

Dynamics of jamming avoidance in echolocating bats

Nachum Ulanovsky¹†, M. Brock Fenton^{2*}, Asaf Tsoar³ and Carmi Korine⁴

¹The Interdisciplinary Centre for Neural Computation and Department of Neurobiology, Hebrew University, Jerusalem 91904, Israel

²Department of Biology, York University, North York, Ontario M3J 1P3, Canada

³Department of Evolution, Systematics and Ecology, The Hebrew University, Givat Ram Campus, Jerusalem 91904, Israel (tsoarasaf@pob.huji.ac.il)

⁴Mitrani Department of Desert Ecology, The Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, 84990 Midreshet Ben-Gurion, Israel (ckorine@bgumail.bgu.ac.il)

Animals using active sensing systems such as echolocation or electrolocation may experience interference from the signals of neighbouring conspecifics, which can be offset by a jamming avoidance response (JAR). Here, we report JAR in one echolocating bat (*Tadarida teniotis*: Molossidae) but not in another (*Taphozous perforatus*: Emballonuridae) when both flew and foraged with conspecifics. In *T. teniotis*, JAR consisted of shifts in the dominant frequencies of echolocation calls, enhancing differences among individuals. Larger spectral overlap of signals elicited stronger JAR. *Tadarida teniotis* showed two types of JAR: (i) for distant conspecifics: a symmetric JAR, with lower- and higher-frequency bats shifting their frequencies downwards and upwards, respectively, on average by the same amount; and (ii) for closer conspecifics: an asymmetric JAR, with only the upper-frequency bat shifting its frequency upwards. In comparison, ‘wave-type’ weakly electric fishes also shift frequencies of discharges in a JAR, but unlike *T. teniotis*, the shifts are either symmetric in some species or asymmetric in others. We hypothesize that symmetric JAR in *T. teniotis* serves to avoid jamming and improve echolocation, whereas asymmetric JAR may aid communication by helping to identify and locate conspecifics, thus minimizing chances of mid-air collisions.

Keywords: echolocating bats; jamming avoidance response; communication; *Tadarida teniotis*; *Taphozous perforatus*

1. INTRODUCTION

Sensory processing in animals is shaped by the ubiquitous presence of background noise, requiring the separation of signal from noise (Dusenbery 1992). This problem may be especially severe in animals using active sensing systems such as electrolocation or echolocation, which may face jamming by the signals of neighbouring conspecifics. Most species of weakly electric fishes show a jamming avoidance response (JAR), achieved by adjusting the discharges of individuals, emphasizing differences between emissions in response to the signals of neighbours (Bullock *et al.* 1972; Heiligenberg 1977, 1991; Scheich 1977; Zelick 1986; Bastian 1994; Heiligenberg *et al.* 1996; Kawasaki 1997; Kramer 1999; Metzner 1999). Weakly electric fishes use two kinds of discharge in electrolocation and electric communication (Heiligenberg 1977; Hopkins 1988; Kramer 1990): ‘pulse species’ generate sequences of short pulses, and ‘wave species’ generate continuous periodic waves. JAR in pulse species involves changes in interpulse intervals (IPIs) minimizing temporal coincidences between pulses of neighbouring conspecifics; JAR in wave species involves changes in discharge frequency, minimizing spectral overlap between frequencies of neighbouring conspecifics (Heiligenberg 1977, 1991; Kawasaki 1997; Metzner

1999). In electric fishes, JAR is supported by neural circuits that were extensively characterized in several species (Scheich 1977; Carr *et al.* 1986; Heiligenberg 1991; Heiligenberg *et al.* 1996; Metzner 1999), and it enhances individual electrolocation performance (Heiligenberg 1991), and possibly also social identification and communication among individuals (Kramer 1999).

The situation in echolocating bats is less clear. Echolocating microchiropteran bats use tonal sonar calls, extracting information about target distance, direction and nature by comparing the original signal with returning echoes (Griffin 1958). When approaching a target, echolocating bats move from ‘search phase’ calls, characterized by stable call parameters and long intercall intervals, to approach, and terminal phases (feeding buzz) involving dramatic shortening of call durations and intercall intervals (Griffin *et al.* 1960; Schnitzler & Kalko 2001). Some species produce echolocation calls at a high duty cycle (call duration/intercall interval), dominated by a narrow constant frequency (CF) band, whereas others echolocate at a low duty cycle, with calls dominated by frequency-modulated (FM) signals of varying bandwidth (Fenton *et al.* 1995; Schnitzler & Kalko 2001).

Several lines of evidence suggest that echolocating bats are susceptible to degradation of the signal-to-noise ratio. Broadcasting white noise affects flight and echolocation behaviour in captive *Plecotus rafinesquii* negotiating an obstacle course (Griffin 1958), and in the wild, foraging *Myotis lucifugus* avoid areas where running water generates high-level background noise (von Frenckell & Barclay 1987). Playback of narrowband signals to flying, captive

* Author and address for correspondence: Department of Biology, University of Western Ontario, Ontario N6A 5B7, Canada (bfenton@uwo.ca).

† Present address: Department of Psychology and Institute for Systems Research, University of Maryland, College Park, MD 20742, USA (nulanovsky@psyc.umd.edu).

Noctilio albiventris interferes with its echolocation behaviour (Roverud 1987), and in laboratory platform experiments, playback presentation of echolocation calls to *Eptesicus fuscus* degrades its distance discrimination performance (Masters & Raver 1996).

In the presence of conspecifics, echolocating bats may need to employ JAR, to avoid masking of the weak echoes coming from prey. Their directional sonar beam may aid in interference suppression (unlike in electric fishes, which use rather omni-directional emissions), but additional JAR strategies may be required, similar to those in weakly electric fishes. High-duty-cycle bats face an almost continuous jamming problem, similar to wave species of weakly electric fishes (which use 100% duty cycle signals). Low-duty-cycle bats may face a hybrid problem, in one sense like that confronting pulse species of weakly electric fishes (which use low-duty-cycle signals), but also like in wave species, because of the continuously arriving echoes with various delays.

