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LETTER

Flowers respond to pollinator sound within minutes by increasing nectar sugar concentration

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Abstract

Can plants sense natural airborne sounds and respond to them rapidly? We show that *Oenothera drummondii* flowers, exposed to playback sound of a flying bee or to synthetic sound signals at similar frequencies, produce sweeter nectar within 3 min, potentially increasing the chances of cross pollination. We found that the flowers vibrated mechanically in response to these sounds, suggesting a plausible mechanism where the flower serves as an auditory sensory organ. Both the vibration and the nectar response were frequency-specific: the flowers responded and vibrated to pollinator sounds, but not to higher frequency sound. Our results document for the first time that plants can rapidly respond to pollinator sounds in an ecologically relevant way. Potential implications include plant resource allocation, the evolution of flower shape and the evolution of pollinators sound. Finally, our results suggest that plants may be affected by other sounds as well, including anthropogenic ones.

Keywords

Communication, nectar, plant bioacoustics, plant–pollinator interactions, pollination, signalling, vibration.

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INTRODUCTION

Plants' ability to sense their environment and respond to it is critical to their survival. Plants responses to light (Jiao *et al.* 2007; Chory 2010), volatile chemicals (Arimura *et al.* 2000; Baldwin *et al.* 2006; Heil & Bueno 2007; Karban *et al.* 2014; Karban 2015) and different forms of touch, including continuous (Darwin 1892; Slack 2000; Braam 2005; Monshausen & Haswell 2013) and vibrating (De Luca & Vallejo-Marín 2013; Appel & Cocroft 2014) are well documented. However, the ability of plants to sense and respond to airborne sound – one of the most widely used communication modalities in the animal kingdom – has hardly been investigated (Chamovitz 2012; Gagliano *et al.* 2012; Hassanien *et al.* 2014). Recent studies demonstrated slow responses, such as changes in the growth rate of plants, after exposure to artificial acoustic stimuli lasting hours or days (Takahashi *et al.* 1991; Xiujuan *et al.* 2003; Yi *et al.* 2003; Bochu *et al.* 2004; Ghosh *et al.* 2016; Choi *et al.* 2017; Gagliano *et al.*, 2017; Ghosh *et al.* 2017; Kim *et al.* 2017; López-Ribera & Vicient 2017; Jung *et al.* 2018). Furthermore, plant tissues have been shown to vibrate to a range of sounds (Telewski 2006; Rebar *et al.* 2012; Davis *et al.*, 2014). In contrast, to the best of our knowledge, a rapid reaction to airborne sound has never been reported for plants; neither has the biological function of any plant response to airborne sound been identified. In this work, we aimed to test rapid plant responses to airborne sound in the context of plant–pollinator interactions.

The great majority (87.5%) of flowering plants rely on animal pollinators for reproduction (Ollerton *et al.* 2011). In these plants, attracting pollinators can increase plant fitness and is achieved using signals such as colour, odour and shape, and by food rewards of nectar and pollen (Willmer 2011). Increased reward quality or quantity can result in longer pollinator visits or in a higher likelihood that a pollinator will visit another flower of the same species in the near future, potentially increasing the flower's fitness by increasing the chances of pollination and reproduction (Faegri & Van Der Pijl 1979; Pappers *et al.* 1999; Stout & Goulson 2002). Producing an enhanced reward can be expensive (Pleasants & Chaplin 1983; Southwick 1984; Pyke 1991; Ordano & Ornelas 2005; Ornelas & Lara 2009; Galetto *et al.* 2018) and standing crop of nectar is subjected to degradation by microbes (Herrera *et al.* 2008; Vannette *et al.*, 2013) as well as to robbery (Irwin *et al.* 2010), including silent robbers like ants (Galen 1999). Thus, a mechanism for timing the production of enhanced reward to a time when pollinators are likely to be present could be highly beneficial to the plant. Here we suggest that a response of plants to the sound of a pollinator can serve as such a timing mechanism. Specifically, we hypothesise that plants could respond to the sound of a flying pollinator by increasing the reward in a way that would increase the probability of pollination and reproduction by the same or similar pollinators.

The wingbeats of flying pollinators, including insects, birds and bats, produce sound waves that travel rapidly through air. If plants were able to receive such sounds and react to

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them rapidly, they could temporarily increase their advertisement and/or reward when pollinators are likely to be present, resulting in improved resource allocation. A possible plant organ that could relay the airborne acoustic signal into a response is the flower itself, especially in flowers with 'bowl' shape. If this is the case, we expect that part of the flower (or the entire flower) would vibrate physically in response to the airborne sound of a potential pollinator. We further predict that nectar sugar concentration would increase in response to the sound. None of these predictions have been tested before. To test these predictions we used the beach evening primrose, *Oenothera drummondii*, whose major pollinators are hawkmoths (at night and early morning) and bees (at dusk and morning) (Eisikowitch & Lazar 1987). We measured petal vibration and nectar sugar concentration in response to sounds. We analysed the effect of different sound frequencies, including both pollinator recordings and synthetic sounds at similar and different frequencies. We show that pollinator sounds, and synthetic sound signals at similar frequencies, cause vibration of the petals and evoke a rapid response – an increase in the plant's nectar sugar concentration.

