

RESEARCH ARTICLE

The Lombard effect emerges early in young bats: implications for the development of audio-vocal integration

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ABSTRACT

Auditory feedback plays an important role in vocal learning and, more generally, in fine-tuning the acoustic features of communication signals. So far, only a few studies have assessed the developmental onset of auditory feedback. The Lombard effect, a well-studied audio-vocal phenomenon, refers to an increase in vocal loudness of a subject in response to an increase in background noise. Here, we studied the time course of the Lombard effect in developing bats, *Phyllostomus discolor*. We show that infant bats produced louder vocalizations in noise than in silence at an age of only 2 weeks. In contrast, the infant bats' morphology and vocalizations changed gradually until 2 months of age. Furthermore, we found that the Lombard magnitude, i.e. how much the bats increased their vocal loudness in noise relative to silence, correlated positively with the age of the infant bats. We conclude that the Lombard effect features an early developmental origin, indicating a fast maturation of the underlying neural circuits for audio-vocal feedback.

KEY WORDS: Animal communication, Audio-vocal integration, Echolocation, Environmental noise, Signal plasticity

INTRODUCTION

Auditory feedback is widely used among birds and mammals for fine-tuning the spectro-temporal features and to guide the adjustments of the loudness of their vocalizations (Lombard, 1911; Brumm and Zollinger, 2011, 2013; Zollinger and Brumm, 2011; Hotchkyn and Parks, 2013). The Lombard effect, an audio-vocal integration phenomenon, refers to an increase in vocal loudness of a subject in response to an increase in background noise. The Lombard effect represents a principal vocal strategy by both birds and mammals (including humans) to reduce noise interference in acoustic communication (Lombard, 1911; Brumm and Zollinger, 2011; Zollinger and Brumm, 2011; Hotchkyn and Parks, 2013). Recent evidence suggests that the Lombard effect also occurs in lower taxonomic groups such as fish (Holt and Johnston, 2014) and frogs (Shen and Xu, 2016), although another tested frog species did not show the Lombard effect (Love and Bee, 2010). Another feature of the Lombard effect is that it is very robust and is not possible to be inhibited in humans with instructions alone (Pick et al., 1989).

Despite the apparent importance of auditory feedback in acoustic communication, only a few studies to date have addressed the developmental onset of auditory feedback (Sanborn, 2010; MacDonald et al., 2012; Takahashi et al., 2013). Sanborn (2010) assessed the effect of delayed auditory feedback on the crying behaviour of human newborns at an age of 4 and 8 weeks. It was found that human newborns changed several acoustic parameters of their cry, despite large individual variability. In contrast, 2- to 3-year-old human toddlers did not compensate for the altered feedback of formant frequency as seen in both older children and adults (MacDonald et al., 2012). Similarly, in the first postnatal week, infant marmoset monkeys did not show evidence of using auditory feedback (Takahashi et al., 2013). At present, no data are available, to our knowledge, regarding the Lombard effect for human infants under 3 years (Siegel et al., 1976) and the Lombard effect has only been examined with adult animals.

Here, we assessed the developmental onset of the Lombard effect in an echolocating bat, the pale spear-nosed bat (*Phyllostomus discolor* Wagner 1843) (Fig. 1A). Because the Lombard effect is widespread in animal groups and is often considered as a basic audio-vocal integration phenomenon (Nonaka et al., 1997; Hage et al., 2006), we hypothesized that the Lombard effect is characterized by an early developmental origin which would thus indicate an early developmental origin of auditory feedback. *Phyllostomus discolor* is a fruit-eating bat relying on echolocation for spatial navigation and is one of the few species of mammals shown to be capable of vocal learning (Esser and Schmidt, 1989; Knörnschild, 2014). Infant bats start to fly at 5–6 weeks of age and wean at 3 months of age (Kwieceński, 2006). Adult bats produce short, frequency-modulated echolocation calls with most sound energy between 40 and 100 kHz (Fig. 1Bv) and a rich repertoire of social communication calls. Our previous work has shown that adult *P. discolor* bats exhibited the strongest Lombard effect when exposed with broadband background noise compared with other noise types (Luo et al., 2015). Although individual bats differed in the compensatory magnitude (i.e. the Lombard magnitude), all tested individuals showed a significant Lombard effect (Luo et al., 2015; Luo and Wiegrebe, 2016).

