ECHOLOCATION

Acoustic cognitive map–based navigation in echolocating bats

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Bats are known for their ability to use echolocation for obstacle avoidance and orientation. However, the extent to which bats utilize their highly local and directional echolocation for kilometer-scale navigation is unknown. In this study, we translocated wild Kuhl's pipistrelle bats and tracked their homing abilities while manipulating their visual, magnetic, and olfactory sensing and accurately tracked them using a new reverse GPS system. We show that bats can identify their location after translocation and conduct several-kilometer map-based navigation using solely echolocation. This proposition was further supported by a large-scale echolocation model disclosing how bats use environmental acoustic information to perform acoustic cognitive map–based navigation. We also demonstrate that navigation is improved when using both echolocation and vision.

Navigation, the ability to plan and execute a goal-directed path, is crucial for almost all aspects of animals' lives (*1*). Echolocating bats with poor vision face a particularly challenging task because their echolocation system is inherently very local and directional, thus severely limiting the amount of information they can obtain per unit of time regarding their environment. Even though bats pose a specifically notable case owing to their agility, small size (usually <20 g), and nocturnality, little is known about how they navigate during their everyday foraging trips (*2*, *3*). A few previous studies investigating navigation in bats suggested that bats can use various of navigation strategies, such as path integration (*4*), spatial memory (*5–7*), and route following (*8*). They can use a (sun-calibrated) magnetic compass (*9–11*) and can even conduct large-scale visual cognitive map–based navigation (*8*, *12*).

Bats' prominent potential sensory modalities for guiding navigation include vision (*13–17*), magnetic sensing, olfaction, and echolocation (*18*). Despite considerable research on echolocation, there is no direct evidence for the ability of bats to rely on echoes alone for kilometer-scale navigation (*13*, *19*, *20*). Using echolocation for such large-scale navigation is not straightforward. Echolocation is short ranged, allowing the detection of large objects from no more than tens of meters (*21*), which is much less than the

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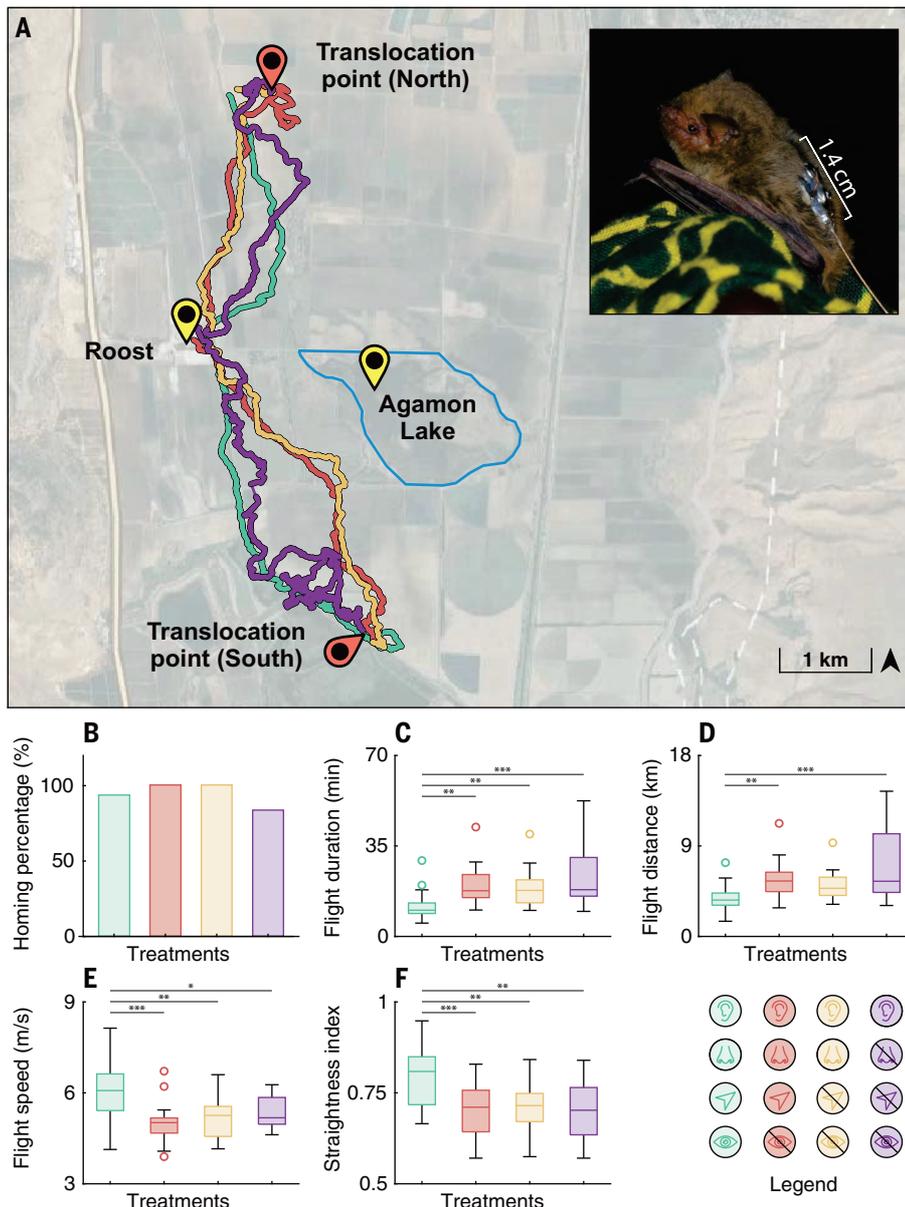‡These authors contributed equally to this work.

