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RESEARCH ARTICLE

The influence of bat echolocation call duration and timing on auditory encoding of predator distance in noctuoid moths

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ABSTRACT

Animals co-occur with multiple predators, making sensory systems that can encode information about diverse predators advantageous. Moths in the families Noctuidae and Erebidae have ears with two auditory receptor cells (A1 and A2) used to detect the echolocation calls of predatory bats. Bat communities contain species that vary in echolocation call duration, and the dynamic range of A1 is limited by the duration of sound, suggesting that A1 provides less information about bats with shorter echolocation calls. To test this hypothesis, we obtained intensity–response functions for both receptor cells across many moth species for sound pulse durations representing the range of echolocation call durations produced by bat species in northeastern North America. We found that the threshold and dynamic range of both cells varied with sound pulse duration. The number of A1 action potentials per sound pulse increases linearly with increasing amplitude for long-duration pulses, saturating near the A2 threshold. For short sound pulses, however, A1 saturates with only a few action potentials per pulse at amplitudes far lower than the A2 threshold for both single sound pulses and pulse sequences typical of searching or approaching bats. Neural adaptation was only evident in response to approaching bat sequences at high amplitudes, not search-phase sequences. These results show that, for short echolocation calls, a large range of sound levels cannot be coded by moth auditory receptor activity, resulting in no information about the distance of a bat, although differences in activity between ears might provide information about direction.

KEY WORDS: Hearing, Sound pressure level, SPL, Neural adaptation, Predator avoidance

INTRODUCTION

Animals co-occur with multiple predators, each of which can provide different cues about their presence. Likewise, the cues from a predator might change during the stages of an attack (Endler, 1991). Sensory systems that accurately encode the level of threat posed by diverse predators during different stages of attack are needed to trigger predator- and context-dependent defensive behavior. Several basic properties of receptor cells and sensory organs can contribute to providing information about the threat posed by a predator. For example, the intensity–response functions for most receptor cells demonstrate an increase in the number or firing rate of action potentials (spikes) with increasing stimulus intensity (Lipetz, 1971). The dynamic range of a receptor cell refers to the range of intensities over which there is a change in neural activity, such as the number of spikes per stimulus or the spike rate (Randall et al., 2002). Therefore, a large dynamic range encodes a large range of stimulus intensities and provides more information to the nervous system. The dynamic range of a sensory organ can be increased if different receptor cells respond to different ranges of intensities (Randall et al., 2002). Using a simple sensory organ, the noctuoid moth ear, we investigated how receptor cell threshold and dynamic range influence the sensory coding of predator cues, namely bat echolocation calls.

Insectivorous bats are voracious predators of nocturnally flying insects (Boyles et al., 2011) and are responsible for the independent evolution of ultrasound-sensitive hearing in numerous lineages throughout the Insecta (Yack and Dawson, 2008; ter Hofstede and Ratcliffe, 2016). Bats produce ultrasonic echolocation calls and use information in the echoes of their calls to avoid obstacles and find insect prey in flight (Moss and Surlykke, 2010). When flying insects hear these echolocation calls, they perform a variety of defensive behaviors to avoid being captured by the bat (Conner and Corcoran, 2012; Yager, 2012). Moths in the families Noctuidae and Erebidae have two ultrasound-sensitive ears, one on either side of their thorax, and each ear contains only two auditory receptor cells, called A1 and A2 (Fullard, 1998). Each receptor cell demonstrates a typical intensity–response function, with the number of spikes increasing with sound amplitude at the ear (Fullard, 1998). The A2 receptor cell, however, is less sensitive than the A1 receptor cell, with thresholds ranging from 14 to 22 dB greater than the A1 threshold depending on the species (ter Hofstede et al., 2013). Therefore, the A2 cell increases the dynamic range of the ear. The large dynamic range of the moth ear (40–60 dB; ter Hofstede and Ratcliffe, 2016) is adaptive for encoding information about the distance of a bat, because the intensity of a bat's echolocation calls increases at the moth as the distance between the bat and moth decreases, at least before the bat is aware of the moth (Roeder, 1966; Goerlitz et al., 2010; Hartley, 1992). Noctuoid moths generally show different types of behavior depending on sound intensity, such as directional flight in response to quiet ultrasound typical of a distant bat and more erratic or drastic evasive flight in response to loud ultrasound typical of a close bat (Roeder, 1962, 1964; Agee, 1967, 1969; Surlykke, 1984), but the precise relationship between neural activity and flight behavior is not known. Graded responses to ultrasound, meaning the type or intensity of behavior changes with the intensity of the ultrasonic stimulus, are known from other ultrasound-sensitive insects as well (reviewed in ter Hofstede and Ratcliffe, 2016).

The echolocation calls of different bat species vary in duration (Fenton and Bell, 1981). In northeastern North America, the durations of search-phase echolocation calls (those that are produced before a bat detects an insect) can vary from 1–3 ms in northern long-eared bats (*Myotis septentrionalis*) to 10–15 ms in

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hoary bats (*Lasiurus cinereus*), with most other sympatric species producing search calls between 5 and 10 ms (Fenton and Bell, 1981; O'Farrell et al., 2000; Murray et al., 2001; Broders et al., 2004). Previous studies investigating the intensity–response functions of the noctuoid moth ear found that the A2 receptor cell threshold occurs at about the same intensity at which the A1 receptor cell saturates, meaning the A1 cell reaches its maximum activity level (Roeder, 1974a; Coro and Pérez, 1983; Boyan and Fullard, 1986; Coro and Alonso, 1989; Fullard et al., 2003, 2007). This phenomenon of one receptor cell's threshold corresponding with the saturation point of another is likely to be an adaptation to provide continuous information about the distance of an approaching bat because the A2 cell can continue to encode changes in intensity when A1 can no longer do so. All of these studies, however, used stimulus durations of 10, 20 or 45 ms, which correspond with, or are greater than, the call durations of bat species with the longest calls in North American bat communities.

Studies investigating the dynamic range of the A1 cell using short-duration stimuli, corresponding with most other bat species, have reported conflicting results. Using a range of stimulus durations, Waters (1996) and Tougaard (1998) found that the dynamic range and maximum number of A1 spikes per pulse increased with pulse duration. Short-duration stimuli (1–3 ms) triggered a maximum of only 2–3 A1 spikes per pulse, representing a very restricted dynamic range. This suggests that the A1 cell conveys little information about intensity, and thus distance to the bat, for bat species that use short-duration calls (Waters, 1996). These results are based on data from three noctuid moth species: *Agrotis segetum* (Waters, 1996), *Spodoptera littoralis* and *Noctua pronuba* (Tougaard, 1998). Pérez and Coro (1984), however, measured the intensity–response functions for the A1 cell in response to 3.5 ms pulses in five noctuid and erebid species and found large dynamic ranges for most species, with no saturation of the A1 cell in one species. These different results suggest variability in the responses to short-duration sound pulses among noctuoid moth species that might influence the ability of each species to encode bat distance for bat species with different duration calls. In addition, several studies have shown that the threshold for A1 responses decreases (i.e. sensitivity increases) with increasing pulse duration, suggesting that, all else being equal, moths should detect bats that use long-duration calls at greater distances than those using short-duration calls (Surlykke et al., 1988; Tougaard, 1998; Nakano and Mason, 2017). However, the activity of the A2 cell was only investigated by Pérez and Coro (1984), who used stimuli of only one duration, so it is not currently known how pulse duration influences A2 threshold or dynamic range.

