Current Biology

Neurons Responsive to Global Visual Motion Have Unique Tuning Properties in Hummingbirds

Highlights

- Neuroanatomy and visual guidance data suggest neural specialization for hovering
- We recorded from neurons responding to visual direction and speed in three species
- Unlike in other species, hummingbird visual nuclei are responsive to all directions
- Motion processing neurons in hummingbirds prefer fast speeds

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In Brief

Direction- and velocity-selective global motion neurons in a key visual nucleus show strong preference for forward motion in all tetrapods studied until now. Gaede et al. show that hummingbirds exhibit expansion in the direction preference domain and differences in velocity tuning, compared to other avian species.



Neurons Responsive to Global Visual Motion Have Unique Tuning Properties in Hummingbirds

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SUMMARY

Neurons in animal visual systems that respond to global optic flow exhibit selectivity for motion direction and/or velocity. The avian lentiformis mesencephali (LM), known in mammals as the nucleus of the optic tract (NOT), is a key nucleus for global motion processing [1-4]. In all animals tested, it has been found that the majority of LM and NOT neurons are tuned to temporo-nasal (back-to-front) motion [4-11]. Moreover, the monocular gain of the optokinetic response is higher in this direction, compared to naso-temporal (front-to-back) motion [12, 13]. Hummingbirds are sensitive to small visual perturbations while hovering, and they drift to compensate for optic flow in all directions [14]. Interestingly, the LM, but not other visual nuclei, is hypertrophied in hummingbirds relative to other birds [15], which suggests enhanced perception of global visual motion. Using extracellular recording techniques, we found that there is a uniform distribution of preferred directions in the LM in Anna's hummingbirds, whereas zebra finch and pigeon LM populations, as in other tetrapods, show a strong bias toward temporo-nasal motion. Furthermore, LM and NOT neurons are generally classified as tuned to "fast" or "slow" motion [10, 16, 17], and we predicted that most neurons would be tuned to slow visual motion as an adaptation for slow hovering. However, we found the opposite result: most hummingbird LM neurons are tuned to fast pattern velocities, compared to zebra finches and pigeons. Collectively, these results suggest a role in rapid responses during hovering, as well as in velocity control and collision avoidance during forward flight of hummingbirds.

RESULTS

We made extracellular recordings from the LM of hummingbirds and zebra finches while presenting large-field random dot patterns in the contralateral visual field (Figure 1A). LM neurons receive direct retinal input and show simple direction selectivity across large, but restricted, receptive fields. We used a random dot-field, rather than a more complex stimulus, because more complicated patterns of optic flow are processed downstream [18, 19]. LM neurons were spontaneously active and exhibited motion opponency, defined as increased firing in response to large-field stimulus motion in a "preferred" direction, and decreased firing in the opposite, "anti-preferred," direction [4, 16, 17, 20].

We first identified the preferred direction of LM neurons by presenting visual motion in each of eight directions, 45° apart. Each motion stimulus lasted 5 s and was bounded by 5 s pauses. Raw extracellular recordings are shown for one hummingbird cell during a full trial (Figure 1A) and two zebra finch cells during a portion of a trial, with higher temporal resolution (Figure 1D). Single units were isolated offline using amplitude or template spike sorting (Figures 1E, 1F, and S1B; see also Supplemental Experimental Procedures).

Individual neurons were defined as directionally tuned if the response to direction was significantly non-uniform (Rayleigh test). The total sample size of directionally tuned neurons was 152 units from ten zebra finches and 88 units from six hummingbirds. Thirteen out of 165 (7.8%) zebra finch cells, and eight out of 96 (8.3%) hummingbird cells, were not direction-modulated, which is similar to the percentage of non-directional cells previously reported in pigeons [4, 21, 22]. For comparison, we also analyzed data from 100 LM units in 38 pigeons from previous studies in which moving large-field sine wave gratings were used as visual stimuli [1, 4, 23–25]. Because speed tuning width is maintained for some but not all visual motion neurons when comparing responses to sine wave gratings and random dot-fields [26], we limited our comparison with pigeon data to preferred direction and preferred speed.

Directional tuning curves are shown for one hummingbird cell (Figure 1B) and two zebra finch cells (Figure 1F). Mean firing rate is plotted as a function of the direction of motion in polar coordinates (forward = 0° , down = -90° , up = 90° , backward = $\pm 180^{\circ}$; Figure S1A; Supplemental Experimental Procedures). An analysis of the direction tuning width is also included in the supplementary materials (Figure S2).

Most zebra finch LM cells prefer temporo-nasal motion (0° in our coordinate system), as is the case for pigeons (Figure 2). A Rayleigh test confirmed that these two distributions were non-uniform (both p < 0.0001). In contrast, most hummingbird neurons are tuned to other directions such that at the population level, the distribution of preferred directions is uniform (Rayleigh test p = 0.379). We determined confidence intervals for the population direction preference by bootstrapping the data within



Figure 1. Representative Data Depicting Preferred Direction Analysis (A) A representative raw trace of an extracellular recording of a hummingbird LM neuron. Arrows indicate direction of dot-field motion; broken lines indicate paused stimulus. The hummingbird illustration shows the bird's head orientation during stimulus presentation.

(B) A polar plot of the mean firing rate (spikes/s) in response to motion in each direction (green circles) for the neuron in (A) with a B-spline fit to the mean firing rates \pm SE (thick magenta \pm thin). The gray line indicates spontaneous activity (spikes/s). F, forward motion (temporo-nasal); U, up; B, backward (naso-temporal); D, down.

(C) A portion of a raw extracellular recording of a zebra finch LM.

(D) A zoomed-in portion of the trace in (C) with spikes from two different neurons (red, blue) sorted from the raw trace (black).

(E) An overlay of the average waveforms of 20 consecutive spikes (\pm SEM) for each of the two classes of spikes identified in (D). PCA cluster analysis for these two cells is provided in Figure S1B.

(F) Polar plots for the direction-modulated response for each cell in (D). Red and blue lines are means \pm SE; gray denotes spontaneous activity. Direction tuning width analysis is provided in Figure S2.

each species (Figures 2D–2F). This analysis confirms overall direction preferences of LM populations for zebra finches and pigeons, but not for hummingbirds. Thus, the uniform distribution observed in hummingbird LM neurons is unique relative to zebra finches, pigeons, and indeed all other tetrapods studied to date.

We next examined LM activity in response to visual motion speed (Figure 3). Cellular responses were measured in both preferred and anti-preferred directions over a range of speeds $(0.24^{\circ}/s, 0.5^{\circ}/s, 1^{\circ}/s, 2^{\circ}/s, 4^{\circ}/s, 8^{\circ}/s, 16^{\circ}/s, 24^{\circ}/s, 32^{\circ}/s, 48^{\circ}/s, 64^{\circ}/s, 80^{\circ}/s;$ presented in random order) similar to other experiments with birds (LM) and mammals (NOT) [4, 6, 10, 16, 17, 20, 27, 28]. Each motion sweep lasted 5 s and was bounded by 5 s pauses. Because recording sites were tested at a single pair of directions, but some measured multiple neurons with different preferred directions, we had to remove cells from further analysis. Only LM cells measured in their preferred direction $\pm 45^{\circ}$ were included in the speed analysis, leading to sample sizes of 56 and 107 units in hummingbirds and zebra finches, respectively. Speed tuning curves were calculated as the mean of five trials.