range of vision, forcing a navigating bat to rely on proximal features when navigating (fig. S1). It is also unclear to what extent can bats reconstruct the world in three dimensions using echolocation (*22*) and, accordingly, to what extent they can use environmental echoes as landmarks for navigation. This combination of limited range and possibly limited object identification ability makes the use of echolocation for navigation challenging, and it is uncertain whether and how bats do so. This challenge has been highlighted (*18*) but has still not been resolved.

We examined the ability of bats to use echolocation solely during navigation over a few kilometers by using a translocation experiment. Solving a translocation homing task first requires identifying the new translocated location and then flying toward a familiar destination. Our aim was to test whether a bat can solve this task acoustically (when deprived from nonacoustic sensory information) when echoes are used both for identifying the translocation location and to inform their internal "compass," guiding the bat in the right direction. Returning home successfully in a directional flight will only be possible if the bat holds some acoustic mental representation of its environment. We used Kuhl's pipistrelle (*Pipistrellus kuhlii*), which possess superb echolocation abilities and have a very limited reliance on vision to evaluate this (supplementary text, section S1).

Results

We caught the bats near their roost and translocated them to one of two translocation points at a distance of ~3 km (Fig. 1A), which is within the scale of their home range size (*23*, *24*).

We manipulated all the main potential sensory modalities the bats have been hypothesized to use (*18*) according to the following treatments (*24*): (i) control group (hereafter referred to as sighted bats with no sensory modality deprivation), (ii) visual deprivation, (iii) visual and magnetic deprivation, and (iv) visual, magnetic, and olfactory deprivation.

We discuss the potential use of other, less likely sensory information in the supplementary text (section S1). Depriving these bats of both echolocation and vision is impossible because they will subsequently not fly. Note that bats in all groups could use echolocation. Transient and short-term visual deprivation was achieved by covering the eyes of the bats (*24*). We hereafter refer to the bats in all treatment groups (excluding the controls) as blindfolded bats. We then tagged the bats using a reverse GPS tracking system [ATLAS (*12*, *25*)] that provided high-resolution semi–real-time tracking at a rate of 0.5 Hz (*24*).

We successfully tracked 76 bats and found that 95% percent of the bats (72) returned successfully within a single night, independent of treatment (Fig. 1B) [$\chi^2(72) = 5.83$, $P = 0.120$, $n = 76$ bats; generalized linear mixed model (GLMM) was fitted to homing percentage, and the treatment was defined as a fixed factor with a binomial distribution]. Returning percentages were: sighted bats, 93% ($n = 30$ bats); visual deprivation, 100% ($n = 17$ bats); visual and magnetic deprivation, 100% ($n = 17$ bats); and visual, magnetic, and olfactory deprivation, 83% ($n = 12$ bats). We analyzed trajectories of the 67 bats that flew directly back to their roost or to the Agamon Lake, which is a prominent landmark in the valley and a familiar foraging site of these bats (Fig. 1A and fig. S2) (*24*).

Although bats of all treatments (all blindfolded) successfully navigated back to their home, the analysis revealed that vision does affect navigation. For all the navigation performance metrics that we tested, sighted (control) bats that could use vision (and all other sensory modalities) to navigate performed better than the visually deprived bats. Sighted bats flew for a shorter duration ($P < 0.006$) and a shorter distance on the way to their destination (visual deprivation, $P = 0.006$; visual and magnetic deprivation, $P = 0.054$; visual, magnetic, and olfactory deprivation, $P < 0.001$), faster ($P < 0.023$), and in a straighter trajectory ($P < 0.003$, GLMM) (Fig. 1, C to F, and Table 1).

Estimated twilight and moon illumination levels during the study were 0.04 ± 0.04 lux ($n = 67$ bats) (*24*). The average ambient light intensity was not correlated with either flight speed or flight distance of sighted bats (Pearson's correlation test: speed, $r = 0.09$ and $P = 0.6$; distance, $r = 0.06$ and $P = 0.7$; $n = 29$ bats), suggesting that the bats relied on distant [e.g., distant anthropogenic lights, such as those generated by the villages around the valley (*26*, *27*); supplementary text, section S3] rather than local visual information.

Except for the sighted bats, there was no significant difference between the flight characteristics of bats in the various sensory deprivation treatments, including the group that could only use echolocation, suggesting that echolocation, more than the other tested modalities,

Fig. 1. Bats use echolocation and vision to conduct kilometer-scale navigation. The different treatments are represented by the following colors: control sighted bats (green); visually deprived bats (orange); visually and magnetically deprived bats (yellow); visually, magnetically, and olfactorily deprived bats (purple; note that these bats could only use echolocation to navigate). (**A**) Homing examples (one per treatment) from the two translocation points (red pinpoints, located 3.7 and 2.7 km from the roost). The inset shows a photo of a Kuhl's pipistrelle bat with an ATLAS tag on its back. (**B**) Homing percentages by the end of the first night. The bats' flight characteristics from the translocation point back to roost or to Agamon Lake are presented in (**C**) flight duration, (**D**) flight distance, (**E**) flight speed, and (**F**) straightness index. All boxplots represent the median and the first and third quartiles, and significance levels are indicated by asterisks: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. Map data is from Google, Mapa GISrael Imagery, and TerraMetrics.

is the modality that allows successful navigation in the absence of vision ($P > 0.1$, GLMM) (table S1).