Three field studies of low-duty-cycle FM bats suggested jamming avoidance, reflected by changes in echolocation behaviour in the presence of conspecifics. Obrist (1995) showed changes in intercall intervals in four vespertilionids (*E. fuscus*, *Euderma maculatum*, *Lasiurus borealis* and *L. cinereus*) when flying with conspecifics, while Habersetzer (1981) and Surlykke & Moss (2000) showed that *Rhinopoma hardwicki* (Rhinopomatidae) and *E. fuscus* (Vespertilionidae) change the frequencies of their echolocation calls when encountering conspecifics, like wave species of weakly electric fishes.

The purpose of our study was to test for the presence and analyse the dynamics of JAR in two species of low-duty-cycle FM bats (the European free-tailed bat, *Tadarida teniotis*: Molossidae, and the Egyptian tomb bat, *Taphozous perforatus*: Emballonuridae), when flying with conspecifics. These species are large aerial feeders (average body mass: *T. teniotis* 25 g, *Tap. perforatus* 32 g), foraging for flying insects in open spaces and around streetlights (Korine & Pinshow 2004). We predicted that, because their search phase echolocation calls are relatively long, JAR, if present, would consist of repulsive frequency shifts as in wave species of weakly electric fishes. Moreover, we predicted that the magnitude of these frequency shifts would be positively correlated with the magnitude of jamming, i.e. with the amplitude of the conspecifics' echolocation calls and with the degree of spectral overlap between the calls. We demonstrate that the molossid (*T. teniotis*) but not the emballonurid (*Tap. perforatus*) exhibits such a JAR. We also demonstrate that the JAR in individual *T. teniotis* consists of both symmetric static and asymmetric dynamic components, which differ from JAR in wave species of weakly electric fishes, where either symmetric or asymmetric JAR occurs in a given species (Heiligenberg *et al.* 1996).

2. METHODS

(a) Recording of bat vocalizations and measurement of pulse parameters

We recorded calls of *T. teniotis* and *Tap. perforatus* between 27 July and 1 August 2002 as they foraged over and around streetlights in Midreshet Ben-Gurion, southern Israel. Both species were actively echolocating, readily avoided mist nets and

pursued and captured flying insects. Individual *T. teniotis* were detected visually using light from the streetlights, and acoustically by following their strong low-frequency calls, which fall into the spectral range audible to humans (table 1). The data were recorded for 4–5 h from sunset.

Recordings were made using a Pettersson D980 Bat Detector (Pettersson Elektronik AB, Uppsala, Sweden; frequency response ± 3.5 dB between 8 and 160 kHz), through an Ines DAQ i508 high-speed card (250 kHz sampling rate) to a Dell Latitude PC running BATSOUNDPRO software (Pettersson). We recorded files 60 s long, separated by *ca.* 10 s intervals of system reset.

After initial inspection of the files in BATSOUNDPRO, we digitally highpass-filtered them (sixth-order Butterworth filter, 7 kHz cut-off), and selected for further analysis files with bat calls ('pulses') that met the following three criteria: (i) 10 s or greater long sequences of calls (long enough for analysis of JAR dynamics), with (ii) high signal-to-noise ratio, that (iii) consisted mainly of search phase echolocation calls (few approaches and buzzes; analysis was carried out on search phase calls only). We analysed 34 such files of recorded *T. teniotis* (total time: 1133 s, total pulses: 2544) and 32 files of *Tap. perforatus* (total time, 1201 s; total pulses, 2327).

We used a combination of BATSOUNDPRO and MATLAB (Mathworks, Natick, MA, USA) to measure the following parameters for bat calls in search phase (table 1): highest frequency (F_{\max}), lowest frequency (F_{\min}), bandwidth ($F_{\max} - F_{\min}$), frequency with maximal energy, pulse duration, pulse amplitude, IPI (between onsets of consecutive pulses) and time relative to file start. Frequencies were measured from the spectrogram (256-point fast Fourier transform, Hanning window), with F_{\min} and F_{\max} as the lowest and highest frequencies above background noise. For *T. teniotis*, the measured pulse parameters were very similar to previously published values (Russo & Jones 2002), while for *Tap. perforatus* this is, to our knowledge, the first report on pulse parameters. F_{\min} , and to a lesser degree F_{\max} , corresponded very well to the bandwidth measured from the power spectrum at 15 dB below the peak power spectral density (256 point resolution). Because lower frequencies undergo less atmospheric attenuation than higher ones (Lawrence & Simmons 1982), we used F_{\min} to represent the frequencies of echolocation calls. If pulses from two bats overlapped in our recordings, we discarded both pulses. In both species we measured the dominant harmonic (*T. teniotis*, first harmonic; *Tap. perforatus*, second harmonic).

(b) Separating the calls of conspecific bats recorded simultaneously

In the search phase, individual bats of both species, when flying alone, used rather fixed values of F_{\min} and interpulse (intercall) interval, the latter reflecting the association between wingbeat frequency and call emission (Speakman & Racey 1991) (figure 1*a,b*). When two *T. teniotis* flew in the same airspace at the same time, the pulses of individual bats were clearly distinguishable by F_{\min} values and by consistent IPIs (figure 2*a,b* and electronic Appendix A, figure 5). When F_{\min} is plotted against duration (figure 2*c*), the presence of two clusters suggests two vocalizing bats (coloured in red and blue). We observed clear pairs of clusters ('two-bat scenario') in 20 out of 34 files of *T. teniotis*; in 14 out of 34 files we observed one cluster ('one-bat scenario'). In a few of the 34 *T. teniotis* files we observed weak calls of one or two additional *T. teniotis* in the background, but we collected data from only the prominent individuals. We

Table 1. Average pulse parameters (\pm s.d.) in one-bat and two-bat scenarios. (In two-bat scenarios the average of both bats is shown. IPI was not measured for *Taphozous perforatus* in two-bat/*N*-bat scenarios, where the pulses from the two bats could not be separated.)

	<i>Tadarida teniotis</i>		<i>Taphozous perforatus</i>	
	one-bat ($n = 14$)	two-bat ($n = 20$)	one-bat ($n = 16$)	two-bat/ <i>N</i> -bat ($n = 16$)
F_{\min} (kHz)	11.25 \pm 0.43	11.23 \pm 1.62	27.54 \pm 0.22	27.41 \pm 0.27
bandwidth (kHz)	5.57 \pm 1.01	5.45 \pm 1.40	2.31 \pm 0.24	2.74 \pm 0.51
duration (ms)	18.3 \pm 2.2	16.6 \pm 1.9	13.1 \pm 1.3	12.4 \pm 1.7
IPI (ms)	540 \pm 86	692 \pm 200	386 \pm 63	—

also had some additional files with three or four prominent *T. teniotis* ('*N*-bat scenarios'), but these were not included in the 34 files analysed here.