In addition to differences in echolocation call duration between species, bats decrease the duration and increase the repetition rate of their echolocation calls when they detect and attack an insect in flight (Moss and Surlykke, 2010). Waters (1996) found that the number of A1 spikes per pulse decreased as the repetition rate of pulses increased in a noctuid moth because the first few pulses resulted in neural adaptation. Similar results were reported by Coro et al. (1998). Intensity–response curves for the moth A1 cell have only been generated in response to the playback of single pulses of sound, so it is not known if a more natural repetition rate might affect the shape of this curve and what pulse trains could tell us about neural encoding of distance at different stages of a bat attack.

To further investigate the role of pulse duration and repetition rate on the activity of moth auditory receptor cells, we had three objectives for this study. First, we replicated previous tests of A1 thresholds and intensity–response curves for different duration acoustic stimuli. Second, we tested whether the A2 cell showed similar patterns of threshold and intensity–response curve differences depending on sound duration. Finally, we tested whether the A1 intensity–response function varies if the stimuli are single pulses or pulses at the durations and repetition rates of a searching bat or a bat that has detected and is approaching the moth. The first two objectives were tested using two subject groups: (1) many individuals of one species to determine variability within a species; and (2) single individuals from many different species to test the generalizability of patterns across moth species. The third objective was tested with individuals from different moth species.

MATERIALS AND METHODS

Study animals

This study was conducted on moths that were both laboratory-raised (Noctuidae, Heliothinae: *Heliothis virescens* Fabricius and *Helicoverpa zea* Boddie) and wild-caught (various families and species). *Heliothis virescens* and *H. zea* were obtained as eggs (Benzon Research, Carlisle, PA, USA) and reared on an artificial diet as larvae. Pupae were stored in plastic containers and checked regularly, and adults were transferred to containers with 10% sugar water provided *ad libitum*. Nerve recordings were made on adults within 21 days after emergence. Wild moths were captured at a mercury vapor light in a forested area bordered by fields near Hanover, NH, USA, and fed 10% sugar water until use. We identified wild moths to family or species when possible using Beadle and Leckie (2012) and Covell (2005). Nerve recordings were made on wild moths within 14 days after capture. We recorded neural activity on the auditory nerve of 18 *H. virescens* and 20 individuals of various other moth species (Erebidae, Erebinae: one *Catocala amatrix* Hübner, one *Catocala cerogama* Guenée, two *Catocala habilis* Grote, one *Catocala relicta* Walker; Erebidae, Arctiinae: one *Halysidota tessellaris* Smith, two *Pyrrharctia Isabella* Smith; Noctuidae, Noctuinae: two *Noctua pronuba* Linnaeus, one *Polia nimbosa* Guenée; Noctuidae, Pantheinae: two *Panthea furcilla* Packard; Noctuidae, Dilobinae: one *Raphia frater* Grote; Noctuidae, Heliothinae: one *H. zea*; five individuals within the family Erebidae or Noctuidae but not identified to species).

Neurophysiological recordings

Animals were mounted with wax to a glass rod ventral side up. The left meso- and metathorax were dissected to reveal the auditory nerve, leaving the dorsal flight muscles and entire right-half of the body intact. Two tungsten electrodes (0.005 inch diameter, Model: 575400, A-M Systems, Carlsborg, WA, USA) were glued together to create parallel hooks that hooked the auditory nerve. Lost hemolymph was replaced with insect saline containing electrolytes. The electrodes were isolated from each other and the body by coating with petroleum jelly. Electrodes were connected to a differential amplifier (model DP-301, Warner Instruments, Hamden, CT, USA). The output of the amplifier was recorded using a computer running Avisoft Recorder software (Avisoft Bioacoustics, Glienicke, Germany) and a multichannel data acquisition board (Avisoft UltraSoundGate 416H). Recordings were made in an anechoic sound chamber (custom predictable field enclosure by ETS-Lindgren, Cedar Park, TX, USA). A 1/4″ microphone (type 4939, Brüel and Kjær, Nærum, Denmark; Avisoft UltraSoundGate 1/4″ Mic Power Module) was placed close to the moth and recorded on a second channel of the data acquisition board to assess timing of neural activity in response to acoustic stimuli.

Although the method of recording neural activity with extracellular electrodes involves cutting open the moth and removing some tissue, this procedure does not appear to have a significant effect on auditory receptor cell activity (ter Hofstede et al., 2011). Moth auditory receptors respond to the displacement of the tympanum, and tympanal displacement does not differ between intact moths and moths that have been prepared for extracellular recordings at the frequencies and amplitudes of sound that we use here (ter Hofstede et al., 2011). Distortion-product otoacoustic emissions (DPOAEs), a non-invasive measure of auditory cell activity, have been used effectively to assess moth hearing (Coro and Kössl, 1998; Mora et al., 2013), but it is currently unknown how these values correspond with the number of action potentials produced by cells, so DPOAEs could not be used to address the objectives of our study.

Acoustic stimuli and measurements of neural activity

Sound pulses were generated using Avisoft SASLab Pro software and saved in .wav files. Sound files were broadcast to the ears of mounted moths using Avisoft Recorder software, an amplifier (Avisoft UltraSoundGate Player 216H) and loudspeaker (Avisoft Ultrasonic Vifa speaker). The moth was placed 50 cm away from the center of the speaker and the ear with the recorded nerve was directed at the speaker. The amplitudes of sound pulses at the position of the moth were calibrated by recording acoustic stimuli using a 1/4″ microphone with a flat frequency response (type 4939, ±2 dB from 0.004–100 kHz; Brüel and Kjær) and adjusting amplitudes relative to a calibration tone (Calibrator type 4231, Brüel and Kjær). Due to the extremely short durations of some of the sound pulses, sound levels were calculated as peak equivalent sound pressure level (peSPL: the rms level re. 20 µPa of a sinusoid with the same peak-to-peak-amplitude as the pulse; Burkard, 2006).

To measure the frequency sensitivity of the auditory neurons, we broadcast pulses of 10 ms duration (plus 1 ms linear ramps) at 20 frequencies (5–100 kHz in 5 kHz increments). Each sound file consisted of a sequence of pulses of the same frequency separated by 0.5 s and increasing in amplitude from 20 dB peSPL to 90 dB peSPL in 2 dB increments. This was designed to simulate the increasing amplitude calls a moth might experience when being approached by an echolocating bat. Frequencies were broadcast in random order for each moth. From the recordings of neural activity (Fig. 1A), we generated audiograms by measuring the thresholds for both the A1 and A2 receptor cell, with threshold being defined as the lowest SPL to which the cell responded with action potentials and continued to respond at greater amplitudes. A1 and A2 action potentials could be distinguished by their different sizes, shapes, timing and thresholds in recordings. Overlapping spikes of A1 and A2 summed to produce a compound action potential (e.g. Fig. 1A).