MATERIALS AND METHODS

Experimental design

Four mother–infant pairs of *P. discolor* were used for experiments. All four infant bats, from two different reproduction cycles, were born naturally in a reproductive colony at Ludwig-Maximilians-Universität München. Infants 1 and 2 were from one reproduction cycle, and infants 3 and 4 were from another reproduction cycle. *Phyllostomus discolor* typically gives birth to only one offspring per reproduction cycle. Details of the behavioural setup, recording and playback system, and testing procedures have been described in an earlier experiment (Luo and Wiegrebe, 2016). In brief, a pair of mother–infant bats was separated into two pyramidal mesh cages

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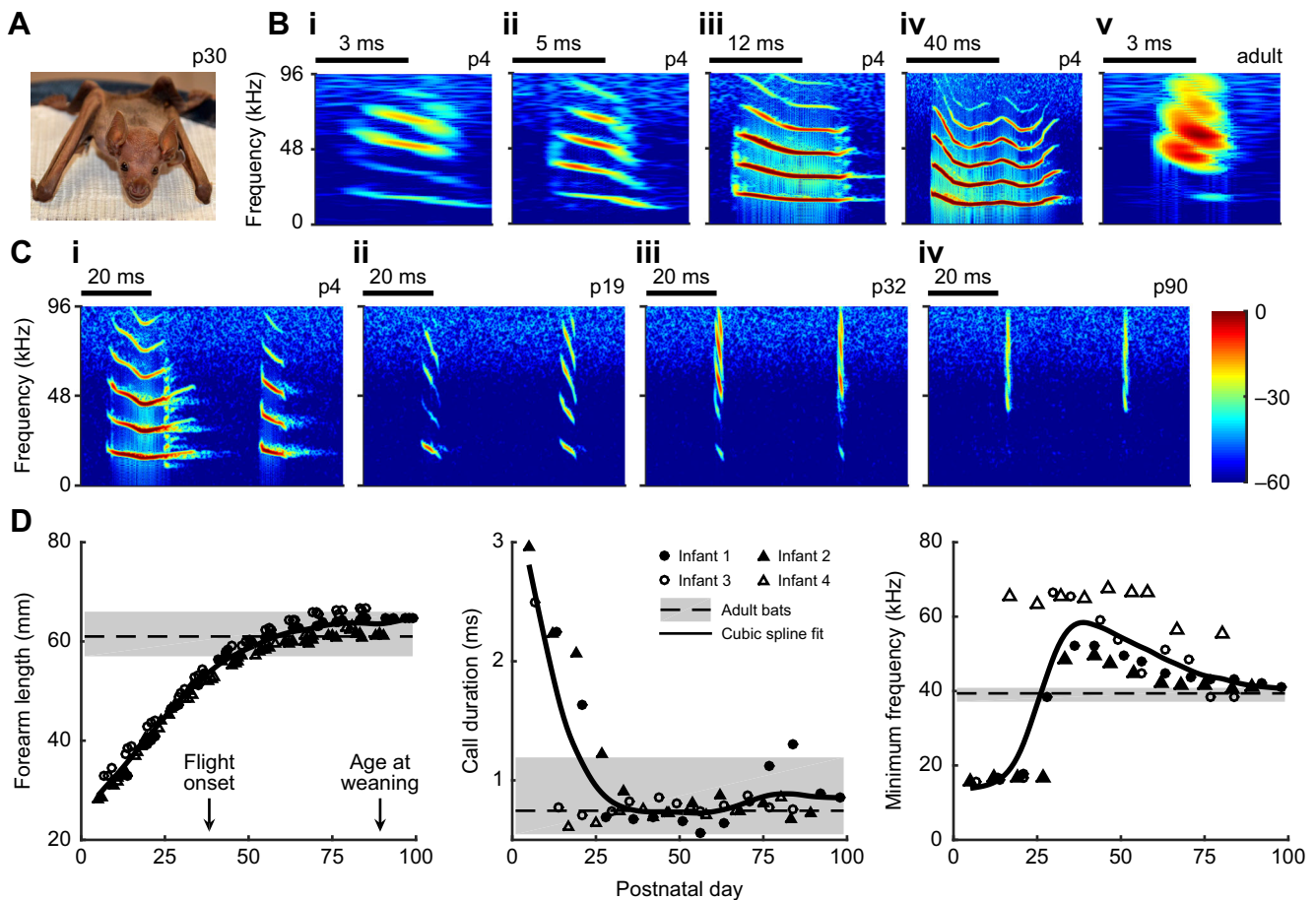


