Current Biology

Airborne Acoustic Perception by a Jumping Spider

Highlights

- We present evidence that jumping spiders, famously visual, perceive airborne sounds

- Spiders responded to low 80 Hz tones by freezing—an acoustic startle response

- Neural recordings revealed units in the brain that respond to airborne acoustic cues

- Neural responses to 80–380 Hz ($\sim$65 dB SPL) persisted at far-field distances (>3 m)

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In Brief

Jumping spiders are renowned visual specialists. Here, Shamble et al. provide evidence that they also respond to airborne acoustic cues. Behaviorally, stimuli caused spiders to freeze, while neural responses to stimuli of $\sim$65 dB SPL persisted even at ranges of 3 m, well beyond what has been previously reported in similar systems.

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Airborne Acoustic Perception by a Jumping Spider

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http://dx.doi.org/10.1016/j.cub.2016.08.041

SUMMARY

Jumping spiders (Salticidae) are famous for their visually driven behaviors [1]. Here, however, we present behavioral and neurophysiological evidence that these animals also perceive and respond to airborne acoustic stimuli, even when the distance between the animal and the sound source is relatively large (~3 m) and with stimulus amplitudes at the position of the spider of ~65 dB sound pressure level (SPL). Behavioral experiments with the jumping spider *Phidippus audax* reveal that these animals respond to low-frequency sounds (80 Hz; 65 dB SPL) by freezing—a common anti-predatory behavior characteristic of an acoustic startle response. Neurophysiological recordings from auditory-sensitive neural units in the brains of these jumping spiders showed responses to low-frequency tones (80 Hz at ~65 dB SPL)—recordings that also represent the first record of acoustically responsive neural units in the jumping spider brain. Responses persisted even when the distances between spider and stimulus source exceeded 3 m and under anechoic conditions. Thus, these spiders appear able to detect airborne sound at distances in the acoustic far-field region, beyond the near-field range often thought to bound acoustic perception in arthropods that lack tympanic ears (e.g., spiders) [2]. Furthermore, direct mechanical stimulation of hairs on the patella of the foreleg was sufficient to generate responses in neural units that also responded to airborne acoustic stimuli—evidence that these hairs likely play a role in the detection of acoustic cues. We suggest that these auditory responses enable the detection of predators and facilitate an acoustic startle response.

RESULTS

Behavior

We used a reaction assay to determine whether the jumping spider *Phidippus audax* responds behaviorally to airborne stimuli (see Supplemental Experimental Procedures). Responses of individual spiders to speaker-generated stimuli were recorded using a digital video camera (60 frames per second) and then categorized. Airborne signals, however, can cause substrate-borne vibrations—a phenomenon that can make it difficult to determine whether an animal is perceiving stimuli via the air or the substrate (see [3]). This is particularly problematic in spiders, whose sensitivity to vibrations is well documented [4–6]. We therefore used a 25 × 25 × 2 cm metal block (14.3 kg) as the arena floor, limiting transmission of airborne sound energy into substrate-borne vibrations [7]. We also verified through analytical calculations and direct vibratory measurements that any sound-induced motion of the block fell below the detection thresholds of spiders (see Supplemental Experimental Procedures). The arena was surrounded by wire mesh (opening diameter 2 mm) to contain spiders while minimizing acoustic reflections. The speaker was located 2 m away and 50 cm below the arena and produced 2 s tones with an amplitude of 65 dB sound pressure level (SPL) (amplitude measured at arena center using a calibrated 0.25-inch pressure microphone; Brüel & Kjær). Each spider was assigned to one of three stimulus conditions—80 Hz (n = 23), 2,000 Hz (n = 22), or silent control (n = 10)—and experienced the stimulus four times.

Spiders responded significantly more to 80 Hz tones than to 2,000 Hz tones or the silent control (ANOVA, Tukey's honestly significant difference [HSD] test, p < 0.0001; see Figure 1A), and there were no significant differences between responses to 2,000 Hz tones and the control (ANOVA, Tukey's HSD test, p = 0.3). Within 80 Hz trials, freezing was the most common response (Figure 1B), characterized by the sudden cessation of movement (Movie S1). Freezing also had a significantly faster onset time (~100 ms) than other behaviors (ANOVA, Tukey's HSD test, p < 0.01) and low onset variability, suggesting that
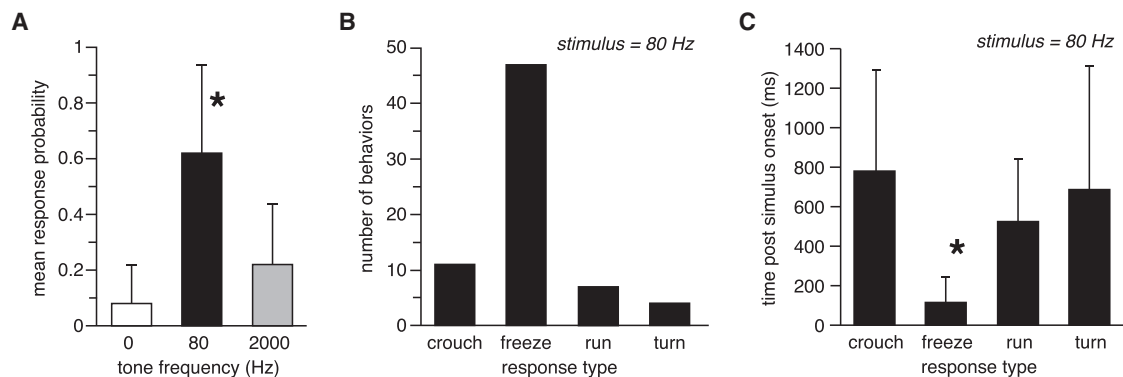
Figure 1. Result of Behavioral Experiments Showing Responses of Individual *Phiddipus audax* Jumping Spiders to Speaker-Generated Tones