MATERIALS AND METHODS

General

We exposed *Oenothera drummondii* plants to different sound playbacks (see below) and measured the concentration of sugar in their nectar. We compared plants' response to different sounds including pollinator recordings, synthetic sounds in pollinator frequencies and in much higher frequencies, and silence. To determine whether the playback sounds result in physical vibration of the flower petals, we used laser vibrometry. To evaluate pollinator temporal distribution in the field, we performed field observations.

Experimental setup: Measuring plant nectar response under different treatments

The nectar response was tested in four different experiments (see Table S1 for summary): Experiment 1a (n = 90 flowers), where the plants were grown outdoors in a natural environment, exposed to natural acoustic conditions in the summer. The response was tested to the acoustic treatments (see Sound signals and playbacks for details): 'Silence' – no sound playback, 'Low' – playback of a low-frequency sound signal with energy between 50 and 1000 Hz, covering the range of pollinator wingbeat frequencies, and 'High' – playback of a high-frequency sound signal with energy between 158 and 160 kHz. This treatment served as a control for the potential effect of the speaker's electromagnetic field, which was absent in the 'Silence' treatment. Experiment 1b (n = 167 flowers), where the plants were grown indoors in the summer, and the response was measured to the previous three stimuli plus a 'Bee' stimulus – playback of the recordings of a single hovering honeybee with a peak frequency of 200–500 Hz; Experiment 2 (n = 298 flowers), where the plants were grown indoors in the fall, and response was tested for 'Low', 'High', and 'Intermediate' stimuli – playback of a sound signal with energy between 34 and 35 kHz. To test the role of the flower itself (rather than other parts of the plant exposed to sound) in the response, the 'Low' and 'High' treatments were also tested for flowers contained in glass jars 'Low in Jar' and 'High in Jar'; and Experiment 3 (n = 112 flowers), where the plants were grown indoors in the spring, and response was tested for 'Low' and 'High' stimuli.

In each experiment, plants were numbered, randomly assigned to treatments and tested at a random order, alternating between the different treatments (see Table S1 for numbers per treatment). We sometimes used different flowers of the same plant in more than one treatment; however, never in the same day, nor in the same treatment. To measure a flower's response, it was emptied of nectar, and immediately exposed to one of the treatments above. Its newly produced nectar was extracted 3 min after the beginning of the treatment (we had to wait 3 min for the amount of nectar accumulated to be measurable by refractormeter). Sugar concentration and nectar volume were quantified before and after the treatment (for details see Nectar measurements methods, Fig. S1).

In the jar manipulation, we used six identical 1 L sound proof glass jars, padded with acoustically isolating foam (see Fig. S2). The jar's ability to block sound was tested by positioning a calibrated microphone (GRAS, 40DP) inside it and playing the 'Low' playback from a 10-cm distance (as in the experiment). This measurement confirmed that jars reduced sound intensity by 14 dB.

Sound signals and playbacks

In the nectar experiments, we used five signals, including bee recordings, three artificial sound stimuli and silence. The artificial sound stimuli were generated using acoustic software (Avisoft, Saslablite). The 'Low' frequency stimulus consisted of a 10-s frequency modulated (FM) sound signal sweeping from 1000 Hz to 50 Hz, covering the frequency range of the wingbeat of natural pollinators. The 'Intermediate' frequency stimulus consisted of a 10-s frequency modulated sound signal sweeping from 35 to 34 kHz. The 'High' frequency stimulus consisted of a 10-s frequency modulated sound signal sweeping from 160 to 158 kHz, a frequency that is clearly out of range for pollinator wingbeat. The 'Bee' stimulus was recorded by positioning a calibrated microphone (GRAS, 40DP) and recording an individual honey bee (*Apis mellifera*) from a distance of 10cm. The 'Silence' control treatment consisted of no playback.

Acoustic playbacks were performed using a Vifa speaker (XT25sc90-04, Vifa). D/A converter (Player 216-2, Avisoft Bioacoustics) at a sampling rate of 500 kHz. All signals were recorded using a calibrated microphone before playback to validate their intensity. Playback intensity in the indoors groups 'Low', 'Bee' and 'Intermediate' were set to resemble the intensity of a bee hovering 10 cm above the plant, with a peak sound pressure level of ca. 75 dBSPL relative to 20 μPa at a distance of 10 cm. 'Low' playbacks in the outdoor group had a peak pressure of *c*. 95 dB SPL (relative to 20 μPa at 10 cm).

For control, we used either 'Silence', where no sound was played, or the 'High' playback which had a weak intensity (ca. 55dBSPL) but served as an additional 'Silence'-like condition controlling for the electromagnetic field, absent in the 'Silence' control. All playbacks were played continuously for 3 min in all treatments, including the silent control. Each playback was played to a group of 5–6 flowers, hovering over each of them with a speaker for a period of 10 s each, returning to the first flower at the end. The speakers were moved from plant to plant for 3 min at a distance of *c*. 10 cm from the nearest flower, mimicking a pollinator hovering around a bush. Thus each flower was exposed to direct sound for 33.8 ± 0.3 s on average (we validated that the number of flowers per group had no effect on the significance of the results, see Results). Such movement of the speakers was done also in the 'Silence' treatment. In both 'grown indoors' and 'grown outdoors' experiments, all playbacks were performed indoors: the flowers were brought into a silent room and were treated there. To control for the accuracy of our playback system, we recorded the playback of the bee sound using a calibrated microphone (GRASS 40DP). The recording obtained that way (Fig. S3) was nearly identical to the original recording used in the experiment.

