



Research

Cite this article: Cvikel N, Levin E, Hurme E, Borissov I, Boonman A, Amichai E, Yovel Y.

2015 On-board recordings reveal no jamming avoidance in wild bats. *Proc. R. Soc. B* **282**: 20142274.

<http://dx.doi.org/10.1098/rspb.2014.2274>

Received: 15 September 2014

Accepted: 23 October 2014

Subject Areas:

behaviour, neuroscience

Keywords:

echolocation, jamming, on-board recordings, sensory segregation, cocktail party, bats

Author for correspondence:

Yossi Yovel

e-mail: yossiyovel@hotmail.com

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2014.2274> or via <http://rspb.royalsocietypublishing.org>.

On-board recordings reveal no jamming avoidance in wild bats

Noam Cvikel¹, Eran Levin³, Edward Hurme⁴, Ivailo Borissov¹, Arjan Boonman¹, Eran Amichai¹ and Yossi Yovel^{1,2}

¹Department of Zoology, Faculty of Life Sciences, and ²Sagol School of Neuroscience, Tel Aviv University, Tel Aviv 6997801, Israel

³Department of Entomology, University of Arizona, Tuscon, AZ 85721, USA

⁴Department of Biology, University of Maryland, College Park, MD 20742, USA

Animals often deal with situations in which vast sensory input is received simultaneously. They therefore must possess sophisticated mechanisms to select important input and ignore the rest. In bat echolocation, this problem is at its extreme. Echolocating bats emit sound signals and analyse the returning echoes to sense their environment. Bats from the same species use signals with similar frequencies. Nearby bats therefore face the difficulty of distinguishing their own echoes from the signals of other bats, a problem often referred to as jamming. Because bats commonly fly in large groups, jamming might simultaneously occur from numerous directions and at many frequencies. Jamming is a special case of the general phenomenon of sensory segregation. Another well-known example is the human problem of following conversation within a crowd. In both situations, a flood of auditory incoming signals must be parsed into important versus irrelevant information. Here, we present a novel method, fitting wild bats with a miniature microphone, which allows studying jamming from the bat's 'point of view'. Previous studies suggested that bats deal with jamming by shifting their echolocation frequency. On-board recordings suggest otherwise. Bats shifted their frequencies, but they did so because they were responding to the conspecifics as though they were nearby objects rather than avoiding being jammed by them. We show how bats could use alternative measures to deal with jamming instead of shifting their frequency. Despite its intuitive appeal, a spectral jamming avoidance response might not be the prime mechanism to avoid sensory interference from conspecifics.

1. Introduction

Revealing how animals segregate important inputs in a flood of incoming sensory information is a fundamental step for understanding the principles of sensory processing. For instance, how do humans keep track of a single conversation within a cocktail party when multiple auditory inputs with similar frequencies arrive simultaneously [1,2]? When flying in the dark, echolocating bats perceive their environment acoustically by emitting ultrasonic signals and analysing the returning echoes [3]. Because bats from the same species (conspecifics) use echolocation signals with overlapping frequencies, it has always been a mystery how bats flying near each other do not interfere with each other's sonar [4–7]. Because bats often fly in groups (which are sometimes composed of dozens to thousands of individuals), this question is even more difficult to answer. Nearby bats should suffer from two types of sensory interference that are often termed jamming. (i) The loud signals emitted by a nearby conspecific might *mask* the faint echoes returning from a small insect, thus impairing the bat's detection abilities. (ii) An echolocating bat might experience difficulties in telling apart its own echoes from the signals of a conspecific. Previous studies suggested that bats deal with jamming by shifting their echolocation frequency (i.e. jamming avoidance [8–14]). This strategy has been shown in electric

fish [15] and should reduce masking by partitioning the frequency range between the individuals.

In this study, we present a novel method to examine how wild bats respond to jamming when flying in the field, over dozens of kilometres, while encountering numerous conspecifics. We used miniature on-board microphones, which also include Global Positioning System (GPS), which were fitted on naturally foraging bats. We chose to study *Rhinopoma microphyllum* bats as these bats are known to be social [16,17], and because they focus their sound energy in a narrow frequency band [18] making them highly prone to be jammed.

All previous field studies on jamming avoidance recorded bats with a single stationary microphone positioned on the ground [10,11,19]. Such recordings do not allow estimation the real frequency that is emitted by the bat, nor the frequency of the conspecific that is received by the bat. This is due to three main reasons. (i) Doppler shifts resulting from the relative motion between the bat and the microphone (as well as the two bats). Doppler shifts might result in a significant recording error of up to 1–2 kHz [12]. (ii) Sound attenuation in the atmosphere is frequency dependent (higher frequencies attenuate more). Unless the exact distance between the bat and the microphone is known, this effect is hard to compensate for and might influence the estimated peak frequency. (iii) The bat's beam is directional and thus the angle between the bat's emission and the microphone will strongly influence the recorded spectrum. It is therefore impossible to use a single stationary microphone to estimate a moving bat's frequency, and more importantly, the frequency of a conspecific as it is received by the bat. On-board recordings, as reported here for the first time in the wild, provide an unbiased measurement of both of these parameters, and thus allow testing of the jamming hypothesis. A microphone mounted on the bat will not suffer from either Doppler shifts or attenuation and directionality effects when recording the emissions of the tagged bat (see §2). It will suffer from Doppler shifts (and the other effects) when recording a conspecific, but importantly, the recorded Doppler-shifted attenuated signal is identical to the signal received by our bat. We thus study the interaction with the conspecific from the bat's 'point of view'.