To separate the calls of the two bats in a two-bat scenario, we need to address possible sources of confusion. First, two clusters in an F_{\min} -duration plot could in principle correspond to a single bat. However, this was unlikely to be the case here, because the variable pattern of IPIs that we observed (figure 2*a*) was inconsistent with the stable intervals expected from a single bat, and because there was no temporal correlation between amplitudes of pulses taken from the two clusters (i.e. no correlation between the two curves in figure 3*b,c*; see figure 4*d* for population analysis). Second, a single cluster in an F_{\min} duration plot could in principle correspond to two or more bats. To assess this possibility, we plotted histograms of IPIs (figure 2*d*): separately for the two clusters (red and blue) and for the mixture of the two clusters taken as one (black). The histogram of the mixture contained many short intervals, which were absent from histograms of the two clusters. In fact, we expect such excess of short intervals when mixing pulses of two bats in search phase, because the two bats use somewhat different intervals, and hence there is often temporal proximity of pulses (e.g. figure 2*a*, short intervals between upper and lower pulses). For individual bats in the search phase, however, these short intervals are almost entirely absent because of their use of rather long intervals (figure 1*a(iv)*). Thus, an excess of short intervals can be taken as evidence for the presence of two bats' calls in our recording. To quantify the excess of short intervals, we used a 'bat separation index' (BSI), which measures the relative number of intervals that are shorter than half the mean interval:

$$\text{BSI} = 1 - \left[\frac{\text{no. intervals} < \text{mean interval}/2}{\text{no. intervals} < 1000 \text{ ms}} \times \frac{1000 \text{ ms}}{\text{mean interval}/2} \right],$$

where the mean interval was computed for each file separately, using only intervals of less than 1000 ms (i.e. ignoring large time gaps). BSI \approx 1 indicates good bat separation, with the cluster corresponding to a single bat (few intervals shorter than half the mean interval), whereas BSI near 0 or below indicates poor bat separation, with the cluster corresponding to a mixture of two or more bats (many short intervals). The distribution of BSIs in the different conditions (figure 2*e*) showed that indeed BSIs were *ca.* 1 for individual bats (one-bat files: mean BSI = 0.997; two-bat files, red and blue clusters: mean BSI = 0.920), and BSIs were low when we mixed the two clusters in two-bat files ('mixed' mean BSI = -0.215). A 'cut-off BSI' of 0.4 produced full segregation between individual bats and mixed pairs of bats (figure 2*e*, horizontal line), so we used BSI > 0.4 as indication of good correspondence between an individual cluster and an individual bat.

To inspect the results of this bat separation procedure, we marked the results back onto the original .wav file, and manually examined (BATSOUNDPRO) the assignment of each pulse to the corresponding bat. Finally, when our field notes clearly documented the presence of individuals or pairs of bats during recording, these notes fully corresponded to the results of the bat separation procedure.

In recordings of *Tap. perforatus*, only single clusters were observed (e.g. figure 1*b*); two clusters were never observed for this species, neither in F_{\min} -duration plots nor in any other two-parameter plots. This is not surprising given the strong similarity in call frequencies between individuals (table 1). However, IPI histograms and BSIs readily allowed us to distinguish recordings of one calling bat ('one-bat scenario', figure 1*b*, BSI > 0.4) versus multiple calling bats ('two-bat/*N*-bat scenario', BSI < 0.4). In the latter case, however, we could not determine how many bats were present, hence 'two-bat/*N*-bat'.

(c) Statistical methods

Recordings of *T. teniotis* suggested that in two-bat scenarios, the two bats maintained quite a large frequency separation (figure 3*a*, separation of red and blue curves). Over the population, this frequency separation (horizontal lines in figure 4*a*) seemed larger than the typical frequency separation between individual bats in one-bat scenarios (figure 4*b*). To check whether this is statistically significant, we employed a Monte Carlo test, as detailed in electronic Appendix A. A small *p*-value in this test would support the hypothesis, H_1 : the mean frequency separation between pairs of bats flying together is larger than the mean frequency separation of randomly chosen pairs of bats flying alone. This would suggest that in two-bat scenarios, *T. teniotis* use 'static JAR', i.e. they shift their mean frequencies away from each other, statically maintaining this frequency difference throughout the recording time (tens of seconds).

However, recordings of *T. teniotis* suggested also the usage of 'dynamic JAR', i.e. fast changes in the call frequencies used by one bat (changes on time-scales of seconds or less), correlated with the call amplitudes of the other bat (figure 3 and electronic Appendix A, figure 6). To test this correlation, we averaged the raw data in 2 s non-overlapping windows, interpolated it (using cubic splines) to obtain smoothed pulse parameters for each bat separately (figure 3), and used the product-moment correlation between smoothed parameter curves as our test statistic. The smoothing and interpolation were necessary to fill in data from pulses that were missing or had low quality. We then used a sign test to examine the null hypothesis, H_0 : the median correlation between the parameters of the two bats is 0. Because we tested four different correlations between pairs of bats (figure 4*d*), we

