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Comparing passive and active hearing: spectral analysis of transient sounds in bats

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SUMMARY

In vision, colour constancy allows the evaluation of the colour of objects independent of the spectral composition of a light source. In the auditory system, comparable mechanisms have been described that allows the evaluation of the spectral shape of sounds independent of the spectral composition of ambient background sounds. For echolocating bats, the evaluation of spectral shape is vitally important both for the analysis of external sounds and the analysis of the echoes of self-generated sonar emissions. Here, we investigated how the echolocating bat *Phyllostomus discolor* evaluates the spectral shape of transient sounds both in passive hearing and in echolocation as a specialized mode of active hearing. Bats were trained to classify transients of different spectral shape as low- or highpass. We then assessed how the spectral shape of an ambient background noise influenced the spontaneous classification of the transients. In the passive-hearing condition, the bats spontaneously changed their classification boundary depending on the spectral shape of the background. In the echo-acoustic condition, the classification boundary did not change although the background- and spectral-shape manipulations were identical in the two conditions. These data show that auditory processing differs between passive and active hearing: echolocation represents an independent mode of active hearing with its own rules of auditory spectral analysis.

Key words: background noise, call analysis, hearing, spectral shape, perceptual constancy.

INTRODUCTION

The colour constancy of the visual system is a well-known perceptual phenomenon that enables the constant perception of an object's colour despite changes in the spectral composition of the light illuminating the object (Smithson, 2005). Humans perceive the colour of a white object still as white and the colour of a red object still as red, independent of illumination by yellowish candle light or greenish neon light.

The timbral constancy of the auditory system (Risset and Wessel, 1982) is an analogous perceptual phenomenon that allows the perception of the spectral shape of a sound (i.e. its timbre or acoustic colour) despite spectral changes caused by the environment (Watkins, 1991). The spectral shape of a sound signal is one major component for the identification, grouping and segregation of different auditory signals (Bregman, 1990; Moss and Surlykke, 2001; Griffiths and Warren, 2004). However, the spectral shape of acoustic waves is distorted during propagation in an unpredictable manner (Wiley and Richards, 1978; Lawrence and Simmons, 1982), thus blurring the information content of the sound. The spectrum of a sound reaching the ear is hence the product of the spectrum of the sound source and the spectrum of the surrounding.

Two options exist to cope with such acoustic distortions: either the sender adapts its vocalization behaviour, or the receiver compensates for these distortions. Species of almost all vertebrate classes show the first option, i.e. changes in their vocalization behaviour, e.g. frogs (Feng et al., 2006), birds (Lengagne et al., 1999; Slabbekoorn and Peet, 2003; Brumm, 2004; Slabbekoorn and den Boer-Visser, 2006), monkeys (Egnor et al., 2007) and whales (Au et al., 1985; Miller et al., 2000; Foote et al., 2004). Bats, in

addition, are generally very adept in adjusting their echolocation calls to changed acoustic conditions (Kalko and Schnitzler, 1993; Gillam et al., 2007). The second option, the timbral constancy of perceived sounds, has only been investigated in humans. Despite the ubiquitous distortions of the spectral envelope of acoustic signals, humans can easily identify them. The auditory system compensates for the spectral characteristics of the environment, resulting in an undistorted perception of the original spectrum of the signal (Risset and Wessel, 1982; Watkins, 1991). When the frequency response of the environment is experimentally manipulated, timbral constancy leads to several perceptual phenomena, such as the 'phoneme boundary shift' between intergradient vowels (Watkins, 1991), the 'flat spectrum vowel effect' (Summerfield et al., 1987) and the 'Zwicker tone' (Zwicker, 1964).

Echolocating bats allow comparison between potentially different mechanisms of auditory spectral processing, since they use both passive and active hearing. The spectral information in both contexts is of great importance and needs to be perceived correctly. Passive hearing is used for vocal communication and rustling prey detection (Esser and Schubert, 1998; Boughman and Wilkinson, 1998; Arlettaz et al., 2001) and we would expect bats to compensate for spectral distortions in the same way as humans. Active hearing, or echolocation, is used for spatial orientation and airborne prey detection (Schnitzler et al., 2003) by listening for the echoes of self-generated ultrasonic calls and evaluating their temporal and spectral properties. For example, bats identify and discriminate objects exclusively on the basis of their different spectral reflection patterns (von Helversen and von Helversen, 2003). Bats even separate and generalize the size-invariant spectral reflection pattern of the same object with different sizes from the

size-variant spectral reflection pattern (von Helversen, 2004; Simon et al., 2006).

The neuronal processing of auditory information is different in passive hearing and active echolocation and is closely coupled to and directly influenced by the vocalizations during echolocation (Suga and Schlegel, 1972; Schuller, 1979). The behavioural responses to auditory stimuli may thus differ in the same experimental task between passive and active hearing. However, whether this is the case was only investigated in one study on the temporal processing of communication sounds and echoes (Schuchmann, 2006).