The responses of neurons to visual motion speed can, in principle, be categorized by both tuning width and speed preference. We estimated the width of tuning curves for each cell by summing the number of velocity values that elicited a firing rate above a given percentage of the maximum firing rate (e.g., number of bins above 50% of max rate) versus that threshold (e.g., 50%) (Figure 3D). Differences between hummingbird and zebra finch cells were first tested using a linear mixed-effects model, but because we found a significant interaction between threshold and species ($F_{1.1465} = 107.207$, p < 0.0001), we next fit a linear model to each species separately. The slope of the relationship between the numbers of speed bins above threshold and the threshold is more negative in zebra finches (-9.92; y intercept =11.45) than in hummingbirds (-6.66; y intercept = 7.59), and the lines do not converge over the meaningful range (thresholds up to 100% of maximum firing). Thus, within the range of velocities tested, hummingbird LM cells exhibit high relative levels of response for fewer speed bins than zebra finch neurons. The distributions of the number of speed bins above 70%, 80%, and 90% thresholds, as well as bootstrapped data for the speed tuning width (number of consecutive speed bins) at 80% of maximum firing rate are presented in Figures S3A-S3D.

From the tuning curves, we also calculated the speed preference of each neuron. We first described the speed preference as a single value: the speed at which maximum firing was achieved (Figure 3E). The hummingbird and zebra finch data are plotted along with similar data from pigeons. It is important to reiterate that the data from our study are derived from experiments using moving dot-fields, whereas the pigeons were tested with sinusoidal gratings. In addition, the speed test values do not overlap completely. The average value for the pattern speed with the highest firing rate across the three cell populations increased from pigeons to zebra finches to hummingbirds. Despite an average preference for higher stimulus velocities, hummingbirds had a larger proportion of the relatively low number of slow cells recorded. In hummingbirds, 20% of the LM population (11 cells) prefers speeds <6°/s, but the majority, 80% of the population (45 cells), prefers speeds >6°/s. Conversely, in zebra finches, only 4% of the population (4 cells) prefers speeds <6°/s, and 96% (103 cells) prefers speeds >6°/s. However, we did not observe strong evidence for distinct populations of "fast" and "slow" LM neurons.

We next considered the overall response of the LM neuron population to increasing motion speeds. When accounting for neurons responding at near-maximal levels for multiple motion speeds, the LM responses of both hummingbirds and zebra finches appear to saturate over the range of speeds tested, and we did not measure a subsequent decline. The saturating



response is illustrated in Figure 3F, which depicts the data for neurons responding with at least 80% of their maximum firing rate. Figures S3E and S3F provide the data for 70% and 90% of maximum firing. We fit sigmoidal curves to the hummingbird and zebra finch LM population responses to increasing speeds, allowing slope or inflection point parameters to vary by cell. Comparisons of the fitted parameters for the two species indicate that hummingbird LM cells show a strong preference for high-velocity visual motion. Responses of zebra finch LM cells to increasing speed saturate more quickly (higher slope, $F_{1,14}$ = 26.78; p < 0.0001) and at lower stimulus velocities (inflection point at lower speed, $F_{1,14} = 25.86$; p < 0.001). Because we did not test higher speeds, we cannot exclude the possibility that hummingbird LM neurons are high-pass rather than band-pass filters. Regardless, the hummingbird LM response is significantly shifted toward higher motion speeds.

Figure 2. Hummingbird LM Cells Have a Uniform Distribution of Preferred Directions, whereas Zebra Finches and Pigeons Prefer Forward Motion

(A–C) Individual cell analysis. Rosette plots show the distribution of preferred directions within the recorded LM populations. Each colored circle represents the preferred direction of a single cell. The circular distributions of preferred directions are calculated as two von Mises parameters: μ , the location of central tendency on the circle, and κ , a descriptor of the concentration at that location. For zebra finches, μ was $6.02^\circ\pm5.761^\circ$ (95% Cl: 8.74° to 2.65°) and κ was 1.24 ± 0.148 . For pigeons, μ was $-7.63^\circ\pm11.57^\circ$ (95% Cl: -5.5° to -9.2°) and κ was 0.722 ± 0.155 . The hummingbird LM population has a uniform distribution.

(D–F) Population analysis. We resampled with replacement the responses of individual neurons 1,000 times each to generate 1,000 LM cell populations for each species. Each circle represents the preferred direction of an entire LM population that passed the Rayleigh test. In hummingbirds (D), 21/1,000 populations had a preferred direction, always generally downward. In zebra finches (E), 1,000/1,000 populations were non-uniform, with population direction preference (μ) of 5.71° ± 0.061° and concentration (κ) of 898.3. In pigeons (F), 1,000/1,000 populations were non-uniform, with population direction preference (μ) of -7.31° ± 0.041° and concentration (κ) of 1,998. Bird illustrations indicate the head orientation.

A notable feature of the speed tuning curves was a difference in the extent of overall excitation and suppression between zebra finch and hummingbird LM neurons (examples in Figure S4). To determine whether this difference was significant, we quantified the level of excitation and suppression as the area under each of the two speed tuning curves (one for each direction) for each unit. Plotting the area under the antipreferred direction tuning curve versus

the area of the preferred direction curve leads to three plausible options for how relative firing rate of a neuron can encode visual motion preference. Values greater than zero indicate overall excitation, whereas negative values indicate overall suppression. Thus, the lower right quadrant of Figure 4A includes LM cells that were excited in the preferred direction and suppressed in the anti-preferred direction relative to the spontaneous firing rate. An example of a zebra finch neuron with these firing characteristics is provided in Figure 4C. The upper right quadrant contains cells that were excited in both directions, and an example cell from a zebra finch is depicted in Figure 4B. The lower left quadrant contains cells that were suppressed in both directions, and an example cell from a hummingbird is provided in Figure 4D. The upper left quadrant contains no cells by definition because the preferred direction is defined by higher relative firing.



Figure 3. Hummingbird LM Neurons Prefer Higher Visual Motion Speed than Zebra Finch LM Neurons

(A) A representative raw trace shows an extracellular recording from the zebra finch LM during the velocity tuning experiment. Arrows indicate direction of dot-field motion; broken lines indicate paused stimulus. The zebra finch illustration shows orientation of the bird's head during stimulus presentation.