Spiders were allowed to move about a 25 × 25 cm arena, with responses to 65 dB SPL tones recorded using a digital video camera (60 frames per second). These recordings were used to categorize behavioral responses and to determine the onset times of observed behaviors. Individual spiders were randomly assigned to a silent control ($n_{spiders} = 10$), 80 Hz ($n_{spiders} = 23$), or 2,000 Hz ($n_{spiders} = 22$) condition and experienced that treatment four times. A dense metal block was used as the arena floor to limit potential for air-to-substrate acoustic transmission (see Supplemental Experimental Procedures). See also Figure S4 and Movie S1.

(A) Spiders in the 80 Hz treatment responded significantly more than spiders in the other conditions (ANOVA, Tukey's HSD test, $p < 0.0001$), and there was no significant difference between responses in the control and 2,000 Hz treatments (ANOVA, Tukey's HSD test, $p = 0.3$). Values plotted are means with error bars extending to one standard deviation (SD), where each data point represents the response frequency of a given spider.

(B) Breakdown of the types of behavior observed by category in response to the 80 Hz condition.

(C) Time elapsed between stimulus onset and observed behavior for responses to the 80 Hz tone. The onset of freezing responses was significantly more rapid than for other behavior types (ANOVA, Tukey's HSD test, $p < 0.01$). Bar heights represent the mean; error bars show one SD.

although "freezing" was a category imposed by our analysis, it constituted a robust and relevant behavioral unit (Figure 1C).

Neural Responses

Recent work has described extracellular methods enabling stable recordings of neural activity in the jumping spider brain [8]. Here we applied these methods to probe for acoustically responsive neural units (see Supplemental Experimental Procedures and [8] for details). In brief, spiders were cold anesthetized, held in place using a 3D-printed spider holder and low-melting-point dental wax, and then placed inside a neurophysiological rig on a vibration-isolating table surrounded by a custom-made Faraday cage and acoustic-isolating foam. An extracellular tungsten microelectrode (4 MΩ, MicroProbes), advanced using a motorized hydraulic microdrive, was guided through a small hole in the cuticle and into the spider's brain. Recordings targeted the area of the CNS ventral to the arcuate body. Resulting neural activity was analyzed using the spike-sorting program Wave_Clus [9] to classify individual units (see Supplemental Experimental Procedures and Figure S1).

Acoustic stimuli were designed using MATLAB, generated via a speaker, and presented in pseudo-random order. Distances between the sound source and the animal were 2 m, 3.0 m, or 3.3 m, depending on the experiment. Signal pressure amplitude was monitored using a calibrated pressure microphone (see above and Supplemental Experimental Procedures) placed adjacent to the animal. We also estimated the particle velocity amplitude of stimuli based on stimulus signal frequency, distance between the speaker and the animal, and parameters of the sound source (see Supplemental Experimental Procedures for calculations). A laser Doppler vibrometer was used to measure whether airborne acoustic signals caused vibrations in

any portion of the experimental setup, including recording electrodes. Vibrations induced by acoustic stimuli were detected at amplitudes of 94 dB SPL and above but were absent at 89 dB SPL (see Supplemental Experimental Procedures). We therefore limited experimental stimulus amplitudes to ≤90 dB SPL to ensure that stimuli were delivered to the animal exclusively as airborne cues.

To determine whether neural units were responsive to airborne acoustic stimuli, we used 0.5 s frequency sweeps (50–400 Hz, linear increase; see Figure 2B inset) with amplitudes between ~45 and 80 dB SPL (speaker-to-animal distance = 2 m). Detection thresholds varied between neural units, from 48 to 77 dB SPL, corresponding to particle velocities estimated at 0.02 and 0.49 mm/s (based on 200 Hz signal) (Figure 2B). These pressure amplitude thresholds are in line with other studies of airborne acoustic perception in arthropods—including systems where receivers possess pressure-sensitive tympanic membranes [10]. Neural activity was also found to increase with stimulus amplitude, suggesting that signal amplitude is represented at this level of the CNS.