Fig. 1. Postnatal development of vocalizations and morphology in *Phyllostomus discolor*. (A) Infant bat at p30 (postnatal day 30) is not entirely furred. (B) Examples of different types of isolation calls of an infant bat at p4 and a typical echolocation call from an adult bat. (C) Short sonar-like vocalizations (panels i, ii and iii) were similar in structure to the echolocation calls (iv). (D) Developmental changes in forearm length, call duration and minimum frequency in infant bats. Data points shown for call duration and minimum frequency were the medians for each infant bat. Black dashed line and the borders of the grey shading indicate the median and the quartiles of the four adult bats. All sound recordings shown here are extracted from the silence control.

(30 cm high, 30×30 cm at the base and 10×10 cm at the top; Bat World Sanctuary, Weatherford, TX, USA) for a period of 19 min per experimental day. The distance between the cages was 1.1 m. The vocalizations of each bat were recorded by three ultrasonic microphones (CO 100K, Sanken, Saitama, Japan) placed horizontally in front of the bats at a sampling rate of 192 kHz. Whenever any of the two centre microphones received a signal of a peak amplitude ≥ 70 dB SPL, recordings of 1 s before and 1 s after the trigger event were saved. Uncorrelated band-pass-filtered white noise (10–90 kHz) that overlapped in frequency with the bats' typical vocalizations (10–100 kHz including both echolocation calls and communication calls) was broadcast from two omnidirectional loudspeakers (Elac 4PI PLUS.2, Elac Electroacoustic, Kiel, Germany) between the bats. We achieved a flat frequency response of the speakers (± 1 dB) between 7 and 90 kHz through digital filtering of the noise with each speaker's compensatory impulse response. Apart from the silence control, there were three noise levels: 28, 40 and 52 dB SPL (sound pressure level re. 20 μ Pa). The 19-min test session comprised a 1-min habituation phase at the beginning, followed by three 3-min noise treatments and three 3-min silence treatments, in an alternating order. The control of the recording and playback systems as well as the testing procedures were automated through SoundMexPro

software (HörTech, Oldenburg, Germany) in MATLAB (v7.5, The MathWorks Inc., Natick, MA, USA) interfacing with an audio interface (Ultralite-mk3 Hybrid, MOTU, Cambridge, MA, USA). This experiment was approved by the Regierung von Oberbayern, Germany (permit no. 55.2-f-54-2532-34-2015).

We conducted the experiment on a weekly basis and typically collected data on three consecutive days per week. We used a balanced design to minimize the effect of noise presentation order. Specifically, for each week, the order of noise presentation was 28, 40 and 52 dB SPL for the first recording day; 40, 52, and 28 dB SPL for the second recording day; and 52, 28 and 40 dB SPL for the third recording day. The dates when the data collection began correspond to an age of postnatal day 4 (p4), p12, p7 and p9 for the four infant bats, respectively. The dates when the data collection stopped correspond to an age of p90, p99, p85 and p81 for the four infant bats, respectively. Additionally, we measured the forearm length and the body mass of the infant bats on each recording day.