In this study, we examined, in two experiments, how bats classify the spectral shape of transient foreground stimuli in relation to a simultaneous noise background with a constant spectral shape. The two experiments differed only in the type of signal that needed to be classified: in the passive-acoustic experiment, the bats had to classify passively presented filtered impulses, which were temporally uncorrelated to their echolocation calls. In the active-acoustic experiment, filtered replica of their recorded echolocation calls were played back in real-time through a loudspeaker, thus generating a virtual echoacoustic object. During both experiments, a continuous noise background was presented, the spectral shape of which was constant during a given trial and could be altered between trials.

During passive hearing, we expected the bats to use the background as a reference for the spectral analysis of the transient foreground stimuli, as humans do (Watkins, 1991). Thus, if the spectral shape of the background was changed, we hypothesized that there would be a shift in the classification as a result of the compensation for the changed environmental transfer characteristics. During echolocation, we hypothesized that there would be no influence of a passively presented constant noise on the spectral classification of echoes, if bats processed echoes differently from passive acoustic signals.

MATERIALS AND METHODS

In two separate experiments on passive and active hearing, bats of the species *Phyllostomus discolor* were trained to classify signals with different spectral shape as containing more energy either in the high or low frequencies. After a training period with two signals that were easily distinguishable by their spectral shape, the bats' spontaneous classification of intermediate test signals was assessed depending on the spectral shape of a noise background.

Animal housing and training procedure

Nine adult, male pale spear-nosed bats, *Phyllostomus discolor* Wagner 1843, were trained in the experiments. They were housed in groups of two to five animals per cage (80 cm×60 cm×80 cm) on a 12 h:12 h dark:light cycle, but were allowed to fly in a large room for several hours each day. Animals had free access to water. On training days, they received food only as a reward in the experiment. Additional food (fruit and mealworms) was given at the weekends. Bats were usually trained daily for 20–30 min on 5 days per week, followed by a 2 days break.

Bats were trained in a two-alternative, forced-choice paradigm to discriminate a highpass filtered training stimulus (+6 dB/octave) from a lowpass filtered training stimulus (–6 dB/octave) during continuous playback of white noise. Bats indicated their decision by crawling into the left or right arm of a Y-shaped maze. Correct decisions were rewarded with banana-pulp; wrong decisions were neither rewarded nor punished. The next trial started when the animal had crawled back to the starting position at the top of the Y-shaped
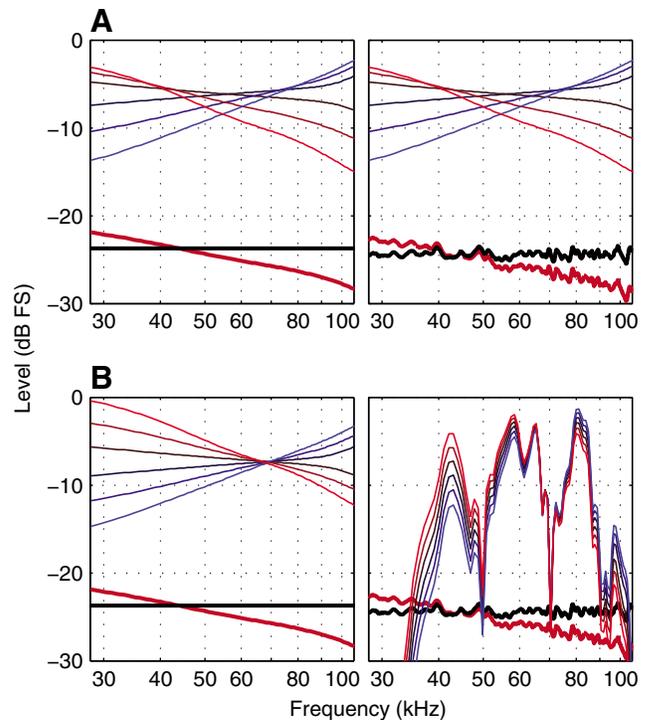

Fig. 1. Filter transfer functions and amplitude spectra of example stimuli. (A) Experiment 1 (passive hearing). (B) Experiment 2 (echolocation). The graphs on the left show the transfer functions of the filters used to generate the foreground stimuli and the noise background. The graphs on the right show examples of the amplitude spectra of the finally presented stimuli, i.e. after convolution of the filters with a foreground signal (an impulse or a recorded echolocation call) and with white noise. FS, full scale. Thick lines, noise background (filter slope of 0 dB/octave or –3 dB/octave); thin lines, foreground stimuli (filter slopes from –6 dB/octave to +6 dB/octave). The amplitudes of the spectra do not illustrate the amplitude of the finally presented stimuli, which cannot be easily compared and additionally depend on the applied attenuation and on the call amplitude.

maze. The presented stimulus, and thus the rewarded side, was selected pseudo-randomly (Gellermann, 1933).

Data collection of the test conditions began after the bats classified the two training stimuli correctly with >75%. Presentation of training stimuli was continued, serving as controls for a constant classification performance, while the test stimuli were interspersed between these control trials with a probability of 20–40% (Experiment 1) or 20% (Experiment 2). During a test trial, one out of 10 different test stimuli was selected randomly (see the next sections for description of the stimuli). Test trials were always rewarded, independent of the bat's decision. Only the test trials of days with a control performance >75% correct were included into the analysis.