To explicitly explore the relationship between stimulus amplitude and frequency, we measured the response threshold, defined as the lowest amplitude that generated a response, for multiple frequencies (Figures 2C–2E). Neural units were determined to have responded to a given frequency-amplitude combination if neural activity (spikes per second) exceeded one standard deviation above the mean activity during the inter-tone intervals for half or more of the eight presentations. Response thresholds (Figures 2C–2E) revealed relatively sharp preferences for low frequencies (80–90 Hz), with threshold amplitudes of ~65 dB SPL. Some responses also showed smaller peaks roughly corresponding with multiples of the frequency of greatest sensitivity, suggestive of resonances in the sensory
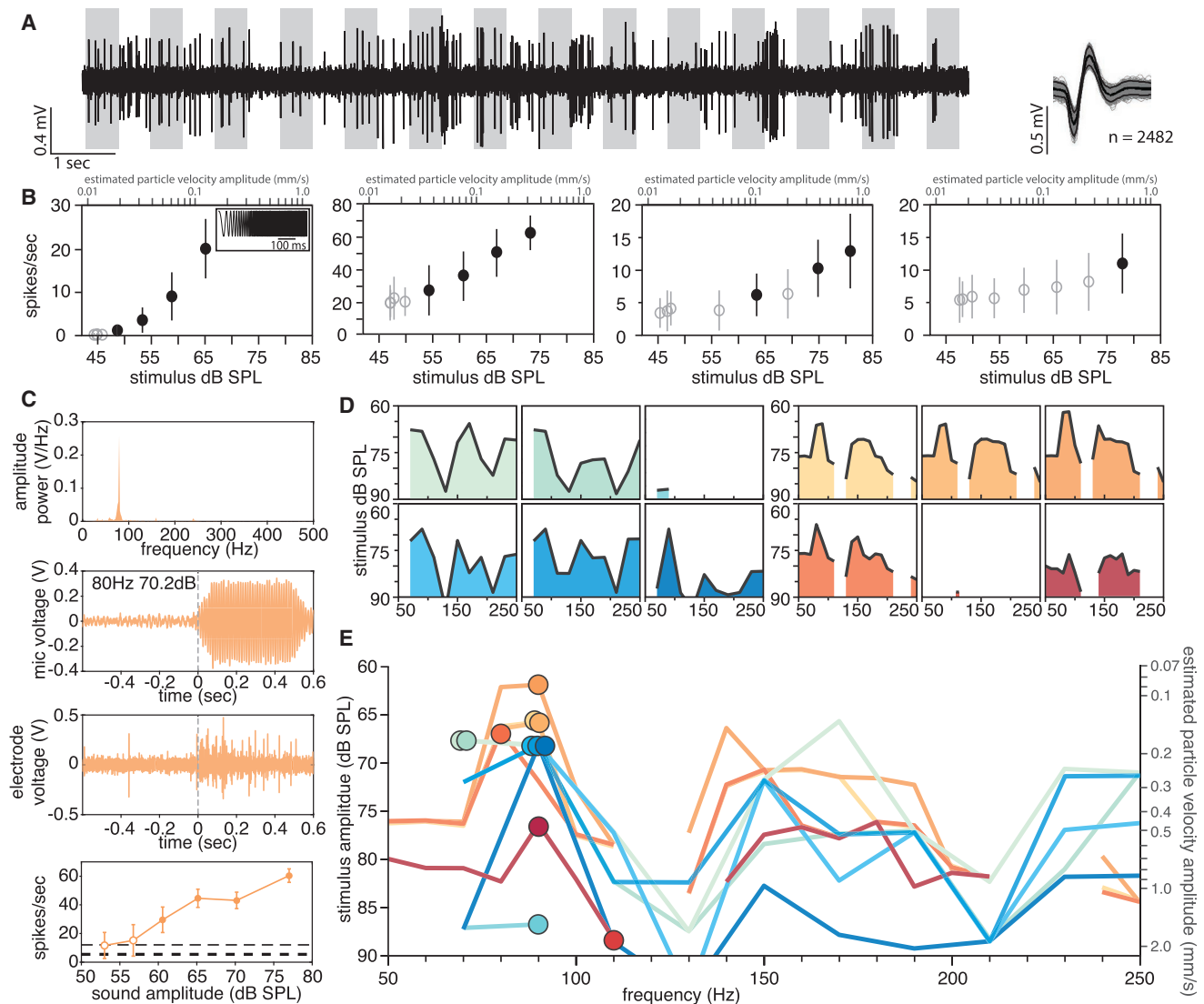
Figure 2. Results of Extracellular Neurophysiological Recordings Made from the Brain of the Jumping Spider *P. audax* in Response to Speaker-Generated Airborne Stimuli

(A) An example trace showing neural activity (left) with stimulus presence indicated by gray boxes and an overlay (right) of all similarly identified spikes following spike sorting [9]. Black center line shows the mean; thin lines denote ± one SD.

