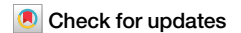




Sensorimotor strategies for rapid leadership takeover in flying echolocating bats



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Coordinated movement in animal groups requires rapid sensorimotor adjustments to maintain cohesion and avoid collisions. In flying organisms this challenge becomes even more pronounced, yet the sensorimotor strategies guiding such rapid flight maneuvers remain poorly understood. We combined high-speed infrared motion capture and on-board miniature ultrasound recorders to investigate the fine-scale kinematic strategies applied by free-flying ghost-faced bats (*Mormoops megalophylla*) to switch their relative positions during tandem-flight. We found that the following bats proactively initiated rapid maneuvers during turns to take over the lead. Specifically, they turned earlier and maintained higher speeds than the leading bats suggesting that they could anticipate the movements of the leader and adapt accordingly. Additionally, following bats likely switched positions to reduce both flight and echolocation costs. Together, our results suggest that bats prefer the leading positions and actively plan overtakes by anticipating the leader's trajectory. This behavior mirroring pursuit principles in fighter jet aviation suggests a general mechanism for role switching in group locomotion.

When flying in a group, animals must constantly negotiate spatial challenges while allocating sensory attention to both conspecifics and the environment^{1–3}. Leading-Following behavior has been observed in various species^{4–9}. Leadership has been shown to emerge if some individuals are more active or better informed than others^{8,10}. Leading is advantageous, enabling earlier access to resources/mates¹¹, but it has also been suggested to be energetically expensive¹² and to increase exposure to predators¹³. On the other hand, following has been linked to lower flight costs^{14–16}, reduced search effort¹⁷ and lower predation risk¹⁸, while it also entails a higher risk of reduced resources and exploitation by the leader¹⁹.

For volant species such as echolocating bats, these challenges are especially acute because sensorimotor decisions must be updated extremely fast²⁰. Specifically, flight requires continuous adjustment of speed, maneuvering, and altitude^{21,22}, while echolocation provides accurate range information but is vulnerable to interference from nearby conspecifics^{23,24}. Bats often fly in groups when emerging from caves and commuting²⁵ or when foraging in small spaces surrounded by vegetation. In these latter situations, they are frequently observed following (or chasing) each other, a behavior which has been suggested to be related to foraging or social competition^{26,27}. Previous work has primarily focused on the sensory aspects of flying in a

group of bats^{26,28–35}, including studies which showed that bats align their flight when commuting^{34,36} and mostly respond to individuals flying in front of them³⁶. Very few studies have so far analyzed the motor strategies applied by the bats when flying in tight groups, especially in a foraging context.

Leader-follower roles are known to be dynamic and changing over time. In flocks of birds, for example, leadership has been shown to temporarily switch during sudden turns^{37–39}. In bats, it has been shown that *Myotis daubentonii* chasing insects over water often engage in coordinated maneuvers and swap leader/follower positions during tandem flights²⁸ but that study focused only on the sensory aspects of chasing and coordinated flight maneuvers and found that following bats use the echoes returning from the leader's body to track the leader and match its flight direction²⁸. However, the fine-scale kinematic strategies that enable rapid position swapping have not been investigated. We hypothesize that two strategies are possible: following bats might use reactive adjustments (responding to the leader's motion and echolocation) or proactive strategies (i.e., changing their trajectory and sensory sampling in advance). Here, we aimed to disentangle these possibilities using simultaneous, high-resolution measurements of flight kinematics and echolocation.

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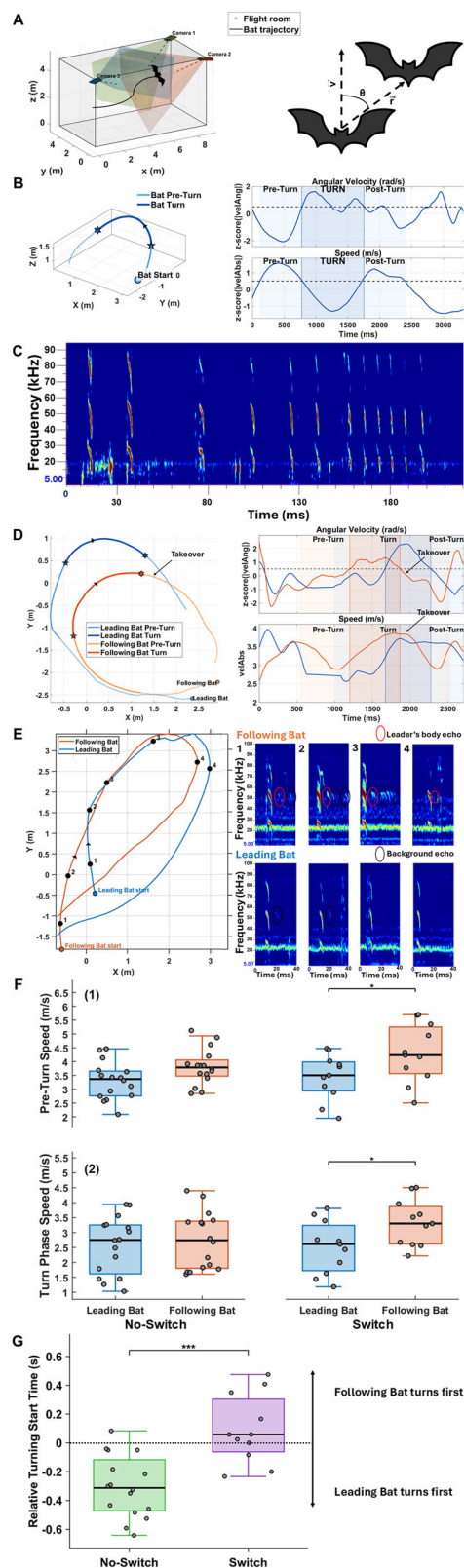


