Why do shrews twitter? Communication or simple echo-based orientation

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Shrews are very vocal animals. We tested behaviourally whether the high-pitched laryngeal 'twittering' calls of as-yet unclear function serve for communication or echo-based orientation. We used a representative species from each of the two largest phylogenetic groups of shrews. In both species, experimental manipulation of substrate density, but not of the likelihood of conspecific presence, affected the shrews' call rate when exploring an unknown environment. This adaptation of call rate to the degree of habitat clutter parallels bat echolocation and suggests that shrews may use the echoes and reverberations of their calls for identifying routes through their habitat or for probing habitat type. To assess the acoustic feasibility of shrew echo orientation, we ensonified shrew habitats in the field with an 'artificial shrew' (small speaker mounted close to a sensitive microphone). The data showed that shrew-like calls can indeed yield echo scenes useful for habitat assessment at close range, but beyond the range of the shrews' vibrissae.

1. INTRODUCTION

Shrews are very vocal animals. They have a considerable repertoire of communication sounds (Gould 1969; Churchfield 1990; Simeonovska-Nikolova 2004). Previous studies provide equivocal evidence whether shrews possess a simple echolocation-like system (Gould *et al.* 1964; Grunwald 1969; Buchler 1976; Tomasi 1979; Forsman & Malmquist 1988; Churchfield 1990; Thomas & Jalili 2004; Catania *et al.* 2008). When moving about, especially in new environments, shrews often emit faint, high-pitched laryngeal calls ('twittering') of unclear function (Churchfield 1990). If the primary role of these calls was communication (e.g. signalling its own presence or calling out for a conspecific), one would expect shrews to vary call rate between an area where shrew scent indicates a high likelihood of conspecific presence and an area with no signs of occupation by other shrews. If however, the function was to gather echo-borne information for habitat assessment (Churchfield 1990), one would predict that shrews

adapt call rate to habitat density, as typically seen in echolocating bats (Schnitzler *et al.* 2003). We behaviourally tested these predictions of the 'communication hypothesis' and the 'echo orientation hypothesis' in a representative species from each of the two largest phylogenetic groups of shrews. To assess acoustic feasibility of shrew echo orientation, we ensonified shrew habitats in the field and analysed returning echo scenes.

2. MATERIAL AND METHODS

(a) *Shrews*
We used seven common shrews (*Sorex araneus*, subfamily Soricinae) and nine greater white-toothed shrews (*Crocidura russula*, subfamily Crocidurinae) caught in live traps and released at the site of capture after completion of the experiments. They were maintained in a fully air-conditioned room (15.5°C, 80% humidity) at a 12 L : 12 D cycle in individual home cages with ad libitum access to water and food (minced meat, mealworms and other invertebrates). Shrews were caught and tested under license by Regierungspräsidium Tübingen (56-2/8852.15 and 56-6/8852.15).

(b) *Experimental setup*
Behavioural experiments were conducted at the University of Tübingen in a completely dark measurement chamber lined with sound absorbing foam. We used glass terraria as experimental cages (40 × 21.5 × 30 cm). The cage floor was covered with paper towel. For the substrate treatment, we used three different densities of hay: single straws, a 2 cm layer ('thin') and a 7 cm layer ('thick'). For the conspecific treatment, we placed an additional paper towel in the cage; it was either fresh (control) or had been in the home cage of a conspecific for 24 h. Our aim was to contrast the situation in which a shrew explores a new area without signs of potential presence of other shrews with that of a shrew entering an area that seems to be inhabited by another shrew, i.e. we aimed at manipulating the likelihood of conspecific presence in the area. We did not want the test shrews to engage in direct interactions with a conspecific and therefore decided against call playbacks or caging another shrew next to the test arena. Rather, we decided on olfactory labelling. Scent is a long-lasting cue and can ideally simulate a high likelihood of conspecific presence in the area. Shrews mark their home ranges by scent (Baxter & Meester 1982; Churchfield 1990), which implies that they can perceive and correctly interpret conspecific scent. Every shrew was tested once in each of the six possible treatment combinations. We used a pseudorandom protocol (Latin squares, Sokal & Rohlf 1995) to factor out effects of task sequence. The experimenter triggered recordings from outside the chamber.

