Title: Echo-acoustic flow affects flight in bats

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Abstract

Flying animals need to react fast to rapid changes in their environment. Visually guided animals use optic flow, generated by their movement through structured environments. Nocturnal bats cannot make use of optic flow, but rely mostly on echolocation.

Here we show that bats exploit echo-acoustic flow to negotiate flight through narrow passages. Specifically, bats' flight between lateral structures is significantly affected by the echo-acoustic salience of those structures, independent of their physical distance. This is true although echolocation, unlike vision, provides explicit distance cues. Moreover, the bats reduced the echolocation sound levels in stronger flow, likely to compensate for the increased summary target strength of the lateral reflectors. However, bats did not reduce flight velocity under stronger echo-acoustic flow.

Our results demonstrate that sensory flow is a ubiquitous principle for flight guidance, independent of the fundamentally different peripheral representation of flow across the senses of vision and echolocation.

Introduction

Flight allows for fast navigation in 3D space. For visually guided animals in flight, stationary objects in the close environment produce patterns of visual motion on the retina, commonly referred to as optic flow (Gibson, 1954). Numerous studies have shown that optic flow is an important entity in perception that guides motion in space in many flying animals (Bhagavatula et al., 2011; Dyhr and Higgins, 2010; Frye and Dickinson, 2007; Srinivasan, 1996). Optic flow is also important for avoiding collisions or estimating time to contact (Wagner, 1982; Wang and Frost, 1992)**.**

Bats as the only flying mammals typically cannot use vision to negotiate flight close to structures due to their nocturnal life style. Instead, bats mostly rely on echolocation, i.e., the auditory analysis of the echoes of self-generated sounds that are emitted at varying rates (Griffin and Grinnell, 1958). Unlike vision, echolocation provides explicit distance information through the analysis of echo delay (Simmons, 1971; Simmons, 1973). Specifically, at a given speed of sound, the delay between a sonar emission and the reception of the echo encodes the distance of the reflective surface in meters. Bats have evolved specialised neural circuits in the auditory brainstem and midbrain to measure echo delay, resulting in a cortical chronotopic map (O'Neill and Suga, 1979; Portfors and Wenstrup, 1999; Portfors and Wenstrup, 2001; Suga, 1970; Suga, 1990). Azimuth and elevation of a reflective surface have to be binaurally computed, because the sensory epithelium for sound (the organ of corti) does not provide explicit spatial information. Thus, compared to vision, echolocation provides relatively sparse spatial information in azimuth and elevation, but more explicit distance information.

For a bat flying through structured 3D space, distances and angles of sound-reflecting surfaces change continuously, effectively creating an echo-acoustic flow.

This continuous flow, however, is discretely sampled by bats and thus not necessarily perceived as continuous.

Especially during commuting flight, when bats follow the edges of vegetation to travel between roosting and feeding sites, echo-acoustic flow is required to keep the lateral distance to passing objects constant as it is typically observed in field studies (Holderied et al., 2006).

Both experimental and theoretical work has indicated that bats might perceive echo-acoustic flow (Bartenstein et al., 2014; Lee et al., 1992; Muller and Schnitzler, 1999; Muller and Schnitzler, 2000) but the unequivocal use of echo-acoustic flow for navigation by bats has not been demonstrated. Here we test the hypothesis that, despite the explicit distance information provided by echolocation, bats still recruit echo-acoustic flow field information to adjust their distance from lateral structures in flight. If this were true, we would expect bats flying between structures that differ in the strength of their echo-acoustic flow to fly closer to that structure that elicits the weaker flow.

Materials and methods
Experimental Setup

The experimental setup was a flight tunnel (Fig. 1A) consisting of two echo-attenuated, terminal cubes and a 3 m long, removable test zone in between. The terminal cubes could be separated from the test zone with curtains and each contained one feeder. Audio was recorded via four ultrasonic microphones (SPU0410LR5H, Knowles, Itasca, IL, USA) positioned centrally on the back walls of the terminal cubes (20 cm and 91 cm height). Analog signals were preamplified (Octopre LE, Focusrite, High Wycombe, England) and AD converted by an audio interface (Ultralite, MOTU, Cambridge, MA, USA) at 192 kHz.