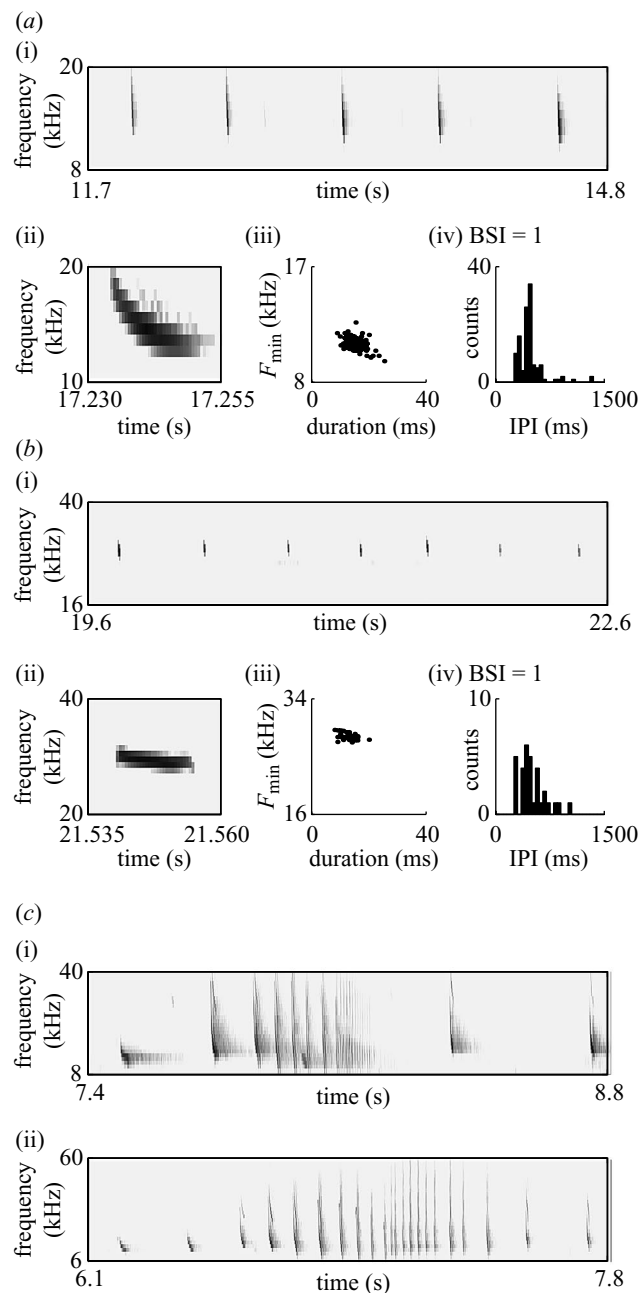


Figure 1. Recordings of *Tadarida teniotis* and *Taphozous perforatus*. (a) Calls of *T. teniotis* recorded in search phase (one-bat scenario). (i) Spectrogram (frequency versus time) of a sequence of pulses, showing the long and relatively stable IPIs in search phase. (ii) Spectrogram of a single pulse, showing the characteristic frequency-modulated sweep. (iii) F_{\min} -duration plot for the entire recording; the small scatter in this cluster demonstrates the stability of these two parameters over the recording. (iv) Histogram of IPIs for the entire recording; the BSI of 1 indicates the absence of short intervals, suggesting the presence of only one individual bat in this recording (see § 2). (b) Calls of *Tap. perforatus*, recorded in search phase (one-bat scenario). Plotted as in (a), with frequency axes of the spectrograms having the same relative extent as in (a) showing that *Tap. perforatus* uses much narrower search calls than *T. teniotis*. (c) Spectrograms of buzzes of *T. teniotis*. (i) Regular feeding buzz, showing the typical decrease in IPI, followed by a pause. (ii) The unusual 'social buzz' observed in multi-bat situations, showing a gradual decrease and then gradual increase in IPI. Spectrograms here and elsewhere were plotted using a 256-point fast Fourier transform.

employed a Bonferroni correction for the p -value, to compensate for multiple testing, so that $p < 0.0125$ ($p < 0.05/4$) was considered significant; for all other statistical tests in this study, a value of $p < 0.05$ was considered significant.

3. RESULTS

We recorded the echolocation calls of foraging *T. teniotis* and *Tap. perforatus*, as they searched, pursued and captured flying insects. Both species produced the full suite of echolocation calls (Griffin *et al.* 1960), including search phase calls (figure 1*a,b*), approach phase calls and feeding buzzes (figure 1*c*(i)). For *T. teniotis* we occasionally observed mixtures of echolocation calls and distinct low-frequency social calls (sinusoidally FM); in some multi-bat situations (but never when bats flew alone) we also observed 'social buzzes' that differed from feeding buzzes (figure 1*c*(ii)). This study focuses exclusively on the search phase echolocation calls.

(a) *Symmetric static frequency shifts in Tadarida teniotis flying together*

We divided the data on *T. teniotis* calls into files representing one-bat scenarios (14 out of 34 files, figure 1*a*) and two-bat scenarios (20 out of 34 files, figure 2), and measured the parameters of bat pulses in the search phase, assigning each pulse to the appropriate bat (table 1). Individual *T. teniotis* in one-bat scenarios used rather stable pulse parameters throughout a single recording (maximum 60 s), as evidenced by narrow clusters in F_{\min} -duration plots and by narrow IPI histograms (figure 1*a*). Moreover, the population distribution for all files showed that *T. teniotis* in one-bat scenarios used a narrow range of frequencies (figure 4*b*).

Tadarida teniotis flying in a two-bat scenario used different frequencies (figures 3*a* and 4*a*): while the population average frequency was identical in one-bat and two-bat scenarios (one-bat: 11.25 kHz, two-bat: 11.23 kHz; Wilcoxon ranked sum test: d.f. = 53, $p > 0.5$), the mean frequency separation between pairs of simultaneously recorded bats (two-bat scenarios, figure 4*a*) was substantially larger than the mean frequency separation between randomly chosen pairs of bats flying alone (one-bat scenarios, figure 4*b*) (Monte Carlo test, see § 2: $p < 0.01$). Thus, when flying together, individual *T. teniotis* maintained a large frequency separation between their echolocation calls.

We will use the following terminology for describing frequency shifts by the bats: 'symmetric' shifts are when both bats shift their frequencies away from the average value used by the bat population, with the shifts having the same magnitude but opposite signs (i.e. mirror symmetry); 'asymmetric' shift is when only one of the bats shifts its frequency. 'Static' shifts are when the bats maintain the frequency separation throughout the recording (tens of seconds); 'dynamic' shifts are fast changes in the call frequency of one bat (on time-scales of seconds or less), correlated with the behaviour of the other bat.