To determine how neural activity changes in response to pulse amplitude and duration, we broadcast sound files containing 50 kHz pulses with durations of 2, 5, 10 and 20 ms (with 0.2, 0.5, 1.0 and 1.0 ms ramps, respectively). Each sound file consisted of a sequence of pulses separated by 0.5 s and increasing in amplitude from 20 dB peSPL to 90 dB peSPL in 2 dB increments. From the recordings of neural activity, we measured thresholds and counted the number of spikes per sound pulse. We measured the range of amplitudes below the A2 cell threshold across which the number of A1 spikes per pulse did not change, and we refer to this as the saturation range. The number of spikes per pulse could increase or decrease by one across the saturation range as long as it returned to the original number of spikes for higher amplitude pulses (e.g. across 5 pulses ranging in amplitude by 10 dB, the number of A1 spikes per pulse might be 4, 4, 5, 4, 4). We additionally measured the interspike intervals (ISIs) of A1 cells (time from the peak of spike to the peak of the next) across the saturation range as an alternative source of information for the moth regarding sound amplitude.

To determine how receptor cells encode a bat that is producing search-phase and approach-phase echolocation calls, we broadcast sequences of 50 kHz pulses that had the same duty cycle (amount of time occupied by sound) but differed in the pulse duration and repetition rate. The search-phase sequence consisted of 8 pulses of 5 ms duration (0.5 ms ramps) repeated every 75 ms. The approach-phase sequence consisted of 16 pulses of 2.5 ms duration (0.5 ms ramps) repeated every 37.5 ms. These values represent search- and approach-phase timing for several bat species sympatric with the moths used in this study (Griffin et al., 1960: *Myotis lucifugus* and *Myotis septentrionalis*; Mukhida et al., 2004: *Myotis leibii*). Stimuli with higher repetition rates typical of the terminal phase (i.e. the final buzz) in bats were not included in our study because moth auditory receptor cells cannot encode such rapid repetition rates (Fullard et al., 2003). Each sequence was broadcast at increasing amplitudes from 20 dB peSPL to 90 dB peSPL in 2 dB increments and separated by 2 s. Thresholds for these acoustic stimuli were defined as the sound level (dB peSPL) at which at least half of the pulses in a sequence were followed by one or more A1 spikes within a 25 ms latency. Data were collected from 10 moths of varying species (five *H. virescens*, two *C. habilis*, one *C. relicta*, one *H. tessellaris* and one noctuid moth of unknown species).

RESULTS

Audiograms

The thresholds for different frequencies of sounds followed the typical patterns observed previously for noctuoid moths (Fullard, 1998; Fig. 1; Table S1). All moths had broadly tuned ears with the best sensitivity (i.e. lowest thresholds) between 15 and 55 kHz. At low frequencies in the audible sound range (5–10 kHz), moths had very high thresholds, and over 55 kHz threshold gradually increased up to the maximum tested frequency (100 kHz). A2 thresholds were generally 15–20 dB greater than A1 thresholds (Fig. 1B).

Influence of pulse duration on dynamic range

The number of A1 and A2 spikes per pulse increased with increasing amplitude for all pulse durations and all moths (Fig. 2, Table S2). We found significant linear regressions between the mean total number of A cell spikes (A1+A2) and sound level above the A1 threshold for all durations for both *H. virescens* (N=8 moths; 2 ms, P<0.001, R^2=0.97; 5 ms, P<0.001, R^2=0.97; 10 ms, P<0.001, R^2=0.98; 20 ms, P<0.001, R^2=0.99) and when multiple species, not including *H. virescens*, are pooled (N=20 moths; 2 ms, P<0.001, R^2=0.97; 5 ms, P<0.001, R^2=0.98; 10 ms, P<0.001, R^2=0.98; 20 ms, P<0.001, R^2=0.99). We observed, however, that the dynamic range of the A1 cell, meaning the range of amplitudes over which the number of spikes per pulse changes, was smaller for shorter-duration pulses than longer-duration pulses.

For short-duration sounds, there is a substantial separation between the amplitude at which the number of A1 spikes saturates and the amplitude at which A2 begins to fire (the saturation range). The saturation range was significantly greater for shorter- than longer-duration pulses (repeated-measures ANOVA: *H. virescens*, $F_{3,21}$=15.6, P<0.001; multiple species pooled, $F_{3,57}$=46.8, P<0.001; Fig. 3). For example, across all moths, the saturation range varied from 8 to 18 dB for 2 ms pulses whereas it varied from only 4 to 8 dB for 20 ms pulses. The number of spikes per pulse was significantly lower for shorter- than longer-duration pulses

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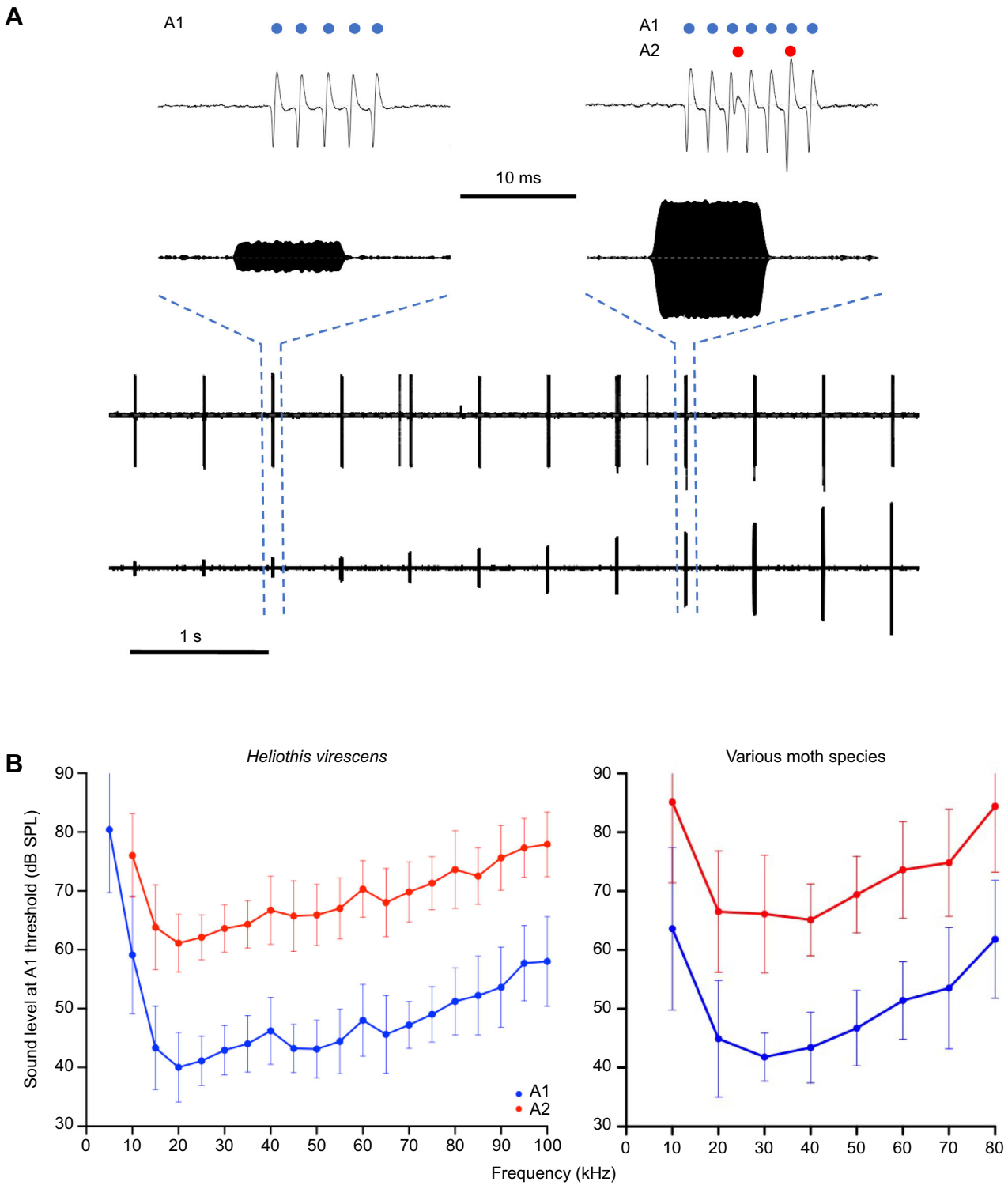