(c) *Call recording and analysis*
Calls were recorded for the first 2 min of exploration with a broadband condenser microphone (custom A/D converter; SR 256 kHz; ultrasonic condenser microphone: frequency response ±3 dB between 20 and 160 kHz, ±8 dB between 4 and 20 kHz; external A/D converter: 16 bit depth, 480 kHz sampling rate; Animal Physiology, University of Tübingen) mounted 32 cm above the cage floor. Sound levels are given as at the microphone. Behaviour was filmed under infrared illumination. Visual counting of all calls on spectrograms was difficult, because they partly overlapped with loud clicks and noise when the shrew moved through the substrate. Therefore, we played the recordings at half the original speed and counted all audible shrew calls. Call rate was measured as calls per recording time. As call rate varied considerably among individual shrews, we normalized it for graphic display by computing the percentage of calls uttered per treatment type. For statistical analysis, we conservatively used the untransformed data. We measured call parameters from a subset (greater than 2000 per species) with good signal-to-noise ratio (Selena, University of Tübingen, 2048 fast Fourier transform (FFT), reading accuracy improved by FFT overlap to 1 ms and by zero-padding to 62 Hz).

(d) *Ensonification experiments*
The echo recordings were conducted in the fields and forests surrounding the Seewiesen Max Planck Institute in natural shrew habitats. An 'artificial shrew' (26HH high-sensitivity measurement microphone and 12HF power module, G.R.A.S., Holte, Denmark; A/D converter as above; sampling rate 192 kHz; speaker from Sennheiser HD 595) was placed on the ground in a shrew-like position. We played artificial, shrew-like calls at naturalistic amplitude (tailored to resemble typical shrew calls as recorded during
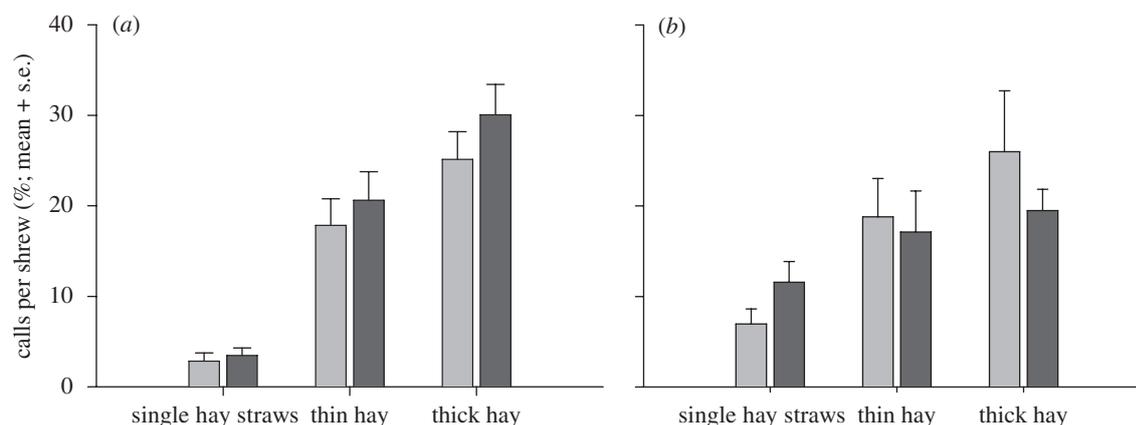
Figure 1. Call rates for (*a*) *Crocidura russula* (*n* = 9) (smell, $F_{1,8}$ = 1.13 and *p* = 0.318; substrate, $F_{2,16}$ = 22.68 and *p* < 0.001) and (*b*) *Sorex araneus* (*n* = 7) (smell, $F_{1,8}$ = 0.52 and *p* = 0.497; substrate, $F_{2,12}$ = 4.19 and *p* = 0.042) in the six experimental settings: three substrate (hay) densities, each with and without conspecific scent. Graphs show percentage data, while statistics (repeated-measures ANOVA; see text) were conservatively calculated with raw data. Grey bars, conspecific smell; black bars, control (no smell).
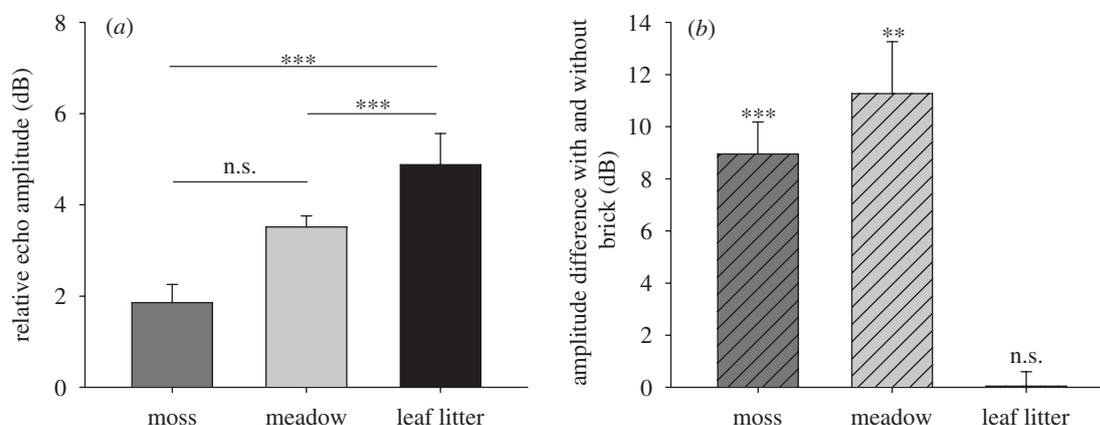