(B and C) Representative velocity tuning curves for a hummingbird (B) and a zebra finch (C) LM cell depict normalized firing rate (±SEM) plotted against the stimulus velocity (log scale) in the preferred (black squares) and anti-preferred (gray diamonds) directions. The dashed gray line indicates a threshold of 80% of the maximum firing rate.

(D) Boxplots of grouped data depict the number of speed bins at successive thresholds (percentages) of the maximum firing rate for hummingbirds (magenta triangles) and zebra finches (orange circles). Magenta and orange diamonds indicate mean.

(E and F) Speed preferences of LM neurons are plotted using two different criteria: (E) the proportion of the LM population for each species that reaches maximal firing at a given stimulus velocity (a single value for each cell); (F) the proportion of the LM cells that have a firing rate above 80% of their maximum firing rate at each stimulus velocity. Figure S3 provides supplemental visualizations of velocity tuning width analysis and speed preference plots showing the proportion of the LM population responding at additional percentages of the maximum firing rate.

[14]. This strong response to global motion direction was not matched with a tuned response to changes in stimulus pattern speed, though only a few pattern speeds were tested [14]. Heightened sensitivity, during hovering flight, to direction rather than velocity suggests that hummingbirds have neural specializations to detect global motion direction stimuli.

The LM is a pretectal nucleus and one of two midbrain nuclei associated with the accessory optic system (AOS) that

At the population level, while still overlapping, hummingbird and zebra finch LM neurons are shifted apart along the suppression-excitation axes (Figure 4A). Hummingbird LM neurons have significantly lower excitation (smaller area under the curve) in the preferred direction ($F_{1,14} = 35.91$; p < 0.0001) and significantly greater suppression in the anti-preferred direction ($F_{1,14} = 8.09$; p = 0.013), compared to zebra finch LM neurons.

DISCUSSION

Hovering hummingbirds are highly sensitive to coherent background motion in all directions in their visual field, and they adjust their three-dimensional position to compensate for this motion process global motion direction and velocity. The LM is hypertrophied in hummingbirds and enlarged, but to a lesser extent, in transiently hovering species [15]. This enlargement may represent a neural specialization related to hovering flight. Iwaniuk and Wylie proposed that a greater relative number of LM neurons preferring slow speeds could aid stabilization during hovering [15]. The goals of the present study were to test this hypothesis and also determine whether the direction preferences of the hummingbird LM conform to the tetrapod pattern.

Previous studies with tetrapods have demonstrated that the direction preferences of LM neurons, or neurons in the homologous NOT, are biased toward temporo-nasal motion. For example, a [¹⁴C]2-deoxyglucose study in chicks has shown



Figure 4. Hummingbird LM Cells Are Less Excited than Zebra Finch Cells by Motion in Their Preferred Direction and Are More Suppressed by Motion in Their Anti-Preferred Direction

The magnitude of excitation and suppression is calculated as the area under the velocity tuning curve (AUC) in response to motion in the preferred and anti-preferred directions, respectively.

(A) The two AUC values are plotted against each other with error bars (SD) calculated from AUCs for 1,000 bootstrapped simulations of each cell's responses.

(B–D) Representative velocity tuning plots demonstrate mean response (±SEM) to motion in the preferred (black squares) and anti-preferred (gray diamonds) directions of cells that fall into quadrants b, c, and d, respectively, in (A). In some cases, the error bars are occluded by the symbol at a given response value. Magenta triangles, hummingbird LM cells; orange circles, zebra finch LM cells. Further examples of speed tuning curves are provided in Figure S4.

not observe a clear distinction between fast and slow LM neuron populations in either zebra finches or hummingbirds. Moreover, when previously published pigeon data are presented in the same

increased glucose uptake in LM cells during motion in the temporo-nasal direction [3]. Furthermore, in pigeons, 53% of recorded LM cells preferred forward (temporo-nasal) motion, whereas the remaining cell preferences were distributed among backward, downward, and upward motion [4]. This bias is consistent with other pigeon LM data [10, 20, 29] and across other tetrapod species, including chicks [3], turtles [30], frogs [31, 32], salamanders [33], wallabies [7], rabbits [34], and cats [6]. It is less clear whether this holds for optic-flow-sensitive neurons in the pretectum of fish, which do not show the same bias for temporo-nasal motion observed in the tetrapod LM or NOT [35–38]. The current study demonstrates that hummingbird LM neurons deviate strongly from the tetrapod pattern by having no directional bias at the population level (Figure 2).

LM neurons are further characterized as being selective for velocity, with a preference for either "slow" or "fast" speeds [10], and as exhibiting a correlation between temporo-nasal direction preference and slow speed preference [4, 17]. Using large-field grating patterns in pigeons, fast cells prefer low spatial frequencies (SFs) and high temporal frequencies (TFs), whereas slow cells prefer high SFs and low TFs [1, 4, 16]. Other previous studies, which used random dot-fields in pigeons, classified 82% of measured LM cells as "fast" (>6°/s) and 18% as "slow" ($<6^{\circ}/s$) [17]. If we apply this threshold ($6^{\circ}/s$), we find that 20% of hummingbird LM neurons are "slow" cells, while only 4% of zebra finch LM neurons had maximal firing at a slow velocity. Compared to zebra finches, we found that hummingbird LM neurons are more selective for a preferred speed over the range of velocities we tested and prefer faster visual motion (Figure 3). Although the percentage of "slow" cells based on a 6°/s threshold is similar in hummingbirds and pigeons, we did manner (Figure 3E), there is no obvious bimodal distribution for this species either. This is likely due to spatiotemporal, rather than velocity, tuning [4].

The LM has a reciprocal relationship with the nucleus of the basal optic root (nBOR) of the AOS; both are retinal-recipient midbrain nuclei and project to each other. Unlike the population-level preference for temporo-nasal motion observed in the pigeon and zebra finch LM (Figure 2), studies in pigeons show that nBOR neurons prefer upward, downward, and naso-temporal motion, with very few cells (~5%-10%) preferring temporo-nasal motion [1, 39]. Similar direction-preference distributions have been shown in the nBOR of turtles [40] and chickens [41]. Furthermore, the nBOR is homologous to the mammalian medial and lateral terminal nuclei of the AOS [5, 8, 42], which contain direction-sensitive neurons that respond best to vertical motion [43-45]. In mammals, the AOS also contains the dorsal terminal nuclei, which have cells that respond preferentially to horizontal motion [45, 46]. The complementary LM-nBOR relationship is further demonstrated by their responses to global motion direction; the LM receives inhibitory inputs from slow nBOR cells that prefer motion of the opposite direction.

Compared to zebra finches, hummingbird LM neurons are more suppressed by motion in the anti-preferred direction and less excited by motion in the preferred direction (Figure 4). The strong inhibition of hummingbird LM neurons by motion in the anti-preferred direction (Figure 4A) could be attributed to an nBOR-mediated mechanism that drives speed tuning (i.e., disinhibition of nBOR). The expansion of the direction preference distribution that we found in the hummingbird LM suggests that the complementary relationship observed in pigeons between the LM and nBOR is not apparent, or may not function in the same way, in hummingbirds.