The successful homing of bats that could sense their environment using only echolocation provides direct evidence that bats can conduct large-scale kilometer navigation using echolocation. The ability of bats to identify their location after translocation and fly in a directional flight to their destination suggests that they possess an acoustic cognitive map.

Both sighted and blindfolded bats could not sense their target from their release point (28). After the bats were released, they performed correlated random walk meandering flights, which transitioned to directed flights toward their target, as was evident from the gradual increase of flight straightness and a decreasing flight angle relative to the target (Fig. 2, A to C, and figs. S3 and S4).

One of the main questions in animal navigation is how animals identify their location in the world. To study this, we first examined the bats' flight between the moment of release and when they started flying straight toward their target. We defined this part of the trajectory as the localization phase. We recognized the localization point (the point where bats start moving in a directed path toward the target) according to their straightness index and flight heading relative to their destination [i.e., when crossing a certain straightness and angle thresholds; see (24) and Fig. 2, A to C]. All bats established the localization phase within minutes (fig. S5), and the vast majority of the bats flew in the direction of within 50° of the roost at an average distance of ~200 m from the translocation point (fig. S6), suggesting that they quickly acquired a general knowledge of their location relative to the roost. Furthermore, both sighted and two of the blindfolded groups achieved localization at similar beeline distances of ~500 m from the translocation point, on average. The visually, magnetically, and olfactorily deprived bats achieved localization within 900 m, a significantly greater distance in comparison to that of the sighted bats ($P = 0.028$) but not significantly larger than that of the other treatment groups ($P > 0.2$, GLMM) (Fig. 2D and table S2).

Bats gradually improved their heading toward the target (Fig. 2C and fig. S4, supporting the cognitive map-based navigation hypothesis. Henceforth, a "cognitive map" will be referred to as a "map"). If the bats were using an alternative strategy, such as route following and flying from one landmark to another, then the angle would decrease and increase, according to the direction toward each of the landmarks (fig. S11).

Supporting the hypothesis that the bats were relying on map-based navigation, the homing duration and flight angle relative to the target of our bats were very similar to those of translocated fruit bats (fig. S7), where we have demonstrated the use of visual map–based navigation in the past (8, 12).

Because acoustically manipulated bats cannot fly and survive in the wild, we further investigated how bats use acoustic information for navigation by using complementary modeling tools. Specifically, we quantified the potential acoustic information available to the bats with Shannon's entropy. We used a Digital Surface Model to reconstruct a three-dimensional (3D) landscape model of the entire study site [at a resolution of 0.35 m; see (24) and Fig. 3A]. We used this model to simulate the echoes each bat would receive along its flight trajectory (Fig. 3B). Lastly, we used the envelope of the simulated echoes to estimate the Shannon entropy of each echo (and hence,

environmental) complexity (24)(Fig. 3B, and movie S1). The entropy of a single spatial cell represents the upper limit of information that can be conveyed by the echo it reflects.

As expected, the acoustic entropy of simple and repeatable environments, such as crop fields or a water surface, were characterized by low values, whereas the entropy of more complex environments, which are characterized by many geometric changes, such as road edges, riverbanks, and orchards, were characterized by high values (Fig. 3, B to D). Although a river and a road are characterized by low entropy, their edges are characterized by high entropy (similar to a visual edge). Moreover, we estimated the visual entropy of the valley (24) and found a significant positive correlation between the echoic and visual entropy of each spatial cell (Pearson's correlation test: $P = 0$, $r = 0.50$, and $n = 15,000$ random spatial cells). This is not surprising when considering that both are measurements of environmental complexity.

There was a significant difference between the echoic entropy of the different landscapes in the region, suggesting that different habitat types are represented by different echoic statistics. Bats could potentially use this information to identify their location or navigate (Fig. 3D) (analysis of variance with echoic entropy and landscape as dependent and explanatory variables, respectively; $P < 0.001$, adjusted $R^2 =$ 0.33, $F_{8,1791} = 110$, $n = 1800$). The bats' ability to use landmarks with high echoic entropy, which provide ample information, is only possible when these distinct features are constant in space and time. For example, a bat could know that it is probably in an orchard based on the high echoic information of the echoes it receives. This would already narrow the number of possible locations of where it might be to all of the orchards with which it is familiar, but it might still not provide an unambiguous location.