We collected data of three bats in Experiment 1 (passive hearing) and of two bats in Experiment 2 (echolocation). Five animals (two in Experiment 1, three in Experiment 2) did not learn to classify the control stimuli and could thus not be used for testing. Most of these individuals were too inactive and did not explore the setup. This was, for example, the case for Bat 2, which was successfully trained in Experiment 1, but did not cooperate anymore in Experiment 2. Other bats were too active and crawled quickly through the setup without paying enough attention. For example, one bat in Experiment 2 learned the task, but only showed a stable performance once or twice within several weeks.

+6 dB to the five selected calls per sequence and calculating their frequency centroid on a logarithmic frequency axis. The frequency centroid divides the amplitude spectrum into two parts with equal energy and can therefore be used as a measure for the frequency distribution.

Statistics

As we were limited to a small number of animals, we used each animal as its own control for the behavioural data. Behavioural classifications of the same foreground stimuli with different noise backgrounds were compared using Fisher's exact test. Behavioural mean data were tested using Student's paired one-sided *t*-tests, testing the null hypothesis against the one-sided alternative hypothesis that the percentage of highpass classification increases with pink-noise background. Student's two-sided *t*-tests were used to compare means of the call parameters across backgrounds (Matlab 7.1).

RESULTS
Experiment 1: perceptual compensation during passive hearing

Three bats were successfully trained to discriminate highpass filtered impulses (+6 dB/octave) from lowpass filtered impulses (–6 dB/octave), which were superimposed on a white-noise background (control, χ^2-test, $P<0.0001$). The open symbols in Fig. 2 show that in these trained conditions, all three bats performed highly reliably, in that highpass filtered impulses were classified as highpass in about 90% of the trials and lowpass filtered impulses were classified as highpass in only about 10% of the trials. With a white-noise background, the bats' spontaneous classification of the test stimuli with intermediate filter slopes depended in general monotonically on the filter slope (solid black symbols in Fig. 2). The perceptual classification boundary (vertical black lines in the lower part of the panels in Fig. 2) is on average at –0.1 dB/octave, and thus very similar to the physical filter boundary of 0 dB/octave. With a pink-noise

background, however, the bats classified the same stimuli more often as highpass (red symbols in Fig. 2). Consequently, the perceptual classification boundary shifted towards negative slopes (vertical red lines in the lower part of the panels in Fig. 2). For the individual bats, this downward shift of the perceptual classification boundary amounted to 1.8, 1.0 and 0.8 dB/octave, with a significant mean downward shift of 1.2 dB/octave [Student's one-sided paired *t*-test, $t(2)=5.52$, $P=0.0156$]. Accordingly, the mean difference in highpass classification between pink and white-noise background (black bar in Fig. 2D) is significantly larger than zero [Student's one-sided *t*-test, $t(5)=2.21$, $P=0.0391$]. In summary, all three bats compensated for the spectral shape of the noise background.

Note that the possible shift of the perceptual classification boundary is limited by ceiling effects. These are apparent in the averaged psychometric functions (Fig. 2D) where the degree of highpass classification of signals with a slope of +3.6 or +6 dB/octave did not increase further when the background was changed from white to pink.

Experiment 2: spectral processing during echolocation

In this experiment, the bats were trained to classify the spectral transfer function of a filter, and not the presented sounds themselves. As the filter was excited by the bats' echolocation calls, the perceptual task was to evaluate spectral changes of the perceived echoes, relative to the emitted calls.