On-board recordings offer several additional advantages. (i) Some previous studies used playbacks from stationary speakers to jam passing bats [11]. Owing to the same two problems described above, it is impossible to estimate exactly which frequency the passing bat is receiving. Moreover, a bat signal emitted from the ground is probably a highly unnatural situation for a passing bat. Here, we studied bats under completely natural jamming situations. (ii) Previous field studies could not assess the position of the bat in space. It is well known that a bat's distance from background objects will have a dramatic influence on its echolocation signal, including its frequencies. Our on-board GPS allowed us to determine whether our bats were flying in open space far from any object and were thus responding to other bats only. (iii) Stationary recordings of randomly passing bats only provide a snap-shot of their behaviour. For instance, when two bats are detected, there is no way to know when they encountered each other. On-board recordings allow us to study the full dynamics of the behaviour from the beginning of the encounter until its end. (iv) Unlike stationary recordings, which greatly vary in their quality depending on the bat's distance from the microphone, the on-board

microphone was always 2 cm from the bat's mouth thus resulting in a consistently high signal-to-noise ratio, without missing a single signal.

In contrast to all previous studies, we found that bats do not show a classical jamming avoidance response when encountering a conspecific at close range. Bats did alter their echolocation signals in response to conspecifics; however, they did so as if they were responding to a nearby (silent) object and not to a masking sound source. These observed shifts might have been interpreted in previous studies as a jamming avoidance response. Finally, we show that even in a sonar cocktail party, previously referred to as the cocktail nightmare in bats [20], individuals exhibit sufficient frequency spread to allow individual recognition without any jamming avoidance response.

2. Material and methods

(a) Animals and research site

Data collection was performed during the summers of 2012 and 2013 in northern Israel, where several male and several female colonies of the species are known [16]. The exact time periods were: 12 July 2012 to 11 August 2012 for the males (which were only studied in 2012) and 19 August 2012 to 15 September 2012, 18 August 2013 to 15 September 2013 for the females, which assured us that the females were postlactation. All bats were captured in their roost early in the morning (around 07.00) using a butterfly net. Bats were treated (see below) within an hour from capture and released in the roost where they were caught. This procedure aimed to allow bats to get used to the extra load for ca 12 h before foraging.

The microphone and tracking device ($30 \times 20 \times 4$ mm) consisted of a GPS data-logger (Lucid Ltd., Israel) and a synchronized ultrasonic microphone (FG-23329, Knowles). The device's total weight (including battery, coating and a telemetry unit—LB-2X 0.3 g, Holohil Systems Ltd.) was on average 3.8 g. We address the effect of this extra loading on the bats below. The telemetry unit was attached to the device to help the experimenters to locate it. The devices were wrapped in coloured balloons for isolation and identification purposes and fitted to the bats using medical cement glue (Perma-Type Surgical Cement, AC103000). Fur was removed by applying hair removal cream for a few seconds (Veet, Reckitt Benckiser). After gluing, bats were held for about 5 min to allow the glue to dry, and then placed in a cloth bag for another 15 min before being returned to the roost.

We retrieved devices from eight bats. Retrieval was achieved either by collecting the device from the roost's floor after it fell off the bat (on average one week after its attachment) or by recapturing the bat in the colony (using a butterfly net). The device was gently removed from the recaptured bats using an adhesive remover (UNI-SOLVE, Smith & Nephew Corp; or Niltac, Triohealthcare Ltd.).

(b) Audio recordings

The microphone was positioned on the bat's back in between the shoulders, ca 2 cm behind the bat's mouth (electronic supplementary material, figure S1), thus ensuring very high signal-to-noise ratio without missing a single bat signal (electronic supplementary material, figure S2). Audio was sampled at 94 kHz in order to allow higher than Nyquist sampling of the bat's second harmonic at ca 26 kHz, where almost all energy is concentrated in search signals. Due to the high power requirement to operate the microphone and the large amounts of data it recorded, we had to use a limited recording duty cycle of 10–20%. We used two main schedules (see the electronic supplementary material, table S1): recording

0.5 s every 5 s—allowing a finer resolution analysis of the bats' behaviour—or recording 5 s every 30 s, aiming to examine longer echolocation sequences.

(c) Sound analysis

Recordings were analysed using a histogram-based threshold detection algorithm for automatic segmentation of signals, which was written for this project (Matlab, MathWorks Inc.). Overall, more than 43 000 audio files including *ca* 80 000 echolocation signals were processed. In brief, the detection algorithm averaged the power (in decibels) along the time axis of the spectrogram (calculated with a window of 256 samples and an overlap of 250) and automatically detected a threshold that segmented echolocation signals from noise. Specifically, recordings were first filtered with a band pass filter around their second harmonic (between 24 and 31 kHz; electronic supplementary material, figure S2*a–b*). Next, the spectrogram was split into shorter windows, and a threshold was detected for each one according to the histogram of the power (red dashed line in the electronic supplementary material, figure S2*c*). Next, each single echolocation signal that crossed the threshold was segmented and the following parameters were estimated (electronic supplementary material, figure S2*d*): signal duration (*sd*)—defined as the part of the signal that was 12 dB below the peak on both sides; signal intensity—defined as the maximum voltage (peak to peak), after removing the baseline direct current; frequency (*f*)—defined as the frequency with maximum intensity in the second harmonic—was estimated using the instantaneous frequency algorithm to improve estimation accuracy; inter-signal interval (*isi*)—defined as the time lag between two consecutive signals, and signal bandwidth (*bw*)—defined as the frequency range of the second harmonic (12 dB drop from both sides of the peak). The algorithm successfully detected a large majority of the echolocation signals; however, it had difficulties in detecting conspecific signals owing to their lower intensity (electronic supplementary material, figure S2). In all analyses, we only used echolocation signals longer than 9 ms. These long signals are classified as search signals that are emitted by the bats in search of prey. We did not include shorter signals, which are commonly emitted by bats that are attacking prey.