Tadarida teniotis whose calls had higher frequencies in two-bat scenarios (henceforth, high-frequency; figure 4*a*, grey dots) shifted their frequency upwards on average from 11.25 to 12.46 kHz (+1.21 kHz shift), whereas bats producing lower-frequency calls (henceforth low-frequency;

black dots) shifted downwards on average from 11.25 to 9.99 kHz (-1.26 kHz shift). Both shifts were significant (Wilcoxon ranked sum test: d.f. = 33, $p < 0.0003$ for both), with identical numerical values but opposite signs (Wilcoxon ranked sum test for the $+1.21$ and -1.26 kHz shifts: d.f. = 39, $p > 0.5$). Thus, the average frequencies of the calls of two *T. teniotis* flying in the same air space were shifted away from each other in repulsive shifts that were, on average, symmetric, and that were maintained throughout the recording ('symmetric static shifts'). In most two-bat recordings the static frequency shifts were already present at the start, but occasionally we observed the development of these shifts: figure 3a(i) shows two bats that started close to the average F_{\min} of one-bat files (11.25 kHz), and then moved their frequencies symmetrically away from each other.

(b) Asymmetric dynamic frequency shifts in *Tadarida teniotis* flying together

The frequencies of *T. teniotis* calls were not static, but changed continuously over time (figure 3a), suggesting a dynamic situation. To examine variability in call frequencies within each file, we used the coefficient of variation (CV; standard deviation/mean) (figure 4c). As expected from the static frequency shifts, the CV of entire two-bat files (mixed high- and low-frequency bats) increased considerably compared with one-bat files (Wilcoxon ranked sum test: d.f. = 33, $p < 10^{-5}$). The CV of individual high-frequency bats in two-bat files increased significantly compared with the CV in one-bat files, but this was not true for low-frequency bats (Wilcoxon ranked sum test: d.f. = 33, $p < 0.01$ and $p > 0.7$ for high- and low-frequency bats, respectively). Thus, individual *T. teniotis* using higher-frequency calls showed increased frequency variability in two-bat scenarios, whereas those using lower frequencies did not.

The dynamic fluctuations did not appear to be random, but rather fluctuations in call frequencies of one bat were influenced by the presence of another, on time-scales of seconds or less. We observed many examples where the F_{\min} of the high-frequency bat fluctuated in correlation with the recorded amplitude of the low-frequency bat (arrows in figure 3a,b and in electronic Appendix A, figure 6). Here, the upper bat's frequency was correlated with the lower bat's amplitude, but not vice versa (see correlation coefficients in figure 3d).

This asymmetry appeared to be a general phenomenon over the population, as indicated by the distribution of correlation coefficients for several comparisons between the frequencies and amplitudes of the two bats (figure 4d). The correlation between the F_{\min} of higher-frequency bats and the amplitude of lower-frequency bats was significantly larger than 0, with 17 out of 20 files showing positive correlations (sign test: d.f. = 19, $p < 0.003$), with median $r = 0.49$, whereas all other correlations were not significant ($p > 0.5$).

The lack of correlation between the recorded call amplitudes of the two bats, when flying together, suggests that their flight patterns were, on average, uncorrelated (that is, they did not tend to fly together e.g. towards the microphone). Because calls with good signal-to-noise ratio usually occurred when bats flew close to the microphone (ca. 3–10 m), this means that when one bat approached

the microphone, it usually also approached the other bat. In addition, the lack of correlation between the F_{\min} of two bats suggests that changes in echolocation calls were not driven by a common external factor, such as wind. Therefore, our results indicate that the only dynamic interaction in the calls of echolocating *T. teniotis* was a frequency shift upwards in the high-frequency bat when a lower-frequency individual approached, but not vice versa.

(c) No frequency shifts in *Taphozous perforatus*

Unlike *T. teniotis*, when two or more *Tap. perforatus* flew in the same airspace, their echolocation calls had almost identical frequencies (figure 4a). Here, IPI histograms allowed us to distinguish between one-bat scenarios (16 out of 32 files) and two-or-more-bat scenarios ('two-bat/*N*-bat scenarios', 16 out of 32 files). In one-bat scenarios, *Tap. perforatus* used a narrow range of average frequencies (figure 4b) whose median did not differ from that of two-bat/*N*-bat scenarios (Wilcoxon ranked sum test: d.f. = 31, $p > 0.2$). Frequency variability in each file (measured by CV) was very low, and, unlike *T. teniotis*, *Tap. perforatus* showed no increase in frequency variability in two-bat/*N*-bat scenarios (CVs in one-bat files versus two-bat/*N*-bat files; Wilcoxon ranked sum test: d.f. = 31, $p > 0.05$; figure 4c). These data demonstrate that when several *Tap. perforatus* flew together, they did not show static or dynamic shifts in the frequencies of their echolocation calls, like the shifts we observed for *T. teniotis*.

4. DISCUSSION

We described two types of JAR in the echolocating bat *T. teniotis*, and the lack of JAR in the bat *Tap. perforatus*. The discussion is structured as follows: first, we discuss some possible sources for these interspecific differences. Second, we discuss the possible communicative role of the JAR in *T. teniotis*. Third, we argue that our results cannot be explained by Doppler shifts. Fourth, we compare the JAR in *T. teniotis* to weakly electric fishes and to humans. Finally, we discuss some hypotheses regarding the asymmetry of dynamic JAR in *T. teniotis*.

Differences in call bandwidths could explain some interspecific differences in the presence and type of JAR. Bats using wideband calls, which produce larger spectral overlap, are more likely to experience jamming than those using narrowband calls, and are therefore more likely to exhibit JAR. In addition, bat species using wideband calls often have a wider audiogram than species using narrowband calls (Neuweiler *et al.* 1984), and may therefore be better able to use frequency shifts for jamming avoidance. Indeed, *T. teniotis* showed a static JAR, coincident with its use of calls of broader bandwidth than *Tap. perforatus*, which showed no JAR (see bandwidths in figure 1 and table 1 (also Rydell & Arlettaz 1994; Russo & Jones 2002)). A bandwidth effect is also indicated by the strong correlation between average call bandwidth and static JAR ($r = 0.80$, d.f. = 34, $p < 10^{-8}$; see electronic Appendix A, figure 7a), which is even stronger when using normalized bandwidth (bandwidth/frequency; data not shown: $r = 0.87$, d.f. = 34, $p < 10^{-12}$). Bandwidth effect also could explain three previous findings: (i) static frequency shifts in *Otomops martiensseni* using wideband calls (Fenton *et al.* 2004); (ii) static frequency shifts in *E. fuscus*