(B) The responses of four independent neural units to a linear frequency sweep signal depicted in the inset (50–400 Hz; 500 ms duration) at a range of stimulus amplitudes presented in pseudo-randomized order. Black markers indicate responses that were significantly greater than background (increased activity during stimuli compared to the post-stimulus interval, repeats per amplitude n = 40, t test, p < 0.05). Gray markers show responses that were not significantly greater than background; vertical bars show ± one SD. Stimulus amplitude was measured at the location of the animal; distance between stimulus source and animal was 2 m. Estimated particle velocities are for a 200 Hz signal.

(C) Example components of a tuning curve experiment, specifically response of a neural unit to 80 Hz tones. From top: amplitude spectrum of recorded stimulus tone, stimulus as recorded at microphone, voltage trace of extracellular recording (dashed line shows stimulus onset), and a summary of neural responses for each amplitude condition showing mean as circles and ± one SD as vertical bars (repeats per amplitude, n = 8). Thick horizontal dashed line shows mean background firing rate, calculated as spikes per second during inter-tone interval. Thin horizontal dashed line shows one SD above mean background activity. Filled circles denote conditions where neural activity exceeded one SD above the mean for a majority of presentations of a given frequency-amplitude combination. The color matches the associated neural unit shown in the upper right panel of (D).

(D) Tuning curve responses for 12 independent neural units: six on the left (blue) from one spider, and those at the right (red) from a second spider. Note the inverted dB y axis such that peaks in the figure show the highest sensitivity. To generate curves, every combination of frequency (50–250 Hz, at 10 Hz intervals) and amplitude (~50–90 dB SPL, at intervals of 5 dB SPL) was presented eight times in pseudorandom order (tone duration = 0.6 s; inter-tone interval = 0.6 s). Lines mark the minimum stimulus amplitude for which activity during at least four out of eight trials exceeded one SD above mean background activity. Colored areas therefore show all amplitudes that were detectable.

(E) An overlay of all curves presented in (D). Colored circles denote the frequency of greatest sensitivity for each unit. For experiments shown in (C)–(E), there was 3 m between the stimulus source and the spider; estimated particle velocity measures are based on an 80 Hz signal.

See also Figures S1, S2, and S3.

structures. Since it is likely that the spiders sense sound through particle velocity [11], we also provide estimates of the particle velocity at the spider's location (right vertical axis, Figure 2E). Spiders responded to particle velocities of ~0.13 mm/s (estimate based on 65 dB SPL, 80 Hz signal at 3 m; see Supplemental Experimental Procedures).

To verify that responses were due to the sensory capabilities of the animals, and not the result of potential acoustic imperfections in our laboratory setup, we repeated our neurophysiological experiments in an anechoic chamber (interior dimensions 4.17 × 5.38 × 3.45 m; base noise level < −10 dB SPL for 200 Hz–30 kHz; verified anechoic properties 100 Hz–30 kHz). Methods for these recordings were identical to previously described laboratory experiments, except that the animal was placed on a vibration-isolated fixture and an on-site speaker system was used to generate stimulus (see Supplemental Experimental Procedures). Stimulus amplitudes were 76–84 dB SPL, with 3.3 m between speaker and animal. Neural responses matched those obtained in our other experiments (Figure 3), demonstrating a sensitivity to low-frequency tones (80–380 Hz).

Since sensory hairs are responsible for detection of airborne stimuli in other spider species [6] and numerous insect species (see [11, 12] for reviews), we investigated the role of hairs in this system. In the non-anechoic laboratory, we presented pure tones between 50 and 80 dB SPL (2 m between source and animal). After identifying an acoustically sensitive neural unit, we used a linearly actuated micro-shaker (Physik Instrumente) to mechanically drive a single long sensory hair on the patella of the foreleg at a range of amplitudes (maximum displacement 10.8 μm). Both airborne stimuli and direct mechanical stimulation of the hair generated increased neural activity across multiple frequencies (64–256 Hz; Figure 4).

DISCUSSION

Hearing at a Distance
Many arthropod species—including spiders—perceive airborne stimuli via specialized sensory hairs: filiform hairs in insects and trichobothria in arachnids [11]. Theoretical and experimental work in the spider *Cupiennius* (Ctenidae) has shown these hair-based mechanoreceptors to be astonishingly sensitive [13–15], allowing these large wandering spiders to capture flying prey at a range of 20 cm without any visual cues [16]. Similarly, sensory hairs have been shown to enable crickets [17], cockroaches [18], and fishing spiders (Pisauridae) [19] to escape from danger by detecting the wave of air that precedes an onrushing predator.