The ability to sustain hovering flight in hummingbirds is unique among vertebrates. The motion preferences and firing properties of LM neurons are also distinct from all other tetrapods in several respects, which supports the hypothesis that hummingbirds have neural specializations for flight mode [15]. The uniform distribution of direction preferences in the hummingbird LM is unique among all tetrapods studied to date and, in combination with their preference for faster speeds, suggests heightened sensitivity to global motion at high speeds. Such sensitivity could be beneficial during hovering when birds are close to visual features that will produce high global motion velocity in response to even small changes in position. This specialization may also play a role in more dynamic behaviors such as competitive interactions, high-speed courtship displays, and insect foraging [47-49]. Testing this hypothesis will require moving to visual stimuli relevant to more complex flight modes [50] and in higher-order brain centers [11, 51].

EXPERIMENTAL PROCEDURES

We used standard extracellular recording techniques to study the LM of anesthetized birds while presenting a computer-generated moving dot-field to the contralateral eye (Figures 1A, 1C, and 3A). Details of the surgical and recording procedures, visual stimulus, and statistical approaches are provided in the Supplemental Experimental Procedures. All spike-sorted data and analysis scripts are available via Figshare (Figshare http://dx.doi.org/10.6084/m9. figshare.c.3590186).

Experimental subjects included ten adult male zebra finches (*Taeniopygia guttata*; Eastern Bird Supplies, Quebec, Canada) and six adult male Anna's hummingbirds (*Calypte anna*; caught on the University of British Columbia campus, October 2014–April 2015). All experimental procedures were approved by the Animal Care Committee of the University of British Columbia.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and four figures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.11.041.

AUTHOR CONTRIBUTIONS

A.H.G. and D.L.A. conceived and designed the experiment. A.H.G. and J.P.M.L. collected the data. A.H.G., B.G., and D.R.W. analyzed the data. A.H.G. and D.L.A. wrote the manuscript. All authors edited the manuscript.

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Hummingbirds Process Motion in Unique Way, Study Shows

Jan 10, 2017 by News Staff / Source

Published in Biology

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The brain area in question is called the lentiformis mesencephali (LM), known in mammals as the nucleus of the optic tract.

"In all four-limbed vertebrates studied to date, most of the neurons in this motion-detecting brain area are tuned to detect motion coming from behind, such as would occur for an impending collision or when being attacked from behind by a predator," said Dr. Douglas Altshuler, an associate professor in the Department of Zoology at the University of British Columbia and corresponding author of the study.

"We found that the LM responds very differently in hummingbirds," he said.

"Instead of most neurons being tuned to back-to-front motion, almost every neuron we found was tuned to a different direction."

"We also found that these neurons were most responsive to very fast motion."

Earlier studies showed that the LM in hummingbirds is enlarged in comparison to that of other birds. Researchers also knew that hummingbirds monitor and correct for any minor drift in their position as they hover.

Those findings had led scientists to suggest that the hummingbird brain might be specially attuned to pick up on slow movements.

To test that hypothesis, Dr. Altshuler and his colleagues recorded neural activity in the LMs of six adult male Anna's hummingbirds (*Calypte anna*) and ten adult male zebra finches (*Taeniopygia guttata*) as the birds watched computer-generated dots move in various directions.

Contrary to expectations, the recordings showed that hummingbirds are most sensitive to fast visual motion.

What's more, unlike other birds, the hummingbirds responded to movement in any direction about equally.

That is, their LM neurons aren't specially attuned to movements in the forward direction as in other animals.

The authors suggest that their visual abilities may play a role in dynamic behaviors, including competitive interactions, high-speed courtship displays, and insect foraging.

"This study provides compelling support for the hypothesis that the avian brain is specialized for flight and that hummingbirds are a powerful model for studying stabilization algorithms," said study co-author Andrea Gaede, also from the Department of Zoology at the University of British Columbia.

The team now plans to investigate the response properties of other nuclei involved in this visual motion-processing pathway, with the ultimate goal of understanding how neural activity in the hummingbird brain is translated into specific flight behaviors.

Andrea H. Gaede et al. Neurons Responsive to Global Visual Motion Have Unique Tuning Properties in Hummingbirds. *Current Biology*, published online January 5, 2017; doi: 10.1016/j.cub.2016.11.041

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For Hummingbirds, the World Moves as Fast As They Do

New research shows how the hummingbird brain allows them to hover and fly precisely



Anna's hummingbirds have brains uniquely adapted for hovering precisely while feeding. (William Leaman / Alamy)

By Ben Panko smithsonian.com 2 hours ago

In the blink of a human eye, a hummingbird can beat its wing dozens of time, dive out of sight and even catch flying insects in midair. How is it possible for these tiny creatures to keep track of the world moving around them?

Their brains may be set up differently to better accommodate visual information coming from all directions, according to new research—which could have implications for the development of precision-flying drones and robots. In the motion-detecting part of the hummingbird brain—which is significantly larger than in other avian species—the neurons appear to be "tuned" differently, says lead author Andrea Gaede, a neurobiology researcher at the University of British Columbia.

"They're processing visual motion in a different way than every other animal studied to date," says Gaede.

In all other birds, amphibians, reptiles and mammals tested, including other species of small birds, the neurons of this brain area, known as the "lentiformis mesencephalic," are tuned to detect motion coming from behind better than other types of motion. This

makes sense for most animals, Gaede says—an animal that can better sense motion on the periphery of its vision would be able to flee from potential predators approaching from the back.

Not hummingbirds. Gaede and her team took six anesthetized Anna's hummingbirds (*Calypte anna*) and put them into a chamber where they could see dots moving on a screen in different directions. They then recorded the signals coming from their brains using electrodes implanted in them in response to the different types of motion, and compared them to tests done the same way on Zebra finches and pigeons.

The researchers overcame significant difficulties to be able to adapt brain recording techniques to the small size and delicacy of the hummingbirds, said University of Chile avian neurology researcher Gonzalo Marín, who was not involved in this study.

Unlike in the finches or pigeons, the neurons in the hummingbirds' motion-sensing brain area appear to be tuned to prefer motion from all different directions fairly equally, according to the study published today in the journal *Current Biology*.

Why would the tiny hummingbird do things so uniquely? Because they have to, according to Gaede.

"They have to be aware of their surroundings in a different way than other animals," Gaede says. Think about it: When you spend a lot of time hovering in front of small flowers to drink, you need to have precise control of their movements—all while beating your wings around 50 times per second. Other birds like falcons may move just as quickly while hunting, but they're usually moving through open air without any obstacles nearby. "They're often hovering at flowers in a cluttered environment [...] they don't want to get knocked away," she says.

Being able to sense motion equally in all directions could also give hummingbirds an advantage when they're flying at high speeds, evading predators and doing intense mating dives to impress females. It would, however, not give them the same advantage in seeing potential predators from behind that other animals have.