Hence, all sound files that were automatically segmented were also manually scrutinized by us, using a quality assurance script that was written for this purpose (Matlab). This allowed us to segment conspecific signals, to detect missed signals (false negatives) and to remove false positives. It was easy to visually determine whether a signal was emitted by a conspecific owing to its dramatically lower intensity (electronic supplementary material, figure S2). Any audio file in which a conspecific signal was present was considered as an encounter with a conspecific.

(d) Estimating the acoustic detection range of the microphone

We used sound physics to estimate the detection range of a conspecific by the microphone. Equation (2.1) describes the sound intensity received by a bat (P_r) at a distance (R) from the emitter (a conspecific) as a function of the intensity of the emitted source (P_t), the atmospheric attenuation coefficient ($\alpha = 0.12$), which depends on signal frequency, temperature, humidity and atmospheric pressure here set to be 26 kHz, 30°C, 60% and 1 atm, respectively.

$$P_r = \frac{P_t * e^{-\alpha R}}{R^2}. \quad (2.1)$$

By plugging in the estimated emission intensity for this species ($P_t = 135$ dB SPL [18]) and the estimated minimum intensity detectable by our microphone, a detection range of *ca* 20 m is

reached (when solving the equation numerically with Matlab). The microphone's P_r —the minimal detectable intensity (or the internal noise floor) of our microphone—was estimated by analysing the internal noise of the microphone by comparison with a calibrated microphone (40DP, GRAS). This procedure yielded a P_r estimation of 85 dB SPL. The procedure was repeated for two different microphones and the differences between them were found to be negligible. We validated this estimation by playing back a *R. microphyllum* signal (Player 116 D/A converter, Scanspeak speaker, Avisoft) at the maximum intensity allowed by the speaker (120 dB) and measuring the detection range, i.e. the maximal range from which conspecific signals were still visible to us (in the on-board recordings device). We found this range to be *ca* 13 m, corroborating the estimated range for a 120 dB signal (the 20 m range was estimated for a 135 dB conspecific signal).

However, when estimating the distances of the conspecifics that were recorded (see below), we found that the farthest detected conspecific was at 12 m. We believe that the discrepancy between these two values (12 versus 20 m) resulted from the fact that the real recordings contained noise (mainly wind noise) that did not exist in the laboratory recording (nor in the theoretical estimation). Moreover, the theoretical estimation was performed assuming that the conspecific is flying on axis towards the bat, which was probably not the case in reality. This means that conspecifics were probably even closer than our estimates.

(e) Estimating conspecific distance

We used equation (2.1) to estimate the distance of a detected conspecific, except that now, P_r (the call intensity of the conspecific) was estimated from the recording, while R (the distance of the conspecific) was the unknown variable. Conspecifics were assumed to call at 135 dB SPL and to be on-axis relative to our bat so that the estimated distance was actually an over-estimation.

(f) Microphone directionality

The microphone was positioned at the centre of the back-lobe of the bat's beam. Bats probably do not move their head much during searching, which is the part of the behaviour that we analysed. But even if they did move their head, the microphone would remain at the centre of the back-lobe, except that its membrane would now be facing this centre at an angle. However, because we used omni-directional microphones, this would almost not affect the signal's intensity or its spectrum, as we confirmed experimentally (electronic supplementary material, figure S3).

(g) Statistics

Unless stated otherwise, all statistical analysis was conducted on the individual bat level to show that all bats responded in the same way. To deal with the problem of pseudo-replicates, in addition to running a *t*-test, we also use the one-sample Kolmogorov–Smirnov test to compare the distributions of specific characters (e.g. frequency and bandwidth) for individual bats when flying with or without conspecifics. In addition, we ran the non-parametric Wilcoxon signed-rank test to compare the bat group under the two conditions (with versus without conspecifics).

(h) Estimating bats' altitude with Global Positioning System

Bats altitude (above ground) was used to validate that they were far from any object (see §3). The altitude accuracy of the GPS measurements was tested by driving on a known road (i.e.