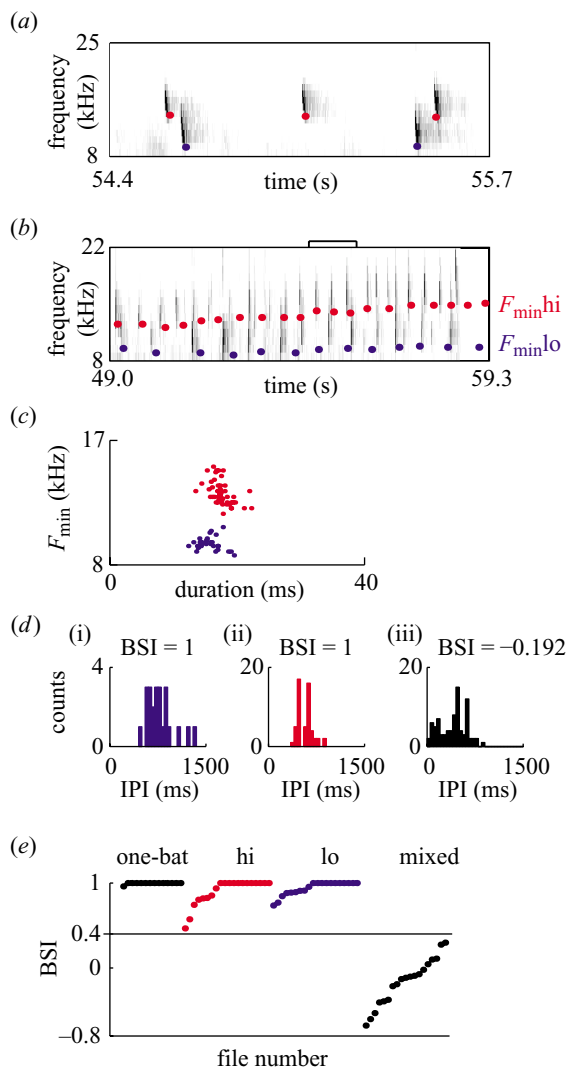


Figure 2. *Tadarida teniotis* calls in two-bat scenarios, and methods for separation of individual bats. (a–d) show a single file (see another file in electronic Appendix A, figure 5), (e) shows population data. (a) Spectrogram of a sequence of several pulses, with marks of our measurements of F_{\min} , coloured separately for the high-frequency bat (red) and low-frequency bat (blue). (b) Spectrogram of a longer time segment, showing the clear separation between F_{\min} of the two bats during the recording. Rectangle at top denotes time of segment in (a). (c) F_{\min} versus duration, showing a clear separate cluster for each bat (red and blue). (d) Histograms of IPIs for the two bats ((i) blue, $BSI = 1$ and (ii) red, $BSI = 1$) and (iii) for their mixture (black), $BSI = -0.192$). (e) BSI values for all the one-bat and two-bat files (each dot represents a single file). ‘hi’, ‘lo’ and ‘mixed’ are two-bat data from high-frequency, low-frequency and mixed high- and low-frequency bats, respectively, sorted in ascending order for each condition (we omitted one ‘mixed’ recording with $BSI = -1.22$). A cut-off BSI of 0.4 allows segregating individual bats (‘one-bat’, ‘hi’, ‘lo’) and pairs of bats (‘mixed’).

using wideband calls (Surlykke & Moss 2000); and (iii) the near absence of static frequency shifts in three hipposiderid bats using very narrowband calls (Jones *et al.* 1994). However, bandwidth does not explain other findings, namely static frequency shifts in *R. hardwickei* using narrowband calls (Habersetzer 1981) and the absence of static frequency shifts in four vespertilionid bats using

broadband calls (Obrist 1995). Moreover, our data on *Tap. perforatus* showed very similar F_{\min} values for individual bats (figure 4, table 1): hence their calls should have often overlapped in two-bat scenarios, despite their narrow bandwidth, and should have elicited JAR. Thus, differences in bandwidth seem to account only partly for differences in JAR.

Further support for the bandwidth hypothesis comes from our findings on dynamic JAR in *T. teniotis*. In all the 20 files with two-bat scenarios, there was spectral overlap between the calls of the two bats flying together, even after static JAR (i.e. $F_{\min}(\text{high-frequency bat}) < F_{\max}(\text{low-frequency bat})$). One may therefore wonder whether the overlapping frequencies might still cause interference (unlike in wave-type electric fishes, where the JAR eliminates any overlap in their signals, which are very narrowband). A possible explanation is that the degree of this interference depends on the distance between the bats: if they are far away, this spectral overlap causes negligible interference, but when they approach each other and the calls become stronger, the interference strengthens and then they need to further shift their frequencies (i.e. dynamic JAR). If this explanation is correct, we expect the dynamic JAR (frequency fluctuations) to be negatively correlated with static JAR (average frequency separation). Indeed, in files with considerable dynamic JAR, this negative correlation was observed ($r = -0.74$, d.f. = 8, $p < 0.02$; see electronic Appendix A, figure 7c).

A second source of interspecific differences may be the different spatial extent of bats’ receiving beams (i.e. the angle from which the bat picks up signals). For ears of identical size and shape, the beam width is inversely proportional to the call frequency (Neuweiler 2000): it is therefore possible that *Tap. perforatus*, which uses higher frequencies than *T. teniotis* (table 1), has a narrower receiving beam, so it is less subject to jamming than *T. teniotis*, which picks interfering signals from a wider angle. Thus, while *T. teniotis* produces frequency shifts and probably uses spectral filtering to suppress interfering signals, *Tap. perforatus* may be using spatial filtering to achieve the same goal, which may explain the absence of frequency JAR in *Tap. perforatus*. Such spatial filtering, however, does not seem to account for the suggested frequency JAR in *R. hardwickei* and *E. fuscus* (Habersetzer 1981; Surlykke & Moss 2000), both of which use higher frequencies.

Finally, a third source of interspecific differences may be the different temporal structures of the dominant harmonics of the calls (compare figure 1a(ii) and 1b(iv)). *Tadarida teniotis* has a frequency-modulated call with a richer temporal structure than the narrowband call of *Tap. perforatus*, which has almost CF with very little temporal structure. Therefore, we can expect only *T. teniotis* to be able to use temporal structure to distinguish their calls from those of conspecifics, while *Tap. perforatus* should use another solution. Because *Tap. perforatus* are not using frequency shifts, they are probably using yet another solution, possibly the spatial filtering discussed above.