The vibration experiments were performed with playbacks of a bee (peak energy at 250–500 Hz) and a moth (peak energy at *c*. 100 Hz and no energy above 400 Hz), and pure tones at the peak frequencies of the signals described above: 'Low' (1 kHz), 'Intermediate' (35 kHz) and 'High' (160 kHz). A control for the bee playback was performed with a live bee, held by its legs with tweezers and hovering at several centimetres from the flower.

Nectar measurements

Nectar was extracted from all the flowers before treatments using PTFE (Teflon) tubes (external diameter = 0.9 mm, internal diameter = 0.6 mm), followed by disposable 1 μL glass capillaries for the nectar remaining after emptying by the Teflon tubes. The treatments were applied immediately after extraction. To avoid differences resulting from variation in emptying times, we left a capillary inside the first emptied flowers to assure that no new nectar has accumulated. When the last flower was emptied, all capillaries were removed and the treatment ('High', 'Low', 'Bee', 'Intermediate' or 'Silence') started. Three minutes later, after the treatment ended, nectar was drawn again from all the flowers. Sugar concentration in each flower was measured by calibrated Bellingham-Stanley low-volume Eclipse refractometers (0–50 Brix), where concentration measurements are accurate in volumes as low as 0.2 μL. Three minutes allowed for enough nectar to accumulate in each flower (see Fig. S4, presenting nectar quantities) sufficient for refractometer measurement.

Measuring petal vibration using laser vibrometry

To determine whether the playback sounds result in physical vibration of the flower petals, we used laser vibrometry. This method allows measuring minute physical vibrations through Doppler shifts of a laser beam reflected from a vibrating surface. To this end, the flowers were positioned on a wafer prober (Karl Suss PSM6, Mitutoyo FS70L-S microscope) and operated in ambient air. The motion of the petals was registered using a laser Doppler vibrometer (Polytec LDV, OFV-5000 controller). The vibrometer was operated in the velocity acquisition mode using VD-02 Velocity Output Decoder, (up to 1.5 MHz bandwidth). The laser beam was focused on the base of the petal (see Fig. S5) using the ×5 long working distance lens of the microscope.

Signals from the LDV were fed into the oscilloscope KEYSIGHT DSOX2004A (70MHz, 1Mpts memory). We compared flower vibrations in response to different playback frequencies and in the absence of playback ('Silence') in a paired experimental design (within the same plant). To validate that the presence of petals was crucial to the vibration, we also compared petal vibration in intact flowers to vibration in intact petal of flowers where some of the petals were removed (see Figs S5). To measure the actual vibration amplitude (i.e. displacement), we subdivided the measured velocity by $\frac{2}{\pi f}$, where f is the frequency of the oscillation. We used vibration models of objects with similar shapes [both a beam and a circular thin plate (Blevins & Plunkett 1980)] to estimate the flower's resonance vibration frequency. The resonance frequency of an object is dictated by the material properties, geometry and boundary conditions. For flower size of *c*. 6 cm and thickness of *c*. 0.4 mm, we estimated a fundamental mode frequency to be in the range of 100–500 Hz. A measured density of *c*. 230 kg/m3 and the Young's modulus of *c*. 1 MPa adopted from Watanabe & Ziegler 2013 were used in calculations.

Monitoring pollinator temporal distribution in the field

In order to assess the temporal distribution of pollinators around the plants in the field, two sets of field observations were done on the Tel Aviv beach: (a) To test whether the presence of a pollinator can indicate the vicinity of additional pollinators, we videoed *Oenothera drummondii* plants during the night. Seventeen plants were videoed over two nights for 4 h after sunset in summer 2017, using IR video cameras (Full Spectrum POV Cam, GhostStop USA, resolution 1920 × 1080, 30 fps). Cameras were positioned at a distance of 1–1.5 m from the plant. The videos were scrutinised manually using Matlab R2016a and VLC media player 2.2.4. A moth passing within a distance of 1 m from a plant was defined as 'near the plant'. We then analysed the distribution of intervals between these events (see Results). (b) To estimate the time that a single pollinator spends close to an *Oenothera drummondii* plant, the plants were visually observed during the day, when it was possible to track the same individual over time. Six plants were observed over 4 days for 3 h in each day. A bee passing within a distance of 10 cm from a plant was defined as 'adjacent to the plant' and the time it spent within this distance was estimated.