Gaede hopes next to study hummingbirds as they're in motion to see how their brains are processing information. "It might be an even more interesting picture," she says, though the small size and dynamism of the birds makes it still unclear how that will be done. Marín said that similar studies of hovering insects have found responses to visual stimulation that were not seen when doing tests while immobilized.

In humans, neurodegenerative disorders such as forms of palsy that impair a person's balance might be harming the human motion sensing brain area, Gaede says. More research into how these areas process motion in hummingbirds could lead to better understandings of how this area works in humans too, and how it could stop working and be fixed. Learning more about hummingbirds hover so well could also help another flying thing that needs to hover precisely, Gaede says: drones.

"This could provide information for determining new algorithms for visual guidance," Gaede says. Companies might be able to better program how the drones use their cameras to avoid obstacles while moving and hovering, for example. One day we might thank hummingbirds when we receive our Amazon packages by drone.

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About Ben Panko

Ben Panko is a staff writer for Smithsonian.com

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Hummingbirds see motion in an unexpected way

Date:	January 5, 2017
Source:	Cell Press
Summary:	Have you ever imagined what the world must look like to hummingbirds as they zoom about at speeds of up to 60 miles per hour? According to new evidence on the way the hummingbird brain processes visual signals you can't. That's because a key area of the hummingbird's brain processes motion in a unique and unexpected way.

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This photograph shows a male Anna's hummingbird near the UBC campus.

Credit: Benny Goller

Have you ever imagined what the world must look like to hummingbirds as they zoom about at speeds of up to 60 miles per hour? According to new evidence on the way the hummingbird brain processes visual signals reported in *Current Biology* on January 5, you can't. That's because a key area of the hummingbird's brain processes motion in a unique and unexpected way.

"In all four-limbed vertebrates studied to date, most of the neurons in this [motion-detecting] brain area are tuned to detect motion coming from behind, such as would occur for an impending collision or when being attacked from behind by a predator," says Douglas Altshuler of the University of British Columbia. "We found that this brain area responds very differently in hummingbirds. Instead of most neurons being tuned to back-to-front motion, almost every neuron we found was tuned to a different direction. We also found that these neurons were most responsive to very fast motion."

The brain area in question is known in birds as the lentiformis mesencephalic, or LM for short. (In mammals, it's called the nucleus of the optic tract.) The LM is responsible for processing visual signals sent to the brain as images move across the retina.

The primary interest of the Altshuler lab is in understanding flight. To understand how birds fly, the researchers needed to understand how they see the world. Hummingbirds were of special interest because of their remarkable ability to zoom quickly and then stop to hover in place while sipping nectar in midair.

Earlier studies showed that the LM in hummingbirds is enlarged in comparison to that of other birds. Scientists also knew that hummingbirds monitor and correct for any minor drift in their position as they hover. Those findings had led researchers to suggest that the hummingbird brain might be specially attuned to pick up on slow movements.

To test that hypothesis in the new study, post-doc and first author of the new study Andrea Gaede recorded neural activity in the LMs of six Anna's hummingbirds and ten zebra finches as the birds watched computer-generated dots move in various directions. Contrary to expectations, the recordings showed that hummingbirds are most sensitive to fast visual motion. What's more, unlike other birds, the hummingbirds responded to movement in any direction about equally. That is, their LM neurons aren't specially attuned to movements in the forward direction as in other animals. The researchers suggest that their visual abilities may play a role in dynamic behaviors, including competitive interactions, high-speed courtship displays, and insect foraging.

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Gaede says her next step is to investigate the response properties of other nuclei involved in this visual motion-processing pathway, with the ultimate goal of understanding how neural activity in the hummingbird brain is translated into specific flight behaviors.

Story Source:

Materials provided by Cell Press. Note: Content may be edited for style and length.

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Science explains why humans may never see the world through a hummingbird's eyes



Scientists have revealed that hummingbirds process visual cues in a way that may be unique in the animal kingdom, according to a study published Jan. 5 in Current Biology. (Jan. 6, 2017)



By Deborah Netburn

JANUARY 6, 2017, 3:00 AM



ummingbirds don't see the world like you or me.

And it turns out they don't see it in the same way as any other known bird, mammal or reptile, either.

In a study published Thursday in Current Biology, scientists reveal that the humming bird's pea-sized brain processes visual cues in a way that may be unique in the animal kingdom.

This doesn't necessarily mean that when a hummingbird flies through a garden the plants look different to it than they do to us, explains lead author Andrea Gaede, a post-doctoral fellow in the department of zoology at

the University of British Columbia.

Instead, her research shows that the hummingbird's brain has evolved to respond to motion in a different way than other vertebrates.

That's actually not a huge surprise. After all, as anyone with a hummingbird feeder knows, these buzzing, fairylike creatures don't move through the world like any other animal, bird or not.

"The way they maneuver is definitely distinct," Gaede said. "There are a few other birds that transiently hover, but generally most birds are just forward fliers."

In general, flying birds occupy a more 3-dimensional space than those of us who are stuck walking on solid ground. But even among its avian cousins, the hummingbird is special.

Hummingbirds have two unusual flight behaviors. They are hovering experts, and during the mating season males will perform what is known as a courtship dive. They fly high in the sky and then dive through the air at a breakneck speed to get the attention of a female.

Studies have shown that hummingbirds have an enlarged lentiformis mesencephali (LM) compared with other birds. This is a region of the bird brain that usually responds to motion going from back to front. For example, if you slipped on an icy sidewalk and fell backward, the neurons in the part of your brain that corresponds to the LM in birds would start firing like crazy.

(Other parts of the brain are responsible for responding to motion coming from different directions.)

Earlier work has also revealed that the LM is slightly enlarged in avian species that hover for a second or two, but not nearly as much as in the brains of hummingbirds, which exhibit sustained hovering. Therefore, scientists have hypothesized that the enlargement of the LM might be important for stabilization, making it worthy of deeper study.

That's where Gaede and her colleagues in the Altshuler Lab at UBC came in.

"In my side of the lab we are interested in how visual signs that birds receive during flight are interpreted in the brain, and ultimately how those are transformed to guide flight," she said.

To learn more about the LM's role in how hummingbirds perceive the world, Gaede anesthetized six hummingbirds and did a little brain surgery that allowed her to listen to individual neurons in the LM part of the brain.

Next, she showed the birds a computer screen with a field of black dots on a white background. She also created a computer program that moved the dots as a collective unit in eight different directions.

She expected that the neurons in the LM would fire rapidly as the dots moved forward, and calm down when the dots moved backward.

But that's not what happened.

Instead, she reports that each neuron in the LM had a preferred direction — meaning it fired more when the dots moved one way rather than another — but there was not an overall bias toward forward motion. Some of the LMs preferred backward motion. Others downward motion. Others upward motion.