Fig. 1. Neural thresholds for sounds in moths. (A) Example recording of the auditory nerve in the noctuid moth *Heliothis virescens* (top traces=nerve, bottom traces=sound stimuli). A1 and A2 spikes are marked in insets with blue and red dots, respectively. (B) Audiogram of A1 and A2 cell thresholds for the noctuid moth *H. virescens* (left panel, *N*=18 moths) and individuals of multiple noctuid and erebid moth species (right panel, *N*=19 moths). See Materials and methods for species and sample sizes. Points are means. Error bars are s.d.

(repeated-measures ANOVA: *H. virescens*, $F_{3,21}$=143.4, P<0.001; multiple species pooled, $F_{3,57}$=134.1, P<0.001; Fig. 3). For example, across all moths, the number of spikes per pulse within the saturation range varied from 2 to 5 spikes per pulse for 2 ms pulses whereas it varied from 8 to 18 spikes per pulse for 20 ms pulses. For all eight *H. virescens* and 18 of the 20 other moths, the number of A1 spikes per pulse saturated at or below the A2 threshold. In two moths (both *C. habilis*), however, the number of A1 spikes per pulse continued to increase across the entire range of amplitudes presented. The ISIs were greater for the spikes in

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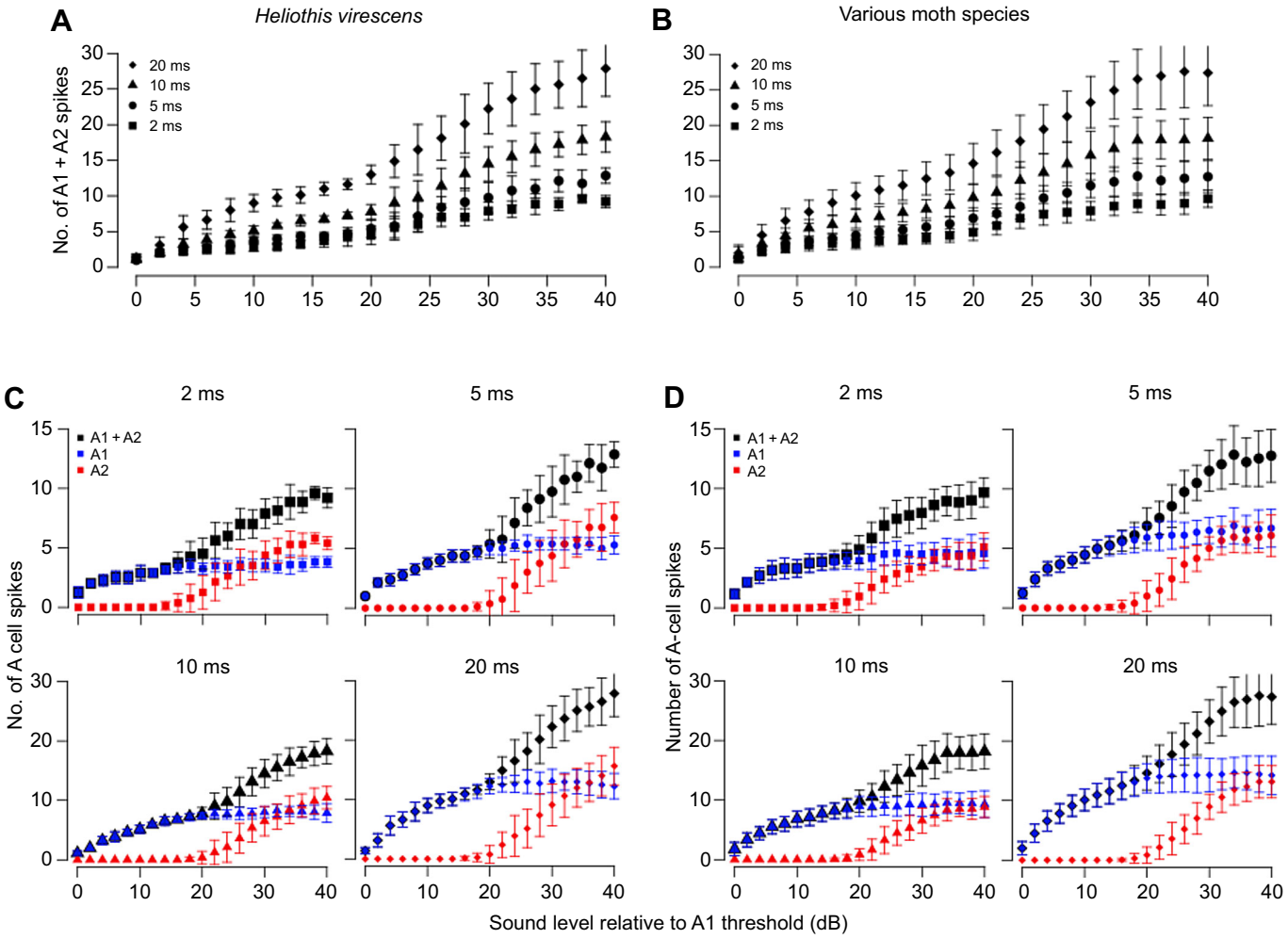

Fig. 2. Intensity–response curves for A cell activity in moths. (A) Intensity–response curves for 50 kHz sound pulses of four durations for the noctuid moth *Heliothis virescens* (*N*=8 moths). Top panel: the total number of A cell spikes per sound pulse (i.e. A1+A2 cell spikes). (C) The number of A cell spikes plotted independently by pulse duration and cell type (blue points, A1 spikes; red points, A2 spikes; black points, A1+A2 spikes). (B,D) The same data as in A and C but for moths of various noctuid and erebid species (*N*=20 moths). See Materials and methods for species and sample sizes. Points are means. Error bars are s.d.

response to the first pulse (the lowest amplitude pulse) but otherwise they did not change significantly across the saturation range (repeated-measures ANOVA: first ISI per pulse: *H. virescens*, $F_{3,45}$=3.7, P=0.019; multiple species pooled, $F_{3,57}$=6.3, P<0.001; mean ISI per pulse: *H. virescens*, $F_{3,45}$=5.0, P=0.005; multiple species pooled, $F_{3,57}$=10.4, P<0.001; Fig. 4).