Plants and growth conditions

Oenothera drummondii plants were propagated from grafts of plants taken from Bet-Yanai coast, Israel. In all experiments, irrespective of the plants growth conditions, the response of the

plants to sound playback was tested indoors, in a quiet room. For Experiment 1a ('grown outdoors, summer 2014'), 200 plants were placed in 3 L pots and grown in the Tel Aviv University Botanical Gardens in an outdoor setting. Flower buds were covered with nets a day before the experiment, to avoid pollination and nectar withdrawal by pollinators. For Experiment 1b ('grown indoors, summer 2015'), 100 plants were placed in 0.5 L pots. We originally expected a difference in sugar concentration between plants grown outdoors and indoors, since a pilot experiment revealed that the nectar volume was dramatically different between these groups, with more nectar in the flowers of plants grown outdoors. For Experiment 2 ('grown indoors, fall 2016'), 400 plants were placed in 1.1 L pots, and for Experiment 3 ('grown indoors, spring 2016'), 200 plants were placed in 0.5 L pots. Experiments 1b, 2 and 3 used indoor-grown plants only, as outdoor plants flower only in the summer. For all indoor experiments, the plants were grown in a controlled growth room, at 27–28 degrees centigrade, with 16 h of artificial daylight, about 1 month prior to the beginning of the experiment. Altogether, more than 650 flowers from these 900 plants were used in the nectar experiments, and another *c*. 200 flowers in the laser experiments (taken from the plants of Experiments 2 and 3). In each experiment, only plants of the same age, season and pot size were tested. See Table S1 for summary of the experiments.

Statistical analysis

Experiment 1: We performed a two-way ANOVA on log (sugar concentration), including the treatment ('Silence', 'High', 'Low' or 'Bee') and group (1a, 'grown indoors' or 1b, 'grown outdoors') variables. The group variable was not found to have a significant effect ($P = 0.793$). Therefore, data from both groups were combined and the sugar concentration and nectar volume between different treatments were compared. Shapiro–Wilks test concluded significant deviation from normality ($P < 0.05$) in some of the cases (nectar volume data), so Wilcoxon rank-sum was used for comparison. Within groups, the reported *P*-values were adjusted for multiple comparisons using the Holm–Bonferroni method.). Experiment 2: nectar traits (sugar concentration and nectar volume) under different treatments were compared using Wilcoxon rank-sum. To test the effect of hydration status (days since watering), number of flowers in group and time of day on our results, we used analysis of variance (ANOVA) model. We used log (sugar concentration) as the dependent variable, and hydration status (or number of flowers in group or time of day), treatment group, and their interaction as predictors. Post-hoc *P*-values were calculated using a Tukey HSD test. Constant variance assumption was corroborated using Levene's Test. All petal vibration levels were compared using paired Wilcoxon test (comparing vibration levels of the same flower under different treatments or petal removal). Pollinator temporal distribution in the field was compared using paired Wilcoxon test as well.

RESULTS

We found that *Oenothera drummondii* flowers produced nectar with significantly increased sugar concentration after exposure to the playback of the natural sound of bee wingbeats ('Bee' treatment) in comparison with flowers exposed to either high frequency sounds ('High') or no sound at all ('silence', Wilcoxon $P < 0.01$ for both comparisons, Fig. 1a and b). The same result was obtained for artificial sounds with bee-like frequencies (the 'Low' treatments, Fig. 1b middle and right). The average sugar concentration was increased by a factor of 1.2 in flowers exposed to pollinator-like frequencies ('Bee' and 'Low' sound signals), in comparison with flowers exposed to 'Silence' or 'High', while no difference was observed between flowers exposed to 'High' frequencies and flowers exposed to the 'Silence' treatment. No difference in sugar concentration was observed between experimental groups before the treatment, and the volume of the nectar produced by the flowers did not change significantly in the 'Bee' and 'Low' treatments (Fig. S4), showing that the increase in sugar concentration in these groups could not be attributed to a decrease in water volume. Analysing the data using Student's *t*-test of log-transformed data resulted in similar significant results ($P < 0.001$ for each of the comparisons between treatment ('Low' and 'Bee') and control ('High' and 'Silence').

To determine whether the pollinator sounds result in physical vibrations of the flower, we used laser vibrometry (see Methods). *Oenothera drummondii* flowers vibrated mechanically in response to the airborne sounds of a bee or a moth recording (Fig. 2a, and Fig. S6 for moth sound spectra), oscillating in velocities that have already been shown to elicit a defence response in a plant that was mechanically moved in such velocities (Appel & Cocroft 2014). The flowers also vibrated in response to the hovering of a live bee similar to their vibration in response to the bee's playback (Fig. S7). The amplitude of the mechanical vibrations (which reached 0.1 mm) depended on the presence of intact petals, and significantly decreased upon removal of petals (Fig. 2b, $P < 0.0005$, see Fig. S5 for details), suggesting that the petals either directly receive, or serve to enhance the received signal.