Fig. 1 | Flight kinematics of switching maneuvers. **A** Scaled Illustration of the experimental system showing three cameras placed on three corners of the room, and an Illustration depicting the angle used to define leading, following encounters. The field of view of the cameras in the experimental setup has been depicted using the colors of the cameras themselves. **B** 3-D and time series plot depicting flight trajectories of one bat in the flight room, highlighting different defined phases of flight- pre-turn and turn (defined above). The time series plot displays changes in the z-score absolute values of different parameters, like angular velocity and speed. The dotted line in angular velocity represents the 0.5 threshold used to define the bounds of the turning phase. **C** Representative echolocation spectrogram of a ghost-faced bat recorded in Raven Pro, showing a typical approach sequence and each echolocation call containing three harmonics with a dominant second harmonic. **D** 2D trajectory plots and a time series plot depicting flight trajectories of two bats in the flight room, highlighting different defined phases of flight- pre-turn and turn (defined above) during a switching event. Leading Bat and Following Bat are depicted in blue and orange colors, respectively. Point of takeover has been denoted on both plots. **E** Leader-follower flight trajectories and echolocation recordings from two tagged bats. Left: Two-dimensional flight paths of the leading bat (blue) and following bat (orange) during coordinated flight in the flight room. Black numbered markers (1–4) indicate four representative frames; matching numbers denote the same time point on both trajectories. Right: 40-ms spectrogram excerpts from the following bat's tag (top row) and the leading bat's tag (bottom row) corresponding to those selected events. Colored circles highlight echo components, including reflections from the leader's body in the following bat's recordings (red circles) and background echoes in both tags (black). The upper and lower spectrogram panels are not time-synchronized with each other, but each row shows matched call events across the two bats. Echoes were annotated as leader's body echo and background echoes by first calculating the apparent distance to the object from the time difference between the echolocation call and the echoes and then comparing them to the actual distance between the bats at that moment. **F** In switching flights, following bats flew faster during the pre-turn (4.3 ± 1.1 m/s vs 3.4 ± 0.8 m/s, respectively, GLMM with Pairwise two-sided Wald tests of linear contrasts, $p = 0.01$, $N = 54$) and the turn phase (3.3 ± 0.8 m/s vs 2.5 ± 0.9 m/s, respectively, GLMM with Pairwise two-sided Wald tests of linear contrasts, $p = 0.03$, $N = 54$) to take the lead. Asterisks denote the level of significance between treatment groups (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). **G** In switching flights, following bats turned earlier than the leading bats to take the lead (GLMM with two-sided Wald tests of linear contrasts, $p = 0.0001$, $N = 27$). Negative values indicate that the leading bat initiated the turn first, whereas positive values indicate that the following bat initiated the turn first.

suit for short-range ranging. These bats roost in large colonies with up to 500,000 individuals⁴³ and frequently forage and commute in groups, creating conditions in which individuals must constantly make rapid sensorimotor adjustments to resolve spatial challenges.

We combined synchronized, high-speed infrared motion capture and on-board miniature ultrasonic recorders to follow free-flying ghost-faced bats during solitary and social flights in a large flight room in nearly complete darkness. We asked (1) How do bats adjust their kinematics when switching between leader-follower roles, and (2) Who initiates the position switches, i.e., do bats prefer to lead or to follow? Our results suggest that leading is the preferred role and highlight the kinematic strategies used by the following bat during or before the turn, particularly following bats fly faster and turn earlier (implying that they predict the movement of the leading bat) to take over the lead without a response from the leading bat.

Results

Bats were released in a large flight cage ($9 \text{ m} \times 5 \text{ m} \times 5 \text{ m}$, Fig. 1A) and their flights, either alone or in smaller groups of up to three individuals (see Methods), were analyzed. Bats flew readily and displayed individual-stable flight patterns circling the flight room in individually stereotypical ellipse-like trajectories (Fig. 1B) flying at an average speed of 3.4 ± 0.5 m/s (Mean $\pm$ SD), turning at the corners by ascending to slow down before the turn (Fig. 1B). The bats' echolocation was recorded continuously with onboard tags (see Methods). Echolocation signals (Fig. 1C) had a maximum frequency of 54.9 ± 1.2 kHz (of the most dominant 2nd harmonic), an inter-pulse interval of 48.6 ± 9.9 ms, and a duration of 2.9 ± 0.3 ms (Mean $\pm$ SD).