The A2 cell also saturated at high amplitudes, with fewer spikes per pulse for shorter- than longer-duration pulses, but this varied across species (Fig. 2). For *H. virescens*, saturation of the A2 cell at 5 spikes per pulse was only evident for the 2 ms pulses, whereas there was a general increase in the number of A2 spikes per pulse with increasing amplitude for all longer-duration pulses. We might not have provided high enough amplitudes to reach the A2 saturation range for these individuals. For the other species, however, there is evidence that the A2 cell saturates for most pulse durations, at about 5–6 spikes per pulse for 2 ms pulses, 7–8 spikes per pulse for 5 ms pulses and about 10 spikes per pulse for 10 ms pulses.

Influence of pulse duration on A cell thresholds

Both A1 and A2 thresholds were higher for shorter- than longer-duration sound pulses (Fig. 5). This pattern occurs both within species (*H. virescens*, repeated-measures ANOVA: A1 cell, $F_{3,21}$=54.7, P<0.001; A2 cell, $F_{3,21}$=13.6, P<0.001) and when multiple species are pooled (A1 cell, $F_{3,57}$=40.7, P<0.001; A2 cell, $F_{3,57}$=36.6, P<0.001). For *H. virescens*, only the 2 ms pulse had a significantly greater A1 threshold than the other duration pulses (Tukey–Kramer HSD *post hoc* test, P<0.05), being 5.5 dB greater than the mean threshold for the 5 ms pulse, whereas A2 thresholds showed a more gradual reduction in threshold across durations (Fig. 5, left panels). When multiple species are pooled, both the A1 and A2 thresholds were significantly higher for the shorter pulse durations (Tukey–Kramer HSD *post hoc* test, P<0.05; Fig. 5, right panels).

Pulse sequences simulating bat echolocation during search and approach phases

For both the search-type and approach-type pulse durations and repetition rates, the intensity–response curves of the mean number of A1 spikes per pulse showed a regular increase with amplitude (Fig. 6A, Table S3). However, for each individual moth, there was usually a range of amplitudes below the A2 threshold across which the mean number of A1 spikes per pulse remained almost constant, showing saturation ranges similar to those seen for short-duration

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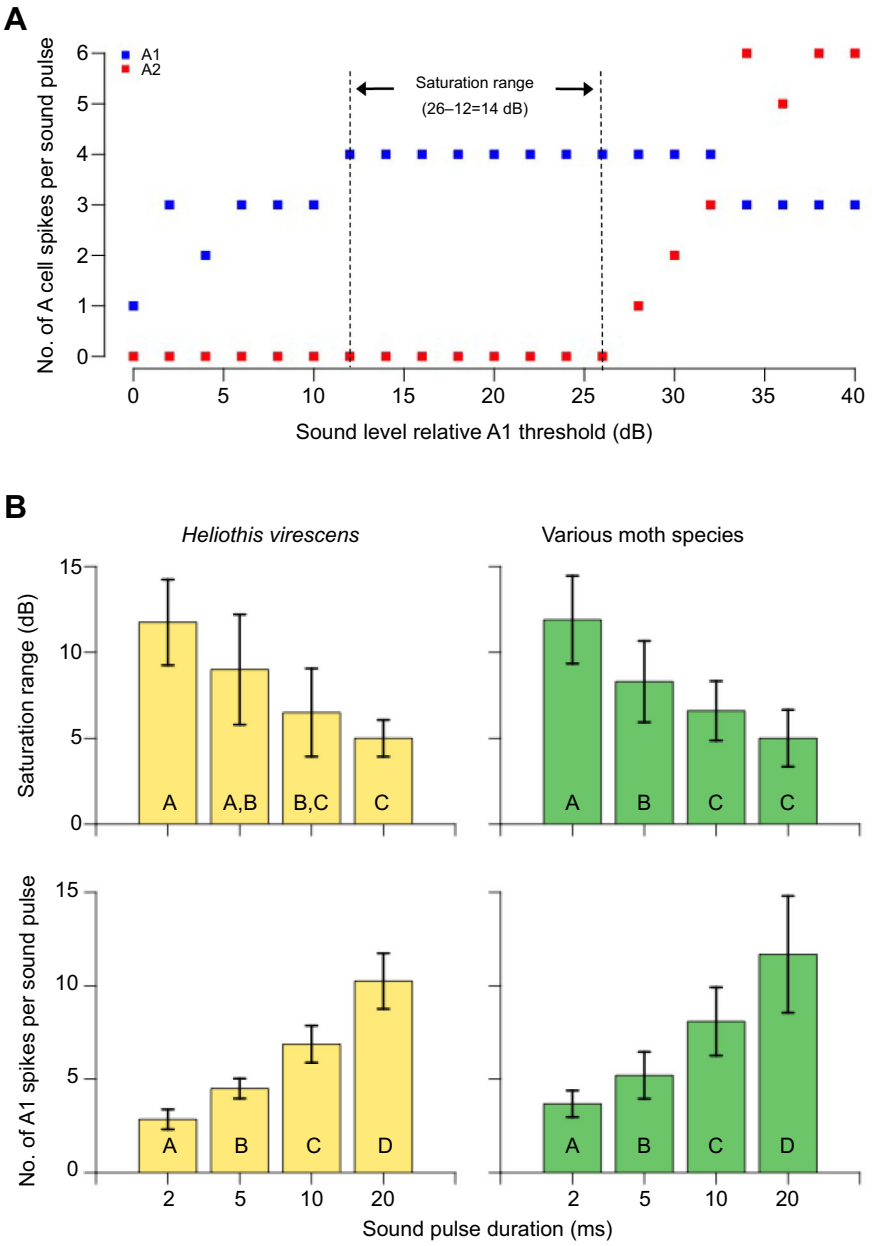

Fig. 3. A1 cell saturation ranges. (A) Intensity–response curve for the moth *Raphia frater* illustrating the saturation range (range of intensities for which the number of A1 spikes per pulse does not change with increasing sound amplitude below the A2 threshold). Stimuli were 2 ms pulses of 50 kHz. (B) The mean saturation range (dB) (top panels) and the mean number of A1 spikes per pulse within the saturation range (bottom panels) for sound pulses of four different durations (*Heliothis virescens* N=8 moths; various moth species N=20 moths). For example, in A, the number of A1 spikes per pulse within the saturation range is 4. Different letters within the bars indicate statistically significant differences (repeated-measures ANOVA, P<0.01). See Materials and methods for moth species and sample sizes. Error bars are s.d.

individual sound pulses (Fig. 6B). For bat-like sequences, we considered saturation ranges to be the range of amplitudes across which the mean number of A1 spikes per pulse did not vary by more than 0.5. Saturation ranges for bat-like sequences ranged from 4 to 12 dB (mean: 7 dB). Interestingly, the moth *C. habilis* demonstrated A1 saturation in response to these stimuli, even though the A1 cell did not saturate in response to short-duration individual pulses (Fig. 6B). Evidence for neural adaptation across bat-like sequences was tested by taking the difference in the number of A1 spikes between the first and last pulse of each sequence at a given amplitude (e.g. the number of A1 spikes for pulse 1 minus pulse 8 for the search sequence and pulse 1 minus pulse 16 for the approach sequence). There was evidence of neural adaptation for the approach-like sequence at high amplitudes, but not at low amplitudes and not for the search-phase sequence (Fig. 7). The mean of the difference in the number of A1 spikes between the first and last pulse increased significantly with increasing amplitude for the approach sequence (N=10, P<0.001, R^2=0.56) but not for the search sequence (N=10, P=0.163, R^2=0.07). The overall difference between the number of spikes for the first and last pulse did not exceed 0.5 spikes per pulse except for approach sequences greater than 10 dB above the A1 threshold.