Unlike the pressure-sensing tympanic ears that have evolved independently in tetrapods [20] and numerous insect lineages [21], sensory hairs are air-flow mechanoreceptors sensitive to the particle-velocity component of airborne stimuli. Airborne sound consists of two coupled fields, pressure and particle velocity, whose relationship is generally nontrivial, depending on frequency as well as the distance from and shape of the sound source [22, 23]. For arthropods that sense airborne disturbances through particle-velocity-sensitive hairs, it is typically assumed that sound detection is only possible close to the sound source in the region termed "near-field," estimated to span 0.5–1 sound

wavelength from the source [2, 21, 22, 24]. This terminology is so common that the particle-velocity component of sound is often referred to as "near-field sound." However, the particle-velocity field does not vanish at larger distances but rather decays continuously even into the "far-field" region. Indeed, the ability to sense sound based on particle velocity depends only on the detection threshold of the sensor and the particle-velocity amplitude at the sensor position. We found that *P. audax* responds to particle-velocity amplitudes of ~0.13 mm/s, an estimate based on observed neural responses to signals of 80 Hz and 65 dB SPL, measured 3 m from the source (Figure 2; see Supplemental Experimental Procedures for calculations). At this range, we calculate that spiders were located well within the far-field region of the sound stimuli. Responses persisted in the nearly ideal acoustic conditions of an anechoic chamber (Figure 3). Indeed, even using the highest traditional estimate for the range of the so-called near-field sound region, 1 sound wavelength, an animal 3 m away would be unable to detect stimuli with wavelengths below this distance; thus, any tone above 115 Hz would be undetectable. That spiders, even under anechoic conditions, responded to stimuli up to 350 Hz (wavelength = 0.98 m) demonstrates that these traditional estimates fail to explain the responses of these animals.

While it is still not clear how *P. audax* detects airborne signals, we hypothesize that air-flow-sensitive hairs that register particle velocity are the most likely candidates for a number of reasons. First, pressure-sensitive tympanic structures have not been found in any spider, or in any other arachnid. Second, neural units were found that respond to both airborne signals and direct mechanical stimulation of single hairs, further suggesting that hair-based sensors are the site of transduction (Figure 4). Indeed, previous work on the spider *Cupiennius* has clearly demonstrated the role of air-flow-sensitive hairs in facilitating responses to airborne stimuli [11, 25, 26]. It has been reported that some spider species may detect airborne stimuli via slit sense organs [27, 28], mechanoreceptors typically thought to be important in detecting cuticle deformation and substrate-based vibrations [6]. However, although these structures exist in jumping spiders, their ability to register airborne cues has not been demonstrated.

Behavioral Relevance of Sound
Spiders exhibited a freezing behavior in response to the low-frequency (80 Hz) stimulus (Figure 1). Freezing is a common reaction to threatening stimuli exhibited across a range of taxa, including rodents [29], fish [30], insects [31], and other arachnids [32], and is generally thought to minimize the chances of attracting the attention of potential predators [33]. Based on the observed behavior and the rapidity and consistency of its onset, the freezing behavior reported here bears the characteristics of an acoustic startle response [34]—a well-defined and well-studied class of behaviors that has also been reported in numerous taxa [34, 35]. The ~100 ms delay between stimulus onset and behavior also fits well within the range of acoustic startle latency times reported in other species (~30–200 ms, [31]).