The ghost-faced bat (*M. megalophylla*), a medium-sized insectivorous bat species (wingspans ranging from 36 to 38 cm), offers a powerful model for studying sensorimotor strategies for fast maneuvers in a group. These bats are highly maneuverable flyers that naturally exhibit coordinated circling and pursuit-like behavior inside roosts and foraging spaces^{40,41}. Their short, broadband, multi-harmonic frequency-modulated (FM) echolocation calls are used for spatial orientation and prey capture⁴² and are well-

Flight kinematics of switching maneuvers

When multiple bats were present in the room, they showed similar individually stereotypical ellipse-like trajectories (Fig. 1D and Supplementary Fig. 1-2) and a strong preference for paired aligned flight. Bats flew synchronously, asynchronously and non-synchronously (see Methods for definitions) for 59%, 6% and 35% respectively of the total paired flight time. During synchronous flights, bats frequently switched between leader-follower roles, at an average rate of ca. 3 switches per minute. On-board recordings show that the following bats received echoes from the leading bats' bodies which could have facilitated their tracking (Fig. 1E). To quantify switching maneuvers and examine the sensorimotor mechanisms allowing these switches, we analyzed the complete kinematics of 11 switching and 16 non-switching events from a total of 12 bats (Supplementary Table 1). Because all switching events occurred during or just after turns, the kinematic analysis focused on turning. We separated each event into two phases: the pre-turn phase - before the bat starts turning, and the turn phase (see Methods).

During the pre-turn phase, the following bats flew significantly faster than the leading bats in switching flights (4.3 ± 1.1 m/s vs 3.4 ± 0.8 m/s, respectively, GLMM with Pairwise Wald tests of linear contrasts, $p = 0.01$, $N = 54$, Table 1 and Fig. 1F1), while in non-switching flights the pre-turn flight speeds for both following and leading bats were similar (3.8 ± 0.7 m/s vs 3.3 ± 0.7 m/s, respectively, GLMM with Pairwise Wald tests of linear contrasts, $p > 0.05$, $N = 54$, Table 1 and Fig. 1F1). Even though both bats slowed down during the turn, the following bats continued flying significantly faster than the leading bats in switching flight (3.3 ± 0.8 m/s vs 2.5 ± 0.9 m/s, respectively, GLMM with Pairwise Wald tests of linear contrasts, $p = 0.03$, $N = 54$, Table 1 and Fig. 1F2). In comparison, in non-switching flights, the bats' speed was not significantly different during the turn (2.7 ± 1 m/s vs 2.6 ± 1 m/s, respectively, GLMM with Pairwise Wald tests of linear contrasts, $p > 0.05$, $N = 54$, Table 1 and Fig. 1F2).

The following bats turned 90 ± 240 ms earlier than the leading bats in switching flights, while in non-switching flights, the following bats began turning 300 ± 210 ms after the leading bats (GLMM, $p = 0.0001$, $N = 27$, Fig. 1G, and Table 1). When taking-over, the following bats also turned farther from the cage wall in comparison to when flying alone suggesting that taking over was intentional and not related to the cage (max distance from center was 3.49 ± 0.36 m vs 2.74 ± 0.65 m for alone and switch following bat respectively; GLMM, $p = 0.037$, $N = 26$, Supplementary Fig. 3). The switching maneuver itself was rapid, lasting only 540 ± 250 ms from the initiation of the follower's turn until the moment of takeover.

In summary, the following bats turned earlier and farther from the wall while flying faster to overtake the leading bats. They did not perform sharper turns (angular velocity was not significantly larger in following bats during switching flight see Table 1 for stats).

Moreover, there was no significant difference in the leading bat's flight kinematics in switching and non-switching flights suggesting that it did not respond to the takeover attempt (Fig. 1F, Table 1 and Supplementary Data 1).

Initiating the overtake

Our results suggest that the following bats initiate the switch. We identified several sensorimotor factors that might explain the disadvantages of the following bat. (1) The use of space was much more restricted when two bats were flying in the arena vs one bat (Fig. 2A). In this situation the leading bat dictates the use of space while the following bat is forced to follow. (2) Tracking the leading bat likely comes with a motor cost: Indeed, in the non-switching flights, the following bats used significantly greater pre-turn angular velocity than the leading bats thus exerting more forces in order to follow (1.4 ± 0.4 rad/s vs 1.0 ± 0.5 rad/s, respectively, GLMM with Pairwise Wald tests of linear contrasts, $p = 0.03$, $N = 43$, Table 1 and Fig. 2B). (3) Tracking the leading bat likely also comes with a sensory and a cognitive cost. Supporting this (on the sensory level) the echolocation calls emitted by the following bat were significantly more intense than those of the leading bat and bats flying alone, even when accounting for call duration

(-74.6 ± 8.7 dB, -78.2 ± 7.9 dB and -78.1 ± 8.9 dB during following, leading and solo flights, respectively, $n = 209$ following calls across 20 flight events, 346 leading calls across 21 flight events, 913 solo calls across 15 solo flights, from 8 bats total (Supplementary Data 2), GLMM with Pairwise Wald tests of linear contrasts, $p = 1.48 \times 10^{-6}$ (Alone vs Follows), 0.0002 (Leads vs Follows), Supplementary Table 2 and Fig. 2C1). Following bats also used higher frequency calls than both leading bats and bats flying alone, even when accounting for call duration and call peak power (55.1 ± 1.2 kHz, 56.0 ± 1.2 kHz, and 55.8 ± 1.2 kHz during solo, following and leading flights, respectively, $n = 209$ following calls across 20 flight events, 346 leading calls across 21 flight events, 913 solo calls across 15 solo flights, from 8 bats total (Supplementary Data 2), GLMM with Pairwise Wald tests of linear contrasts, $p = 0.003$ (Alone vs Follows), 0.04 (Leads vs Follows), Supplementary Table 2 and Fig. 2C2).

