two-way analysis of variance test, using the carrier frequency and
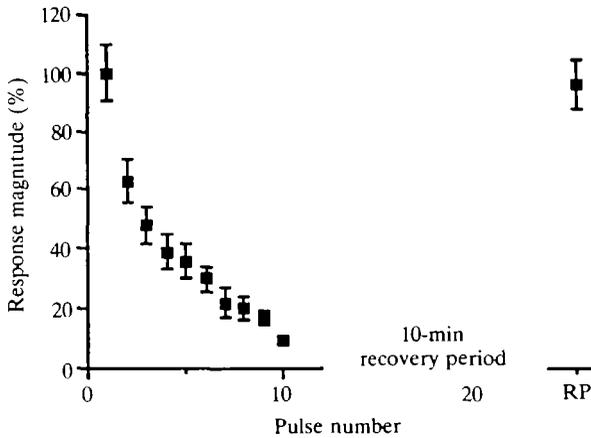

Fig. 4. Spontaneous recovery. Ten crickets received 10 pulses with a 20 kHz carrier frequency, an IPI of 500 ms and an intensity of 10 dB over threshold from the right. After a 10-min recovery, a pulse (RP) with a 20 kHz carrier frequency and 10 dB over threshold was given from the right side. Values are mean±S.E.M.
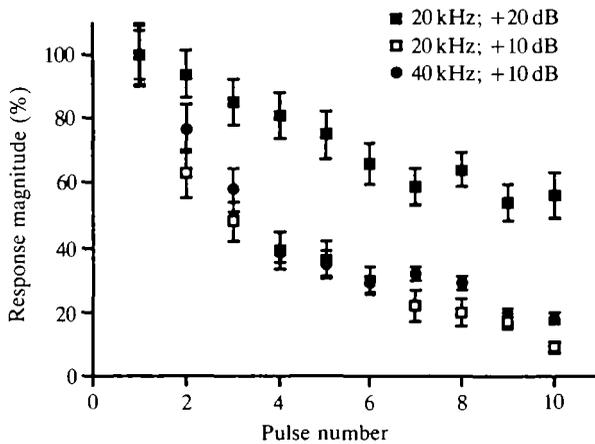

Fig. 5. The effect of the carrier frequency and intensity on the habituation response. In each case, 10 crickets received 10 pulses with an IPI of 500 ms. The characteristics of the pulse series were divided into three groups: (1) a 20 kHz carrier frequency at 20 dB over threshold; (2) a 20 kHz carrier frequency at 10 dB over threshold (same data shown in Fig. 2 for the 500 ms IPI); and (3) a 40 kHz carrier frequency at 10 dB over threshold. For each group, the points show the relationship between the magnitude of the leg swing over the series of pulses. Values are mean±S.E.M.

pulse number as factors, showed that both frequencies induced a significant decrease in response magnitude across the series of pulses ($F=51.6$; $P<0.0001$) but that there was no significant difference in magnitude caused by the selection of the carrier frequency ($F=3.0$; $P>0.05$).

Discussion

The negative phonotactic response of the Australian field cricket, as measured by the swing of the metathoracic leg, does show habituation in response to a series of ultrasonic stimuli. The above experiments show that the cricket's response satisfies eight of the nine principles of habituation as defined by Thompson and Spencer (1966). In particular, we showed the following points: (1) the magnitude of the response declines along a negative exponential function during a series of stimuli; (2) the response recovers spontaneously if the stimulus is withheld; (3) a series of habituation sessions induces more rapid and stronger habituation; (4) more rapid stimuli produce more rapid and stronger habituation; (5) a weaker stimulus intensity produces more rapid and stronger habituation; (6) the habituation response shows stimulus generalization (i.e. the response is similar for frequencies of 20 and 40 kHz); (7) a novel stimulus produces dishabituation; and (8) the dishabituating stimulus shows habituation after repeated trials. These results characterize the cricket's response in the traditional context of habituation.