To test the frequency specificity of both the physical vibration and the nectar response, we performed another indoors experiment (Experiment 2, in the fall) in which we repeated the use of the previous sound stimuli (Low and High) and introduced another 'Intermediate' sound signal with a peak frequency of 35 kHz (240 new flowers were used in this experiment, in the fall, see Table S1). The flowers showed some frequency specificity, both functionally and mechanically: they vibrated significantly (paired Wilcoxon $P < 0.0001$, $n = 21$) in response to sound signals of the 'Low' signal, 1 kHz, but not in response to the peak frequency of an 'Intermediate' signal, 35 kHz ($P > 0.9$, $n = 23$), or the 'High' signal, 160 kHz ($P > 0.9$, $n = 21$, see Fig. 2c and d black line). Similarly, the flowers increased sugar concentration in response to 'Low' sound signals significantly ($P < 0.002$, 2D red dotted line) in comparison to the 'Intermediate-' or 'High'-treated flowers. 'Low' sounds resulted in significantly higher sugar concentration than all other treatments (High, Intermediate, High in jar, Low in jar) also when accounting for hydration status, number of flowers in group, or the time of day ($P < 0.03$). We cannot report how the flower responds between 1 kHz and 35 kHz. Differences between the four other treatment groups were not significant. The ratios of post-treatment to

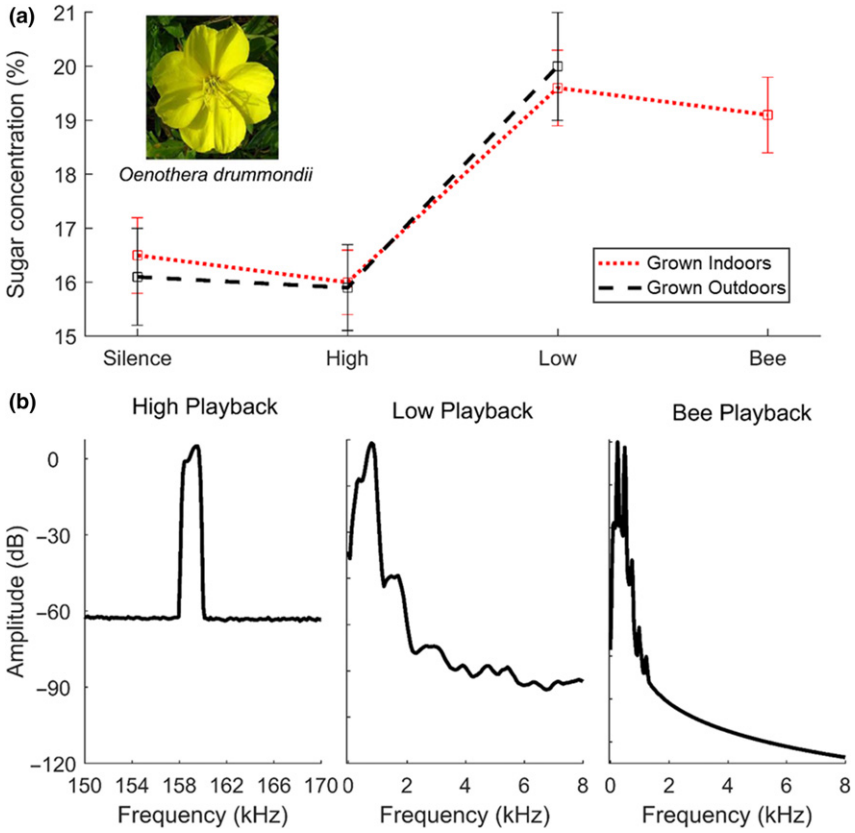

Figure 1 Flowers respond rapidly to pollinator sounds by producing sweeter nectar (a). Mean sugar concentration under the different treatments in plants grown outdoors (dashed black) and indoors (dotted red). Mean sugar concentration across both indoors and outdoors groups differed significantly ($P < 0.01$) between flowers exposed to frequencies below 1 kHz (sugar concentration 19.8% ± 0.6, $n = 72$ and 19.1% ± 0.7, $n = 42$ for 'Low' and 'Bee' after 3 min respectively), compared to flowers exposed to 'Silence' or 'High' frequency sound (16.3% ± 0.5, $n = 71$, and 16.0% ± 0.4, $n = 72$ respectively). Insert shows a flower of *Oenothera drummondii*. (b) Spectra (frequency content) of the playback signals used in the experiment. Both 'Bee' and 'Low' signals contain most energy below 1000 Hz, while the 'High' control peaked at *c*. 159 000 Hz.

pre-treatment concentration and vibration, per plant, revealed an identical pattern: the ratios were significantly higher ($P < 0.002$ for concentration ratio, see Fig. S8A, $P <$ e-07 for vibration ratio) in plants exposed to 'low' sounds in comparison with plants exposed to 'high' or 'intermediate' sounds (Table S2). The volume of the nectar produced by the flowers did not decrease in response to the 'Low' treatment (Fig. S8B), so the increase in sugar concentration in this group could not be attributed to a decrease in water volume. In another experiment (Experiment 3, $n = 112$ flowers, in spring) where only 'Low' and 'High' stimuli were tested, there was again significant increase in the sugar concentration in response to the 'Low' stimuli (see Table S3). The plants showed different flowering phenotype in different seasons probably reflecting the season experienced before entering the growth room: summer plants (Experiment 1) had larger flowers with higher sugar concentration before treatment in comparison with either fall plants (Experiment 2) or spring (see Table S4). Regardless, the major pattern – an increase in nectar sugar concentration in response to pollinator sound playbacks – was highly significant in all seasons (Fig. 2D, 1ATable S3).