The floor of the test zone was lined with white cloth to achieve high contrast in the video, its ceiling consisted of visually and acoustically transparent gauze. It was lit along both side walls with IR LED strips (Synergy 21 LED Flex Strip infrared 86417, ALLNET GmbH Computersysteme, Germering, Germany). An infrared camera (A602f, Basler, Ahrensburg, Germany) at 3.54 m height recorded videos at 20 fps. For audio-visual synchronization, the camera was triggered via the audio interface.

Stimuli and Experimental Procedure

Stimuli for this experiment were the structured side walls of the test zone. Each side wall was planked vertically on one and horizontally on the other side with tongue-and-groove panelling that creates periodic ridges and grooves. Vertical ridges induce strong echo-acoustic flow because they are orientated perpendicular to the flight direction and result in time-variant echoes. Horizontal ridges induce weaker echo-acoustic flow because they are orientated parallel to the flight direction. Two experiments were conducted, using stimuli that vary in the strength of echo-acoustic flow when presented in vertical orientation:

(i) Broad panelling (weaker echo-acoustic flow), ridge width 7.5 cm; groove width 1.5 cm and (ii) Fine panelling (stronger echo-acoustic flow), ridge width 3 cm; groove width 1.5 cm.

Rotating the side walls changes the orientation of the ridges between horizontal and vertical. This resulted in eight experimental conditions (four arrangements of walls (both vertical, both horizontal, one vertical, the other horizontal or vice versa) times two flight directions). A sequence of random permutations of the eight conditions was pre-generated and experimental trials for each animal acquired according to this sequence.

Training

Seven adult bats (3 female, 4 male) of the species *P. discolor* were trained to fly back and forth between the two feeders. Five training days were followed by two resting days. Training took place in a dark, echo-attenuated flight room (2.1 x 1.2 x 2.4 m).

Data acquisition

Data acquisition took place on ten consecutive days. The start of a trial was initiated by opening the curtain. After the animal had passed the test zone, the experimenter closed the curtain behind the animal. 5 s audio and video ringbuffer recordings were saved. All technical equipment was controlled with a custom-written Matlab program (MathWorks, Natick, MA, USA) using Soundmexpro (HörTech, Oldenburg, Germany), and the Matlab image acquisition and data acquisition toolboxes.

Data Analysis

Only trials without reversal of flight direction were analyzed. Custom-written Matlab programs were used for all data analyses: automatic 2D flightpath reconstruction, calculation of flight velocity and audio analyses. Some trials could not be analyzed for audio because of a microphone defect.

All analyses were applied on the individual level for each experimental animal. Tests comparing the broad and fine panelling were applied on the results of one specific bat, i.e. only on data recorded with bats which participated in both experiments.

Flightpath analyses were performed using all data points in the respective combination of flight direction and wall arrangement that lay within the central one meter of the test zone.

Homogeneity of flight paths: A Brown & Forsythe Test was used to test if an animal's flight paths in the central meter of the test zone showed equal variances with concordant vertical and concordant horizontal ridges. The range between the first

and the third quartile was used as a measure for the homogeneity of the flight paths of all flights of one bat. These values were compared to determine with which ridge orientation flight paths were more homogenous.

Analysis of number of calls and inter-call intervals (ICIs): We tested whether the number of calls produced in the central two meters of the flight tunnel differed between flights between vertically ridged walls and flights between horizontally ridged walls (two-sided Wilcoxon rank sum test). We checked with a Kruskal-Wallis test whether the distributions of ICIs differed across these conditions. The skewness of the distributions, which quantifies the extent to which a distribution deviates from symmetry, was calculated. A Gaussian distribution has a skewness of zero (fully symmetric) whereas the ICI distributions (cf. Fig. 3C-.F) show an asymmetry in favour of short ICIs. In this case the skewness is larger than zero.