Of Thompson and Spencer's (1966) nine points, one did not apply to crickets. In some organisms exposed to a series of stimuli, the behavioral response can become negative. In this study, the abduction of the metathoracic leg never declined to zero, let alone negative values. With more rapid stimuli than those examined here, the response might decline to zero. However, a negative response might be constrained by the contact between the metathoracic leg and the abdomen; the normal posture of the legs and body does not permit the legs to 'cross'.

The neural locus of the habituation is not specified by our experiments. This work, for example, does not eliminate the possibility that sensory adaptation is responsible for behavioral habituation of the leg's abduction. If sensory adaptation does occur, then the afferent input should decline and, thereby, decrease the response of the first interneuron. A single interneuron, Int-1, has been shown to be both necessary and sufficient for initiating the negative phonotactic response (Nolen and Hoy, 1984). Using ultrasonic pulses of 0.5 ms duration and an IPI of 100 ms, there is no apparent decrement in Int-1's response even after six pulses (Moiseff and Hoy, 1983). Using 30 ms ultrasonic pulses and an IPI of 66 ms, four pulses did not produce an appreciable decrement in Int-1's spike number (Nolen and Hoy, 1987). These findings suggest that sensory adaptation is not occurring at the rates of stimulation used in our work. However, the stimulus paradigms for the behavioral and cellular work are not identical. In the future, the response of Int-1 should be examined using the same stimulus parameters that are used for the behavioral habituation.

Although this is the first formal description of habituation in an ultrasound-

induced escape response by a flying insect, previous studies also suggested habituation. Wang and Robertson (1988) examined the ultrasound-induced increase in the wingbeat frequency in tethered, flying Australian field crickets. Using 30 ms pulses and an IPI of 500 ms, their Fig. 5 shows a decline in the magnitude of the frequency increase during a series of stimuli. Miller and Olesen (1979) found that free-flying green lacewings, which generally exhibit a dramatic response to ultrasound, sometimes failed to respond after a series of similar stimuli. Given that Miller and Olesen examined free-flying green lacewings, their work supports the idea that flying insects may habituate to ultrasonic stimuli.

Furthermore, many organisms show a decremental response to a series of stimuli in behavior that may be classified either as alarm reactions or as escape responses. A visual stimulus induces movement or recoil by neonatal garter snakes, but with a series of stimuli the response decreases (Hampton and Gillingham, 1989). A moving hand can induce a garter snake to strike but this response, too, decreases with repeated stimuli (Herzog *et al.* 1989). The mechanically induced shortening reflex in the leech habituates over time and can be dishabituated with a shock (Boulis and Sahley, 1988). Mechanical stimuli can also induce swimming in the leech. However, this response also habituates and can be dishabituated with a more intense mechanical stimulus (Debski and Friesen, 1985). Many fish habituate to the presence of a predatory fish or predatory models (Czanyi, 1985; Magurran and Girling, 1986; Huntingford and Coulter, 1989). Praying mantids produce a fright response when exposed to a bird, but repeated stimuli reveal a decremental response (Balderrama and Maldonado, 1971). Finally, the escape responses in crayfish (Wine and Krasne, 1971) and cockroaches (Baxter, 1907) also decrease in response to repeated stimuli. These studies suggest the widespread nature of the habituation of escape and startle responses, even though the stimuli may indicate danger.

Nevertheless, most studies of behavioral habituation have been investigated in a laboratory setting. Shalter (1984) claimed that antipredator responses are easier to habituate in the laboratory than in a natural environment. According to Schleidt (1961), this occurs because laboratory experiments fail to use an adequate stimulus. For example, laboratory experiments often use a stationary stimulus and this seems unlikely to occur in nature. In some experiments, simply moving the location of the stimulus produced a renewed response (Shalter, 1975). In our work on crickets, moving the stimulus also dishabituated the abduction of the metathoracic leg. So, there is no doubt that laboratory experiments do not adequately replicate the natural environment.