It has been proposed that acoustic startle responses may facilitate attention-altering effects, enabling an animal to refocus limited attentional resources [34]. This is an especially
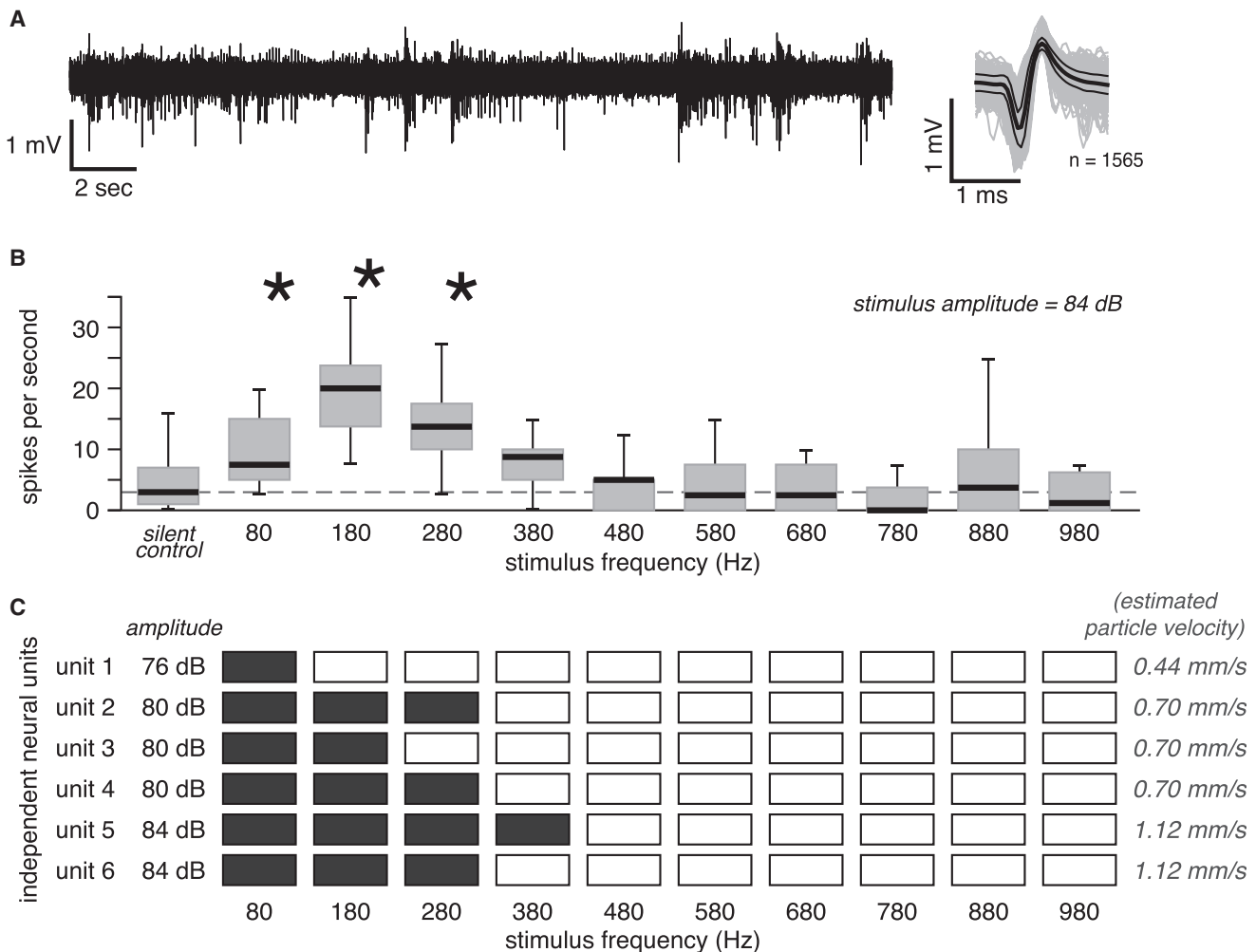
Figure 3. Extracellular Activity in the Brain of the Jumping Spider *P. audax* in Response to Pure Tone Airborne Acoustic Stimuli under Anechoic Conditions

Frequencies, including a silent control, were presented in pseudo-random order. See also Figures S1 and S3.

(A) Trace showing extracellular activity in response to a 84 dB SPL signal (left) and an overlay of spikes determined to represent a single neural unit based on spike sorting (right). The black center line represents the mean; thin lines represent ± one SD.

(B) Response of the unit shown in (A) to specific pure tone frequencies (repeats per frequency, n = 30). Asterisks indicate responses that were significantly greater than the response to the silent control condition (Kruskal-Wallis, p < 0.05 after Bonferroni correction). Thick black lines represent the median, gray boxes extend to the 25th and 75th percentiles, and whiskers extend to cover 99 percent of a normal distribution. The dashed line shows median activity for the control condition.

(C) Schematic depicting the responses of six independent neural units in a spider to pure tones, for the stated stimulus amplitudes. Independence of units was based on spike sorting [11] and electrode location (see Figure S1). Black boxes indicate conditions in which neural activity was significantly elevated compared to the silent control (Kruskal-Wallis, p < 0.05 after Bonferroni correction); white boxes indicate no significant difference. The distance between stimulus and the animal was 3.3 m; estimated particle velocity is based on an 80 Hz signal.

compelling possibility in jumping spiders, given the importance of vision in shaping their behaviors. Such a reaction would enable an individual, upon registering an airborne stimulus, to rapidly reallocate sensory and decision-making resources to best inform subsequent behavior. For example, spiders could become more responsive to visual cues that immediately follow an acoustic stimulus. Freezing also limits optical flow due to self-motion, likely improving visual performance. All this might be particularly important in the context of potential threats, and for species with vagabond lifestyles such as jumping spiders, where the location of the threat and the subsequent route to

safety may not be immediately apparent, instead requiring rapid and flexible decision-making.