Two bats were successfully trained to discriminate highpass filtered echoes (+6 dB/octave) from lowpass filtered echoes (–6 dB/octave), superimposed on white-noise background (control, χ^2-test, $P<0.0001$; open symbols in Fig. 3). As we showed for the passive-acoustic classification of impulses, the spontaneous classification of filters with intermediate spectral slopes and a white-noise background depended monotonically on the filter slope (solid black symbols in Fig. 3). However, in contrast to the passive-acoustic experiment, the classification of the same test filters was not affected by the change from a white
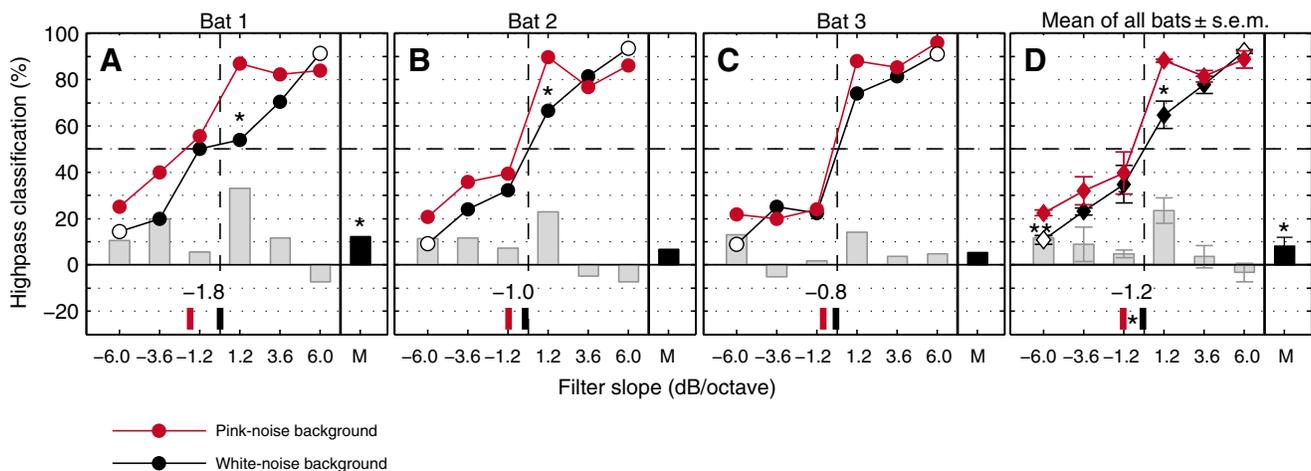
Fig. 2. Experiment 1 (passive hearing): classification of filtered impulses by three bats (A–C) and their means ± s.e.m. (D). The performance is plotted as percentage of highpass classification *versus* the filter slope. Trials with presentation of white-noise background are shown with black symbols, and trials with pink-noise background are shown with red symbols. The two training/control conditions (±6 dB/octave and white noise) are indicated with open symbols. The grey bars show the difference in highpass classification between pink- and white-noise background. Their mean difference across all six filter slopes (indicated by M) is shown as a black bar. The perceptual classification boundaries per background are indicated by vertical lines in the lower part of each panel (black, white-noise background; red, pink-noise background). The shift in the perceptual classification boundary from white- to pink-noise background is given above the vertical lines in units of dB/octave. Only the mean perceptual classification boundary could be tested for significance. *$P<0.05$, **$P<0.01$.
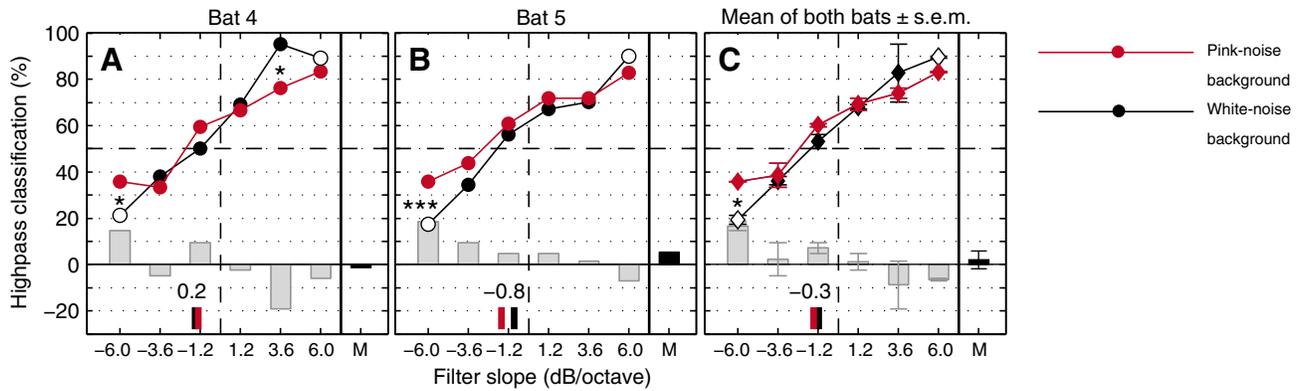
Fig. 3. Experiment 2 (echolocation): classification of filtered echolocation calls by two bats (A,B) and their means ± s.e.m. (C) during presentation of white-noise (black symbols) and pink-noise background (red symbols). Notation as in Fig. 2. *P<0.05, ***P<0.001.

to a pink-noise background (red symbols in Fig. 3). The shift of the perceptual classification boundary was positive in Bat 4 and negative in Bat 5, with a non-significant mean shift of –0.3 dB/octave. Accordingly, the mean difference in highpass classification between pink- and white-noise background equals almost zero (black bar, Fig. 3C).

Effect of the roving level

In both experiments, the foreground level was roved to prevent the bats from using loudness cues for classification. In addition to the filter slope, which was the reinforced cue, this roving level also influenced the classification during Experiment 2 (echolocation), but not during Experiment 1 (passive hearing). Fig. 4A,B illustrates this effect for the control data of Experiment 2, which are plotted as a

function of echo level. This shows that highpass controls were mostly classified as highpass (>90%), with a small decrease in performance for louder echoes. By contrast, lowpass controls were classified correctly at high levels, but incorrectly at low levels with errors of up to 60%. A similar, more pronounced pattern is visible for the test echoes (Fig. 4C,D).