Experiments were approved by the Regierung von Oberbayern (55.2-1-54-2532-221-14) and conducted under the principles of laboratory animal care and the regulations of the German Law on Animal Protection. Approval to keep and breed the bats was issued by Munich district veterinary office.

Results and discussion

Exemplary flight paths of a bat from left to right between vertical, concordant ridges are shown in Fig. 1B (black). When ridging was changed to horizontal on one wall, the bat chose to fly significantly closer to that wall and, consequently, further from the vertically ridged wall (Fig. 1B, blue). Fig. 1B, right shows the medians and interquartiles of the bat's deviation from corridor midline within the central one meter of the corridor. Overall, 645 flight paths from 5 bats were analyzed with a spacing of the ridges of 9 cm. Figure 1C shows how median flight paths differed between orthogonal (blue) and concordant vertical (black) conditions when the vertical ridges were presented on the one wall (Fig 1C, left) or on the other (Fig 1C, right). Net

lateral deviations for both flight directions are represented by the yellow arrows. All bats consistently and significantly shifted their flight paths towards the wall with horizontal ridges inducing lower echo-acoustic flow (p<0.05, two-sided rank sum test).

We repeated the whole experiment, replacing the side walls with walls where the ridge spacing was reduced from 9 cm to 4.5 cm. 750 trials from 5 bats were analyzed. Data show that also with this finer spacing of the ridges, the bats significantly deviated in their flight trajectory between concordant and orthogonal ridges, again flying significantly closer to the horizontal ridges (Fig. 1D, red arrows). The magnitude of this deviation, however, is not significantly different from the 9 cm spacing (Wilcoxon signed rank test).

Second, we compared peak flight velocity to assess whether bats adjust their flight velocity to balance echo-acoustic flow. With the 9 cm ridges, all bats tended to fly faster when the horizontal ridges were presented on both walls than with vertical ridges (Fig. 2A). This was, however, only significant for bat 5 (p ≤ 0.05, two-sided Wilcoxon rank sum test). With the finer spacing (Fig. 2B), the differences in flight velocity between concordant vertical and concordant horizontal ridges were even less pronounced. We conclude that flight velocity was not significantly affected by echo-acoustic flow as presented here.

We tested how homogenous the flight paths were between the lateral walls when both of them had either horizontal or vertical ridges. Specifically we tested whether the stronger echo-acoustic flow of the vertical ridges leads the bats to fly along more homogeneous paths than with horizontal ridges. With broad ridge spacing, we found this to be the case in 8 of 10 cases (5 bats times 2 flight directions). With fine ridge spacing, we found this to be the case in 6 of 10 cases (p ≤ 0.05, Brown & Forsythe Test). Note, however, that we also found the opposite effect (less homogenous flight

paths with vertical ridges) in 1 of 10 cases each for broad and fine ridges. Overall, the bats showed more homogenous flight paths when exposed to stronger echo-acoustic flow.

The ultrasonic recordings during flights show that all animals produced significantly fainter calls when both walls were vertically ridged than when they were horizontally ridged ($p \leq 0.05$, two-sided Wilcoxon rank sum test). This is true both for the broad ridge spacing (4715 calls from 595 flights, Fig. 3A) and the fine ridge spacing (5702 calls from 704 flights, Fig. 3B). Only call onsets (RMS of the first 0.4 ms) were analysed to make sure that echoes from the reverberant test zone did not contaminate the analysis. The bats did not alter their rate of sonar emission, neither per distance, nor per time, between the vertical and horizontal ridges. Again this is true for both the broad and the fine ridge spacing (data not shown). However, some of the bats changed their temporal ensonification strategy: specifically, the distribution of inter-call intervals (ICI) changed significantly (cf. Fig. 3C-F for exemplary ICI histograms of Bat1; significant differences in ICI distribution are depicted as red asterisks in Fig. 3G and H) in that the skewness of the ICI histogram became less positive when the vertical ridges were replaced with horizontal ridges. This means that, while the bats did not produce significantly more calls with vertical ridges, they produced more often shorter ICIs. Quantitative results for the analysis on the skewness of ICI histograms are shown in Fig. 3G and H.