Although entropy is a measurement of information, it does not measure how distinct an echoic scene is, whereas localization would require distinguishable echoes. We used the Kullback-Leibler (KL) divergence distance to assess the similarity of echoic information across landscape types; a higher KL distance indicates lower similarity between reflected echoes, a required property for distinguishing between acoustic scenes. We found that many landscapes tend to be differentiable acoustically from different and also similar landscape categories (Fig. 3E), suggesting that they might provide site-specific information allowing acoustic localization. A KL map of the region, which represents the differentiability between each spatial cell and 1000 random locations in the area, suggests which locations are more distinguishable acoustically and could serve as landmarks for localization and naviga- tion (Fig. 3F). Habitats with high echoic entropy that also exhibit more distinguishable echoes, that is, high KL distances (such as orchards and settlements), may be more useful as acoustic landmarks. For example, when encountering a familiar echo, a bat that realizes that it is in an orchard based on echo entropy might be able to identify the specific orchard if the site is characterized by a sufficiently high KL distance to other orchards, as we present here (Fig. 3E). Navigation in a complex environment probably requires both the triangulation of informative environmental features (with high echoic entropy) that the bat encounters in a sequence and the identification of specific locations (using KL distance), which could explain why bats exhibit wandering during the localization phase.

We next examined the individual-specific echoic entropy bats experienced during the entire flight from the translocation point to their destination and compared it to two alternative movement strategies (hereafter referred to as flight modes): (i) direct flight and (ii) maximum entropy based–flight, where, in each step, bats choose their flight direction according to the highest available echoic entropy in the direction of the target (24). We found that both sighted and blindfolded bats experienced significantly higher average entropy during their flight from the translocation point in comparison to the entropy that

Table 1. Bats' movement characteristics from the release point to their destination according to different sensory deprivation treatments. Analysis was conducted with a GLMM; flight parameters were set as the dependent variables, treatment was set as a fixed factor, and translocation point (i.e., point one or two) and destination (roost or lake) were set as random effects. Est., estimate; SE, standard error; t stat., t statistic; DF, degrees of freedom; lower, the lower bound of the confidence interval; upper, the upper bound of the confidence interval; SD, standard deviation.

	Est.	SE	t stat.	DF	P value	Lower	Upper	Mean ± SD (number of bats)
Flight duration (min)								
Control (Intercept)	11.7	1.5	7.9	63	5.1×10^{-11}	8.7	14.6	11.7 ± 4.7 (29)
Visual deprivation	8.5	2.6	3.3	63	0.002	3.3	13.6	20.1 ± 8.3 (14)
Visual and magnetic deprivation	7.1	2.5	2.8	63	0.006	2.1	12.2	18.8 ± 8.0 (15)
Visual, magnetic, and olfactory deprivation	13.0	3.0	4.3	63	6×10^{-5}	7.0	19.1	24.7 ± 14.9 (9)
Flight distance (km)								
Control (Intercept)	3.8	0.4	10.2	63	6.3×10^{-15}	3.1	4.6	3.8 ± 1.2 (29)
Visual deprivation	1.9	0.7	2.8	63	0.006	0.6	3.2	5.7 ± 2.2 (14)
Visual and magnetic deprivation	1.3	0.6	2.0	63	0.054	0.0	2.6	5.1 ± 1.5 (15)
Visual, magnetic, and olfactory deprivation	3.6	0.8	4.7	63	1.5×10^{-5}	2.1	5.2	7.5 ± 4.2 (9)
Flight speed (m/s)								
Control (Intercept)	6.1	0.15	40.6	63	6.4×10^{-47}	5.8	6.4	6.1 ± 1.0 (29)
Visual deprivation	−1.0	0.26	−4.0	63	1.6×10^{-4}	−1.6	−0.5	5.0 ± 0.8 (14)
Visual and magnetic deprivation	−0.9	0.26	−3.5	63	0.001	−1.4	−0.4	5.2 ± 0.7 (15)
Visual, magnetic, and olfactory deprivation	−0.7	0.31	−2.3	63	0.023	−1.3	−0.1	5.3 ± 0.5 (9)
Straightness index								
Control (Intercept)	0.79	0.02	34.7	63	9.6×10^{-43}	0.7	0.84	0.79 ± 0.1 (29)
Visual deprivation	−0.10	0.02	−3.9	63	2.7×10^{-4}	−0.1	−0.05	0.70 ± 0.1 (14)
Vision and magnetic deprivation	−0.08	0.02	−3.1	63	0.003	−0.1	−0.03	0.71 ± 0.1 (15)
Visual, magnetic, and olfactory deprivation	−0.10	0.03	−3.3	63	0.002	−0.2	−0.04	0.70 ± 0.1 (9)

they would have experienced if they had flown in a straight line to the same destination and a significantly lower entropy in comparison to that of the maximum-entropy step-selection model ($P < 0.001$). In addition, both sighted and blindfolded bats flew significantly longer distance than if they were to conduct a straight flight and a significantly shorter distance in comparison to the trajectory expected from the maximum-entropy step-selection model ($P < 0.001$, GLMM) (Fig. 3C, Table 2, and fig. S8). These findings imply that bats flew near environmental features that provide sufficient information to navigate, regardless of the sensory modality they could use, but did not search for the maximum entropy, probably because this would be less efficient in terms of flight distance and duration.