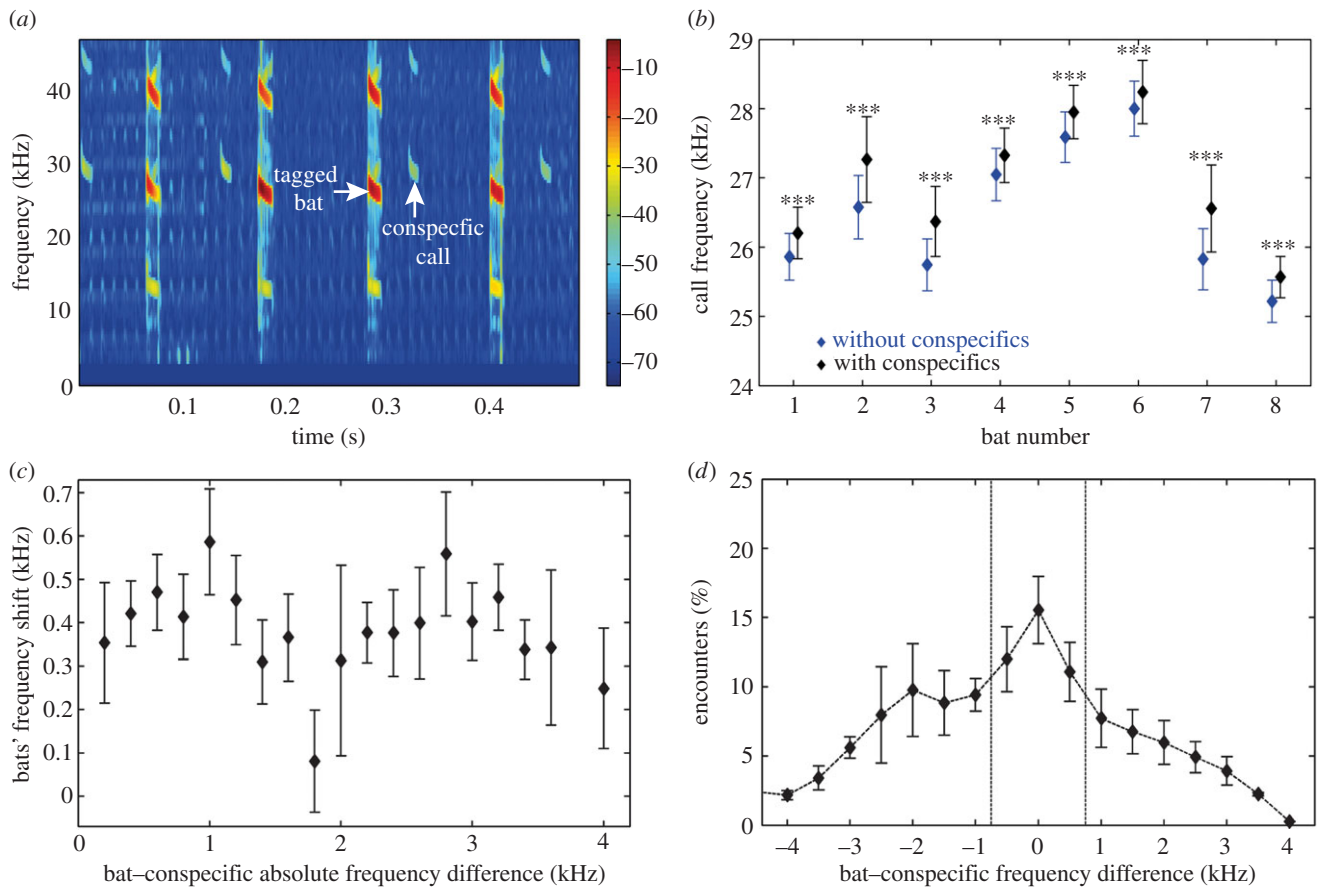


Figure 1. Changes in bats' signals in response to conspecifics negate a jamming avoidance response. (a) A spectrogram showing an on-board recording with signals of both the tagged bat and a conspecific (both depicted by arrows). The signal-to-noise ratio of both bats is high, but it is easy to discriminate the two according to the difference in their intensity. The conspecific's call intensity is around 110 dB SPL, thus louder than any possible prey echo. (b) Bats' signal frequency with (black) and without (blue) conspecifics (mean \pm s.d.). All bats significantly increased signal frequency in the presence of conspecifics. *** $p < 0.001$. (c) Bats' shift in frequency as a function of the absolute difference between the frequencies of the tagged bat and the frequency of the conspecific (mean \pm s.e., zero difference means maximum masking). The graph shows no correlation between the two—bats always shifted their frequency upwards by the same amount—suggesting that jamming avoidance is not the cause for the bats' response (Pearson correlation, $R = -0.08$, $p = 0.77$). (d) The distribution of the difference in frequency between the tagged bat and the conspecifics (average and s.e. for all bats). If the bats were trying to avoid jamming (i.e. trying to avoid a difference of zero), there should have been a minimum at zero. The distribution, however, peaks at zero, as would be expected if bats always increased their frequency independently of the frequency of the conspecific.

where the altitude above ground is 0 m) and estimating the error of the GPS measurement (after using the 'LOESS' local regression smoothing filter [21]). We found that the altitude error was -5 ± 11 m (mean \pm s.d.), proving that errors were small enough to allow our analysis of only high conspecific interactions.

(i) The effect of the extra loading on the bats

Rhinopoma microphyllum is a medium sized insectivorous bat whose mass dramatically changes (by up to 100%) throughout the year. At the end of the summer (before migration), large males can reach 45 g, while large females reach as much as 35 g (E. Levin 2003–2010, unpublished data collected from over 1000 bats of this species). Because much of the weight increase during summer in this species results from accumulating fat in the tail membrane [17,22] and not from building muscles, higher weights do not necessarily correspond to better carrying capacity. We therefore did not choose bats with the highest mass, but bats with high mass that suggests good physical shape and long forearms, suggesting high loading potential. As the study was performed during the end of the season, when bats are most fit, we assumed that these criteria were adequate to select bats that could best handle such weights. All females that were tagged weighed at least 27 g and had a forearm of at least 68 mm, corresponding to a potential body mass of up to 34 g at

the end of the season. All males weighed at least 30 g and had forearms of at least 71 mm, corresponding to a potential weight of up to 45 g. The actual weight loading reached 11–14% (12% on average) of body mass. All eight bats flew long distances (50 km on average) and performed foraging during their tracking, showing 'normal' behaviour comparable to that previously described [16]. Importantly, this paper concentrates on bats' echolocation behaviour in response to the presence of a conspecific. It is highly unlikely that such a sensory response would change due to the extra loading carried by the bats, especially not during their first night of carrying it.