In addition to further reducing confusion in echolocation, the dynamic JAR in *T. teniotis* may also have a communicative role, as suggested for electrolocation (Kramer 1999; see also Barclay 1982). For flying bats, such a role could be to enhance their ability to identify, locate and track

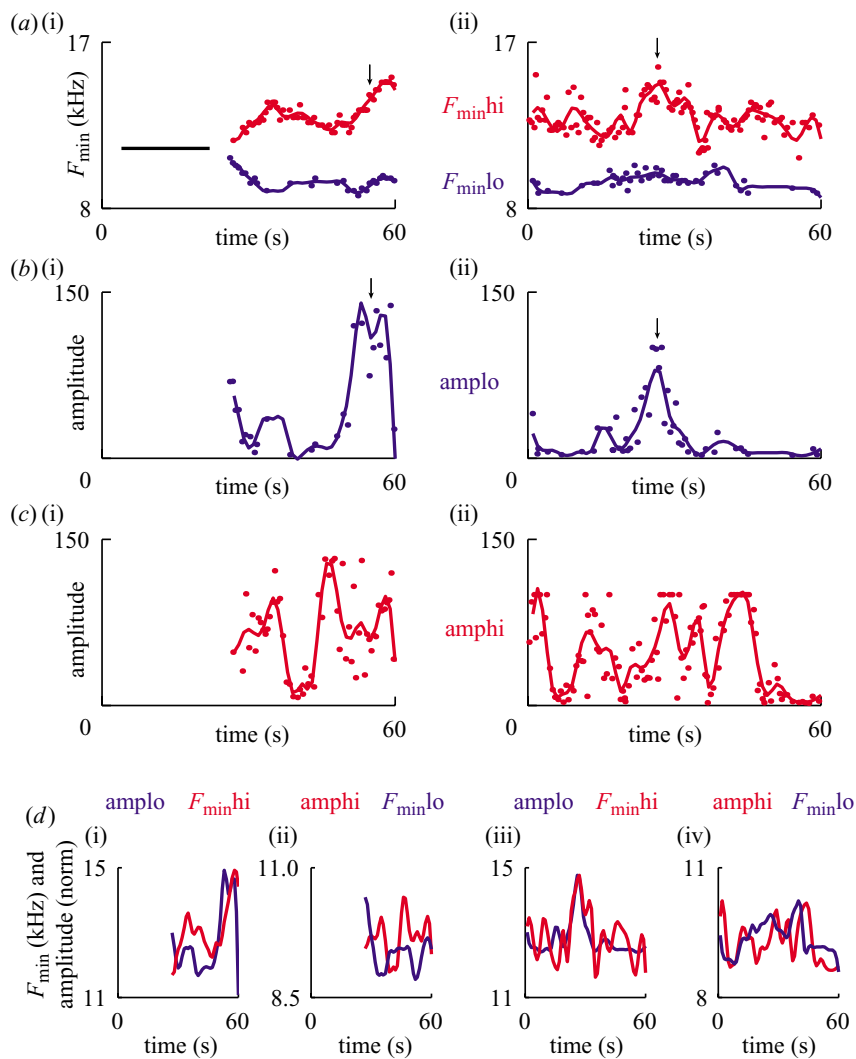


Figure 3. Examples of JAR in *Tadarida teniotis* recorded in a two-bat scenario. The two columns show two different recordings; see another recording in electronic Appendix A, figure 6. (a) F_{\min} of the calls of both bats over an entire recording, with dots showing raw data and solid lines showing smoothed data. Horizontal line in (i) denotes the average population frequency in one-bat scenarios (11.25 kHz), suggesting that these two bats started from the same frequency, and then developed a static frequency shift. (b) Amplitude of calls over an entire recording, for the lower-frequency bat (amplo). Arrows, times when the F_{\min} of the higher-frequency bat ($F_{\min,hi}$) behaved similarly to the amplitude of the lower-frequency bat (amplo). (c) Amplitude of calls for the higher-frequency bat (amphi). (d) Overlay of the smoothed F_{\min} of one bat over the smoothed amplitude of the other bat (amplitudes were normalized to fit F_{\min} ranges), with the correlation coefficients of the two curves. (i) $r = 0.506$, (ii) $r = -0.074$, (iii) $r = 0.656$, (iv) $r = 0.305$.

conspecifics, which might minimize the chances of mid-air collisions, improving ‘air traffic control’ in multi-bat situations. This suggestion is consistent with the observations of bats’ repeatedly using predictable flight paths when numerous individuals approached a water hole (Adams & Simmons 2002). This is also consistent with bats’ reported ability to communicate in-flight, as evidenced by their use of modified echolocation calls for communication, e.g. in the ‘honking behaviour’ of *Noctilio leporinus* on a collision course (Suthers 1965). Evidence of acoustic communication between foraging *T. teniotis* comes from our occasional observation of mixtures of echolocation calls and distinct low-frequency social calls (see also Belwood & Fullard 1984; Fenton 1985; Racey & Swift 1985), and also from the ‘social buzzes’ that were observed only in multi-bat situations, not when bats flew alone (figure 1c(ii)).

The changes in frequency that we observed in *T. teniotis*

cannot be accounted for by Doppler shifts. To observe at our microphone a Doppler shift of 2.47 kHz (the average observed static frequency separation), given an average baseline of 11.25 kHz, the two bats would have had to be: (i) flying towards one another each at 11% of the speed of sound; (ii) been flying collinearly with our microphone; and (iii) maintained such straight flight for the 60 s of the recording. This is highly unlikely, because after 60 s the bats would be 2 km away from our microphone, and hence undetectable, and 4 km away from each other, and hence in no need to perform JAR.