We aimed to examine whether bats used acoustically informative environmental features at times when they make movement decisions, that is, when taking large turns (fig. S9) (24). Both sighted and blindfolded bats experienced significantly higher average echoic entropy and KL distance (i.e., distinct echoes) when taking large turns (>25°) in comparison to when flying straight (<25°, $P < 0.001$) (Fig. 3G, Table 2, fig. S10A, and table S4). Moreover, bats experienced significantly higher echoic entropy and KL distance during the localization phase compared with that of the rest of the flight ($P < 0.004$, GLMM) (Fig. 3H, Table 2, fig. S10B, and table S4). Indeed, examining specific trajectories suggests that the bats localized themselves after encountering high-entropy features (fig. S11), while they probably also sampled adjacent features

within an informative area. In comparison to at least one of the blindfolded groups, sighted bats experienced significantly higher entropy when turning and higher KL distance when turning and during the localization phase, ($P < 0.049$) (Table 2 and table S4). Bats would benefit from memorizing such high-KL sites because they are distinctive, but bats could memorize any landmark they choose to.

Discussion

Homing after translocation requires identification of the new location and determining the direction toward a desirable target. We translocated bats a few kilometers away from their roost to examine evidence for cognitive map–based navigation within their familiar home range (2). Both sighted and blindfolded bats

Table 2. Bats use environmental features to guide navigation. The echoic entropy bats experienced during different sensory deprivation and different flight modes, i.e., during their real trajectory, straight flight, and entropy based step selection flight to their destination, while turning versus flying in a relatively straight flight (turning angle >25° versus <25°), and during versus after the localization phase. Analysis was conducted using a GLMM with echoic entropy set as the dependent variable; treatment and flight mode were defined as fixed factors; and translocation point, destination, and bat ID were defined as random effects. Est., estimate; SE, standard error; t stat., t statistic; DF, degrees of freedom; lower, the lower bound of the confidence interval; upper, the upper bound of the confidence interval; SD, standard deviation.

	Est.	SE	t stat.	DF	P value	Lower	Upper	Mean ± SD (number of bats)		
Real, straight, and maximum entropy–based flights (bit/echo)								**Real track**	**Straight line**	**Step selection**
Control (Intercept)	1.67	0.05	32.2	194	1.2×10^{-79}	1.57	1.78	1.5 ± 0.12 (29)	1.6 ± 0.24 (29)	2.4 ± 0.44 (29)
Visual deprivation	0.03	0.06	0.4	194	0.661	0.14	0.09	1.4 ± 0.09 (14)	1.6 ± 0.16 (14)	2.5 ± 0.5 (14)
Visual and magnetic deprivation	0.06	0.06	1.1	194	0.277	0.18	0.05	1.5 ± 0.12 (15)	1.6 ± 0.14 (15)	2.3 ± 0.42 (15)
Visual, magnetic, and olfactory deprivation	0.08	0.07	1.2	194	0.245	0.22	0.06	1.4 ± 0.1 (9)	1.8 ± 0.15 (9)	2.1 ± 0.45 (9)
Flight mode (Straight line)	0.72	0.05	15.2	194	5.2×10^{-35}	0.63	0.82			
Flight mode (Step selection)	0.20	0.05	4.2	194	4.2×10^{-5}	0.29	0.11			
Turning versus straight flight (bit/echo)								**Turning**	**Straight flight**	
Control (Intercept)	1.79	0.05	33.4	129	2.7×10^{-65}	1.68	1.89	1.8 ± 0.29 (29)	1.7 ± 0.2 (29)	
Visual deprivation	0.20	0.07	3.0	129	0.003	0.33	0.07	1.6 ± 0.18 (14)	1.5 ± 0.19 (14)	
Visual and magnetic deprivation	0.02	0.06	0.3	129	0.765	0.15	0.11	1.8 ± 0.33 (15)	1.7 ± 0.18 (15)	
Visual, magnetic, and olfactory deprivation	0.12	0.08	1.6	129	0.111	0.28	0.03	1.6 ± 0.19 (9)	1.6 ± 0.16 (9)	
Flight mode	0.11	0.02	4.7	129	7.8×10^{-6}	0.15	0.06			
During versus after the localization phase (bit/echo)								**During**	**After**	
Control (Intercept)	1.21	0.04	33.32	109	5.6×10^{-59}	1.14	1.28	1.2 ± 0.33 (21)	1.1 ± 0.04 (21)	
Visual deprivation	0.08	0.05	1.65	109	0.102	0.18	0.02	1.1 ± 0.07 (13)	1.1 ± 0.03 (13)	
Visual and magnetic deprivation	0.08	0.05	1.56	109	0.122	0.17	0.02	1.1 ± 0.06 (14)	1.1 ± 0.04 (14)	
Visual, magnetic, and olfactory deprivation	0.03	0.06	0.49	109	0.626	0.14	0.08	1.2 ± 0.5 (9)	1.0 ± 0.09 (9)	
Flight mode	0.11	0.04	2.95	109	0.004	0.19	0.04			

could not directly sense their roost from the translocation release points, which was located far beyond their maximum sensing range for both echolocation and vision (*28*). At the beginning of their flight, bats performed a meandering flight, which we defined as the localization phase, during which they flew in a correlated-random flight and turned next to environmental features that provided ample acoustic and visual information and gradually transitioned to a direct flight toward their destination (fig. S12). A similar switch from a wandering phase to a return (to home) phase was described for translocated Egyptian fruit bats (*29*), Stone curlews (*30*), and honeybees (*31*).