Sound analysis

We performed sound analysis with custom-written programs in MATLAB adapted from Luo and Wiegbe (2016). Recordings were high-pass filtered at 5 kHz and compensated for the uneven frequency response of the microphones. Subsequently, all calls with

the peak amplitude ≥ 70 dB SPL (the recording threshold) were detected, extracted and measured. For each call, we measured its duration, RMS amplitude across the duration, and minimum and maximum frequencies. Here, a call was taken as the recording samples with its amplitude ≥ 3 times of the maximum amplitude of the noise floor after smoothing. To estimate the minimum frequency and the maximum frequency, we artificially separated calls into two groups based on call duration: short vocalizations (call duration < 4 ms) and long vocalizations (call duration ≥ 4 ms). Short vocalizations of the infant bats were similar in structure to the adult echolocation calls (Fig. 1B,C) and might be a precursor of echolocation calls in some bat species (Habersetzer and Marimuthu, 1986). Long vocalizations are social calls and are approximately 20–30 dB louder than short vocalizations. Then, -10 dB and -30 dB threshold criteria were applied to the short vocalizations and long vocalizations, respectively. Here, a fixed threshold criterion is not suitable because of the large amplitude difference between short vocalizations and long vocalizations (up to 60 dB). Thus, the minimum/maximum frequency was estimated as the frequency component with 10 dB lower intensity than the frequency component with the maximum intensity from the power spectrum for the short vocalizations. More details of sound analysis were presented in another study (Luo and Wiegrebe, 2016).

To ensure the quality of the sound analysis, we additionally conducted systematic manual checks. Specifically, for each mother–infant pair, 60 s of recordings consisting of 30 randomly chosen 2 s sound files were manually checked graphically by examining the waveform, spectrogram and power spectrum, with all analyzed signal parameters displayed simultaneously. This procedure of manual check confirmed the high quality of the sound analysis program. The average error rates, defined as incorrectly analyzed calls to the total calls checked, were 4.3% (363/8441), 2.0% (297/15,230), 1.6% (49/3081) and 0.7% (21/2917) for the four mother–infant pairs, respectively. Here, incorrectly analyzed calls referred to the calls that would be excluded or reanalyzed if they were analyzed manually.

Statistics

Differences in call amplitude between different background noise levels and silence control were evaluated statistically by ANOVA in MATLAB (R2015b). Specifically, the ANOVA1.m function was used to calculate the mean differences between noise levels. Then, the MULTCOMPARE.m function was used for the *post hoc* pairwise comparison to estimate the Bonferroni-corrected *P*-values, which are denoted as P_{adj} . Before the statistical analysis, we first pooled the data for each recording week to increase the sample size and to control for the effect of the order of the noise presentation. Throughout the paper, all the statistical results are referring to the short vocalizations of durations < 4 ms or the echolocation calls of the adults. The 4 ms call duration criterion was chosen because it is slightly longer than the maximum call duration of the echolocation calls of the adult bats (~ 3.5 ms). Moreover, nearly all < 4 ms vocalizations in the infant bats were similar in structure to the adult echolocation calls, which was confirmed during the manual checking of the sound analysis procedure mentioned above. Nevertheless, we also performed all the statistical analysis and re-examined the main conclusions of the paper for two other duration criteria based on the histogram of the duration for each infant bat (Fig. S1). As can be seen, our conclusions hold for all the three evaluated duration criteria (Fig. S1, Tables S1, S2). For long vocalizations alone, we found little evidence for the Lombard effect. This is probably because the high signal-to-noise ratio between the

long vocalizations and the noise level: even for the maximum noise level of 52 dB SPL, the bats still had a signal-to-noise ratio of more than 50 dB.

RESULTS

We tested the Lombard effect in both infant bats and their mothers across the developmental stage of the infants from a few days after birth to 3 months. Bats were exposed to white noise (10–90 kHz) at three faint to moderate sound levels – 28, 40 and 52 dB SPL (re. 20 μPa) – in addition to a silence control. We analyzed between 23,000 and 34,000 short sonar-like vocalizations (call duration < 4 ms; e.g. Fig. 1Cii–iv; see Materials and methods for details) from four infant bats and between 6400 and 202,000 echolocation calls from their mothers. The exact sample sizes are provided in Table S1.