Echolocation calls

P. discolor emits multiharmonic, downward frequency-modulated calls. Calls were very short, having 90% of their energy within less than 0.7 ms (median ~0.4 ms; Fig. 5A). The mean fundamental frequencies were 18.4 and 19.5 kHz for Bats 4 and 5, respectively (Fig. 5H). The –20 dB bandwidth was around 55 kHz with cut-off frequencies at 36–38 kHz and at 91–93 kHz (Fig. 5C–E), which was
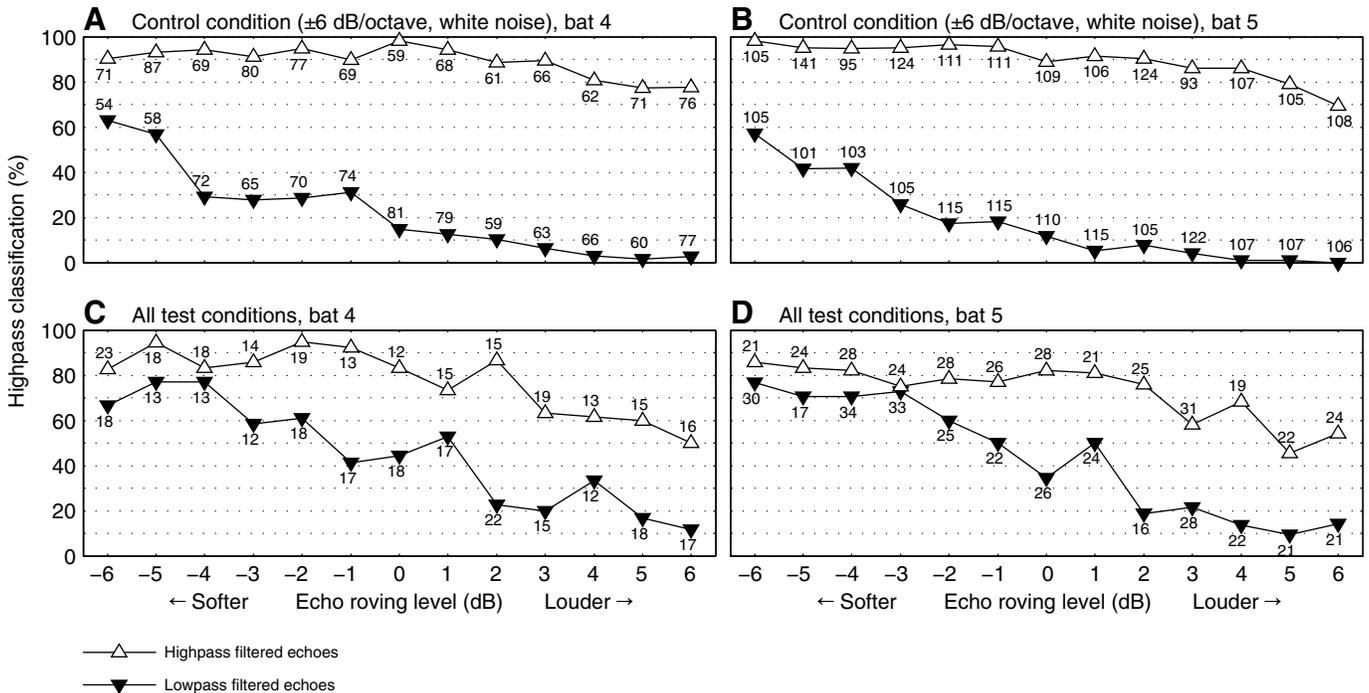
Fig. 4. Experiment 2 (echolocation): influence of the roving level on signal classification. Classification of the same filtered echoes by the same bats as in Fig. 3, but here plotted as a function of echo level. (A,B) Control signals (±6 dB/octave, white-noise background). (C,D) Test signals (white noise: ±1.2 and 3.6 dB/octave, pink noise: ±1.2, 3.6 and 6.0 dB/octave). Numbers above the data points give the number of trials.
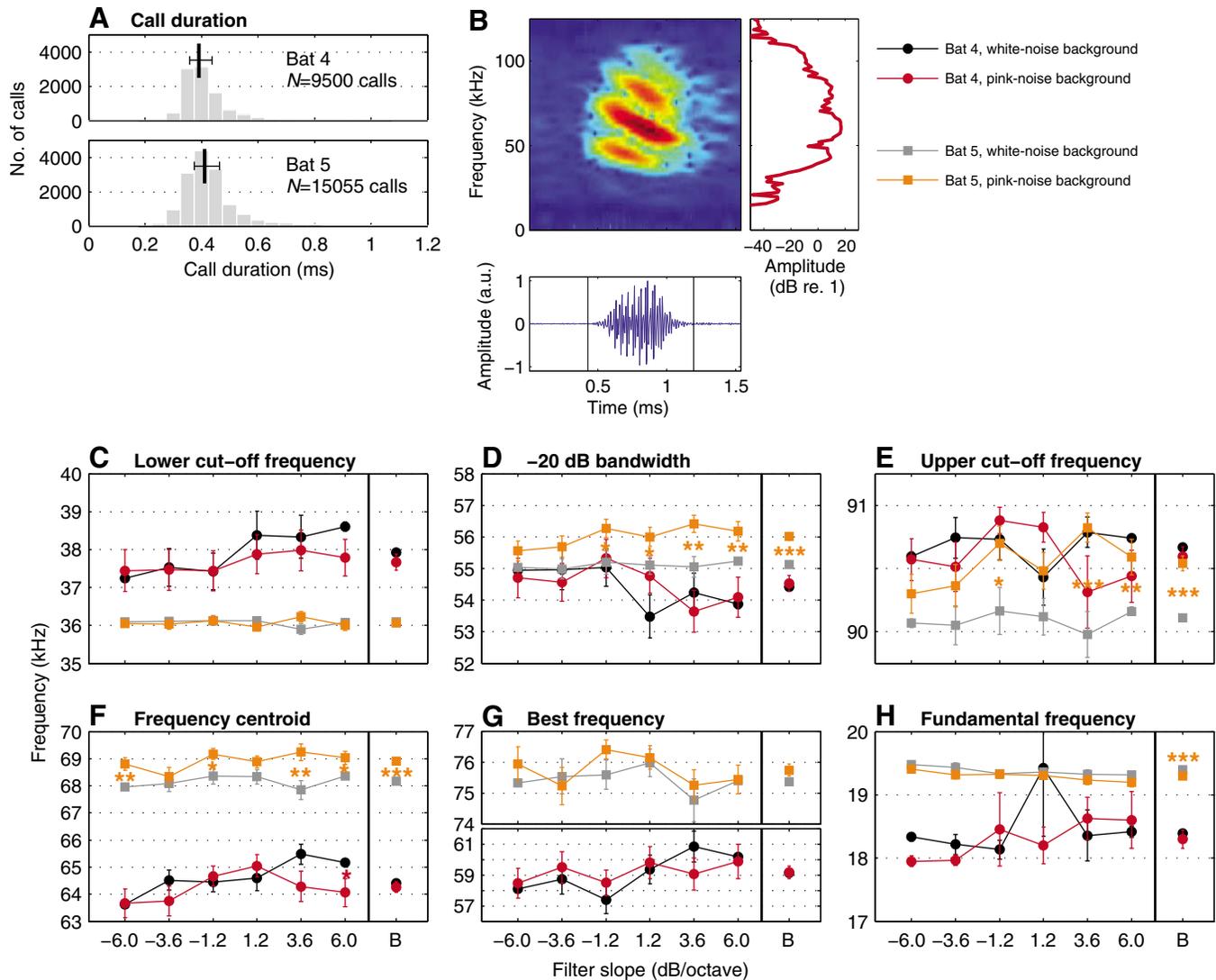
Fig. 5. Call parameters of *Phyllostomus discolor* in Experiment 2 (echolocation). (A) Histogram of the durations of the analysed calls. Median and quartiles are indicated by the vertical lines. (B) One example call of Bat 4 plotted as spectrogram (top), as oscillogram (bottom) and as amplitude spectrum (right). The amplitude spectrum was calculated from the section between the vertical lines in the time signal. (C–H) Spectral parameters. For analysis, we used the five calls with the highest signal-to-noise ratio per sequence and calculated the mean per sequence of every parameter. The means per sequence were then grouped, either per stimulus (i.e. the combinations of filter slope and noise backgrounds; the larger part of the panels, between –6.0 and +6.0 dB/octave; N=33–59 sequences per test stimulus, 766–1252 sequences per control stimulus) or per noise background (small right part of the panels, marked B; N=214–2694 sequences per background), and their second order mean ± s.e.m. was plotted. Note the different scales of the y-axes. Grey symbols, white-noise background; coloured symbols, pink-noise background. *$P<0.05$, **$P<0.01$, ***$P<0.001$.