Our field experiments suggest that bats can perform map-based navigation while relying on echolocation, and our modeling provides insight into how they could do so. Specifically, modeling the acoustic information that the bats could acquire by using the echoic entropy

suggests that the bats flew along trajectories that provided more acoustic information than the direct path to their destination, despite the cost of flying ~1.8-times-longer trajectories, and that they turned at points of higher acoustic information (which were not obstacles). This additional flight distance of 2.3 ± 2.2 km (*n* = 67 bats) is not negligible and represents 6% of the total cumulative flight distance undertaken in a regular foraging night (38.3 ± 23.7 km, *n* = 117 bats) (*24*).

We show that the acoustic information of certain environmental features can be distinguishable (i.e., large KL distance) and could allow the bats to identify their specific location in their familiar area, which is essential for map-based navigation. As expected, complex environments (such as orchards) provide more-distinguishable acoustic information (even when compared to other orchards; see upper right, Fig. 3E). These results are in line with previous

findings that showed that bats can recognize natural objects by their specific acoustic signature (*32–34*) and use acoustic landmarks for spatial navigation in models (*34*) and in lab conditions (*5, 35*). After localization, bats had to use acoustics to inform their compass to guide flight direction. Bats flew next to environmental features with greater acoustic information while turning, supporting our hypothesis that more complex landscapes, which create more complex acoustic signals, provide essential information for orientation and navigation. Flying over a low-entropy environment, such as a harvested field, might create ambiguity and make heading maintenance difficult. Moreover, such a landscape has little distinct features in the region and might confuse the animal regarding its location.

Although the bats might have sometimes flown along landscape elements during part of the way home, it does not negate the hypothesis that they maintain a mental acoustic map, as (after localization) they always chose a path in the direction toward their final target, and they gradually and continuously decreased the angle of flight relative to the target [in comparison to route following, where linear movement segments are typically disrupted by sharp turns at landmarks (*2*)]. Moreover, even when a more accurate visual map is used, animals and bats, specifically, might not use direct route for various sensory reasons (fig. S13), as we have previously shown for visually navigating bats (*8, 36*).

When they could, the bats also appeared to use vision in addition to echolocation to assist navigation, as sighted bats exhibited significantly faster and straighter flights (Figs. 1, E and F, and 2, B and C). Visually guided navigation is common in bat species with large eyes and good vision; however, it has rarely been demonstrated in small echolocating bats (*37–39*) with relatively small eyes and lower acuity (*40*). Furthermore, although echolocation is sometimes advantageous over vision for recognizing proximal objects at short distances (<10 m), vision has a significantly greater sensing range (up to 2 km). We suggest that, when using vision for navigation, bats perhaps rely on more distant environmental features, such as distant anthropogenic lights, as there was no correlation between flight straightness and general ambient illumination. In our experiment, we did not find any evidence that bats use magnetic sensing or olfaction to perform the homing task (supplementary text, section S1).

We demonstrate that (6-g) Kuhl's pipistrelle can navigate over a few kilometers using solely echolocation and that, when available, they can also use vision to improve navigation performance. These small echolocating bats first identify their new location after translocation and then conduct directional flight home using environmental features that provide enough acoustic information to be distinguished as
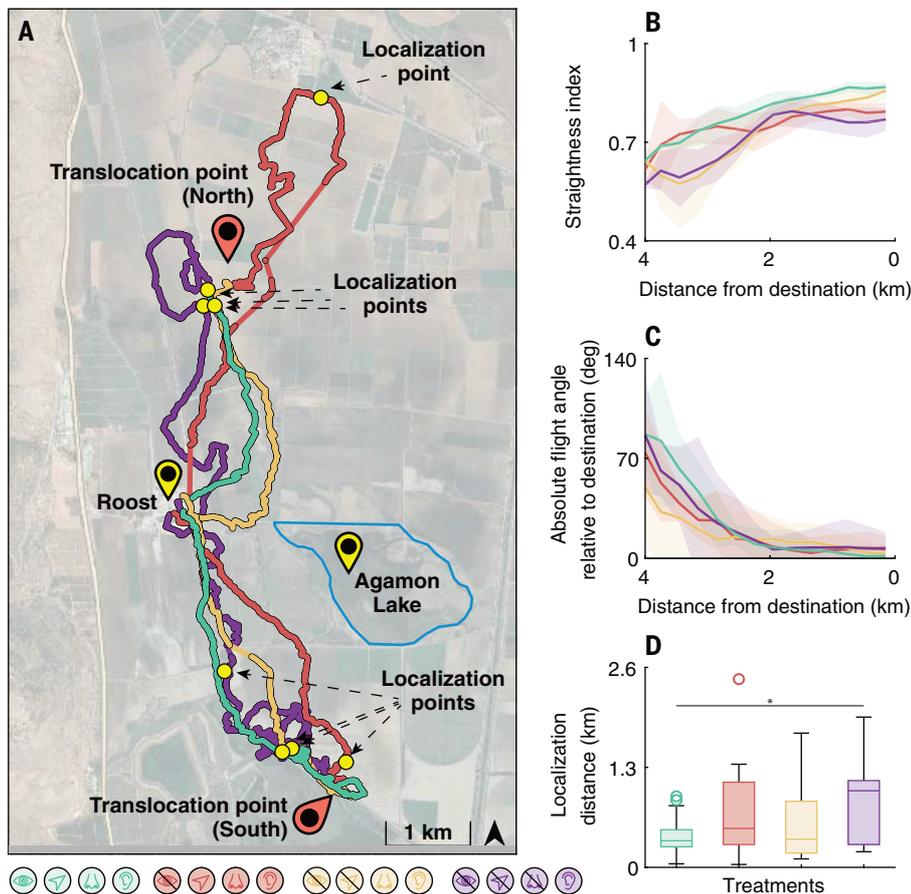