In the context of threat detection, the observed frequency sensitivity of *P. audax* seems to make it well suited to detecting acoustic signals generated by potentially dangerous flying insects, especially predatory wasps (Insecta: Hymenoptera) and dipteran parasitoids (notably adult small-headed flies, Insecta: Diptera: Orthorrhapha: Acroceridae—although not their mobile larvae), many of which specialize on spiders and are a major cause of spider mortality [36–39]. Dominant acoustic frequencies of flying hymenopterans are ~100 Hz (depending on
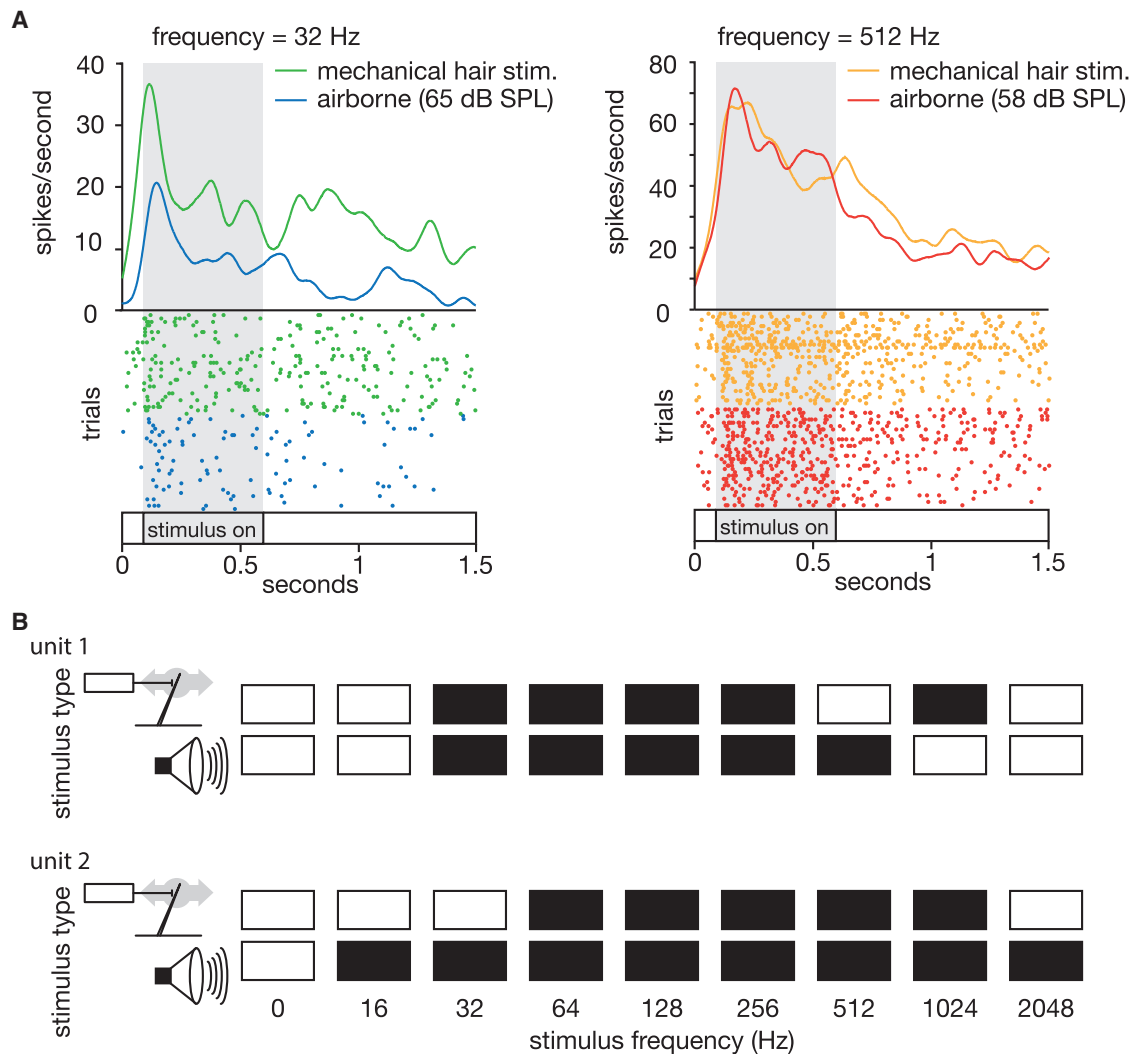
Figure 4. Activity of Neural Units in the Brain of the Jumping Spider *P. audax* in Response to Airborne Acoustic Stimuli and to Direct Mechanical Stimulation of an Air-Flow-Sensitive Hair on the Patella of the Foreleg

Airborne stimuli were generated using a speaker, while hairs were driven using a linearly actuated piezo micro-shaker. Neural activity was recorded in response to pure frequency tones (0.5 s duration), presented in pseudo-random order within each stimulus type (airborne or mechanical stimulation of the hair). The amplitude of airborne acoustic stimuli was between 50 and 80 dB SPL, and the distance between the stimulus source and the animal was 2 m. The amplitude of the direct mechanical stimuli also varied, up to a maximum amplitude of 10.8 μm (peak to trough). Activation of the micro-shaker when near (within ∼1 cm) but not in contact with the hair resulted in no increased neural activity. See also Figure S1.