To test one potential advantage of increasing reward within minutes after a pollinator's sound, we video-monitored the distribution of pollinators near *Oenothera drummondii* flowers in the field over two nights. We found that one pollinator flying in the vicinity of the plant – and producing sound in the process – is a strong indication that another or same individual may be in the plant vicinity within a few minutes. Specifically, a pollinator was > 9 times more common near the plant if a pollinator was near the plant in the preceding 6 min, than if no pollinator was around in the preceding 6 min (see Fig. S9 and Monitoring pollinator visitations methods). This activity pattern of the pollinators suggests that a response of the plant within minutes of the sound could more often be relevant to pollinators than a response not preceded by a sound. We further quantified the time pollinators tend to stay next to *Oenothera drummondii* flowers in the field (Methods). Two species of bees were observed around the flowers, and the observed time spent within a distance that would allow the bee sound to generate flower vibrations ('adjacent to the plant') were 27.8 ± 7.7 s for honey bees ($n = 44$), and 38.9 ± 11.8 sec for carpenter bees ($n = 23$), see Fig. S10. In reality, plants may of course be exposed to longer sound stimuli due to multiple bee pass one after the other. Notably, as our playback lasted 3 min and we had six plants at each session, each plant was exposed to 30 s of direct playback, on average.

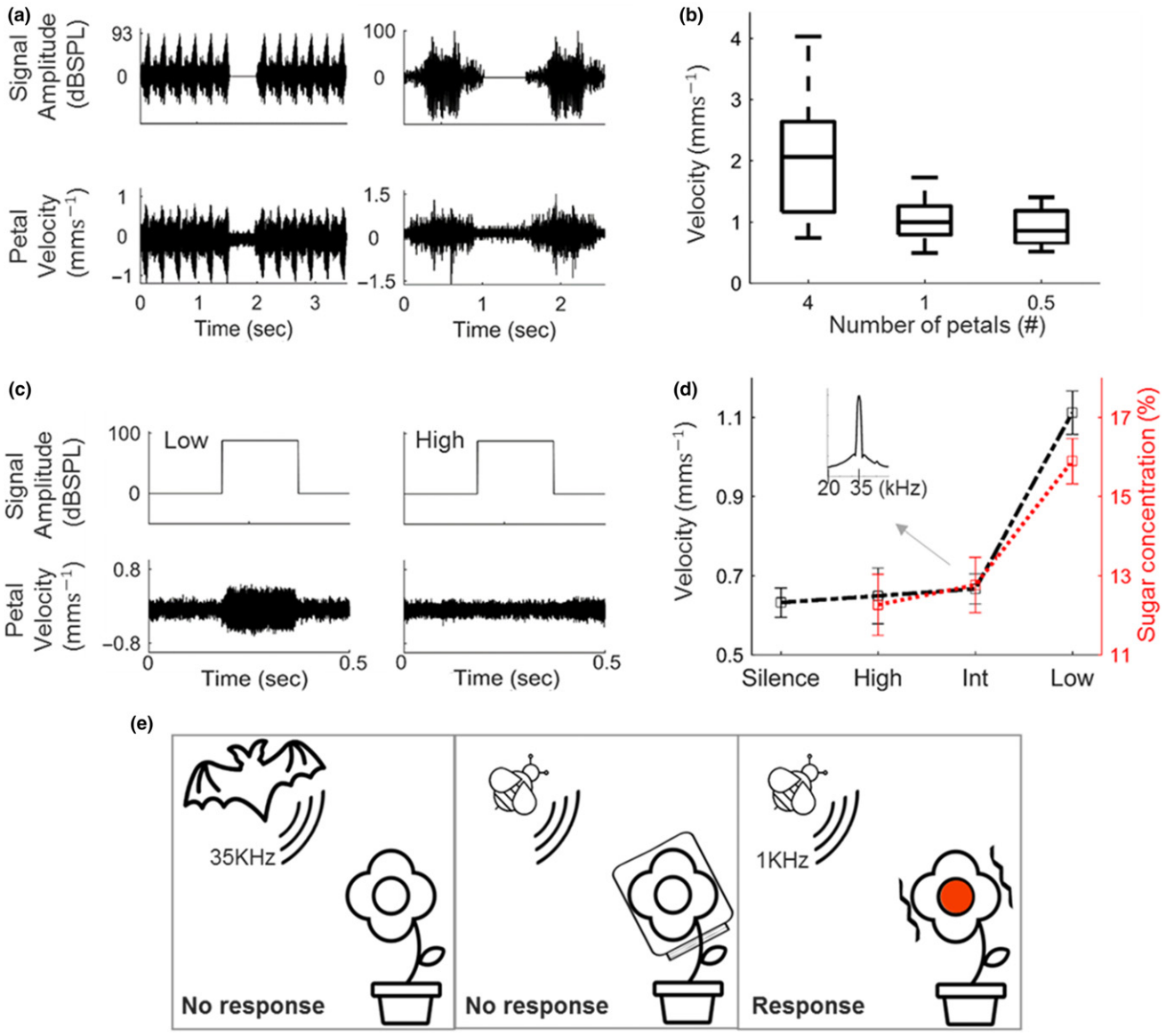

Figure 2 (a) Flowers vibrate mechanically in response to airborne sound of a pollinator. Top: Left – time signal of a honey bee sound signal (airborne signal recorded using a microphone). Right – time signal of a flying *Plodia interpunctella* male moth (the signal's spectrum peaks at *c*. 100 Hz, see Fig. S6). Bottom: Mechanical vibration recorded in an *Oenothera drummondii* flower in response to the playback of the bee (left) and moth (right) sound signals. (b) Vibration velocity in response to the bee signal depended on the presence of petals: a significantly stronger vibration was recorded when all four petals were intact in comparison to when flowers were trimmed and had only 1 or 0.5 petals (paired Wilcoxon, $P < 0.0005$ for the comparison between four and one petal and $P < 0.005$ for the comparison between 4 and 0.5 petals). (c) Flowers vibrated in response to playback of low frequencies around 1 kHz (left) while they did not vibrate above background noise to playbacks at higher frequencies of *c*. 35 kHz (right). Top: the time that the playback was 'on'. Bottom: Vibration time signals of the flowers. (d) Frequency specificity in both vibration and sugar concentration response. The flowers vibrated (dashed black) significantly more than background noise in response to sound signals in low frequencies around 1 kHz (paired Wilcoxon $P < 0.0001$, $n = 21$) but not in response to high frequencies around 160 kHz ($P > 0.6$, $n = 23$) or to intermediate frequencies around 35 kHz ($P > 0.9$, $n = 21$); The flowers also increased sugar concentration (dotted red line) in response to 'Low' signals significantly more than in response to the 'Intermediate' signal presented in the inset ($P < 0.002$), or to the 'High' signal serving as control ($P < 0.0001$). (Sugar concentration 15.9% ± 0.57, $n = 81$, 12.8% ± 0.7, $n = 49$, and 12.3% ± 0.77, $n = 51$, for Low, High and Intermediate respectively). Inset shows the spectrum of the 'Intermediate' playback signal used in the nectar experiment. (e) Summary of experimental results. Flowers vibrate in response to airborne sound at pollinator's frequency range, and increase nectar sugar concentration (right panel). Glass covered flowers do not respond (middle), suggesting that the flower serves as the plant's 'ear'. The flowers response is frequency specific, and they do not vibrate or respond to frequencies around 35 kHz (left).