about the same for both bats. Inter-individual differences were only found in the energy distribution across frequencies: the frequency centroid of Bat 4 is about 4–5 kHz lower than in Bat 5 (Fig. 5F), and its best frequency is about 15 kHz lower than in Bat 5 (Fig. 5G). Thus, calls of Bat 4 had most energy in the third harmonic (58–60 kHz), whereas calls of Bat 5 had most energy in the fourth harmonic (75–76 kHz). Hence, both bats performed the spectral classification task with partially different spectral call structures.

The noise background and the different filter slopes only partially influenced the call structure. Bat 4 showed no systematic background-correlated differences in its call parameters. Bat 5 slightly increased the level of the higher harmonics of its calls during the presentation of pink-noise background: the –20 dB bandwidth and the frequency centroid was about 1 kHz higher [Fig. 5D,F,

$t(3099)=-4.04$, $P<0.0001$], which was caused by an increase in the upper cut-off frequency [Fig. 5E, $t(3099)=-4.04$, $P<0.0001$]. Alternatively, it is possible that the bat accomplished this frequency increase by reducing its fundamental frequency by 0.1 kHz [Fig. 5H, $t(3099)=3.49$, $P=0.0005$], thus also reducing its fifth harmonic by 0.5 kHz. In consequence, the fifth harmonic moves further down into the pass band of the bat's vocal tract, and thus shifts the frequency centroid upwards.

DISCUSSION
In both experiments, bats were successfully trained to classify the spectral shape of transient foreground signals that differed in filter slope by 12 dB/octave (Fig. 1). Despite the differing spectral shape of impulses and echolocation calls, both source stimuli were

sufficiently broadband for a stable classification of these spectral changes. As the stimulus level was roved, the bats were prevented from using potential loudness cues introduced by the filtering. The bats thus learned to evaluate the filter-generated spectral changes.