Echolocation and communication calls develop gradually in infant bats

When infant bats are separated from their mothers, they produce a suite of vocalizations, termed isolation calls, which function to attract their mothers (Brown, 1976; Brown and Grinnell, 1980). The isolation calls of *P. discolor*, as shown in Fig. 1B, varied greatly in structure. It is interesting to note that some of the isolation calls of newborn infants (Fig. 1Bi,ii) were similar in structure to the echolocation calls of the adult bats (Fig. 1Bv). The same phenomenon was described in an earlier study for the same species of bat (Esser and Schmidt, 1989). Here, we found that during development, the short vocalizations of infants converged gradually to the adult echolocation calls (Fig. 1C). Quantification of call duration showed that by approximately 1 month of age, call duration was shortened to the adult call duration, while minimum frequency showed no vocal convergence until at least 2 months of age (Fig. 1D). Similarly, forearm length of the infant bats reached the adult level at approximately 2 months of age (Fig. 1D). In this study, the short vocalizations likely comprised both short isolation calls and echolocation calls, as spontaneous echolocation calls were observed from 10-day-old *P. discolor* (Rother and Schmidt, 1985).

Early onset of the Lombard effect

We found that, at around 2 weeks of age, all four tested infant bats produced significantly louder short vocalizations in the 52 dB background noise than in silence (Fig. 2A,B, Table S1). The average increases in vocal loudness (i.e. the Lombard magnitude) were 4.2 ± 0.4 , 2.8 ± 0.7 , 4.6 ± 0.9 and 2.0 ± 0.5 dB for the four infant bats (mean \pm s.e.m.; P_{adj} -values < 0.0001 , 0.001, 0.054 and 0.0015, respectively). Fig. 2A shows a sequence of short sonar-like vocalizations in silence, followed by a similar sequence in the 52 dB background noise. The waveform (Fig. 2A, top panel) readily shows that peak amplitudes of the bat's call increase as soon as the background noise is switched on. This is a clear manifestation of the Lombard effect.

Three of the four infant bats were also tested before 10 days of age (infants 2–4), but infant 4 did not produce short vocalization before p10. In infant 2, a significant Lombard effect occurred at p5 (mean \pm s.e.m. difference between 52 dB SPL noise condition and silence: 2.9 ± 0.6 dB; $P_{\text{adj}} < 0.0001$; Fig. 2B). Between p7 and p9, infant 3 produced on average 2.1 ± 1.1 dB louder calls in the 52 dB SPL noise condition than in the silence condition, but the difference was not significant (Table S1).

Assuming a transition around p60 between infancy and adulthood, based on the morphological and vocal similarity (Fig. 1D), the four infant bats exhibited the Lombard effect in 23