When she tried the same experiment with zebra finches, more than half of the neurons in their LM's had a preference for forward motion as she anticipated.

So, what does that mean?

Mostly it means that hummingbirds are processing motion in a different way than zebra finches and almost every other known animal. And, because of the hummingbird's unusual flight patterns, it is likely that this alternative processing evolved to help these birds stabilize while hovering. It might also be useful for flying in a cluttered environment — like a field of flowers.

"This could be a shortcut, or a sidestep to some other processing, so they are faster at responding to some types of motion," she said. "It's definitely different than what has previously been described."

Gaede added that there is still more work to be done to show how the hummingbird brain is specialized for its specific type of flight.

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"Now that we know LM functions differently, we want to know if other areas of the brain that the LM interacts with behave differently and how important that is during flight," she said.

Eventually, this work could help engineers design robots or drones that use the brain processes of the hummingbird to fly— or at least hover and dive more effectively.

We may never be able to see for ourselves how hummingbirds interpret the world, but perhaps one day, our machines might.

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How Hummingbirds Sense Movement While Hovering

A visual motion-sensing brain region found in all four-limbed vertebrates displays unique properties in Anna's hummingbirds.

By Anna Azvolinsky | January 5, 2017





Hummingbirds are efficient hoverers, suspending their bodies midair using rapid forward and backward

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researchers have now shown. According to a study published today (January 5) in Current Biology, a highly conserved area of the brain-the lentiformis mesencephali (LM), which receives panoramic visual motion information directly from the retina-processes the movement of objects from all directions. In contrast, the LMs of other bird species and all other four-limbed vertebrates studied to date predominantly sense back-to-front motion.

While the authors had predicted the neurons of this hummingbird brain region would be tuned to slow motion, they in fact found the opposite: LM neurons were sensitive to quick visual motion, most likely because hummingbirds must process and respond to their environments quickly to avoid collisions, both during hovering and in other modes of flight.

"This ancient part of the brain the authors studied has one job: to detect the motion of the image in front of the eyes," explained Michael Ibbotson, a neuroscientist at the University of Melbourne who penned an accompanying editorial but was not involved in the research. The results of this study suggest that "hummingbirds evolved this area of the brain to have fine motor control to be able to hover and push in every direction possible," Ibbotson said.

"The authors show that the LM of hummingbirds contains neurons tuned to almost any direction of motion, which goes against previous assumptions, and which should certainly relate to the particular high demands of this bird's flight maneuvers," Gonzalo Marin, who studies avian vision at the University of Chile in Santiago and was also not involved in the work, wrote in an email to The Scientist.

In a 2007 anatomical study, researchers at the University of Alberta in Canada showed that the LM of a hummingbird is proportionally larger compared to the same brain region in other bird species. "What's remarkable about the enlargement is that this is a brain region that has some very basic and fundamental functions and we generally do not consider highly conserved brain regions like this to vary so much in size across species," said Andrew Iwaniuk, a coauthor on the anatomical study who is now at the University of Lethbridge in Canada but was not involved in this latest work.

To study the function of the LM in hummingbirds, study coauthor Andrea Gaede, a postdoctoral fellow in Douglas Altshuler's laboratory at the University of British Columbia, Canada, and colleagues recorded the activities of LM neurons of six Anna's hummingbirds (Calypte anna) and 10 zebra finches (Taeniopygia guttata) while the anesthetized avians were shown hundreds of 2-D dots moving in unison on a screen. Gaede's team compared those data with similar information generated from a study on pigeons (Columba livia domestica).

The researchers exposed the birds to moving dots in eight different directions for five seconds each, identifying the directional preferences of active LM neurons. They then tested whether the neurons responded to fast or slow movement, both in their preferred direction and in the opposite direction. The team found that most pigeon and zebra finch LM neurons spontaneously fired when the dot field moved forward and were inhibited when the dot field moved backward. In hummingbirds, LM neurons were excited by motion in a single direction, but that direction could have been any one of the eight tested, Gaede explained. The researchers also found that 80 percent of the hummingbird LM neurons examined responded to quick visual movement.

"As a comparative biologist I think it's really cool that someone followed up the anatomical study I did and actually showed that the physiology backs up the anatomy," said Iwaniuk.

"Hummingbirds have a massive enlargement of the LM that is also associated with this improved ability to detect global motion. These LM cells are tuned to forward motion in other vertebrates, but in hummingbirds, these neurons are responsive to motions in any direction," he added. "When you think about hummingbird flight, this makes complete sense, because you have an animal that floats in the air in the same way that a fish swims in water, basically."

Gaede said her team would next like to understand how the hummingbird brain processes visual information and translates it into motor outputs mid-flight. The technical challenge now will be probing LM neurons in awake, moving animals, she noted.

To Marin's mind, the work tied into the broader question of how visual systems control body posture while navigating an environment."Normally one thinks of vision as a system dedicated to detect and react to



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A.H. Gaede et al., "Neurons responsive to global visual motion have unique tuning properties in hummingbirds," *Current Biology*, doi:10.1016/j.cub.2016.11.041.

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Hummingbirds see motion in an unexpected way January 5, 2017



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Male Anna's hummingbird near the UBC campus. Credit: Benny Goller

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More information: Current Biology, Gaede et al.: "Neurons Responsive to Global Visual Motion Have Unique Tuning Properties in Hummingbirds" http://www.cell.com/current-biology/fulltext/S0960-9822(16)31394-X , DOI: 10.1016/j.cub.2016.11.041

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Hummingbirds See Motion in an Unexpected Way

Fri, 01/06/2017 - 10:18am by Cell Press



This photograph shows a male Anna's hummingbird near the UBC campus. (Credit: Benny Goller)

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The brain area in question is known in birds as the lentiformis mesencephalic, or LM for short. (In mammals, it's called the nucleus of the optic tract.) The LM is responsible for processing visual signals sent to the brain as images move across the retina.

The primary interest of the Altshuler lab is in understanding flight. To understand how birds fly, the researchers needed to understand how they see the world. Hummingbirds were of special interest because of their remarkable ability to zoom quickly and then stop to hover in place while sipping nectar in midair.

Earlier studies showed that the LM in hummingbirds is enlarged in comparison to that of other birds. Scientists also knew that hummingbirds monitor and correct for any minor drift in their position as they hover. Those findings had led researchers to suggest that the hummingbird brain might be specially attuned to pick up on slow movements.

To test that hypothesis in the new study, post-doc and first author of the new study Andrea Gaede recorded neural activity in the LMs of six Anna's hummingbirds and ten zebra finches as the birds watched computer-generated dots move in various directions. Contrary to expectations, the recordings showed that hummingbirds are most sensitive to fast visual motion. What's more, unlike other birds, the hummingbirds responded to movement in any direction about equally. That is, their LM neurons aren't specially attuned to movements in the forward direction as in other animals. The researchers suggest that their visual abilities may play a role in dynamic behaviors, including competitive interactions, high-speed courtship displays, and insect foraging. "This study provides compelling support for the hypothesis that the avian brain is specialized for flight and that hummingbirds are a powerful model for studying stabilization algorithms," Gaede says.