DISCUSSION

The first objective in this study was to replicate previous results demonstrating differences in A1 cell activity in response to different duration sound stimuli for a greater number of moth species. Our results support previous studies showing that the dynamic range of the A1 cell increases, and the A1 cell threshold decreases, with increasing sound stimulus duration. The A1 cell usually saturated at intensities below that of the A2 cell threshold, resulting in ranges of sound amplitudes at which the moth ear could not encode increases in intensity, which we refer to as the saturation range. The saturation range was large for short-duration pulses and small for long-duration pulses. We found these patterns to be consistent between multiple individuals of one moth species (*H. virescens*) and these

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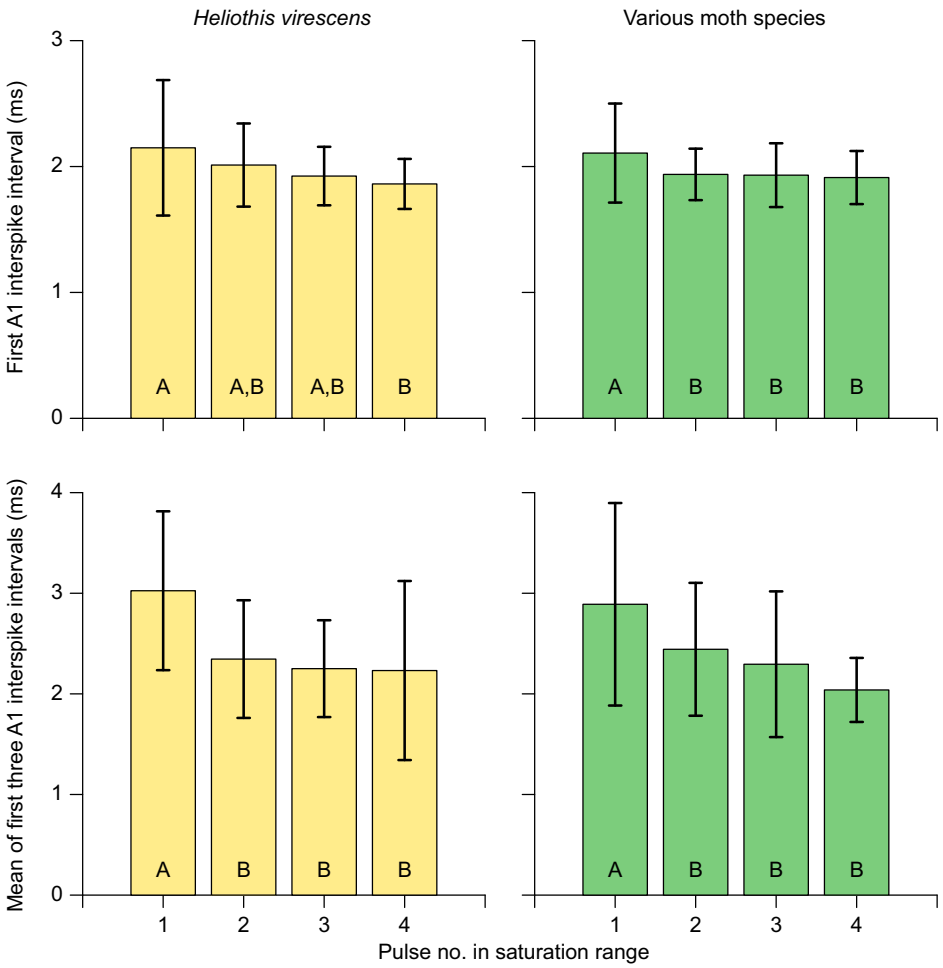

Fig. 4. A1 cell interspike intervals across the saturation range. The mean for the first A1 interspike interval (time from the first A1 spike to the second A1 spike) (top panels) and the mean of the first three A1 interspike intervals (bottom panels) for pulse numbers 1–4 within the saturation range (*Heliothis virescens* *N*=8 moths; various moth species *N*=20 moths). Stimuli were 2 ms pulses of 50 kHz. Different letters within the bars indicate statistically significant differences (repeated-measures ANOVA, $P<0.01$). See Materials and methods for species and sample sizes. Error bars are s.d.

patterns were also found for individuals of 15 other noctuid and erebid moth species, although the absolute values of the saturation ranges differed among individuals across these species. The second objective was to test whether the A2 cell shows similar response properties. We found that, like the A1 cell, the dynamic range of the A2 cell increased, and the threshold decreased, with increasing sound stimulus duration. The third objective was to test if the repetition rate of sound pulses, specifically those relevant to cues produced by predatory bats, influenced these results. Although saturation ranges were not found in response to the bat-like pulse patterns for pooled data from multiple individuals of different species, each individual moth showed A1 cell saturation ranges below the A2 threshold typical of the individual pulse data.

The linear increase in number of A cell spikes with amplitude provides moths with information about the distance of an approaching bat but only for bat species that produced long-duration (10–20 ms) echolocation calls. For the many bat species that produce shorter-duration echolocation calls (2–5 ms), there is a large range of call amplitudes that trigger the same response in the moth ear (the saturation range), meaning that the moth is not receiving information about the changes in distance between the bat and the moth. However, information about distance might not be important to moths at the distances encoded only by the A1 receptor. Most bats produce exceptionally intense echolocation calls, in the range of 120–140 dB SPL at 10 cm (Waters and Jones, 1995; Holderied and von Helversen, 2003; Holderied et al., 2005; Surlykke and Kalko, 2008). A few aerial-hawking bat species are known to produce significantly lower amplitude echolocation calls, and these bats largely escape detection by eared prey (Goerlitz et al., 2010; Corcoran and Conner, 2017). Various studies have estimated or measured maximum detection distance of moths for typical aerial-hawking bats ranging from 15 to 40 m (Roeder, 1966; Surlykke, 1988; Surlykke et al., 1999; Goerlitz et al., 2010). For the moth *H. virescens*, the mean A1 threshold for a 2 ms pulse at 50 kHz is 50 dB SPL, with the saturation range starting at approximately 6 dB above threshold. The mean saturation range is 12 dB, making the range of sound levels across the saturation range 56–68 dB SPL. As a rough estimate, for a bat producing echolocation calls at 120 dB SPL, the A1 receptor of *H. virescens* will produce three spikes per echolocation call when the bat is between ca. 11.5 and 15 m away (calculation incorporating attenuation due to spherical spreading and atmospheric attenuation at 20°C and 75% relative humidity; Griffin, 1971; Møhl, 1988). These distances are greater than the distances predicted for bats to detect the echo from the moth (5–10 m; Surlykke, 1988; Surlykke et al., 1999; Goerlitz et al., 2010). Therefore, moths might only need information about direction, not distance, to fly away from bats that have not yet detected their echo.