Fig. 2. Bats identify their location after translocation during the localization phase. (**A**) Examples of homing trajectories from the two translocation points. Bats flew in a correlated random walk until they identified their new location (i.e., the localization points, indicated by yellow circles) and then flew in a relatively straight flight toward their destination. (**B**) Straightness index according to flight distance from destination. Data represent mean ± standard error. (**C**) Absolute flight angle relative to destination according to flight distance from destination. Data represent mean ± average variance. (**D**) The beeline localization distance of the different groups. Boxplots represent the median and the first and third quartiles, and significance levels are indicated by asterisks: *P < 0.05; **P < 0.01; ***P < 0.001. Map data are from Google, Mapa GIsrael Imagery, and CNES/Airbus. Landsat/Copernicus. Maxar Technology.
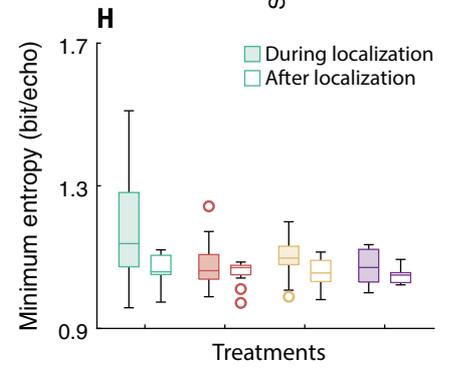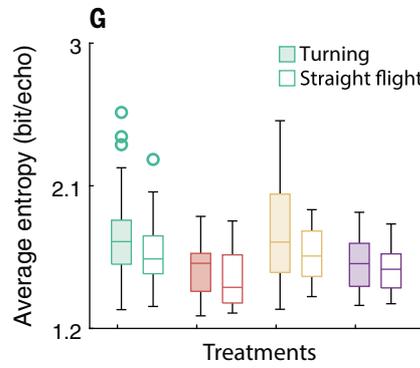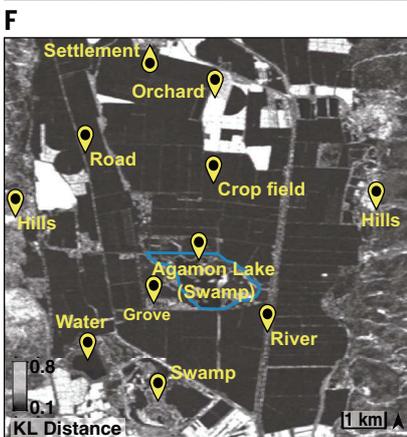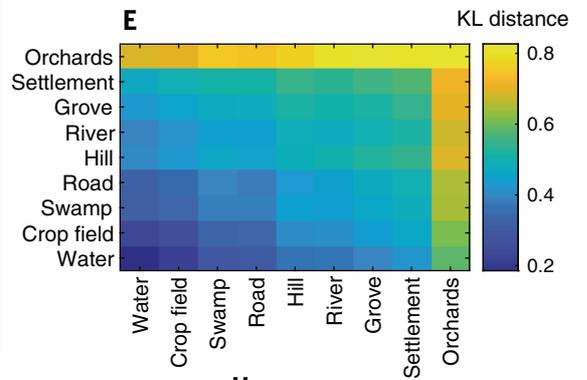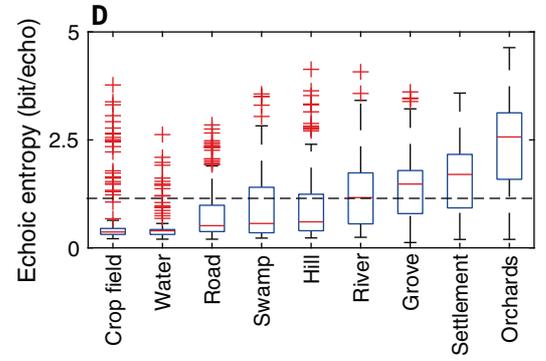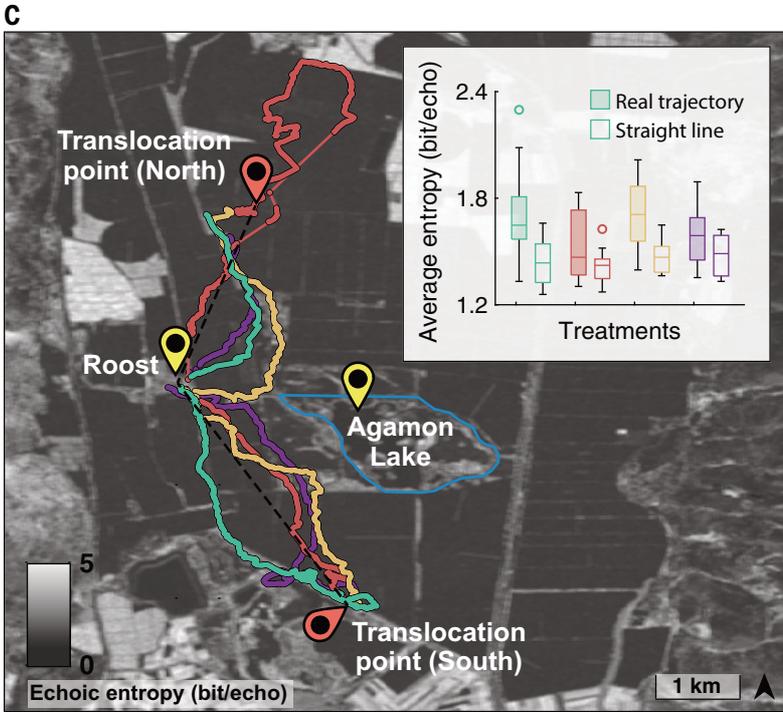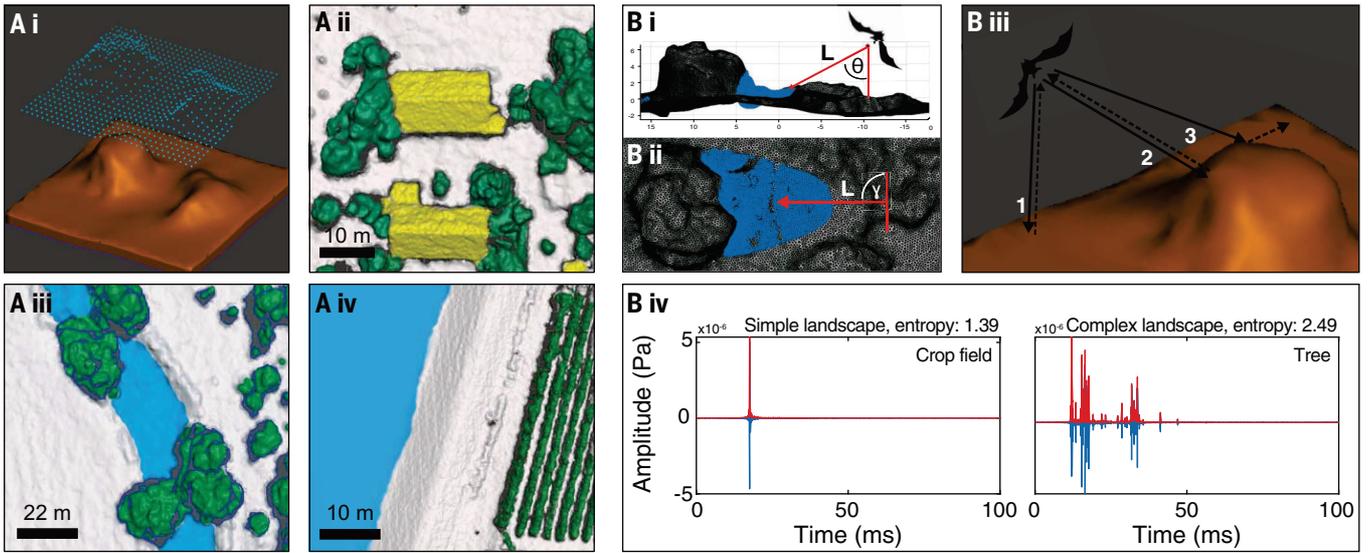
Fig. 3. Bats use echoic environmental features to guide navigation. (**A**) 3D landscape reconstruction of the study site using a high resolution digital elevation model. (i) The 3D point cloud (cyan points) was converted into a surface mesh. (ii) to (iv) Three examples of 3D landscapes. (**B**) Echo simulation. (i) A side and (ii) top view of the bat's position. The distance between the bat and the center of the landscape (L), elevation angle (θ), and azimuth (γ) are presented. (iii) A schematic of three reflections