Finally, to validate the importance of the flower itself as an organ responsible for reception of pollinator sounds, we ran another experiment. When the flowers (but not the stem or leaves) were covered with glass jars that blocked sound (see Fig. S2), then the 'Low' playback had no effect on the sugar concentration: For flowers enclosed in jars, there was no significant difference between exposure to 'Low' treatment and exposure to 'High' ($P > 0.64$, for $n = 58$ and 59 flowers respectively), and none of these groups differed significantly from the no jar 'High' treatment, that served as a control

($P > 0.49$, $n = 49$ flowers, see Table S2). Mean nectar volume did not differ significantly between any of the groups (Table S2). These results suggest that flowers are important for hearing pollinators, but we cannot exclude the possibility that other parts of the plant may also respond to pollinator sounds, resulting in nectar response later than 3 min, or that other parts of the plant may serve as sensory organs for sounds at other frequencies.

DISCUSSION

We found that plants respond rapidly to specific airborne sound frequencies (Figs 1, 2d) in a way that could potentially increase their chances of pollination, and that flowers can serve as sound sensing organs (Fig. 2). Consistent results were obtained in four independent experiments (Table S1) with over 650 flowers in total. The flowers responded similar to bee wingbeat sounds and to artificial sound waves that were similar in their frequency spectrum but differed greatly in their temporal pattern, suggesting that the frequency of the sound is sufficient to elicit a response. The flowers responded rapidly, within 3 min. The concentration of sugar in the nectar produced following the exposure to sound increased by a factor of 1.2 on average.

Bees have been shown to be capable of perceiving differences in sugar concentration, as small as 1-3% (Afik *et al.* 2006; Whitney *et al.* 2008). Thus, even if the new sugar-rich nectar is diluted by lower concentration nectar already present in the flower, the bees would be able to detect the difference in many cases.

Increased sugar concentration can enhance the learning process of the pollinators, and facilitate the pollinator constancy – the tendency to visit flowers from the same species (Cnaani *et al.* 2006) – thus increasing the effectiveness of pollination. Enhanced reward can also increase visit duration, further enhancing pollination efficiency (Manetas & Petropoulou 2000; Brandenburg *et al.* 2012). This is not without caveats: too high sugar concentration could result in too viscous nectar for some pollinators, but the values measured here are below the optimum for both bees and moths (Josens & Farina 2001; Krenn 2010; Kim *et al.* 2011), suggesting that the pollinators can benefit from the increased concentration. It may also result in a higher number of flowers visited per plant, possibly leading to geitonogamous selfing (Klinkhamer & de Jong 1993; Hodges 1995; Dafni *et al.* 2005). Yet, if only part of the flowers in the plant carry enhanced rewards – for example due to depletion – then the response could result in increased variation in nectar standing crop within the plant, encouraging the pollinators to move to the next plant and facilitating outcrossing (Ott *et al.* 1985; Biernaskie & Cartar 2004; Pyke 2016).