Figure 2. Echo amplitudes for reflections recorded from calls of the artificial shrew (for details, see §2). (*a*) Comparison of three different habitat types. Lines indicate *p*-values from a *post hoc* Tukey test. (*b*) 'Acoustic visibility' through substrate of a solid object (brick stone) positioned at 50 cm; bars depict differences between echo amplitudes with and without brick. Asterisks indicate *p*-values from *post hoc* paired *t*-tests: **<0.01; ***<0.001; n.s., not significant.

behavioural experiments: 10 ms; first harmonic sweeping from 5 to 8 kHz and 8 to 5 kHz, respectively; second harmonic present; 45 dB sound pressure level (SPL) at 32 cm). We recorded echoes from different habitat types: meadow, moss (mainly *Polytrichum* spp.) and forest floor covered in dry leaf litter (mainly *Fagus sylvatica*). We extracted the highest amplitude values for the time–frequency region where an echo of the second harmonic from 50 cm ahead would be expected from spectrogram pixels using SELENA and a custom MATLAB (The MathWorks) program. With these data, we assessed two questions. (i) Does the echo SPL differ between substrates; i.e. could shrews potentially get echo-borne information on the type of habitat in front of them? (ii) Does a large object (landmark or obstacle) reflect an echo perceivable *through* substrate; i.e. could shrews extract routing information from reverberations of their calls? For the latter question, we placed a brick stone (24.5 × 11.5 × 5.0 cm) 50 cm ahead of the artificial shrew *in* the substrate.

Statistical analyses were computed with SPSS 15.0 for Windows.

3. RESULTS

Olfactorily simulated increased likelihood of conspecific presence did not influence call rates in either species (figure 1). In contrast, substrate density clearly affected call rate in both species.

Calls were on average 8–16 ms multi-harmonic tonal signals, with a frequency range of 4–8 kHz for the first harmonic (range of individual means for nine *C. russula* and seven *S. araneus*) at sound levels of 40 ± 2 dB SPL (mean ± s.d.; *Crocidura*) and 46 ± 2 dB SPL (*Sorex*). Higher harmonics were usually present, but the main call energy was always in the sonic range (<20 kHz). The frequency modulation pattern was quite variable (upward, downward, constant or first up- and then downward modulated calls). Median pulse interval was 0.5 s (interquartile range, 0.2–1.4 s, *Crocidura*) and 0.4 s (0.2–1.1 s, *Sorex*).