3. Results

As expected from a social forager, the eight *R. microphyllum* bats we monitored frequently encountered conspecifics. We analysed a total of 853 events in which our bats encountered conspecifics at distances of 12 m or less (6 ± 2 m on average; figure 1a and see §2d,e). At such proximity, the physics of sound determine that the signals of the conspecific are far louder than the loudest echo an insect can produce (a conspecific at 12 m can be as loud as 110 dB SPL, while a large ant echo from 3 m will only reach *ca* 60 dB SPL [23]). This means that a

conspecific call would impose a real danger of jamming the faint echo returning from an insect. The fact that we recorded many conspecifics, but never recorded an echo of a prey—even in 85 events during which our bats were attacking prey—confirmed this theoretical assumption (electronic supplementary material, figure S4).

All bats significantly changed their signal's frequency in the presence of conspecifics, seemingly suggesting a jamming avoidance response (figure 1*b*; electronic supplementary material, figure S5; $p < 0.001$ for all individual bats and $p < 0.01$ for the group, t -test, Kolmogorov–Smirnov and the Wilcoxon signed tests; see §2*g*). However, all bats shifted their frequency upwards (figure 1*b*; electronic supplementary material, figure S5). Such a response cannot solve the jamming problem because jamming would reoccur at higher frequencies. A classical jamming avoidance response in the frequency domain [15] should result in an increase in the difference between the frequency of the reacting bat and the conspecific. Therefore, if bats tried to reduce masking, we would expect them to shift their frequency more when the overlap with a conspecific's frequency happened to be higher. Results did not support this expectation. All bats always *increased* their frequency (by the same amount on average), irrespective of the frequency of the conspecific (figure 1*c*; the slope of the regression line was not significantly different from 0, $p > 0.6$). Moreover, the distribution of the frequency difference between the two nearby bats shows that bats did not attempt to minimize the frequency overlap. On the contrary, the distribution peaked at zero, as expected if bats were responding independently of the conspecific's frequency (figure 1*d*). Importantly, as explained in §1, unlike stationary recordings, what we record is exactly what our bat hears, notwithstanding Doppler shifts and other acoustic errors.

One of the disadvantages of recordings with stationary microphones is that they only allow the recording of bats that are relatively close to the ground. In this situation, bats already change their frequency due to the background, which limits our ability to assess their response to jamming. Using the GPS data, we selected and analysed only the encounters in which the bats were at least 40 m above ground, thus ensuring that they were responding to conspecifics and not to some nearby background object or to the ground. The results remained exactly the same when analysing only this part of the data (electronic supplementary material, figure S6).

4. Discussion

Altogether, our results strongly imply that bats do not exhibit a spectral jamming avoidance response. Why then do bats shift their frequencies in the presence of conspecifics? An alternative explanation for this behaviour would be that a nearby conspecific is a moving object entering our bat's acoustic 'field of view', thus drawing the sensory attention of our bat. Echolocating bats constantly adjust their signals according to the presence of obstacles usually referred to as 'background' [24–26]. It is well established that when approaching an object, bats shorten their signals and increase their bandwidth, and this is accompanied by an increase in signal frequency [24,27]. Indeed, all of our bats exhibited a response that is typical for bats flying near background objects. They shortened their signals in the presence of conspecifics (figure 2*a*, $p < 0.001$ for all