Noctuoid moths appear to show directional flight away from low-amplitude ultrasound and more erratic or drastic evasive maneuvers in response to high-amplitude ultrasound (Roeder, 1962). The body of moths provides a sound shadow that reduces sound levels by 10–20 dB from the ipsilateral to the contralateral ear (Payne et al., 1966; Surlykke, 1984), allowing for information about the direction of

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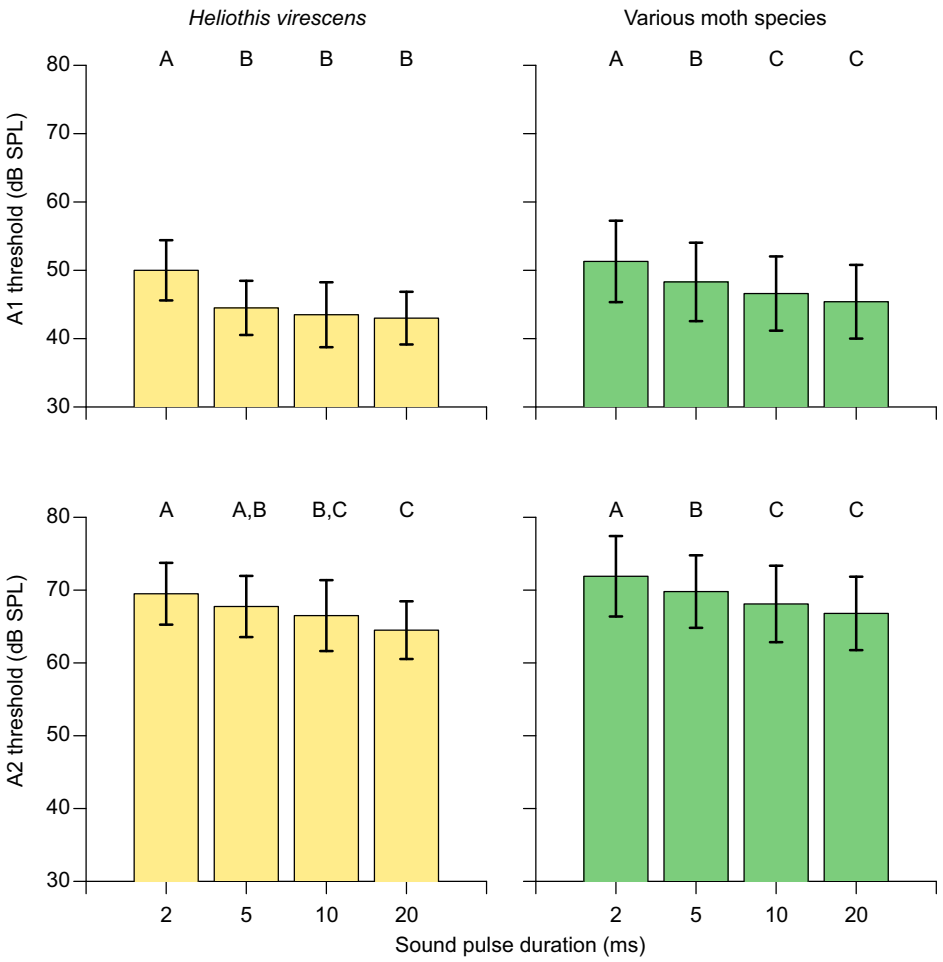

Fig. 5. A1 and A2 cell thresholds for four sound pulse durations. *Heliothis virescens* N=8 moths; various moth species N=20 moths. Different letters above the bars indicate statistically significant differences (repeated-measures ANOVA, P<0.01). See Materials and methods for species and sample sizes. Values are means. Error bars are s.d.

sound based on differences in the number of spikes between ears (Roeder, 1964). The directional cues provided by the sound shadow, however, would no longer be encoded by the A1 cell at 10–20 dB above the start of the saturation range because sound levels increase such that the A1 cell is saturated on both sides. Based on our results, this corresponds with the amplitude at which the A2 cell starts to fire (ca. 20 dB above the A1 threshold). This is adaptive for two reasons. First, close to the A2 threshold, the sound shadow might maintain differences in amplitude between ears such that the difference in activity of the A2 cell could be used for directional information when the A1 cell can no longer encode this information. In support of this idea, the last-ditch diving response of the erebid moth *Bertholdia trigona* has a directional component (Corcoran and Conner, 2012). Second, the A2 cell will provide information about the distance of an approaching bat across its dynamic range.

In addition to the number of receptor cell spikes per stimulus, the ISI or spike rate is known to be important for triggering behavioral responses to sound in insects (Nabatiyan et al., 2003; Marsat and Pollack, 2012). Bursts of spikes are thought to be more reliable indicators of the presence of a stimulus and are more likely to trigger the activity of the postsynaptic neuron(s) due to temporal summation (Nabatiyan et al., 2003). In noctuoid moths, the A1 receptor cell exhibits spontaneous firing activity (Roeder, 1966; Waters, 1996), meaning that the individual A1 spikes do not provide information to the moth about the presence of a bat. These spontaneous spikes, however, generally occur individually and not in rapid succession, whereas multiple A1 spikes with short ISIs, i.e. a burst of spikes at a high spike rate, are typical for responses to sound (Roeder, 1966). Based on a combination of electrophysiological and behavioral experiments, Roeder (1964) estimated that an A1 ISI of 1.5–2.6 ms is needed to trigger evasive flight in moths. In our recordings of multiple moth species, for 2 ms pulses of sound, ISIs less than 2.6 ms occur at amplitudes 3.1±1.5 dB greater than A1 threshold with an average of 2.4±0.5 A1 spikes per pulse. For 20 ms pulses of sound, ISIs less than 2.6 ms occur at amplitudes 5.2±2.7 dB greater than A1 threshold with an average of 7.2±1.7 A1 spikes per pulse. Therefore, there are some subtle differences in the combination of number of A1 spikes per pulse and ISIs that correlate with different pulse durations. Having low ISIs in response to short-duration pulses at low amplitudes might compensate for the production of only a few A1 spikes per pulse.