Discussion

Bats in our flight room moved through space in individually repeatable, stereotyped ellipse-like trajectories echoing previous observations in the laboratory settings⁴⁴, in the wild while foraging^{45,46}, and near roosting⁴⁷ and swarming sites⁴⁸. When flying in a group, bats must make sensorimotor decisions within hundreds of milliseconds, and our combined acoustic and kinematic analysis demonstrate how following bats maneuver to take over the leadership.

To overtake the leader, the following bats flew faster, turned earlier both in time and space and did not slow down as much as the leading bats did during turns. This strategy reduces the need for large lateral accelerations during the maneuver (i.e., to turn more sharply), thereby likely minimizing collision risk which is high during the takeover. In contrast, during non-switching flights both bats had similar pre-turn speeds, turning timing, and speed during the turn. These patterns suggest that the following bats executed a deliberate overtaking maneuver, taking advantage of the expected turn.

Interestingly, the maneuver performed by the following bats resembles pursuit-curve strategies used in fighter jet aviation. Instead of simply reacting to the leader's motion, the follower increases its speed and initiates the turn early, allowing it to "cut the corner" and takeover. In fighter jet aviation, this corresponds to the lag-to-lead pursuit transition performed during turning engagements, where a pursuing aircraft anticipates an opponent's turn and uses early turn initiation to obtain positional advantage without requiring a tighter turn radius⁴⁹. This strategy of geometry-based, anticipatory maneuvering closely parallels the kinematic pattern observed in our bats, suggesting that predictive trajectory shaping is a convergent solution in both biological and engineered flyers operating in constrained 3-D environments.

In our controlled environment, the cage walls constrained the bats to turn near the boundaries of the space. A similar situation occurs in nature when multiple bats forage in edge-space environments near vegetation (e.g., a forest opening) or other obstacles or even in caves. The bats are confined at least on some sides, and they often exhibit following behavior and overtaking²⁸. In such situations, a following bat might be able to take advantage of predictable turns. Our study thus suggests that bats can predict the motor plan of a conspecific and act accordingly. However, we cannot completely exclude alternative explanations such as that the bats were turning due to the cage and then maneuvering to avoid collision with the conspecific. This might have been possible if everything was always fixed, but in reality, there is much variability in the exact trajectory (Fig. 2A) and speed (preturn: 3.4 ± 0.8 m/s, turn: 2.5 ± 0.9 m/s) of the leading bat and thus if the following bat did not track the leading bat (and predict when it is about to turn) such precise maneuvers would likely fail. Prior studies have described the turning mechanics of bats⁵⁰ and shown that while turning at edge spaces, bats will slow down by ascending and converting kinetic energy into potential energy momentarily before diving and speeding⁵¹, similar to what we observed in our flight room (Fig. 1C and Supplementary Fig. 4). This is an energetically rational action, because when braking before a turn in a confined space, kinetic energy can be lost. By gaining altitude, the energy is stored as

Table 1 | Flight kinematics of switching versus non-switching maneuvers

Parameter (Units)	Comparison	Estimate (1-2)	CI Low	CI High	pValue	PseudoR2	GLMM Model Formula
Pre-Turn Speed (m/s)	No-Switch Leading vs No-Switch Following	-0.509	-1.035	0.016	0.063	0.071	Pre-Turn Speed ~ Flight Type*Position + (1 Bat)
	No-Switch Leading vs Switch Leading	-0.110	-0.692	0.472	0.713	0.071	
	No-Switch Following vs Switch Following	-0.461	-1.044	0.121	0.127	0.071	
Turn Phase Speed (m/s)	Switch Leading vs Switch Following	-0.861	-1.495	-0.227	0.010	0.071	
	No-Switch Leading vs No-Switch Following	-0.156	-0.757	0.446	0.614	0.041	Turn Speed ~ Flight Type*Position + (1 Bat)
	No-Switch Leading vs Switch Leading	0.078	-0.588	0.744	0.820	0.041	
	No-Switch Following vs Switch Following	-0.587	-1.253	0.080	0.090	0.041	
	Switch Leading vs Switch Following	-0.820	-1.546	-0.095	0.031	0.041	
	No-Switch Leading vs No-Switch Following	-0.430	-0.806	-0.054	0.031	0.085	Pre-turn Angular Velocity ~ Flight Type*Position + (1 Bat)
	No-Switch Leading vs Switch Leading	-0.297	-0.696	0.103	0.154	0.085	
	No-Switch Following vs Switch Following	0.092	-0.284	0.468	0.635	0.085	
	Switch Leading vs Switch Following	-0.041	-0.441	0.359	0.841	0.085	
Turn Angular Velocity (rad/s)	No-Switch Leading vs No-Switch Following	0.288	-0.842	1.418	0.620	0.015	Turn Angular Velocity ~ Flight Type*Position + (1 Bat)
	No-Switch Leading vs Switch Leading	0.960	-0.292	2.211	0.139	0.015	
	No-Switch Following vs Switch Following	0.605	-0.646	1.857	0.348	0.015	
Relative Turning Start Time (s)	Switch Leading vs Switch Following	-0.067	-1.429	1.296	0.924	0.015	
	No-Switch vs Switch	-0.357	-0.511	-0.204	0.0001	2.537	Relative Turning Start Time ~ FlightType + (1 LeadingBat) + (1 FollowingBat)

Pairwise comparisons derived from GLMMs with two-sided Wald tests of linear contrasts, assessing the effects of Flight Type (Switch vs. No-Switch) and Position (Leading vs. Following) on pre-turn and turning kinematics. For each parameter we report the estimated group difference (Estimate = Group 1 – Group 2), its 95% confidence interval, the *p*-value, the pseudo-*R*², and the model formula. All models include bat identity as a random intercept, except the model for Relative Turning Start Time, which includes separate random intercepts for leading- and following-bat identity. Negative estimates indicate lower values in the first group relative to the second. All parameters retain their original physical units.