Gaede says her next step is to investigate the response properties of other nuclei involved in this visual motionprocessing pathway, with the ultimate goal of understanding how neural activity in the hummingbird brain is translated into specific flight behaviors.

Animal Studies





Brain Cells "Reprogrammed" Using Thin Beam of Light

ANIMAL



Researchers 'Reprogram' Network of Brain Cells in Mice with

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Die Gehirne der Flugvirtuosen

06.01.2017 16:03 Uhr

Wie der Schwirrflug der Kolibris möglich wird

Nicht nur die Flugmanöver des Kolibris sind einzigartig. Auch das Gehirn der Vögel nimmt Bewegung anders wahr. VON JANA SCHLÜTTER



Spektakulär. Die Flugmanöver der Kolibris sind einzigartig. FOTO: M: CAMPBELL, PICTURE ALLIANCE / DPA

Ein Angriff aus dem Hinterhalt ist für die meisten Tiere die größte Gefahr und so schlagen die Nervenzellen in ihrem Gehirn vor allem Alarm, wenn die Tiere aus dem Augenwinkel sehen, dass sie ein Räuber verfolgt. So ist es bei Tauben und bei Zebrafinken, bei Kaninchen und bei Wallabys, bei Schildkröten und bei Salamandern. Nur Kolibris scheren aus, berichten Forscher um Douglas Altshuler von der Universität von British Columbia in Vancouver im Fachblatt "Current Biology". Die Neuronen in ihren Sehzentren reagieren auf Bewegung aus allen Richtungen gleichermaßen. Besonders heftig feuern sie, wenn sich etwas sehr schnell bewegt. Das bestätige die These, dass der einzigartige Schwirrflug der Kolibris mit Anpassungen des Gehirns einhergeht.

Kolibris gelten als Flugvirtuosen, sie können quasi in der Luft "stehen", seitwärts und rückwärts fliegen. Bezogen auf ihre Körpergröße gehören sie zu den schnellsten Tieren der Welt. Auch das Balzen ist mit Hochgeschwindigkeits- Flugmanövern verbunden. Angesichts des "Auf-der-Stelle-Schwebens", während die Vögel Nektar trinken, rechneten die Forscher aber damit, dass die Neuronen auf langsame Bewegung mindestens ebenso reagieren. Sie pflanzten zehn Zebrafinken, acht Kolibris und einigen Tauben Elektroden in ein bestimmtes Sehzentrum ein und zeigten den Vögeln auf seitlichen Bildschirmen Punkte, die sich aus zufälliger Richtung und mit zufälliger Geschwindigkeit auf sie zubewegten. Die Aktivität der Neuronen unterschied sich bei den Kolibris deutlich von der der anderen Vögel. Dies könne den Kolibris unter anderem helfen, während des Nektartrinkens ständig ihre Position zu korrigieren. Zusätzlich hätten sie so vermutlich einen Vorteil beim Balzwettbewerb und bei der Jagd nach Insekten.



SUCHE

06.01.2017 | von Jana Schlütter

DIE GEHIRNE DER FLUGVIRTUOSEN Wie der Schwirrflug der Kolibris möglich wird von Jana Schlütter

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Spektakulär. Die Flugmanöver der Kolibris sind einzigartig. Foto: m: Campbell, picture alliance / dpa

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ADVERTISING

BALTIMON & SUN

Science explains why humans may never see the world through a hummingbird's eyes



Scientists have revealed that hummingbirds process visual cues in a way that may be unique in the animal kingdom, according to a study published Jan. 5 in Current Biology. (Jan. 6, 2017)



By Deborah Netburn

JANUARY 6, 2017, 6:00 AM

ummingbirds don't see the world like you or me.

And it turns out they don't see it in the same way as any other known bird, mammal or reptile, either.

In a study published Thursday in Current Biology, scientists reveal that the humming bird's pea-sized brain processes visual cues in a way that may be unique in the animal kingdom.

This doesn't necessarily mean that when a hummingbird flies through a garden the plants look different to it than they do to us, explains lead author Andrea Gaede, a post-doctoral fellow in the department of zoology at the University of British Columbia. Instead, her research shows that the hummingbird's brain has evolved to respond to motion in a different way than other vertebrates.

That's actually not a huge surprise. After all, as anyone with a hummingbird feeder knows, these buzzing, fairylike creatures don't move through the world like any other animal, bird or not.

"The way they maneuver is definitely distinct," Gaede said. "There are a few other birds that transiently hover, but generally most birds are just forward fliers."

In general, flying birds occupy a more 3-dimensional space than those of us who are stuck walking on solid ground. But even among its avian cousins, the hummingbird is special.

Hummingbirds have two unusual flight behaviors. They are hovering experts, and during the mating season males will perform what is known as a courtship dive. They fly high in the sky and then dive through the air at a breakneck speed to get the attention of a female.

Studies have shown that hummingbirds have an enlarged lentiformis mesencephali (LM) compared with other birds. This is a region of the bird brain that usually responds to motion going from back to front. For example, if you slipped on an icy sidewalk and fell backward, the neurons in the part of your brain that corresponds to the LM in birds would start firing like crazy.

(Other parts of the brain are responsible for responding to motion coming from different directions.)

Earlier work has also revealed that the LM is slightly enlarged in avian species that hover for a second or two, but not nearly as much as in the brains of hummingbirds, which exhibit sustained hovering. Therefore, scientists have hypothesized that the enlargement of the LM might be important for stabilization, making it worthy of deeper study.

That's where Gaede and her colleagues in the Altshuler Lab at UBC came in.

"In my side of the lab we are interested in how visual signs that birds receive during flight are interpreted in the brain, and ultimately how those are transformed to guide flight," she said.

To learn more about the LM's role in how hummingbirds perceive the world, Gaede anesthetized six hummingbirds and did a little brain surgery that allowed her to listen to individual neurons in the LM part of the brain.

Next, she showed the birds a computer screen with a field of black dots on a white background. She also created a computer program that moved the dots as a collective unit in eight different directions.

She expected that the neurons in the LM would fire rapidly as the dots moved forward, and calm down when the dots moved backward.

But that's not what happened.

Instead, she reports that each neuron in the LM had a preferred direction — meaning it fired more when the dots moved one way rather than another — but there was not an overall bias toward forward motion. Some of the LMs preferred backward motion. Others downward motion. Others upward motion.

When she tried the same experiment with zebra finches, more than half of the neurons in their LM's had a preference for forward motion as she anticipated.

So, what does that mean?

Mostly it means that hummingbirds are processing motion in a different way than zebra finches and almost every other known animal. And, because of the hummingbird's unusual flight patterns, it is likely that this alternative processing evolved to help these birds stabilize while hovering. It might also be useful for flying in a cluttered environment — like a field of flowers.