A1 cell saturation at higher intensities appears to be the most typical pattern for noctuid and erebid species but this is not universal. Similar to results found by Pérez and Coro (1984), the A1 cell in two of the moths in our study did not saturate in response to 2 ms pulses but continued to produce more spikes per pulse with increasing amplitude up to 40 dB above A1 threshold, reaching up to 8 spikes per pulse, whereas the mean across all species was a maximum of only 4.6±1.5 spikes per pulse. Interestingly, both these moths were individuals of the species *C. habilis*, whereas individuals of congeneric species (*C. amatrix*, *C. cerogama* and *C. relicta*) showed the pattern of A1 cell saturation typical of the other species tested. It remains unclear why the A1 cell shows saturation at high sound levels in some moths and not in others. Further tests across many species should be conducted to investigate

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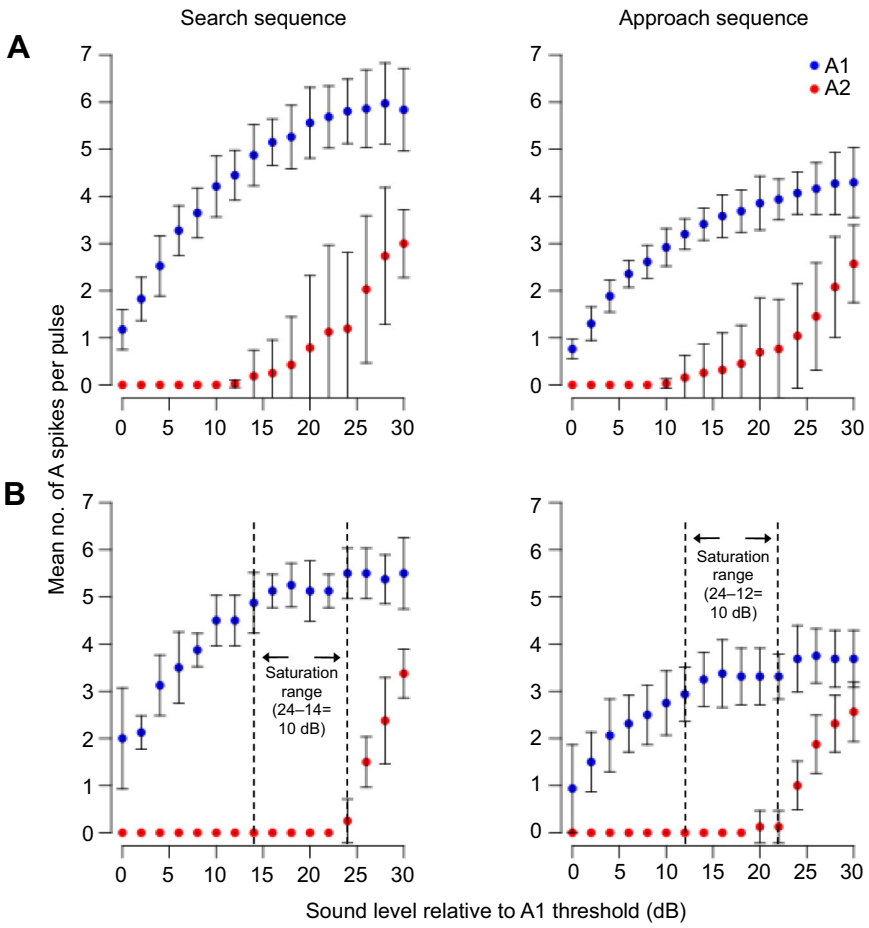

Fig. 6. Intensity–response curves for the bat-like pulse sequences. (A) The mean number of A1 and A2 spikes per pulse for sequences of pulses in the timing of bat search- or approach-phase echolocation calls (*N*=10 moths). See Materials and methods for moth species and species sample sizes. (B) Same as A but for the moth *Catocala habilis* showing the saturation ranges. Error bars are s.d.

phylogenetic patterns or possible correlations with other parameters of A cell activity.

Our results suggest that A1 cell adaptation is negligible at repetition rates typical of search-phase echolocation calls of bats, even at high intensities. Adaptation, however, does result in a decrease of the number of A1 spikes per pulse at high amplitudes for calls produced at faster repetition rates typical of the approach sequence of bats. Individual moths still had ranges of amplitudes below the A2 threshold in which the number of A1 spikes per pulse varied little (i.e. saturation ranges). Therefore, data collected using individual pulses appear to provide valid information about the limitations of the A1 cell to encode changes in amplitude relevant to bat echolocation calls.

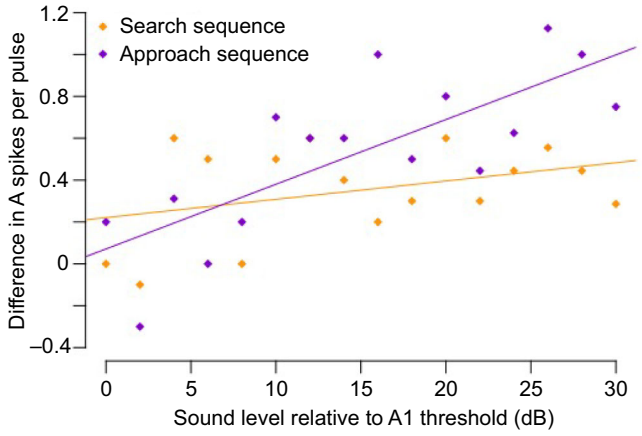

Fig. 7. Difference in the number of A1 spikes for the first and last pulse in the bat-like pulse sequences. The difference in A1 spikes increased with amplitude for the approach sequence but not for the search sequence (*N*=10 moths). See Materials and methods for moth species and species sample sizes.

Despite decades of interest and research, the relationship between receptor cell activity and moth behavior is still not well understood. Many studies have reported that moths from various families have two types of anti-bat behavior depending on sound intensity: directional flight away from a quiet (distant) bat and more drastic flight maneuvers in response to a loud (close) bat (Roeder, 1962, 1964; Agee, 1967, 1969; Surlykke, 1984; Rydell et al., 1997; Svensson et al., 1999). Likewise, range fractionation by the two receptor cells in the moth ear, with A1 encoding low-amplitude sound and A2 encoding high-amplitude sounds, has also been well documented (Roeder, 1964; Fullard, 1998). Therefore, Roeder (1974b) suggested that the A1 cell might primarily function to trigger directional flight away from an approaching bat and the A2 cell might trigger the last-ditch maneuvers seen in response to a nearby bat. Other authors have since suggested that this might be a simplification; notodontid moths, which have only one receptor cell per ear, show both types of behavior (Surlykke, 1984) and arctiid moths produce sounds back to bats as aposematic signals of toxicity or to jam the bat's echolocation (Hristov and Conner, 2005; Ratcliffe and Fullard, 2005; Corcoran et al., 2009) when only the A1 cell is activated (Ratcliffe et al., 2009). Together with these results, our data suggest the hypothesis that the A2 cell might be sufficient but not necessary to elicit last-ditch behavior in noctuoid moths. Perhaps a large number of A1 cell spikes would be sufficient to

trigger last-ditch behavior in response to bats that produce long-duration calls, whereas a few A1 spikes and the A2 cell firing could trigger the same response to bats that produce short echolocation calls. This hypothesis remains to be tested. Of particular interest would be behavioural and neurophysiological data in response to varying pulse durations from moth species belonging to the family Notodontidae, with only one receptor cell per ear.

In conclusion, the A1 receptor of noctuid and erebid moths is able to provide information about both the distance and direction of bats that use long-duration calls but only direction for bats that use short-duration calls. Directional information is useful for triggering the 'far-bat' directional flight response, and this might be all that is needed for the distances between bats and moths for which only the A1 cell is activated. Considering this result, the activity of the A2 cell at higher amplitudes appears to be an important adaptation to provide information about the distance of an approaching bat that produces short-duration echolocation calls.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: S.D.G., H.M.tH.; Methodology: S.D.G., H.M.tH.; Formal analysis: S.D.G., H.M.tH.; Writing - original draft: S.D.G., H.M.tH.; Writing - review & editing: S.D.G., H.M.tH.

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