Experiment 1: perceptual compensation during passive hearing

With pink-noise background, the bats classified the same passively heard impulses more often as highpass than during the presentation of a white-noise background. This shows that bats employ a compensatory mechanism during passive hearing similar to the one described in humans (e.g. Summerfield et al., 1987; Watkins, 1991). The perceptual compensation in humans is presumably based on the different rate of spectrotemporal variation between two different filters (Furui, 1986; Repp, 1987; van Dijkhuizen et al., 1987; Haggard et al., 1987): while the spectrum of transmission channels is fairly constant over time, the spectrum of natural sound sources varies rapidly. By taking the constant fraction of the overall perceived spectrum as a reference, the auditory system compensates for it and evaluates only relative changes to it. This results in a perceptual whitening of the environmental spectrum and in the perception of the undistorted spectral shape of the transmitted sound.

We found the same compensatory mechanism during passive hearing in bats. When the noise background was filtered with a constant lowpass filter, the bats compensated for this filter and perceived the same transient foreground stimuli as containing more high frequencies. Such a compensation allows animals to perceive the spectral shape of acoustic signals as it had been at the sound source, i.e. to perceive the spectral characteristics of the sound source despite changes in the absolute spectral shape of the acoustic signal that is impinging on the ear.

This timbral constancy of the auditory system is a high-level perceptual process (Watkins, 1991), as is the colour constancy of the visual system (Smithson, 2005); the colour constancy being mediated by cells in area V1 and V4 of the visual cortex (Zeki, 1983; Wachtler et al., 2003). As such, they are likely to be under cognitive control and may be employed only if necessary.

Experiment 2: spectral processing during echolocation

In contrast to passive hearing, the classification of echoes during active hearing was independent of the passively presented noise background. This shows (i) that the spectral processing of echoes differs from the spectral processing of transient passive acoustic stimuli, even in the identical experimental situation, and (ii) that the spectral processing of echoes is independent of simultaneous, passively presented acoustic signals.

In contrast to the auditory processing of passive sounds, the neuronal processing of echoes is coupled to, and influenced by, the vocalisation pattern (Suga and Schlegel, 1972; Schuller, 1979), for example by opening temporal processing windows (Roverud and Grinnell, 1985). Based on neurophysiological data, it was suggested for the gleaning bat *Antrozous pallidus* that it processes passively heard prey sounds and actively acquired echoes in two different, parallel auditory pathways (Fuzessery, 1994; Razak and Fuzessery, 2002), which converge later in the auditory cortex (Razak et al., 1999). Behaviourally, it was suggested that the auditory mechanisms for the temporal analysis of spatial echo information are under cognitive control and that they may be employed during passive hearing, but not during echolocation (Schuchmann et al., 2006; Schuchmann, 2006). The current study provides behavioural evidence that spectral processing also differs between passive and
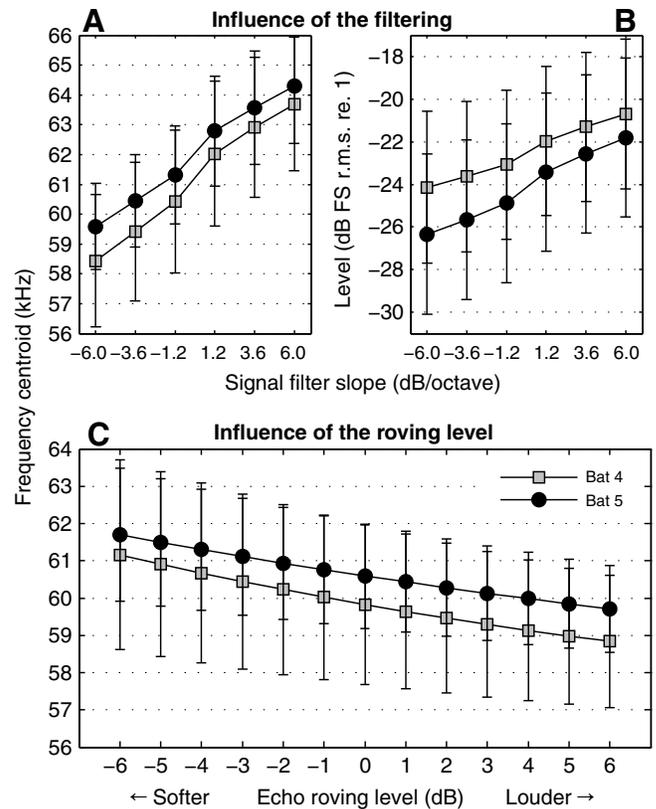
Fig. 6. Calculated influence of the stimulus filters and the roving level on the frequency centroid and the level of the recorded calls (mean ± s.d. of 9500 calls for Bat 4 and 15055 calls for Bat 5). (A) The stimulus filters, going from lowpass (–6 dB/octave) to highpass (+6 dB/octave), increased the frequency centroid of the recorded calls by about 5 kHz. (B) The stimulus filters, going from lowpass (–6 dB/octave) to highpass (+6 dB/octave), increased the r.m.s. level of the recorded calls by 2–3 dB SPL. (C) Increasing roving levels, i.e. higher overall levels, reduced the frequency centroid of the recorded calls by about 2 kHz.

active hearing. The reference for the spectral evaluation of echoes is thus not the constant spectral characteristics of external passive acoustic signals, but an internal reference, which can either be an efference copy of the motor signals that generated the last call, or an auditory reference generated from hearing the outgoing call.