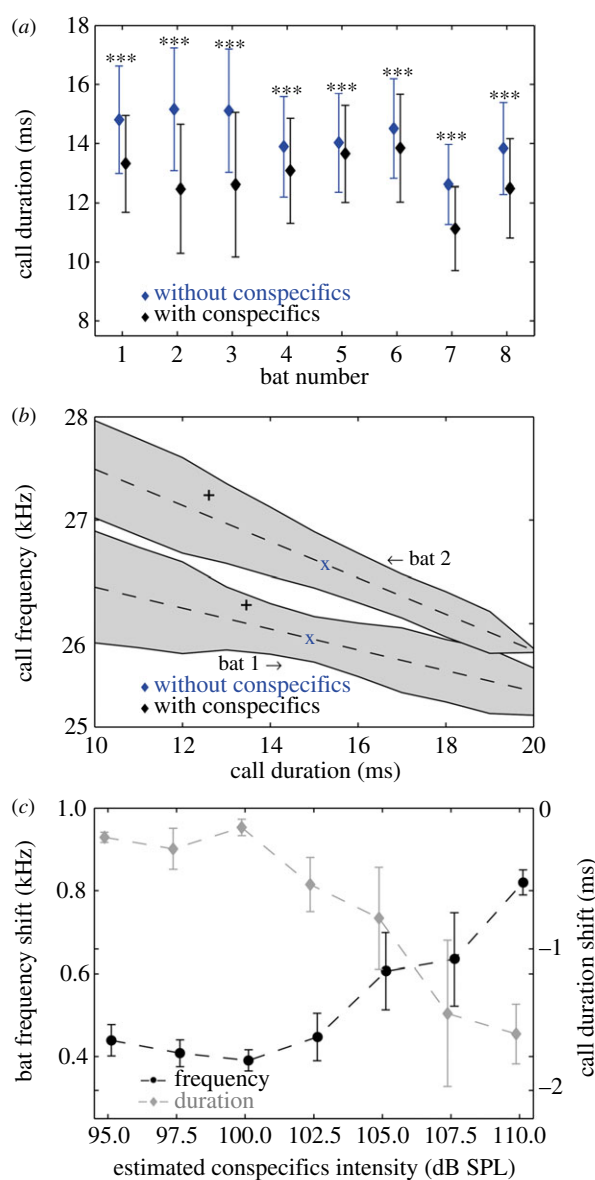


Figure 2. Changes in bats' signals in response to conspecifics imply that bats respond to a conspecific in the same way as to a close object. (*a*) Signal duration with (black) and without (blue) conspecifics shows that all bats significantly decreased signal duration in the presence of conspecifics (mean \pm s.d.). Note that signal duration changes due to foraging (even with no conspecifics) and thus the s.d. is high. (*b*) Signal frequency as a function of signal duration. All bats showed a significant negative linear relation between signal frequency and signal duration (correlation was significantly negative $p < 0.001$ for all bats; electronic supplementary material, table S2). The dashed lines show the linear regression fit for two bats, while the grey shaded areas represent the s.d. around the regression line. For each bat, the blue crosses depict the mean signal duration and the mean frequency for all instances of foraging without conspecifics and the black crosses depict the mean signal duration and the mean frequency for all instances of foraging with conspecifics. Note how signal duration shortens and signal frequency increases for all bats in the presence of conspecifics. (*c*) Bats increased their frequency (black circles) and decreased the signals' duration (grey diamonds) as a function of the conspecific's intensity, which is related to its distance (closer conspecifics are louder). This clear correlation shows that a closer conspecific increases the bat's response as expected if the bat is coming closer to an object but not if it was responding to jamming (correlation coefficients—frequency: $R = 0.88$, $p = 0.008$; duration: $R = -0.92$, $p = 0.003$).

bats and $p < 0.01$ for the group; see §2*g*) and their signal frequencies increased accordingly (figure 2*b*). When flying near conspecifics, all eight bats also significantly increased

their signal bandwidth, and six out of eight significantly decreased the interval between signals—exactly as bats who are approaching an object do (electronic supplementary material, figure S7, $p < 0.001$ for all bats and $p < 0.01$ for the group, see §2). Interestingly, the bandwidth is an acoustic parameter that allows disentangling of the two hypotheses (jamming versus background approach). It is assumed that jamming can be avoided by *reducing* the bandwidth, while approaching background requires *increasing* the bandwidth. We observed the latter response, supporting the background hypothesis. Finally, the bats' response to the conspecific was gradual and distance-dependent, i.e. when the conspecific was closer (or louder), the bat shortened its signals more and increased the frequency accordingly (figure 2c). Such a gradual (distance-dependent) response is known for bats approaching an object and makes perfect sense because the object is gradually becoming closer [27]. In the case of jamming, however, there is no reason to respond in a way that depends on the distance. As explained above, all of the conspecific signals we recorded were much louder than any potential prey echo and could therefore potentially jam our bats. If the bats were responding to jamming by shifting their frequencies, one would expect a full response (i.e. frequency shift) if the frequency of the conspecific was overlapping, or no response if there was no overlap, but there is not much sense in a gradual response in which the frequency shifts gradually when the conspecific comes closer. We conclude that the observed changes in echolocation resulted from attending a nearby moving object (the conspecific) and not from sensory jamming.

If not by shifting their signals' frequencies, how then did bats deal with potential jamming? Within the bat population, individual bats differ in their echolocation frequencies (figure 1b). In fact, we found that in 72% of the encounters, the difference between the frequencies of the two nearby bats happened to be more than 500 Hz (figure 1d, vertical dotted lines depict the ± 500 Hz lines and 72% of the interactions were above or below these lines). This is more than the minimal distinguishable frequency that has been found for bats using similar frequencies [28,29]. In these 72% of the encounters, bats could therefore distinguish their own signals from the signals of the conspecific based on the peak frequency only. Obviously, bats could also use other acoustic features such as signal duration, signal bandwidth and others to further improve signal recognition [30]. Although often encountering conspecific, these bats might not need to respond in order to avoid jamming at all (see below).

In conclusion, our main finding suggests that in most cases, bats do not need to use the classical jamming avoidance response even when encountering a nearby conspecific. This was the case despite the narrow frequency band of *R. microphyllum*, which makes this bat highly sensitive to jamming. Bats did alter their echolocation signals in the presence of conspecifics; however, their response could clearly be classified as a response to background and not to jamming. Our results did not change even when reanalysing only the 30% most intense conspecific calls emitted by extremely close conspecifics (less than *ca* 5 m; electronic supplementary material, figure S8a–b). Interestingly, the bats' response to conspecifics included an increase in frequency, which was also observed in some of the previous studies on jamming avoidance [10,11]. However, these studies did not control for signal duration and therefore might have interpreted this

increase as a jamming avoidance response. Naturally, we cannot preclude that other bat species do exhibit some sort of jamming avoidance in certain situations. A frequently suggested explanation, namely that bats increase their frequency to narrow their emitted beam and thus to avoid jamming, does not appear to be an adequate explanation because the beam is only expected to narrow by a negligible amount of less than 3° with such a frequency shift (of less than 1 kHz).