of bat sonar beam. (iv) Exemplar reflected echoes of a single peak (left) and complex multipeak echo (right). (**C**) Examples of bat flight trajectories are represented by scattered points, and straight lines between the same departure and destination points are represented by black dashed lines on a background of the echoic entropy map. The inset shows the average echoic entropy bats experienced during their flight from the translocation point to their destination (solid boxes) compared with the average entropy that they would experience if they had flown in a straight line between the same departure and destination points (transparent boxes). (**D**) The echoic entropies and (**E**) echoic KL distance across landscapes range from low (water and crop fields) to high (settlements and orchards). (**F**) The echoic KL distance map was used to measure the differentiability between spatial cells. The average KL distance values for each cell are presented in a black to white color scale that represents a low to high differentiability, respectively. The echoic entropy bats experienced (**G**) when turning (solid boxes) compared with flying straight (transparent boxes) as well as (**H**) during (solid boxes) and after (transparent boxes) the localization phase. In (C), (G), and (H), the different treatments are represented by the same colors as in Figs. 1 and 2. Boxplots represent the median and the first and third quartiles.

landmarks. This behavior also implies that they hold an acoustic mental map of their home range.

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SUPPLEMENTARY MATERIALS

Materials and Methods
Supplementary Text
Figs. S1 to S14
Tables S1 to S5
References (*42 81*)
MDAR Reproducibility Checklist