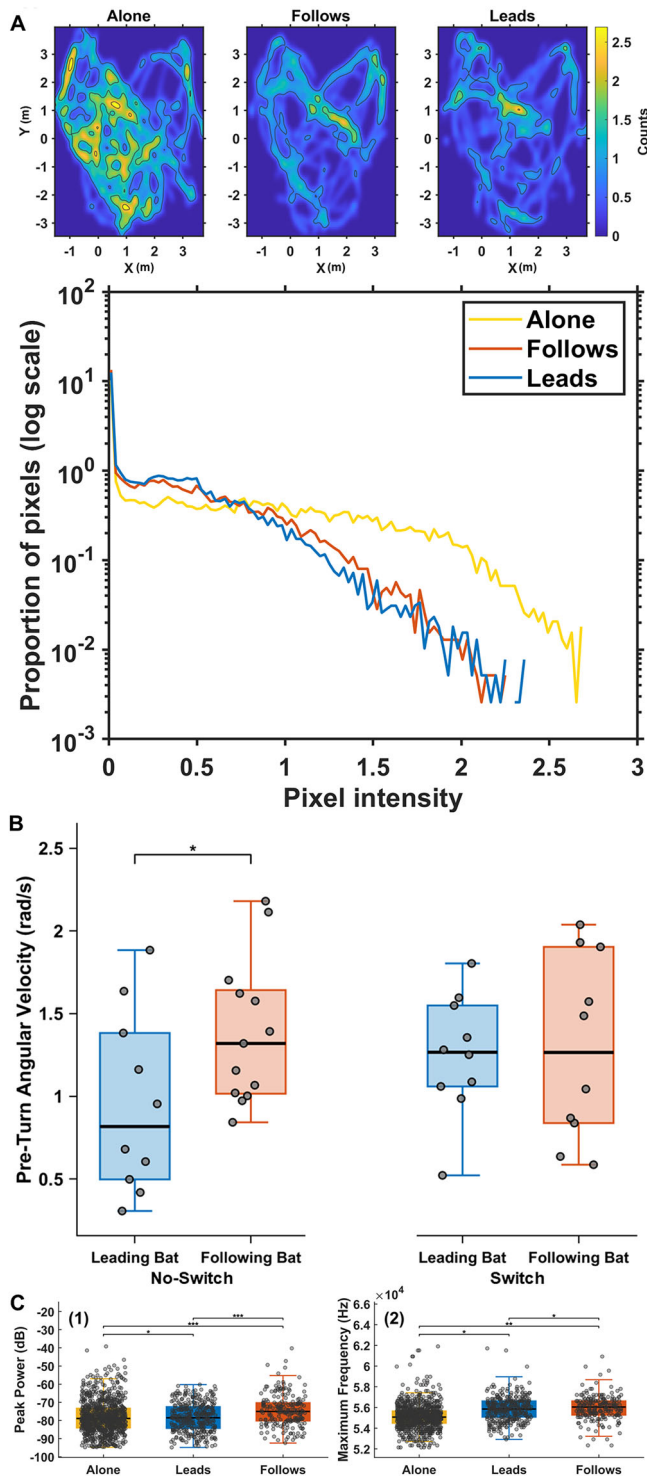


Fig. 2 | Initiating the overtakes. A Heat-maps (hotter colors mean bats spent more time at that location) of the arena for bats flying alone, or when leading / following. The bottom row shows the corresponding pixel-intensity distributions, demonstrating that when flying alone – bats use a much broader part of the arena – note the long tail of hot-color pixels. This suggests that when flying in a pair, the use of space is much more restricted. **B** In the non-switching flights, the following bats used significantly greater angular velocity than the leading bats (1.4 ± 0.4 rad/s vs 1.0 ± 0.5 rad/s, respectively, GLMM with Pairwise two-sided Wald tests of linear contrasts, $p = 0.03$, $N = 43$). Asterisks denote the level of significance between treatment groups (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). **C1** Call Peak Power significantly increases when the bat is following compared to when it is leading or flying alone (-74.6 ± 8.7 dB, -78.2 ± 7.9 dB and -78.1 ± 8.9 dB during following, leading and solo flights, respectively, $n = 209$ following calls across 20 flight events, 346 leading calls across 21 flight events, 913 solo calls across 15 solo flights, from 8 bats total (Supplementary Data 2), GLMM with Pairwise two-sided Wald tests of linear contrasts, $p = 1.48E-06$ (Alone vs Follows), 0.0002 (Leads vs Follows)). **C2** Call Maximum Frequency significantly increases when the bat is following as compared to when it is leading or during solitary flights (55.1 ± 1.2 kHz, 56.0 ± 1.2 kHz, and 55.8 ± 1.2 kHz during solo, following and leading flights, respectively, $n = 209$ following calls across 20 flight events, 346 leading calls across 21 flight events, 913 solo calls across 15 solo flights, from 8 bats total (Supplementary Data 2), GLMM with Pairwise two-sided Wald tests of linear contrasts, $p = 0.003$ (Alone vs Follows), 0.04 (Leads vs Follows)).