Rhinopoma microphyllum bats are known to emerge from their roosts in swarms of thousands of individuals. In such situations, bats might suffer from actual jamming; however, it makes little sense to deal with such a situation by shifting one's frequency, because all frequency bands will be in use. In such situations, *R. microphyllum* probably turn to use other sensory modalities, such as vision, as well as relying on spatial memory. Moreover, bats are often observed touching each other during the emergence.

We argue that bats do not need to shift their frequency owing to the wide variability in the populations' frequencies [31,32]. The frequencies of the bats we monitored spanned a range of *ca* 3 kHz (figure 1b). Each of these bats dynamically shifted its frequency according to the sensory task it was performing, but when doing so, the signal's duration changed accordingly (figure 2b). Therefore, even when two bats were operating at the same frequency, they could probably easily tell apart their signals according to their respective signal durations. Even in the case that two bats share the same peak frequency (for a given duration), bats could extract other acoustic cues that would allow self-recognition, such as the signal's spectral resonances [30] and the exact spectro-temporal modulation of the signal. There are more measures unrelated to the signal itself that allow the distinguishing of a bat's own echoes from the signals (or echoes) of another bat. First, the bat could direct its ears to narrow the received beam, thus reducing the sector from which it receives auditory input. Second, unless the echo and the conspecific signal return simultaneously, the bat could use spatial hearing to distinguish between the two [33]. Third, a bat that is already pursuing prey can extrapolate information from previous echoes to generate expectations regarding the delay, amplitude and direction of the next echo, which will assist in distinguishing it from other incoming signals. Finally, shifting one's frequency might be disadvantageous if the bat maintains a reference of its signal in the brain, which serves as a template that is matched to incoming signals [34]. These numerous sources of information provide sufficient measures to segregate the important signals from the irrelevant ones, making the cocktail nightmare a party after all.

Ethics statement. All experiments were performed with permission from the Israeli National Park Authority (permit numbers: 2011/38346 and 2012/38346) and the Tel-Aviv University IACUC (number: L-11-054).

Data accessibility. Data will be given upon request from the corresponding author.

Acknowledgements. We are also grateful to the Israel Nature and Parks Authority for allowing us to work in the field, and especially to Hanoach Tal, Aviram Shani and the team of Yehudia Reservoir; and to Eldad Eitan and the team of Gamla Reservoir, for helping us with fieldwork.

Funding statement. This work was supported by the Human Frontier Science Programme, grant no. RGP0040, and by the Israeli National Foundation, grant no. 559/13.