Taken together, the current psychophysical experiments show that echolocating bats (*P. discolor*) adjust their flight paths between structured surfaces according to the strength of echo-acoustic flow elicited by these surfaces. Our bats always chose to fly closer to the side wall that elicited the weaker echo-acoustic flow. This is surprising because, unlike all visually guided flyers (insects and birds), bats have explicit information about their distance to objects, through the neural analysis of

echo delay. Our data show that the perceptual valence of echo-acoustic flow was ranked over these explicit echo-acoustic distance cues. Thus, our results demonstrate that sensory flow elicited by self-motion is a ubiquitous principle for guidance of flight in the animal kingdom, independent of the sensory modality and the fundamentally different peripheral sensory representation of the perceptual cues mediating the flow information.

The neurobiological basis for the stronger perceptual valence of echo-acoustic flow compared to explicit echo-acoustic distance cues is not completely clear, but recent research has thrown some light on this: It has been known for some decades that target distance is explicitly encoded by specialized neurons in the brain of various bat species (Mittmann and Wenstrup, 1995; O'Neill and Suga, 1979; Olsen and Suga, 1991) and represented in a chronotopic map of echo delay in the bat auditory cortex, (e.g. Bartenstein et al., 2014; Hagemann et al., 2010; O'Neill and Suga, 1979). However, it has recently been shown that this map is 'blurry' and responses depend critically on the actual combination of echo intensity and delay (Hechavarria et al., 2013). Indeed, in Bartenstein et al. (2014), it was found that neurons in the auditory cortex encode echo-acoustic flow information on the geometric relation between targets and the bats' flight trajectory, rather than echo delay. Thus, the classical chronotopic map as it has been described in the bat cortex, may not encode echo delay per se. It may rather encode echo delay as it changes over time in typical fly-by situations that elicit echo-acoustic flow. This may provide a neurophysiological basis for the bats' perceptual preference described in our experiments.

How is echo-acoustic flow represented in the bat auditory system? Clearly the peripheral sensory representation of flow fields is fundamentally different across vision and echolocation: while in vision the retina provides explicit spatial information for the time-variant structures, it is not even clear to which extent these structures are

perceptually resolved in echolocation. A vertical ridge that generates the flow information in the current experiments can be approximated as a vertical line reflector that reflects into all azimuths. In response to a bat's call, many of these line reflectors will generate reflections that add up as a complex echo with increasing delays and decreasing amplitudes (due to geometric and atmospheric attenuation). Horizontal ridges, in contrast, will reflect relatively little energy back to the bat. Thus, it is conceivable that the bats did not perceive the vertical passing ridges as time-variant but simply as louder. In line with this, the bats reduced the call level with vertical ridges compared to horizontal ridges, an exemplification of automatic gain control, as it is ubiquitously observed in echolocating bats and whales (Au and Benoit-Bird, 2003; Hartley, 1992; Kick and Simmons, 1984; Linnenschmidt et al., 2012). On the other hand, the complex echoes generated by the ridges change periodically with a repetition rate equal to the product of ridge spacing and flight velocity. With the current (broad) ridge spacing of 11/m and peak flight velocity around 4.5 m/s (cf. Fig. 2), echoes change periodically with 49.5 Hz. However, our bats produced much fewer calls in flight, on the order of 16/s (not shown). Thus the ridge periodicity is strongly undersampled by the bats. Fontaine and Peremans (2011) have shown how bats can reconstruct the wing beat of insects despite such echo-acoustic undersampling, namely by adaptively adjusting and distributing ICIs. The fact that some of our bats showed indeed changes in the skewness of the ICI histograms (cf. Fig. 3C-H) corroborates this hypothesis.