A response within 3 min is advantageous when pollinators move between nearby flowers, or when the presence of one pollinator is a good predictor of other nearby pollinators, such as in bees (Goulson 1999; Slaa *et al.* 2003) and in moths according to our field observations (Fig. S9). Such a response would allow the plant to identify the beginning and intensity of pollinator activity which can differ from day-to-day due to various factors such as weather conditions (Corbet *et al.* 1993). The plant could then switch to an increased sugar production mode, in order to reward the first actual visitors. Rapidly increasing nectar sugar concentration would be advantageous also in the case of a sporadic pollinator remaining in the area of the plant for a long time. Note that in a plant like the evening primrose, characterised by multiple flowers (dozens of flowers in a mature bush), the response to the sound of a nearby pollinator could be beneficial even if the pollinator avoids visiting the specific flowers that had recently been visited (Giurfa & Núñez 1992; Goulson *et al.* 1998), since it can still visit other flowers of the same plant. Other pollinators actually prefer occupied or recently occupied food sources (Schmidt *et al.* 2003; Kawaguchi *et al.* 2006; Lihoreau *et al.* 2016), and might especially benefit from enhanced refilling.

The plants responded to sound frequencies characteristic of pollinators' wingbeat (Figs 1, 2). How could frequency specificity be attained? We estimated the resonance frequency of the evening primrose petal to be a few hundred Hz based on vibration models developed for objects with similar shapes (Blevins & Plunkett 1980). This is close to the sound frequencies typically generated by bee and moth wingbeat. Furthermore, the flower should vibrate mostly around the resonance frequency, and vibrate less in response to higher or lower frequencies. Indeed, we observed that the flower-filtered frequencies above 350 Hz produced by the hovering bee, responding less to these frequencies (Figure S7). This could explain how the flower increased sugar concentration in its nectar only in response to low frequencies. Moreover, this frequency specificity might also explain, in theory, how the flower filters wind-induced vibrations, which are typically at lower frequencies (Appel & Cocroft 2014).

The current work is the first step in a new field, and can be extended in several ways. First, the response to sound can be further studied in the wild, on the background of other natural sounds. Second, all our nectar measurements were performed by first emptying the flower and then measuring refilled nectar. Testing the response to sound without prior manipulation will be more realistic (Corbet 2003), but would require large sample sizes due to the high variation in the nectar standing crop present in the model species. Third, the actual functionality of the response has yet to be tested – that is, do pollinators indeed prefer plants exposed to sound, and to what extent? Fourth, we tested the response to sound in a single plant species. Additional species might reveal different responses according to their specific ecologies (e.g. bat pollinated plants may respond to different frequencies).

The petal vibrations that we measure could be picked up by mechanoreceptors, which are common in plants (Monshausen & Gilroy 2009), and have been shown to respond to vibrations with similar velocities (Appel & Cocroft 2014). We hypothesise that the flower serves as an external 'ear' in terms of receiving pollinator airborne sounds by the plant. We posit that the petals of other flowering species could have evolved to detect sound, similar to our findings in *Oenothera drummondii*. The resonance frequency of a flower will be dictated by its mechanical parameters: size, shape and density, which could be under natural selection. If plant responses to airborne acoustic signals are indeed adaptive in the context of

pollination, we expect plants with 'noisy' pollinators – such as bees, moths and birds – to have evolved large ear-like flowers with proper mechanical parameters making them sensitive to the sounds of their pollinators.

Much is known about the response of pollinators to plant signalling from a distance (Patiny 2011; Schaefer & Ruxton 2011). In contrast, the response of plants to pollinators from a distance has never been demonstrated. The implications of such a response to the ecological system might be far reaching, since pollination is critical to the survival of many plant species, including many agriculturally important crops (Kremen *et al.* 2002; Fægri & Van der Pijl 2013). Plant response to sound could allow bidirectional feedback between pollinators and plants, which can improve the synchronisation between them, lowering nectar waste and potentially improving the efficiency of pollination in changing environments. These advantages can be diminished in very noisy environments, suggesting possible sensitivity of pollination to external noises, including antropogenic ones. Finally, plants' ability to sense airborne sounds has implications way beyond pollination: plants could potentially sense and respond to herbivores' airborne sounds, other animals, and possibly other plants (Khait *et al.,* 2018).

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AUTHOR CONTRIBUTIONS

LH conceived the idea. LH, YY, YS and DAC designed the research. MV, IK, UBD, PE, AB, AK, DP, IR, AG, KS, RS, and EZ performed the experiments. IK, UO, MV, YY and LH analysed the data. YY LH and SK supervised the acoustic experiments. YS and LH supervised the nectar experiments. LH, YY and YS contributed equally to the study. All the authors discussed the results and took part in writing the manuscript.

DATA ACCESSABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.6n5h0pb.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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