maneuvers in order to follow the leading bat. These turns likely imposed greater energetic demands, due to the larger centripetal and reorientation forces. This is supported by previous work showing that bat turning maneuvers are energetically demanding; for example, bats have been shown to consume about 0.67 W to execute a turning-ascending maneuver, approximately twice the power consumed during level flight⁵³. Tracking likely also comes with a sensory cost. Indeed, the echolocation calls emitted by the following bats were significantly more intense (by an average of 3.6 dB), again probably because of the need to track the leading bat using echolocation²⁸ while avoiding obstacles. High-intensity echolocation imposes some metabolic costs on flying bats⁵⁴ and an additional sensory cost which we did not quantify is that of the cognitive processes entailed by tracking (which the leading bat does not have). The following bats also used slightly higher frequency calls which may likewise reflect the demands of tracking^{55,56}. Consistent with this interpretation, we further showed that following bats received echoes from the leading bat's body (Fig. 1E). So, in total, the following bat spent additional sensori-motor energy for both tracking the leading bat and adjusting its flight to keep track of it. In addition to the cost of following, the leading bat might have a sensory advantage – being the first to spot prey or obstacles (although in our setup, the bats never attacked the mealworms we hung). Indeed, our analysis of the space used by the bats suggested that when flying in pairs, bats were more limited in their space use than when flying alone and specifically they stuck more to their ellipse stereotypical trajectories and avoided use of the center of the arena (Fig. 2A). So, another reason to take the lead would thus be to control the use of space.

It is worth noting that our finding that the following bats increased echolocation output rather than suppressing it differs from previous work on paired bats³⁰ and an alone bat under acoustic masking⁵⁷. Chiu et al. found that paired big brown bats briefly ceased vocalizing at close range, but this was observed under artificial laboratory conditions in trained bats pursuing a tethered mealworm presented at a largely fixed, predictable location that was repositioned only occasionally rather than a spontaneous, unconstrained flight and role-switching behavior examined here. Similarly, Taub & Yovel showed that echolocating bats adjust their flight movement to manage acoustic masking, but that study concerned a single bat landing on a static target, not two bats flying together, and therefore does not bear on the social flight interactions that are the focus of the present study.

Interestingly, we found no response from the leading bats to switching attempts (e.g., by increasing speed or angular velocity), suggesting that they might not be aware of the following bats switching intention. This makes

potential energy and then converted back for subsequent acceleration in the opposite direction. Although this species has been recorded to fly much faster during commuting flights⁵², the speeds recorded by us are normal for flights in confined spaces⁵⁰, and there is no reason to assume that in nature, in a restricted space, these bats would fly faster.

Our results shed some light on bats' motivation for preferring the leading position during pairwise interactions. Tracking and following a small object such as a bat that is moving in a small environment comes with a sensorimotor cost (even if part of the movement is repeatable – it is not exactly the same). Indeed, the following bats used significantly higher pre-turn angular velocities in non-switching flights, suggesting tighter

sense as sensing in the back is not easy using echolocation. Based on our analysis, the following bat only began its turn ~90 ms earlier, which resembles the fast end of reported bat behavioral latencies with a previous study of sudden prey-removal perturbations, where median acoustic and behavioral reaction times of approximately 80–90 ms were observed¹⁵⁸. The response time was also supported by other studies^{34,59}. Although, on one occasion we observed a double switch during a single maneuver (i.e., after the following bat overtook the leader, the leader immediately regained its frontal position). We did not include that singular case in our analysis. More broadly, leadership dynamically changed in some pairs, with bats alternating between leading and following across encounters and flights, whereas in others it was stable, with one bat consistently leading and the other consistently following (Supplementary Table 3). In one pair, the follower initially overtook the leader, after which it remained the leader in all subsequent encounters (Supplementary Table 3). These different social dynamics suggest that more factors, such as social status might play a role in the decision to take-over the leader.

Although our bats carried additional weight (14–16% of body mass including tags and reflective markers), comparisons with untagged individuals revealed no significant differences in flight speed or angular velocity (Methods), indicating that tagging did not measurably impair flight performance. Tagging remained within the range of loads that have been used in free-ranging insectivorous bats^{60,61} and is also consistent with the natural variability observed in insectivorous bats: in *Nyctalus noctula*, one individual was recaptured immediately after foraging having gained 8 g, or 27% of its previous capture mass⁶², and in *Micronycteris microtis* individuals consumed an estimated 4.6 ± 1.6 g of arthropods per night, equivalent to 61–84% of body mass⁶³. Accordingly, the added mass in our study likely fell within the range of nightly load variation that these bats can naturally experience. Additionally, all bats had extra weight, so the echolocation and interactions that we studied should not be impacted.

Together, these findings reveal rapid and precise sensorimotor adjustments that allow a following bat to transition into the leading position during coordinated flight, indicating anticipatory control rather than purely reactive behavior. This overtaking strategy, characterized by predictive kinematic modulation under sensory constraints, may represent a general principle of role switching in collective movement and could extend to other taxa that navigate in groups, including echolocating cetaceans, flocking birds, and schooling fish.

Material and methods

Animals

Bats were captured early in the evening as they emerged from their cave roosts in the Emiliano Zapata municipality, near Xalapa city, state of Veracruz, México (around latitude 19.4°, longitude -96.6°), on the 6th and 8th of July 2023, using butterfly and mist nets. A total of five individuals were caught on 6th July, and eight individuals on 8th July, with body masses between 14 and 16 g.