In summary, the current experiments demonstrate that echolocating bats recruit flow-field information to adjust their flight paths along structured layouts. These findings are in agreement with previous reports on birds and insects and thus corroborate the ubiquitous nature of flow-field guided navigation. However, bats assess lateral structures by echolocation, not vision, and the peripheral sensory representations of

spatial information across these senses are fundamentally different. It is tempting to speculate that this difference results in the remarkable finding that our bats did not reduce flight velocity under stronger flow, an effect readily observed in birds and insects, (e.g. Baird et al., 2005; Bhagavatula et al., 2011; David, 1982; Srinivasan, 1996). Our bats also did not change the ensonification rate and showed only small variations in temporal ensonification patterns. These data suggest that the explicit distance cues provided by echolocation, unlike vision, lead to a lower perceptual weighting of flow-field information in bats, compared to visually guided flyers. As all of our experiments were conducted in the dark, it may be informative in future studies to assess the extent to which bats flying by light can recruit (optic) flow field information to negotiate flight through narrow passages. The relative salience of optic versus echo-acoustic flow field percepts may also vary strongly across bat species, as some bats are quite active in day light or dusk (e.g. *Saccopteryx bilineata*) while many purely nocturnal, insectivorous bats appear to have somewhat reduced vision (e.g. Pteronotus parnellii).

Author contributions

K Kugler, U. Firzlaff, and L. Wiegrebe designed the experiments; K. Kugler and W.

Greiter built the setup; K. Kugler executed the experiments and analysed the data; K.

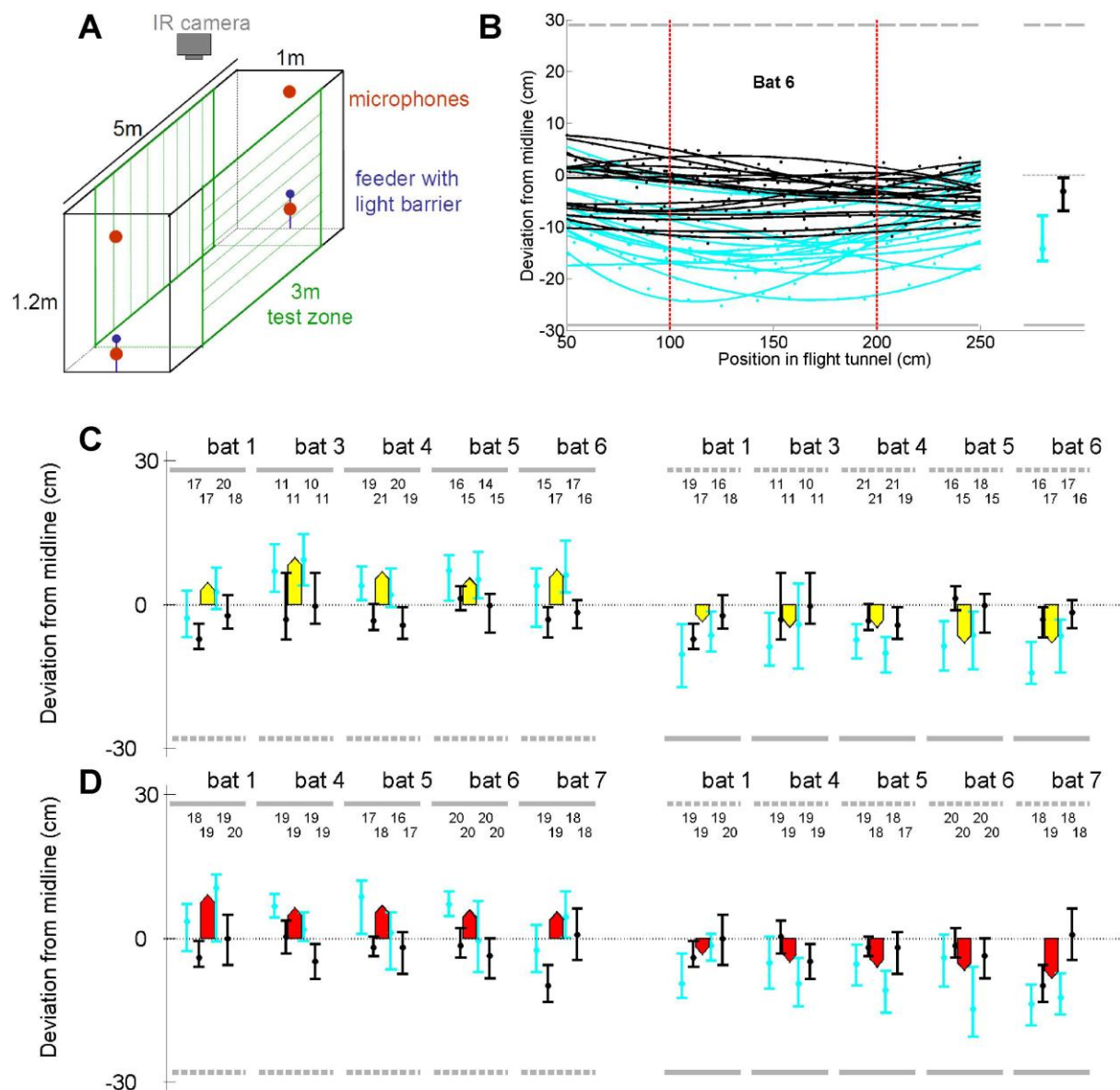Kugler, W. Greiter, H. Luksch, U. Firzlaff and L. Wiegrebe wrote the paper.