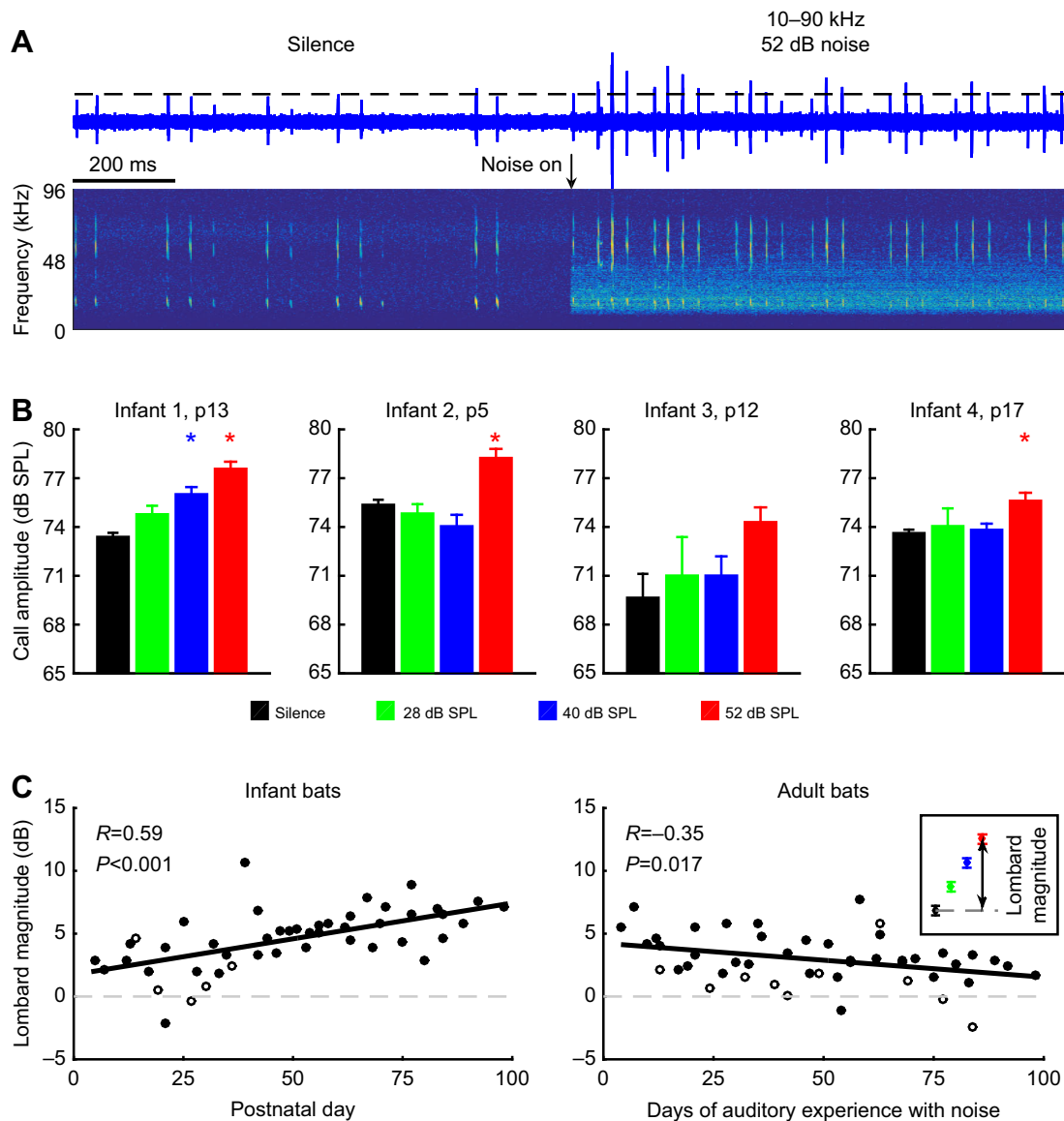


Fig. 2. Postnatal development of the Lombard effect in infant bats. (A) An illustration of the Lombard effect in an infant bat at p12. After the noise started (vertical arrow), the infant bat produced louder short vocalizations. Note that the background-noise spectrum is not correctly illustrated here because the microphone was directed towards the bat, not towards the noise sources. (B) The Lombard effect is present in all tested infant bats at an age of ~2 weeks. Data are mean±s.e.m. Asterisks above the error bar indicate a significant difference from the silence control ($P_{\text{adj}}<0.05$). For infant 3, the P -value was 0.054. The sample size (the number of calls) for the silence control, and 28, 40 and 52 dB noise conditions were: 392, 89, 126 and 129 for infant 1; 369, 107, 72 and 114 for infant 2; 13, 5, 20 and 34 for infant 3; and 499, 19, 157 and 92 for infant 4. (C) The Lombard magnitude is positively correlated with the age of the infant bats, while it is negatively correlated with the auditory experience of the adult bats. Filled circles indicate data points of statistical significance; unfilled circles are not significant.

out of the 30 testing weeks before reaching 2 months of age, with a mean±s.e.m. increase in vocal loudness of 4.5 ± 0.4 dB in the 52 dB SPL noise condition (range: 1.8–10.7 dB; Fig. 2C, left panel). For the same testing period, the four adult bats exhibited the Lombard effect in 22 out of 30 tests, with a mean±s.e.m. increase in call amplitude of 4.0 ± 0.4 dB (range: 1.6–7.7 dB; Fig. 2C, right panel). Thus, the stability of the Lombard effect was similar in infant and adult bats regarding both the probability of the occurrence (GLM, d.f.=58, $t=-0.3$, $P=0.77$) and the Lombard magnitude (t -test, $t=0.9$, d.f.=43, $P=0.4$).