This does suggest that laboratory scenarios may not reveal the natural occurrence of habituation. However, field experiments offer additional limitations. With an animal moving freely in the field, few techniques allow reliable measurements of behavioral parameters, particularly if the animal is flying. The complex and often subtle nature of habituation can be sufficiently difficult to measure even under controlled laboratory conditions. Therefore, these constraints produce a problem beyond current resolution.

Nevertheless, the habituation described here for ultrasound-induced negative phonotaxis in crickets seems reasonable from an evolutionary perspective. When a cricket responds to an echolocating bat, the first ultrasonic pulse should induce the most dramatic response. Given the superior speed and maneuverability of bats, crickets must respond quickly. Failing to respond to repeated pulses from a similar location appears functional. If the pulses do indeed come from a bat, only the response to the first few pulses determines whether the cricket survives or becomes captured prey. However, if the pulses are not from a hunting bat, there is no need to respond. Furthermore, given that moving the location of the stimulus, even for a single pulse, induces dishabituation, the cricket should continue to respond as a bat closes during an attack. As the bat closes in and the cricket performs evasive maneuvers, the relative location, intensity and duration of the stimulus would change. Therefore, these laboratory experiments seem to provide valuable information about negative phonotaxis in crickets.

References

ARNOLD, J. W. (1971). Feeding behaviour of a predaceous bug (Hemiptera: Nabidae). *Can. J. Zool.* **49**, 131–132.

BALDERRAMA, N. AND MALDONADO, H. (1971). Habituation of the deimatic response in the mantid (*Stagmatoptera biocellata*). *J. comp. Physiol. Psychol.* **75**, 98–106.

BAXTER, C. (1907). Habituation of the roach to puffs of air. *Anat. Rec.* **128**, 521.

BOULIS, N. M. AND SAHLEY, C. L. (1988). A behavioral analysis of habituation and sensitization in the semi-intact leech. *J. Neurosci.* **8**, 4621–4627.

BUCKLEY, F. G. AND BUCKLEY, P. A. (1972). The breeding ecology of Royal Terns *Sterna* (*Thalasseus*) *maxima maxima*. *Ibis* **114**, 344–359.

CZANYI, V. (1985). Ethological analysis of predator avoidance by the paradise fish (*Macropodus opercularis*). I. Recognition and learning of predators. *Behav.* **92**, 227–240.

DAVIS, M. AND FILE, S. E. (1984). Intrinsic and extrinsic mechanisms of habituation and sensitization: Implications for the design and analysis of experiments. In *Habituation, Sensitization, and Behavior* (ed. H. V. S. Peeke and L. Petrinovich), pp. 287–323. Orlando: Academic Press, Inc.

DEBSKI, E. A. AND FRIESEN, W. O. (1985). Habituation of swimming activity in the medicinal leech. *J. exp. Biol.* **116**, 169–188.

HAMPTON, R. E. AND GILLINGHAM, J. C. (1989). Habituation of the alarm reaction in neonatal eastern garter snakes, *Thamnophis sirtalis*. *J. Herpetol.* **23**, 433–435.

HERZOG, H. A., JR, BOWERS, B. B. AND BURGHARDT, G. M. (1989). Development of antipredator responses in snakes. IV. Interspecific and intraspecific differences in habituation of defensive behavior. *Dev. Psychobiol.* **22**, 487–508.

HOY, R., NOLEN, T. AND BRODFUEHRER, P. (1989). The neuroethology of acoustic startle and escape in flying insects. *J. exp. Biol.* **146**, 287–306.

HUMPHREY, G. (1930). Le Chatelier's rule and the problem of habituation and dehabituation in *Helix albolabus*. *Psychol. Forsch.* **13**, 113–127.