In the current experiments, the background was never loud enough to mask the transient foreground. The evaluation of the echo spectral shape independent of ambient background sounds, as it was demonstrated here, does not mean that the bats would not suffer from masking at considerably higher background levels.

Effect of the roving level

In Experiment 2, echo classification was influenced by echo level; softer echoes were more often classified as highpass than louder echoes. Three explanations are conceivable for this: first, the bats might have used residual loudness cues to discriminate the filter slopes of –6 dB/octave and +6 dB/octave, thus rendering the applied roving level ineffective. To test this hypothesis, we filtered the recorded calls with the experimentally used filters and calculated their r.m.s. level. The level of lowpass filtered calls was 3–4 dB lower than the level of highpass filtered calls (Fig. 6B). This finding is in contrast to the experimentally observed level effect (Fig. 5)

which showed that softer echoes were more likely to be classified as highpass. Therefore, we reject this hypothesis.

Second, the spectral shape of the echo above hearing threshold might vary with echo level. To test this hypothesis, we applied a roving level of –6 to +6 dB to every recorded call and calculated the frequency centroid of the roved echo above hearing threshold on a logarithmic frequency axis as a measure for the perceived spectral shape. The hearing threshold of *P. discolor* was taken from Hoffmann et al. (Hoffmann et al., 2008), and for frequencies above 80 kHz from Esser and Daucher [(Esser and Daucher, 1996); magnitudes reduced by 28.5 dB to match the audiogram of Hoffmann et al. (Hoffmann et al., 2008)]. The frequency centroid increased by about 2 kHz for softer echoes (Fig. 6C). In comparison, the filters used for echo generation changed the frequency centroid by about 5 kHz (Fig. 6A), which is about twice as much as caused by the roving level. Frequency cues caused by the roving level should therefore be overruled by the direct spectral changes and are thus not sufficient to explain the influence of the roving level on their own.

Third, timbre, pitch and loudness are auditory perceptual dimensions that mutually interact in a complex non-linear fashion. For example the reaction time for stimulus classification in one of these dimensions depends in non-reciprocal ways on the other dimensions (Melara and Marks, 1990), with high pitch and high timbre both corresponding to loud signals, but high timbre corresponding to low pitch. In echolocation, small targets give more high frequent echo content than larger ones. Therefore, the bats may tend to classify faint targets similarly to high-pass filtered ones.

In summary, the joined effects of the bats perceptual associations between different stimulus qualities and the spectral composition of the echolocation calls combined with the bats' absolute hearing threshold can at least qualitatively explain the level dependence of the behavioural performance in Experiment 2. Note that the shape of the psychometric functions did not change if only a part of the trials was analysed, e.g. all trials with a roving level above 0 dB. Thus, the observed effect of the roving level does not confound the main result, i.e. the lack of influence of background spectral shape on echo spectral classification.

Echolocation calls

In addition to perceptual compensatory mechanisms, which are used during passive hearing, bats could compensate for spectral distortions during echolocation by adapting the call spectrum to the spectral shape of passive acoustic signals. Bats constantly adjust their signals to meet changing perceptual requirements. For example, call bandwidth is changed during prey interception (Schnitzler et al., 2003), presumably to increase object resolution (Siemers and Schnitzler, 2004; Boonman and Ostwald, 2007), and depending on the surroundings (Kalko and Schnitzler, 1993) and the calls of conspecifics (Gillam et al., 2007). If bats compensated for the lowpass characteristic of the passively presented noise background, they would need to shift the frequency centroid of their calls to lower frequencies. However, every consistent effect we found was in the opposite direction, i.e. with a pink-noise background, the frequency centroid was shifted to higher frequencies. These findings do not support the compensation hypothesis. Instead, this is further evidence that echo spectral processing is not influenced by passive acoustic stimuli. Passive and active hearing thus represent two different and separate modes of operation of the auditory system, where the spectral shape of passive sounds does not influence the evaluation of signals during active hearing.

CONCLUSION

The presented data show that the bat *Phyllostomus discolor* adapted the processing of passive acoustic signals to compensate for spectral distortions. Communication signals, or other passively heard sounds, can thereby be corrected for spectral changes generated by the environmental transfer function. Such changes are discernible from the constant spectrotemporal part of the same or other ongoing signals, such as ambient sounds, transmitted through the same transmission channel. By contrast, when the bats had to classify self-generated echoes instead of passively presented transient signals in exactly the same experimental paradigm, their classification was independent of the passively heard noise background. The spectral analysis of transient stimuli during echolocation, i.e. spectral echo analysis, thus recruits different auditory processing mechanisms than the spectral evaluation of passively heard sounds. The data provide psychophysical evidence for the hypothesis that bats switch to an independent mode of auditory processing during echolocation, which does not necessarily obey to the general rules of auditory spectral analysis. Thus, during echolocation, spectral echo analysis is not confounded by the spectral shape of faint ambient sounds.

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