Possibly our most surprising finding is the existence of two types of JAR in *T. teniotis*: symmetric static JAR (figure 4a) and asymmetric dynamic JAR (figure 4d). In electric fishes, JAR acts as an early warning system and occurs in response to very weak interfering stimuli (Heiligenberg 1977), resembling the static JAR that we observed in *T. teniotis*. Some wave species of electric fishes

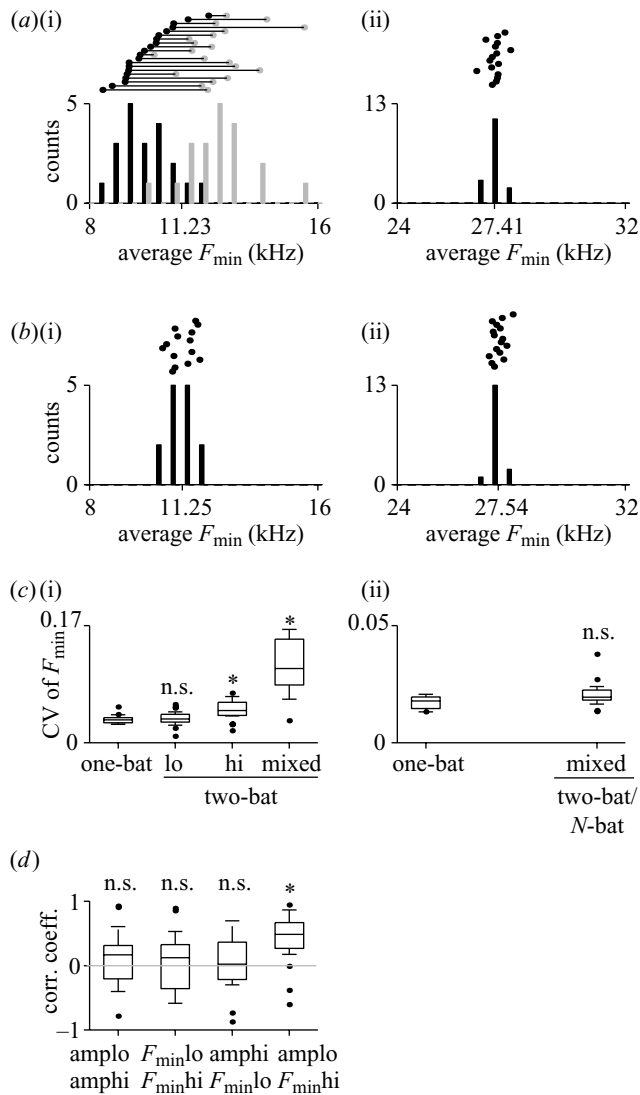


Figure 4. Population analysis of recordings of *Tadarida teniotis* (a(i), b(i) and c(i)) and *Taphozous perforatus* (a(ii), b(ii) and c(ii)). (a) Distribution of average frequencies (F_{\min}) in two-bat files, separately for low-frequency bats (black) and high-frequency bats (grey). Horizontal lines show frequency differences in individual *T. teniotis* files (for *Tap. perforatus* we could not separate individual bats, so there are no horizontal lines). (i) Two-bat, $n = 20$, (ii) two-bat/ N -bat mixed, $n = 16$. (b) Distribution of average frequencies in one-bat files. (i) $n = 14$, (ii) $n = 16$. Note that the typical frequency difference between individual *T. teniotis* in (b) is smaller than in (a) (horizontal lines), suggesting static JAR in (a). (c) Distributions of the CV of F_{\min} for one-bat files and two-bat files, for which separate data are shown for low-frequency bats (lo), high-frequency bats (hi) and mixtures of the two bats (mixed). Asterisks denote significant difference between the medians of CV distributions in two-bat versus one-bat scenarios. (d) Distributions of correlation coefficients for four different comparisons between frequencies and amplitudes of individual *T. teniotis* in two-bat files. 'amplo- F_{\min} hi' (correlation between the amplitude of the lower-frequency bat and the F_{\min} of the higher-frequency bat) is the only significant correlation, demonstrating the asymmetric dynamic JAR.

(Eigenmannidae) show symmetric JAR, increasing their discharge frequencies in response to low-frequency signals and decreasing their frequencies in response to high-

frequency signals. Other wave species (Apterontidae) show asymmetric JAR, increasing their discharge frequencies only in response to interfering signals (Heiligenberg *et al.* 1996). The symmetry or asymmetry of the JAR is a characteristic of fish species, and is served by functionally different neural circuitry (Heiligenberg 1977; Metzner 1999). *Tadarida teniotis* shows both symmetric and asymmetric JAR.

Interestingly, humans talking in the presence of masking noise tend to increase their fundamental frequency (pitch), as well as changing other acoustic parameters, in an attempt to improve speech intelligibility: an effect known as the 'Lombard reflex' (e.g. Summers *et al.* 1988). Also, when presented via earphones with a fed-back version of their speech whose pitch is shifted in real time, most humans try to correct their pitch in the opposite direction, to make the auditory input 'sound right'; an effect known as the 'audio-vocal reflex' (e.g. Burnett *et al.* 1998). Thus, auditory input can affect vocal output, both in echolocating bats and in humans.

What accounts for the asymmetry of dynamic JAR in *T. teniotis*? Two hypotheses could provide simple explanations. The first hypothesis proposes that because of static JAR, the lower-frequency individual is close to its lowest possible frequency, precluding further lowering of frequency. This implies that when the lower-frequency individual 'has room' to shift its frequency downwards, it will do so. The lack of the expected negative relationship between the magnitude of dynamic JAR and the F_{\min} of lower-frequency bats ($r = 0.17$; electronic Appendix A, figure 7b) argues against this hypothesis. However, this lack of correlation could also stem from bats having different individual lowest frequencies, determined, for example, by size or sex. The second hypothesis proposes that *T. teniotis*, which specializes in long-range detection of large insects (Rydell & Arlettaz 1994) might be more sensitive to interference in the lower-frequency portion of its echolocation call, which is the portion that provides echo information from the longest distance (because it contains the most energy and also undergoes the least atmospheric attenuation). While this hypothesis remains to be tested, it is clear that under this hypothesis, once a static JAR has occurred, the higher-frequency individual will still have interference in the lower-frequency portion of its call, necessitating dynamic JAR; while the lower-frequency individual will be free of interference there. Our observations (electronic Appendix A figure 7c) are consistent with this hypothesis.

In summary, JAR is not a general requirement for successful foraging when aerial-feeding, echolocating bats fly in the immediate presence of conspecifics. While an emballonurid (*Tap. perforatus*) showed no evidence of JAR, a molossid (*T. teniotis*), operating in the same space at the same time, exhibited both symmetric static JAR and asymmetric dynamic JAR. This indicates that two mammalian species, using the same foraging habitat and facing a similar signal-detection problem, may have evolved very different sensory processing solutions to this problem.

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