References

- Formisano E, De Martino F, Bonte M, Goebel R. 2008 'Who' is saying 'what'? Brain-based decoding of human voice and speech. *Science* **322**, 970–973. (doi:10.1126/science.1164318)
- Mesgarani N, Chang EF. 2012 Selective cortical representation of attended speaker in multi-talker speech perception. *Nature* **485**, 233–236. (doi:10.1038/nature11020)
- Griffin DR. 1958 *Listening in the dark*. New Haven, CT: Yale University Press.
- Griffin DR, McCue JGG, Grinnell AD. 1963 The resistance of bats to jamming. *J. Exp. Zool.* **152**, 229–250. (doi:10.1002/jez.1401520303)
- Chiu C, Xian W, Moss CF. 2008 Flying in silence?: echolocating bats cease vocalizing to avoid sonar jamming. *Proc. Natl Acad. Sci. USA* **105**, 13 116–13 121. (doi:10.1073/pnas.0804408105)
- Jarvis J, Jackson W, Smotherman M. 2013 Groups of bats improve sonar efficiency through mutual suppression of pulse emissions. *Front. Physiol.* **4**, 140. (doi:10.3389/fphys.2013.00140)
- Jarvis J, Bohn KM, Tressler J, Smotherman M. 2010 A mechanism for antiphonal echolocation by Free-tailed bats. *Anim. Behav.* **79**, 787–796. (doi:10.1016/j.anbehav.2010.01.004)
- Chiu C, Reddy PV, Xian W, Krishnaprasad PS, Moss CF. 2010 Effects of competitive prey capture on flight behavior and sonar beam pattern in paired big brown bats, *Eptesicus fuscus*. *J. Exp. Biol.* **213**, 3348–3356. (doi:10.1242/jeb.044818)
- Bates ME, Stamper SA, Simmons JA. 2008 Jamming avoidance response of big brown bats in target detection. *J. Exp. Biol.* **211**, 106–113. (doi:10.1242/jeb.009688)
- Ulanovsky N, Fenton MB, Tsoar A, Korine C. 2004 Dynamics of jamming avoidance in echolocating bats. *Proc. R. Soc. Lond. B* **271**, 1467–1475. (doi:10.1098/rspb.2004.2750)
- Gillam EH, Ulanovsky N, McCracken GF. 2007 Rapid jamming avoidance in biosonar. *Proc. R. Soc. B* **274**, 651–660. (doi:10.1098/rspb.2006.0047)
- Habersetzer J. 1981 Adaptive echolocation sounds in the bat *Rhinopoma hardwickei*. *J. Comp. Physiol. A* **144**, 559–566. (doi:10.1007/BF01326841)
- Ibáñez C, Juste J, López-Wilchis R, Núñez-Garduño A. 2004 Habitat variation and jamming avoidance in echolocation calls of the sac-winged bat (*Balantiopteryx plicata*). *J. Mammal.* **85**, 38–42. (doi:10.1644/1545-1542(2004)085<0038:HVAJAI>2.0.CO;2)
- Ratcliffe JM *et al.* 2004 Conspecifics influence call design in the Brazilian free-tailed bat, *Tadarida brasiliensis*. *Can. J. Zool.* **82**, 966–971. (doi:10.1139/z04-074)
- Metzner W. 1999 Neural circuitry for communication and jamming avoidance in gymnotiform electric fish. *J. Exp. Biol.* **202**, 1365–1375.
- Levin E, Roll U, Dolev A, Yom-Tov Y, Kronfeld-Schor N. 2013 Bats of a gender flock together: sexual segregation in a subtropical bat. *PLoS ONE* **8**, e54987. (doi:10.1371/journal.pone.0054987)
- Levin E, Yom-Tov Y, Barnea A. 2009 Frequent summer nuptial flights of ants provide a primary food source for bats. *Die Naturwiss.* **96**, 477–483. (doi:10.1007/s00114-008-0496-3)
- Boonman A, Bar-On Y, Cvikel N, Yovel Y. 2013 It's not black or white—on the range of vision and echolocation in echolocating bats. *Front. Physiol.* **4**, 248. (doi:10.3389/fphys.2013.00248)
- Obrist MK. 1995 Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design. *Behav. Ecol. Sociobiol.* **36**, 207–219. (doi:10.1007/BF00177798)
- Ulanovsky N, Moss CF. 2008 What the bat's voice tells the bat's brain. *Proc. Natl Acad. Sci. USA* **105**, 8491–8498. (doi:10.1073/pnas.0703550105)
- Hen I, Sakov A, Kafkafi N, Golani I, Benjamini Y. 2004 The dynamics of spatial behavior: how can robust smoothing techniques help? *J. Neurosci. Methods* **133**, 161–172. (doi:10.1016/j.jneumeth.2003.10.013)
- Levin E, Yom-Tov Y, Hefetz A, Kronfeld-Schor N. 2013 Changes in diet, body mass and fatty acid composition during pre-hibernation in a subtropical bat in relation to NPY and AgRP expression. *J. Comp. Physiol. B Bioch. Syst. Environ. Physiol.* **183**, 157–166. (doi:10.1007/s00360-012-0689-0)
- Holderied MW, von Helversen O. 2003 Echolocation range and wingbeat period match in aerial-hawking bats. *Proc. R. Soc. Lond. B* **270**, 2293–2299. (doi:10.1098/rspb.2003.2487)
- Schnitzler H-U, Moss CF, Denzinger A. 2003 From spatial orientation to food acquisition in echolocating bats. *Trends Ecol. Evol.* **18**, 386–394. (doi:10.1016/S0169-5347(03)00185-X)
- Jones G, Holderied MW. 2007 Bat echolocation calls: adaptation and convergent evolution. *Proc. R. Soc. B* **274**, 905–912. (doi:10.1098/rspb.2006.0200)
- Holderied MW, Jones G, von Helversen O. 2006 Flight and echolocation behaviour of whiskered bats commuting along a hedgerow: range-dependent sonar signal design, Doppler tolerance and evidence for 'acoustic focussing'. *J. Exp. Biol.* **209**, 1816–1826. (doi:10.1242/jeb.02194)
- Melcón ML, Denzinger A, Schnitzler H-U. 2007 Aerial hawking and landing: approach behaviour in Natterer's bats, *Myotis nattereri* (Kuhl 1818). *J. Exp. Biol.* **210**, 4457–4464. (doi:10.1242/jeb.007435)
- Höller P, Schmidt U. 1996 The orientation behaviour of the lesser spear-nosed bat, *Phyllostomus discolor* (Chiroptera) in a model roost. Concurrence of visual, echoacoustical and endogenous spatial information. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **179**, 245–254. (doi:10.1007/BF00222791)
- Roverud RC, Rabitoy ER. 1994 Complex sound analysis in the FM bat *Eptesicus fuscus*, correlated with structural parameters of frequency modulated signals. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **174**, 567–573. (doi:10.1007/BF00217377)
- Yovel Y, Melcon ML, Franz MO, Denzinger A, Schnitzler H-U. 2009 The voice of bats: how greater mouse-eared bats recognize individuals based on their echolocation calls. *PLoS Comput. Biol.* **5**, e1000400. (doi:10.1371/journal.pcbi.1000400)
- Jones G, Sripathi K, Waters D, Marimuthu G. 1994 Individual variation in the echolocation calls of three sympatric Indian hipposiderid bats, and an experimental attempt to jam bat echolocation. *Folia Zool.* **43**, 347–362.
- Masters W. 1995 Sonar signals of big brown bats, *Eptesicus fuscus*, contain information about individual identity, age and family affiliation. *Anim. Behav.* **50**, 1243–1260. (doi:10.1016/0003-3472(95)80041-7)
- Koay G, Kearns D, Heffner HE, Heffner RS. 1998 Passive sound-localization ability of the big brown bat (*Eptesicus fuscus*). *Hear. Res.* **119**, 37–48. (doi:10.1016/S0378-5955(98)00037-9)
- Suga N, Niwa H, Taniguchi I, Margoliash D. 1987 The personalized auditory cortex of the mustached bat: adaptation for echolocation. *J. Neurophysiol.* **58**, 643–654.