(A) Examples from extracellular recordings of two independently recorded neural units in response to the indicated frequency tone of both stimulus types. Rasters show spike times, and line histograms (smoothed with a Gaussian filter, SD = 36 ms) show a summary of all 30 tone presentations for each stimulus set. The gray bar denotes the 500 ms time interval when the stimulus was present.

(B) Summary of responses to direct mechanical stimulation of a hair (top) and airborne stimulation (bottom) for two distinct neural units. Black boxes indicate responses in which neural activity (spikes/s) was significantly greater in response to the stimulus than was activity during the post-stimulus interval (time window for stimulus response = 0.7 s to capture potential post-stimulus effect; post-stimulus window = 1.3 s; each tone repeated 30 times, t test, p < 0.05); white boxes indicate no significant response. Note that because stimuli were delivered at a range of amplitudes, these findings do not represent a true response tuning curve (e.g., in contrast to Figure 2E; see Supplemental Experimental Procedures for details); instead, these results simply provide evidence that single neural units responded to both stimuli types across multiple stimulus frequencies.

the species) with harmonics up to ∼1,000 Hz [40]—properties that match the frequency sensitivities reported here. Indeed, air-flow-sensitive hairs have been shown to be important in detecting flying predatory wasps in other systems, though only to a maximum range of 70 cm [41]. The ability to detect these predators may be especially important for jumping spiders since

(unlike sedentary web-dwelling spider species) they are diurnally active, moving through the environment in search of prey and potential mates—a lifestyle that likely increases exposure to similarly diurnal predators such as wasps. Furthermore, unlike their web-dwelling cousins, jumping spiders lack the built-in defensive advantages that accompany life on a web [38]. Thus,

the ability to detect the presence of threats—even before they become visually apparent—could provide these animals with an important fitness advantage.

Sensitivity to low frequencies may also enable *P. audax* to detect and respond to more general disturbances, such as the movement of leaves or breaking of twigs, that might signal the presence of larger threats. Such disturbances produce broadband signals [42] with frequencies that these spiders are sensitive to, and could be of sufficient amplitude to make them detectable at a distance. Although not themselves threatening, such signals could be important in shaping adaptive behavioral responses to dangerous circumstances.

From an ecological perspective, perception of airborne cues could benefit these spiders in contexts beyond threat avoidance, including prey detection and conspecific signaling. For example, although the frequency sensitivities observed here overlap with those generated by flying predatory wasps, they would also be sufficient to register the presence of other flying insects. Extensive work in the spider *Cupiennius* has demonstrated the utility of air-flow-sensitive hairs in enabling spiders to detect and capture flying insect prey [16]. Jumping spiders, too, have been found to be capable of capturing prey in the absence of visual cues, though successful captures seemed to require repeated physical contact with prey, facilitated by an enclosed arena [43]. Since the acoustic fundamental frequency produced by a flapping insect is typically equal to its wingbeat frequency, and since wingbeat frequency is generally inversely proportional to insect size [40], the frequency sensitivities reported here could make these spiders capable of detecting even relatively small insects in flight (e.g., fruit fly wingbeat frequency is roughly 200 Hz, [44])—though detection range would be limited by the low amplitude of such signals.

Particle-velocity cues might also mediate conspecific interactions, as has been demonstrated in other arachnids [45], including a possible role in courtship, as has been suggested in wolf spiders [46]. Many spider species, and jumping spiders in particular, have complex courtship displays consisting of multiple components and often multiple signaling modalities—complexity that may be related to the simultaneous challenges of maintaining female attention while reducing female aggression [47]. These courtships often involve rapid leg movements and elaborate acoustic signals produced by specialized stridulatory structures [5]. Although stridulatory signals have been shown to convey information via substrate-borne vibrations and leg waving provides visual information [5], both components could also generate particle-velocity-based airborne signals, potentially adding another signaling dimension to displays. Such a role for airborne acoustic signals in courtship may also help explain why some spider species respond to acoustic stimuli even when placed on substrates that prevent vibratory signaling [7, 46].

Conclusions

Although jumping spiders are best known as visual specialists, we report that the jumping spider *P. audax* is capable of perceiving airborne acoustic cues, evidenced by both behavioral responses and neural activity in the CNS. Behaviorally, the freezing responses observed here constitute an acoustic startle response, a reaction that has been shown to have important implications for mediating anti-predatory behavior. Regarding signal reception, we hypothesize that air-flow-sensitive hairs are the site of detection. Detection thresholds were in the region of 65 dB SPL, corresponding to an estimated particle-velocity amplitude of 0.13 mm/s, with greatest sensitivity to relatively low frequencies (∼80 Hz). Responses persisted even when the distance between the animal and the stimulus exceeded 3 m—well beyond the 70 cm range [41] that was, to our knowledge, the greatest detection distance previously reported for sensory systems that detect air flow [11]. These findings bring into question the distinction commonly made by biologists between "near-field" and "far-field" sound, demonstrating that these animals—believed to be only able to detect particle velocity—respond to airborne stimuli even at "far-field" distances.

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