Flight room

Experiments were conducted in a dedicated flight cage with walls made of mosquito nets (9 m × 5 m × 5 m, Fig. 1A) at the La Mancha Field Station, located east of Xalapa, Mexico. The net covering the cage was mounted on plastic poles holding its infrastructure. A small, insulated wooden chamber with a mosquito net roof was used to temporarily house the bats between trials. To minimize reverberation, a carpet was laid over the concrete floor.

Sensors

Infrared camera. Three Opti Track infrared cameras (two model S250e and one model Prime41) were mounted at three corners of the flight room on tripods at a height of 20–30 cm from the ceiling, operating at 120 frames per second. Cameras were positioned to maximize the overlapping field of view, ensuring that the majority of the flight volume was covered by at least two cameras simultaneously to enable 3D reconstruction.

On-board tag fixation

A miniature modular audio logger (Pipistrell, ASD, 17 mm × 30 mm × 3.5 mm) incorporating an ultrasound microphone was affixed to each bat between the shoulders using TORBOT - Liquid Bonding Cement. The tag weighed 2.2–2.3 g (including batteries and protective wrapping). Before attachment, hair was carefully removed using a commercial depilatory cream. Bats flew readily in the room with the tags, and no obvious impairment in flight ability or kinematics was observed following tag attachment. The flight speed (tagged = 3.9 ± 1 m/s, untagged = 3.9 ± 1.1 m/s) and angular velocity (tagged = 1.4 ± 1.4 rad/s, untagged = 1.9 ± 1.8 rad/s) of 8 tagged and 4 untagged bats were found to be similar in our analysis (mean ± SD). Additionally, there was no noticeable qualitative difference in landing rates, landing and take-off ability or behavior upon release between tagged and untagged bats.

Experimental design

On 6th July, five bats were simultaneously released into the flight room and allowed to fly freely at their own time in a single trial of 75 minutes. Though all five bats were free to fly, for most of the time, bats only flew in pairs or triplets at most. On 8th July, each 4.5 min trial followed a staggered release design. One bat was first released and allowed to fly alone for 4.5 min, after which a second bat was introduced, and the two bats flew together for another 4.5 min. The first bat was then removed, leaving the second bat to fly alone for 4.5 min, after which a third bat was introduced. This sequence was continued until eight bats had been tested. A binomial mixed-effects model with random intercepts for bat identity and test number showed that prior alone time did not predict leader position ($\beta = 0.29$, SE = 0.66, $p = 0.66$; OR = 1.33, 95% CI [0.36, 4.90]).

Each bat was tested only on the same night in a continuous experiment, without reintroducing the bat and only a limited number of trials were performed to avoid development or use of spatial memory in the bats as their navigation is heavily influenced by their spatial memory of the environment^{34,44,64}. Four wires, each holding five to seven tethered mealworms, were suspended from the flight-room ceiling (about one meter); however, no hunting attempts were observed in any trials. Bats were marked with lightweight (0.01 g) reflective markers affixed to their heads and wings using TORBOT Liquid Bonding Cement to enable motion tracking and individual identification in the dark. Tags and reflectors were removed from the bats after the experiment using UNI-SOLVE adhesive removal wipes and bats were released unharmed at the capture site on the same night they were collected.

Flight tracking

Calibration: Wand and ball tracking were used to calibrate the tracking system, using the semi-automatic and automatic modes in the DLTdv® package⁶⁵ in MATLAB (version- R2023a). A wand marked with three reflective markers was waved and the movement of the markers was tracked after which a ball marked with a single reflective marker was manually dropped within the flight room, and its movement was recorded and tracked. DLT coefficients and tracking error were estimated using EasyWand⁶⁶. This procedure found that the positional errors were 5.0 ± 3.7 cm (X), 6.2 ± 4.4 cm (Y), and 3.0 ± 1.5 cm (Z).

Three-dimensional flight trajectories were reconstructed using the DLTdv8a MATLAB package⁶⁵. Marker positions were tracked in the videos using semi-automatic, automatic, and multitrack modes.

Video post processing

A custom MATLAB script was employed to post-process the DLT tracking output. Outlier locations were removed by computing a moving median position and discarding samples whose Euclidean distance to that median exceeded a fixed threshold of 0.12 meters. Interpolation was then carried out to fill the gaps in the tracking. Only gaps shorter than 0.3 seconds were interpolated using the spline method. Smoothing was applied to the interpolated point positions using a moving-average filter (window size = 0.1 seconds, i.e., 12 samples) to reduce random fluctuations and noise. After

smoothing, movement parameters, including speed and angular velocity, were calculated. We calculated angles using trigonometric functions based on the tracked velocities in the x, y, and z directions. The allocentric angle of motion (commonly referred to as heading or azimuth angle) was calculated using the arctangent function (atan2) of the y and x velocity components. Angular velocity, representing the rate of change of angle over time, was calculated by taking the derivative of the angle with respect to time. Outliers were removed using the following thresholds: - maximum angular velocity as $\pi \times 1.5$ rad/s and maximum absolute velocity as 7 m/s (96th percentile).