HUNTINGFORD, F. A. AND COULTER, R. M. (1989). Habituation of predator inspection in the three-spined stickleback, *Gasterosteus aculeatus*. L. *J. Fish Biol.* **35**, 153–154.

MAGURRAN, A. E. AND GIRLING, S. L. (1986). Predator model recognition and response habituation in shoaling minnows. *Anim. Behav.* **34**, 510–518.

MAY, M. L., BRODFUEHRER, P. D. AND HOY, R. R. (1988). Kinematic and aerodynamic aspects of ultrasound-induced negative phonotaxis in flying Australian field crickets (*Teleogryllus oceanicus*). *J. comp. Physiol.* A **164**, 243–249.

MAY, M. L. AND HOY, R. R. (1990a). Ultrasound-induced yaw movements in the flying Australian field cricket (*Teleogryllus oceanicus*). *J. exp. Biol.* **149**, 177–189.

MAY, M. L. AND HOY, R. R. (1990b). Leg-induced steering in flying crickets. *J. exp. Biol.* **151**, 485–488.

MILLER, L. A. AND OLESEN, J. (1979). Avoidance behavior in green lacewings. I. Behavior of free flying green lacewings to hunting bats and ultrasound. *J. comp. Physiol.* **131**, 113–120.

MOISEFF, A. AND HOY, R. (1983). Sensitivity to ultrasound in an identifiable auditory interneuron in the cricket: a possible neural link to phonotactic behavior. *J. comp. Physiol.* **152**, 155–167.

MOISEFF, A., POLLACK, G. S. AND HOY, R. R. (1978). Steering responses of flying crickets to sound and ultrasound: mate attraction and predator avoidance. *Proc. natn. Acad. Sci. U.S.A.* **75**, 4052–4056.

NOLEN, T. G. AND HOY, R. R. (1984). Initiation of behavior by single neurons: The role of behavioral context. *Science* **226**, 992–994.

NOLEN, T. G. AND HOY, R. R. (1987). Postsynaptic inhibition mediates high-frequency selectivity in the cricket *Teleogryllus oceanicus*: Implications for flight phonotaxis behavior. *J. Neurosci.* **7**, 2081–2096.

RUSHFORTH, N. B. (1965). Behavioural studies of the coelenterate *Hydra pirardi Brien*. *Anim. Behav.* **13**, 30–42.

SCHLEIDT, W. M. (1961). Reaktionen von Truthühnern auf fliegende Raubvögel und versuche zur Analyse ihrer AAM's. *Z. Tierpsychol.* **18**, 534–560.

SHALTER, M. D. (1975). Lack of spatial generalization in habituation tests of fowl. *J. comp. physiol. Psych.* **89**, 258–262.

SHALTER, M. D. (1984). Predator–prey behavior and habituation. In *Habituation, Sensitization, and Behavior* (ed. H. V. S. Peeke and L. Petrinovich), pp. 349–391. Orlando: Academic Press, Inc.

SOKAL, R. R. AND ROHLF, F. J. (1981). *Biometry*. New York: W. H. Freeman & Company.

THOMPSON, R. F., GROVES, P. M., TEYLER, T. J. AND ROEMER, R. A. (1973). A dual-process theory of habituation: Theory and behavior. In *Habituation* (ed. H. V. S. Peeke and M. J. Herz), pp. 239–271. Orlando: Academic Press, Inc.

THOMPSON, R. F. AND SPENCER, W. A. (1966). Habituation: A model phenomenon for the study of neuronal substrates of behavior. *Psychol. Rev.* **173**, 16–43.

WANG, S. AND ROBERTSON, R. M. (1988). Changes of the hindwing motor pattern associated with phonotactic steering during flight in the cricket, *Teleogryllus oceanicus*. *J. comp. Physiol.* A **164**, 219–229.

WINE, J. J. AND KRASNE, F. B. (1971). The organization of escape behaviour in the crayfish. *J. exp. Biol.* **55**, 1–18.