Figures

Figure 1: A Schematic of the set-up with central test zone and two terminal cubes, separable with curtains. Bats' flights were monitored via an infrared camera centred above the test zone, and echolocation calls were recorded with two ultrasonic microphones (at 20 and 91 cm height at midline) in each of the terminal cubes. After each flight, the bat was rewarded from the feeder platform. The structures of the

lateral walls in the test zone (either vertical or horizontal ridges) could easily be changed in between trials by rotating the lateral walls. **B** left: exemplary flight paths from Bat 6 for lateral walls with orthogonal orientation to each other (blue paths, ridging illustrated by grey lines) and for lateral walls with concordant orientation (black paths, both walls with vertical ridges). Medians and interquartiles of the flight paths are shown on the far right. **C** Medians and interquartiles of flight paths for all bats with broad ridges oriented either concordantly vertical (black) or orthogonally (blue). The first two bars for each bat represent flights from left to right; the third and fourth bars flights from right to left. The number of flights is given above the respective bar. Mean deviations between concordant and orthogonal ridges are represented by the coloured arrows. The direction and magnitude of the coloured arrows clearly show that the bats always flew closer to the side with the weaker echo-acoustic flow. **D** shows the data for the experiment with the fine ridges in the same format as **C**.
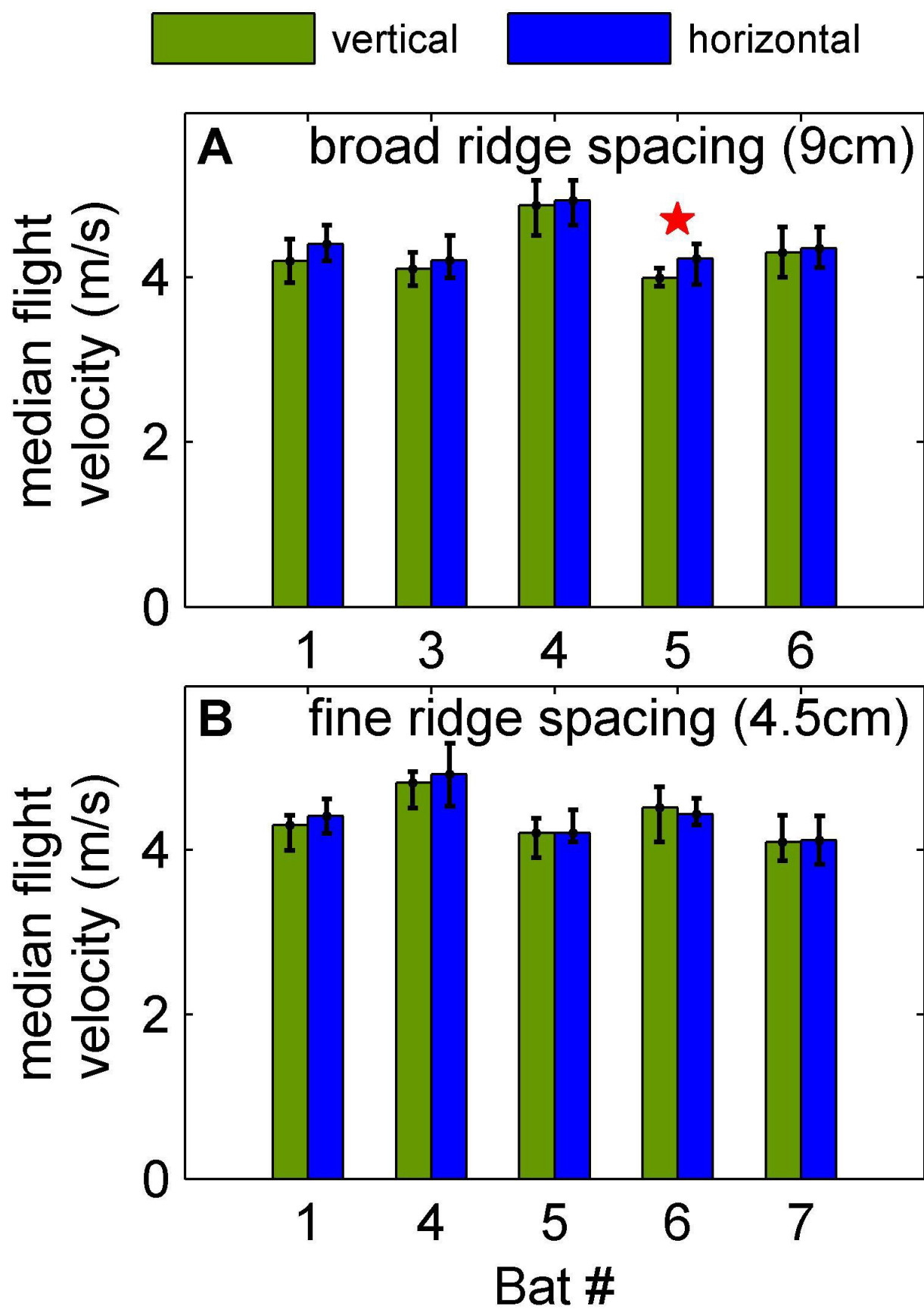
Figure 2: Medians of bat flight velocities: the green bars represent flight velocities with concordant **vertical** ridges; the blue bars represent flight velocities with concordant **horizontal** ridges. Error bars represent interquartiles. The asterisk indicates a significant difference in flight velocity (Wilcoxon rank sum test, p<0.05). **A** and **B** show data for the broad and fine ridges, respectively.
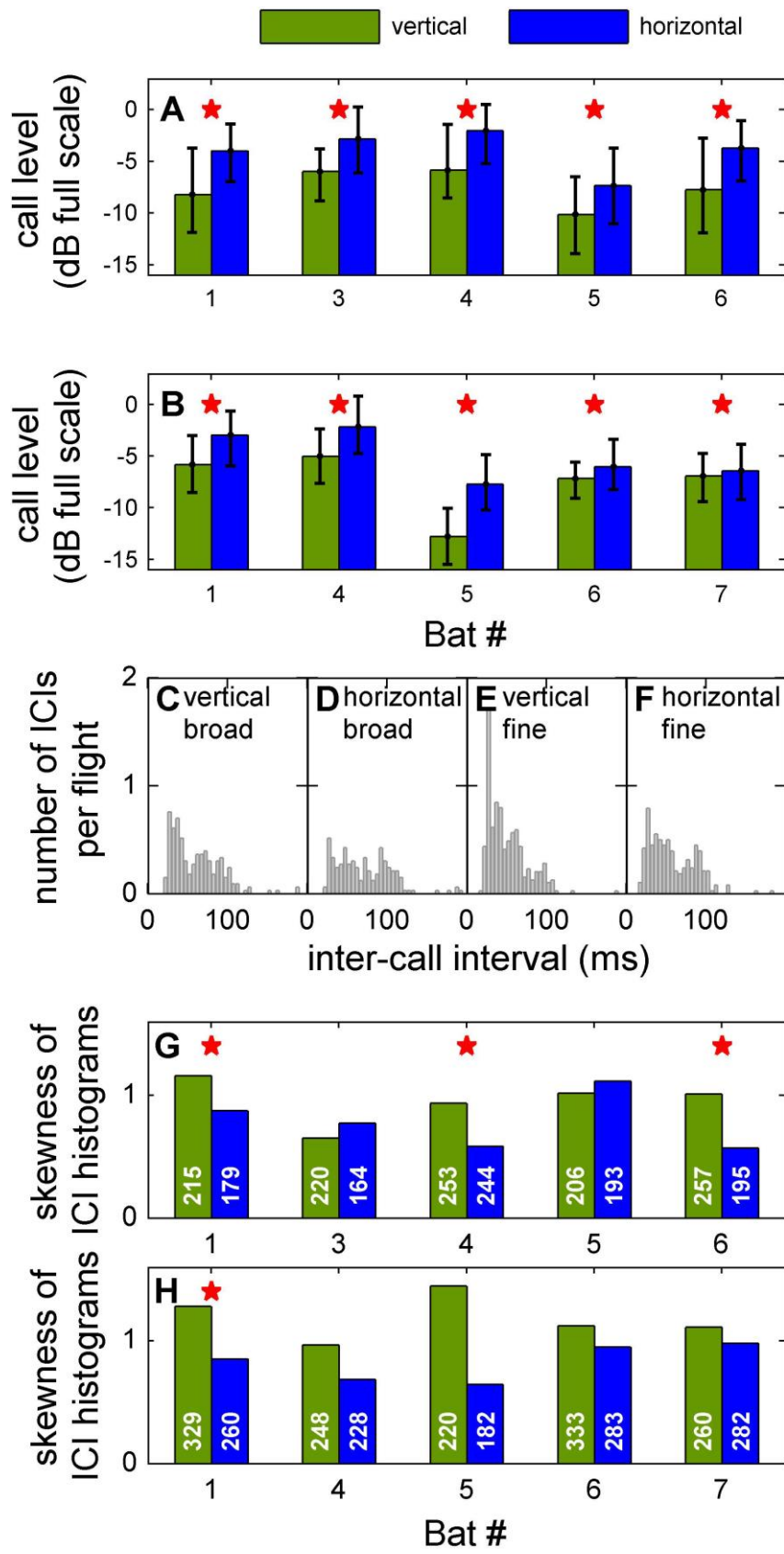
Figure 3: Analyses of ensonification parameters: Analyses of echolocation call levels are shown in **A** and **B** for the broad and fine ridges, respectively. Data show that bats called significantly fainter with concordant vertical ridges (green) than with concordant horizontal ridges (blue). Error bars show interquartiles; asterisks show significant differences (two-sided Wilcoxon rank sum test, p<0.05). Exemplary inter-call interval histograms of Bat 1 are shown in **C-F**. The inter-call interval axis is truncated at 200 ms; maximal inter-call intervals across bats and exp. Conditions ranged between 102 and 233 ms. Analyses of the skewness of the inter-call interval distributions are shown in **G** and **H** for the broad and fine ridges, respectively. Asterisks show where the distribution of inter-call intervals differs significantly between concordant vertical ridges and concordant horizontal ridges. The white numbers within the bars represent the number of inter-call intervals on which each skewness analysis was based.

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