The Lombard effect is not static

We found a positive correlation between the Lombard magnitude in the 52 dB SPL noise condition and the age of the infant bats

(Pearson correlation, $R=0.59$, $P<0.001$; Fig. 2C, left panel). For the infant bats, the Lombard magnitude was on average 3.8 dB greater at 3 months of age than at 2 weeks of age (95% confidence interval: 0.65–8.9 dB). When the correlation analysis was performed infant by infant, we found that this positive correlation was true for three of the four infants (Pearson correlation, infant 1, $R=0.81$, $P<0.001$; infant 2, $R=0.68$, $P=0.011$; infant 3, $R=0.69$, $P=0.012$). Similarly, the Lombard magnitude was positively related to both the forearm length (Pearson correlation, $R=0.58$, $P<0.001$; Fig. 3A) and the body mass of infant bats (Pearson correlation, $R=0.56$, $P<0.001$; Fig. 3B). These data show that while the Lombard effect starts to emerge at a very early age, it increases in magnitude across development.

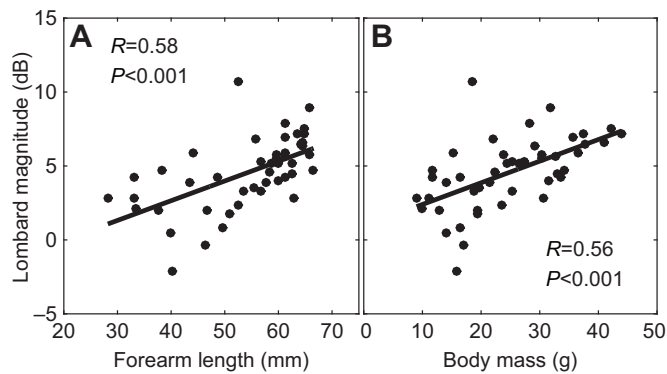


Fig. 3. The Lombard magnitude is positively related to the morphological features of developing bats. (A) Forearm length. (B) Body mass. Data were pooled from all four infant bats. The Lombard magnitude was calculated as the difference in call amplitude between the silence control and the 52 dB SPL noise condition for each infant bat, as shown in Fig. 2C.

DISCUSSION

Our data show that very young *P. discolor*, around p14, reliably increased the loudness of their vocalization in the presence of moderate-level background noise. This is rather a conservative estimate, considering that in one of the two infants for which we had data available before p7 a significant Lombard effect was observed. In contrast, *P. discolor* did not fly until p30, did not reach the adult morphology or vocalization patterns until p60, and did not wean until p90. Given all these behavioural benchmarks, it is quite surprising that 2-week-old infant bats showed the Lombard effect. At first glance, the Lombard effect appears to be a simple behavioural phenomenon. In fact, it requires integration of auditory sensory processing with vocal-motor control (Lombard, 1911; Lane and Tranel, 1971; Eliades and Wang, 2012) and thus it is a good marker for the emergence of audio-vocal feedback.

Does the Lombard effect emerge earlier in *P. discolor* (or echolocating bats in general) than in birds or other mammals? In humans, one study has compared the Lombard effect between adults and 3- to 4-year-old children (Siegel et al., 1976). Both age groups exhibited a Lombard effect of a similar magnitude, indicating that in humans, the origin of the Lombard effect is earlier than 3 years of age. A study on crying behaviour of human infants showed that 1-month-old infants cried louder in the presence of cries from other infants (Geangu et al., 2010). This study suggests that humans might also feature a very early onset of the Lombard effect. At present, there is no comparable data available from other animal species. One study shows that deafened kittens called significantly louder than those with normal hearing at an age of 9 days (Romand and Ehret, 1984). Although this work is not a direct test of the Lombard effect, it demonstrates an early onset of an audio-vocal integration circuit that might regulate the Lombard effect as well.