Audio signal processing

On-board audio tags recorded continuously at 200 kHz. Audio was processed using Batalef, an in-house MATLAB script⁶⁷. Echolocation Analysis was performed only on data collected on 8th July. The audio was first bandpass filtered using a forward-backward Butterworth filter (8th order) in the frequency range of 35–62 kHz to isolate the dominant second harmonic (Fig. 1B). Automatic call peak detection and acoustic parameter extraction were implemented, and all detections were manually inspected and corrected on a call-by-call basis. In trials involving conspecifics, own calls and conspecific calls were manually differentiated. The call parameters that were extracted included: The call's Maximum Frequency (highest frequency at the start of the FM sweep), Duration (default criteria before manual inspection: 12 dB below the peak amplitude), Peak Power, and Inter-Pulse Interval (IPI)- the time from the start of one call to the start of the next successive call. In parallel with Batalef, spectrograms were visualized using Raven Pro® 1.6.5 (Yang Center, Cornell Lab of Ornithology) for manual inspection. To avoid unreliable measurements of the very short and low buzz calls, we omitted them from the analysis by setting the minimum IPI threshold to 0.008 seconds and the minimum call level to -95 dB relative to the noise floor.

Synchronization

To ensure precise temporal alignment between video and audio recordings, a synchronizer emitted a single light and sound pulse at the start of each trial. The signal was recorded by one camera and by the audio tag, enabling synchronization of the data streams with an accuracy of 1/120 s.

Classifying paired behavior

Pairwise flight was classified using geometric and temporal criteria derived from the 3-D trajectories and instantaneous flight directions. For each pair, we computed the inter-bat distance and the 3-D angle (θ) between a bat's instantaneous velocity vector ($\rightarrow v$) and the position vector ($\rightarrow r$) to the other bat (Fig. 1A). Flight was termed as paired if the inter bat distance was less than two meters. Further bats were classified as flying synchronously, asynchronously, or non-synchronously when, for at least three consecutive frames (equivalent of 25 ms), the angle θ was less than 45°, more than 135°, or between 45° and 135°, respectively. Additionally, in synchronous flights we defined two encounter types- Leading and Following depending on the spatial position of the bat that is- bat in front was termed as 'Leader' while bat behind was termed as 'Follower'.

Identifying switch events

Switch maneuvers were defined as events in which the following bat became the leading bat (Supplementary Video). We refer to the 'following bat' as the bat that started the maneuver behind, while the 'leading bat' was the bat that started ahead. Since the observed switches happened during or after turns, we divided the flight into two parts: Pre-turn and turn. We used the z-score of the absolute Angular Velocity metric and set a threshold of 0.5 to identify the start and end time of the turn phase (Fig. 1D and Supplementary Fig. 5). The pre-turn phase was defined as 0.67 seconds before the beginning of the turn phase. since bats were thought to plan a switch in the period between their previous turn and the upcoming turn. Both parts of the flight described above were analyzed separately in this study. All the switching events we identified occurred when two or three bats were flying in the cage (Supplementary Table 1).

Statistics

All statistical analysis used generalized linear mixed-effects models (GLMM, identity link) using the `fitglme` function in MATLAB 2023a after testing for normal distribution to quantify how Flight Type (No-Switch vs. Switch) and Position (Leading vs. Following) influenced kinematic variables across bats and how Encounter Type (Alone vs Leads vs Follows) influenced echolocation variables across bats. All tests were two-sided, with statistical significance assessed at $\alpha = 0.05$, and 95% confidence intervals reported for all estimates. Because each bat contributed multiple flights across conditions, we explicitly modeled Bat identity as a random intercept, allowing individual-level variation to be accounted for while estimating population-level fixed effects. Additionally, since the echolocation analysis was done on call level data, with the random intercept for each bat we also included random intercepts for SessionID, and FlightID, where SessionID represents sessions (Test Number) nested within bats and FlightID represents flights (Flight Number) nested within sessions. This structure accounts for repeated calls within flights and repeated flights within sessions for each individual. All post-hoc pairwise comparisons were performed using model-based linear contrasts (Wald tests) on estimated marginal means derived from each GLMM. Where interactions were present, results proceeded entirely based on pairwise EMM contrasts rather than main-effect coefficients, because the biological question concerns differences between specific combinations (e.g., Switch-Following vs. Switch-Leading), not the average effect of Flight Type or Position pooled across the other factor.

Ethics. Ethics Statement Bats were captured and handled with permit from the Secretariat of Environment and Natural Resources, Government of Mexico- SEMARNAT number 30/K4-0470/06/23. Animals were cared for and experiments were performed according to the American Society of Mammalogists manual⁶⁹. No anesthesia or euthanasia procedures were used since the study did not involve any kind of surgery, invasive handling, or prolonged immobilization.

Reporting summary

Further information on experimental design is available in the Nature Portfolio Reporting Summary linked to this Article.

Data availability

The numerical source data underlying all graphs and charts presented in this study are available in an open-access repository in Mendeley (Sensorimotor strategies for rapid leadership takeover in flying echolocating bats - Mendeley Data)⁶⁸. Additional data supporting the findings of this study are available in the Supplementary Information or from the corresponding author upon reasonable request.

Code availability

Codes have been deposited in an open-access repository in Mendeley (Sensorimotor strategies for rapid leadership takeover in flying echolocating bats - Mendeley Data)⁶⁸. All other related information is included in the article and/or supplementary material.

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Author contributions

O.M., and Y.Y. designed the experiments; O.M. and A.G.S. performed the field experiments and data collection; P.N.P. and O.M. analyzed the data; P.N.P. wrote the original draft, P.N.P., O.M. and Y.Y. edited the manuscript. All authors reviewed and approved the final version of the manuscript. P.N.P. and O.M. contributed equally to this work.

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