The echo SPLs recorded with the artificial shrew differed between habitat types; they were lower for moss vegetation than for both meadow and leaf litter (figure 2). A brick stone, a potential landmark or obstacle to a shrew, increased the echo SPL through moss and meadow, but not through leaf litter.

4. DISCUSSION

The lack of any change of call rate in response to simulated increased likelihood of conspecific presence argues against a predominantly communicative function of twittering in shrews. Yet, the frequency

modulation pattern was quite variable and partly matched previous descriptions of shrew vocal repertoires (Churchfield 1990; Simeonovska-Nikolova 2004), which might indicate an additional communicative function. In bats, echolocation and communication are mutually non-exclusive call functions (Fenton 2003). We consider it unlikely that the shrews vocalized less in more open situations to reduce conspicuousness to predators, because even the denser substrate treatments would not have provided shelter from an attacking carnivore or raptor.

The finding that substrate density affected call rate in both species supports the echo-orientation-hypothesis and suggests that shrews use the echoes and reverberations of their calls for probing habitat routing or type. The shrew signals were tonal, larynx-produced calls in the sonic range and matched well with the range of best hearing for shrews (2–20 kHz; Konstantinov & Movchan 1985). We found no 'echolocation clicks'. In shrews, there is no evidence for the degree of sophistication present in bat echolocation; rather, we suggest that they may use call reverberations for simple, close-range spatial orientation. The low amplitude of the shrew calls probably avoids eliciting the middle-ear reflex (cf. Pilz *et al.* 1997), which would impair perception of returning echoes from close distances. However, overlap of outgoing call and returning echoes from nearby objects will confront the shrews with the problem of forward masking (Schnitzler *et al.* 2003). For example, at the end of emitting a 10 ms call, a shrew would receive reflections of the call onset from objects up to 1.7 m distance. Further, the perception of single echo targets will be hampered by overlapping background echo (backward masking). Use of echo information for foraging thus appears extremely unlikely, because shrew prey is substrate borne and often at only a few centimetres distance from the shrew. Prey echo will overlap with and not differ from substrate echoes and outgoing calls (Churchfield 1990; Siemers & Schnitzler 2004). Dealing with masking was surely a major challenge for the evolution of echolocation (Fenton *et al.* 1995). Bats reduce masking by shortening call duration as they come closer to objects of interest (Schnitzler *et al.* 2003). Broad call bandwidth probably helps bats to separate call and echoes in time within the different frequency channels of the hearing system (Siemers & Schnitzler 2004). Many of the shrew calls we recorded were broadband, multi-harmonic and frequency modulated and accordingly reduce masking. This was also evident in our echo analyses. Nevertheless, shrews will typically experience call–echo overlap and a multitude of overlapping substrate echoes. Except for large and thus strongly reflecting objects, such as a big stone or tree trunk, they will probably not be able to disentangle echo scenes, but rather derive information on habitat type from the overall call reverberations. This might be comparable to human hearing whether one calls into a beech forest or into a reverberant wine cellar.

Our ensonification experiments showed that shrew-like calls can indeed yield echo scenes useful for habitat assessment at close range, but beyond the reach of the shrews' vibrissae. Assessment of large objects in the substrate would be important for shrews to plan routing, avoid barriers and find escape routes

(Tomasi 1979; Forsman & Malmquist 1988) and shelters. As evidenced by our measurements, a large object is echo-acoustically detectable through grass or moss vegetation because of the rather low frequencies and hence long wavelengths of shrew calls (5 kHz approx. 6.9 cm; 15 kHz approx. 2.3 cm; echo intensity drops when the wavelength of the incident sound increases to well above the reflector size (Morse & Ingard 1986)). In contrast, leaf litter reflected a strong echo and was acoustically 'opaque'. The differences in reflection strengths between substrates might be a simple means for shrews to coarsely assess the habitat type. Indeed, Buchler (1976) had successfully trained shrews to discriminate stone from vegetation using echolocation. Bats probably distinguish different foliage types by their echo patterns (Grunwald *et al.* 2004; Yovel *et al.* 2008); birds possibly probe terrain echo acoustically using flight calls (Griffin & Buchler 1978). Performance tests will be needed to investigate further how shrews assess their close-range surroundings by echo information.

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