The neural substrate underlying the Lombard effect is not entirely known. Although some studies suggest the involvement of higher cortical areas (Lane and Tranel, 1971; Jürgens, 2009; Eliades and Wang, 2012), audio-vocal neurons that might regulate the Lombard effect have been found in the pontine brainstem of squirrel monkeys (Hage et al., 2006). There is also evidence that auditory stimulation can result in an increased vocal loudness in decerebrate cats whose vocalizations were evoked by electrical stimulation in the periaqueductal gray of the brainstem (Nonaka et al., 1997). The very early developmental onset demonstrated in the present study suggests that the Lombard effect might be controlled by quite basic, and likely lower-level, sensory-motor brain processes.

We found that the Lombard magnitude in infant bats increased gradually from p14 to p90. This finding emphasizes the dynamics of the Lombard effect. In humans, the expression of the Lombard effect is affected by the content (Patel and Schell, 2008) and the context (Garnier et al., 2010) of the speech. Specifically, humans show a greater Lombard magnitude for information-bearing contents than for non-information-bearing contents, and a greater compensation magnitude for communicative tasks than reading tasks. Here, we provided evidence that the developmental stage influences the Lombard effect. Nevertheless, the exact mechanism underlying the observed developmental changes in the Lombard effect is unknown. Because the Lombard effect involves both auditory and vocal production systems, changes in the expression of the Lombard effect across development might be related to the developmental changes in the auditory system, the vocal production system, or the neural interface between the two.

In bats, the maturation of the neural substrates for audio-motor coupling have been studied for two bat-specific behaviours, namely, for Doppler-shift compensation in horseshoe bats and for target-distance measurement by terms of delay-tuned neurons. Doppler-shift compensation, i.e. the lowering of emission frequency in flight to keep echo-reception frequency constant, can already be observed in juvenile bats from the fourth postnatal week on (Vater et al., 2003). The representation of target distance measured by delay-tuned neurons is already established in the first week of postnatal development (Kössl et al., 2012). Both Doppler-shift compensation and delay-tuning undergo further refinement and maturation in the postnatal development. Similarly, our data suggest that the Lombard effect, another type of audio-vocal integration, is also linked to the developmental stage. It would be very interesting to determine whether the developmental change in the Lombard effect is specific to echolocation in bats or whether it is an intrinsic property of the Lombard effect itself. Developmental data on the Lombard effect from humans and other animal groups are essential in teasing apart these two hypotheses.

In conclusion, we show that infant bats exhibit a significant Lombard effect at an age of only 2 weeks. In contrast, the morphology and the vocalizations of the infant bats changed gradually until 2 months of age. These results suggest that the Lombard effect is under strong selection pressure. Early onset of the Lombard effect in echolocating bats could be adaptive, as echolocating bats typically live in the dark and rely strongly on sounds for daily activities. The strong selection pressure may also be appreciated by its wide taxonomic spread: it is demonstrated in all tested species of birds and mammals, including humans (Brumm and Zollinger, 2011; Brumm, 2013; Hotchkiss and Parks, 2013), in addition to the very recent evidence from frogs and fish (Holt and Johnston, 2014; Shen and Xu, 2016). The early developmental onset of the Lombard effect thus demonstrates that auditory feedback features an early developmental origin. Moreover, we provide evidence that the developmental stage acts as another factor influencing the Lombard effect, emphasizing its dynamics, which probably result from the interaction between multiple brain areas such as the brainstem (Nonaka et al., 1997; Hage et al., 2006), basal ganglia (Tressler et al., 2011) and higher cortical areas (Jürgens, 2009; Eliades and Wang, 2012).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

J.L. and L.W. designed this experiment; J.L. conducted the experiment and analyzed the data; A.L. obtained the experimental permit; J.L., L.W., A.L. and U.F. interpreted the data and wrote the paper.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.151050.supplemental>

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