"This could be a shortcut, or a sidestep to some other processing, so they are faster at responding to some types of motion," she said. "It's definitely different than what has previously been described."

Gaede added that there is still more work to be done to show how the hummingbird brain is specialized for its specific type of flight.

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"Now that we know LM functions differently, we want to know if other areas of the brain that the LM interacts with behave differently and how important that is during flight," she said.

Eventually, this work could help engineers design robots or drones that use the brain processes of the hummingbird to fly— or at least hover and dive more effectively.

We may never be able to see for ourselves how hummingbirds interpret the world, but perhaps one day, our machines might.

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Hummingbirds see motion in an unexpected way

CELL PRESS



IMAGE: THIS PHOTOGRAPH SHOWS A MALE ANNA'S HUMMINGBIRD NEAR THE UBC CAMPUS. view more > CREDIT: BENNY GOLLER

Have you ever imagined what the world must look like to hummingbirds as they zoom about at speeds of up to 60 miles per hour? According to new evidence on the way the hummingbird brain processes visual signals reported in *Current Biology* on January 5, you can't. That's because a key area of the hummingbird's brain processes motion in a unique and unexpected way.

"In all four-limbed vertebrates studied to date, most of the neurons in this [motion-detecting] brain area are tuned to detect motion coming from behind, such as would occur for an impending collision or when being attacked from behind by a predator," says Douglas Altshuler of the University of British Columbia. "We found that this brain area responds very differently in hummingbirds. Instead of most neurons being tuned to back-to-front motion, almost every neuron we found was tuned to a different direction. We also found that these neurons were most responsive to very fast motion."

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VICE

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The Mighty Hummingbird Can Perceive Motion From Every Angle

Written by GRENNAN MILLIKEN (/AUTHOR/GRENNANMILLIKEN)

January 5, 2017 // 12:00 PM EST

Current Biology Dispatches



Current Biology

Figure 1. Flow fields generated by multiciliated cells aid olfaction.

Multiciliated cells in the larval zebrafish nose pit beat with asymmetric strokes, generating flow fields around the nose (left panel; warm colors and arrow size indicate flow strength). These flow fields push water into the nasal pit and eject them laterally. This effectively flushes odors over the sensory olfactory epithelium, enhancing odor detection and dynamic odor processing (adapted from [6] with major help from Marion Haug).

But the importance of directed, multiciliated cell-generated flows over epithelia does not stop here. Recently, multiciliated cells have been shown to play a crucial role in mammals as well [8]. Failure of these cells to generate directed fluid flows across their respective epithelia has been associated with diseases of the respiratory, reproductive and nervous systems [9]. Hence, the study of multiciliated cells in the accessible zebrafish may very well help us to not only understand the mechanism of how these fascinating cells generate fluid flow at the cellular and molecular level, but also gain insight into the corresponding human diseases as well.

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Visual Neuroscience: Unique Neural System for Flight Stabilization in Hummingbirds

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The pretectal visual motion processing area in the hummingbird brain is unlike that in other birds: instead of emphasizing detection of horizontal movements, it codes for motion in all directions through 360°, possibly offering precise visual stability control during hovering.

The pretectum and accessory optic system (AOS) are essential visual pathways between retina and brain. They are found in all classes of vertebrates and have a critical role in detecting the direction of image motion [1]. Signals from the pretectum/AOS feed into the motor system to provide information relevant for maintaining eye, head and



Current Biology Dispatches

body stability in the face of unintentional body movements. As an example of how this sensory-motor system operates, an unexpected backward body movement will generate forward image motion; the body tracks the image motion to move the body forward, thus returning it to its original position. To make this possible, the pretectum/AOS contains directionselective neurons: these neurons respond to image motion in one direction along their preferred motion axis, and their background activity is usually inhibited by motion in the opposite direction (Figure 1A). The cells have broad directional tuning widths, meaning that similar firing rates can represent a broad range of directions, leading to ambiguity in the precise direction being indicated - more on this later. The neurons also respond optimally only when the whole visual scene moves simultaneously, as during body movements. Along with balance detectors in the inner ear (the vestibular system), pretectal/AOS neurons form an integral part of the sensory-motor circuitry that keeps humans from falling over and birds from falling out of the skies.

In birds, the main brain nuclei are the pretectal lentiformis mesencephalic (LM) and the nucleus of the basal optic root (nBOR). In most birds, the preferred directions of LM neurons are horizontal-forward motion in the contralateral eye (Figure 1B, red), while preferred directions for nBOR neurons are most often vertical (up or down), or horizontal backward motion in the contralateral eye (Figure 1B, black). While many consider these visual pathways a closed chapter in vision science, as they report in this issue of Current Biology, Gaede et al. [2] have uncovered a unique feature in hummingbirds - instead of preferring just horizontal-forward image motion, neurons in the hummingbird LM have preferences for all directions through 360°.

The vestibular system detects rotations about the roll, yaw and pitch axes. Roll and pitch generate vertical visual motion over the eyes and yaw generates horizontal motion. Having a pretectum/AOS that detects image motion generated by body movements around the same axes as the vestibular apparatus makes for a robust, multi-sensory control circuit for stability control, found in species from mammals to insects [3,4]. Motion directions at non-vertical or horizontal angles can, theoretically, be calculated using the information from the orthogonally aligned detectors using principles that are equivalent to trigonometry (Figure 1C). For example, if both forward-tuned LM neurons and vertical-up tuned nBOR neurons fire at half their maximum spike rate, this could be interpreted at higher neural levels as upward-forward motion at 45° (Figure 1C). But because of the broad direction tuning of the neurons and noise in the system, such solutions run the risk of imprecision.

Gaede et al. [2] investigated the LM of hummingbirds, which have a unique flying behavior, and compared them to the LMs in pigeons and finches, which fly using more conventional methods. Most birds utilize wing movements that generate lift partly through forward movement. Many birds are capable of hovering but this is non-optimal. Hummingbirds, on the other hand, use rapid wing beats to hover in front of flowers, which provide their food supply. It turns out that the pretectal LM in hummingbirds does not conform to the standard bird model. Instead, the neurons in the LM have several unique characteristics. It is enlarged relative to brain size compared to LMs in other birds [5], implying a special role for the nucleus. Moreover, there is a uniform distribution of preferred directions at the population level (Figure 2A) and the neurons are tuned selectively to high image speeds [2].

Let us try to make sense of the different neural machinery found in the pretectum of the hummingbird in the context of its visual environment. Most birds want to stay level relative to the visual environment, which from daily observations of bird behavior is clearly achievable using primarily vertical and horizontal tuned pretectal/AOS detectors (Figure 1C). Hummingbirds have a different problem. While staying level, they need accurately to maneuver between flowers by adjusting their wing beats from stationary-hover to movinghover using visual cues, much like a helicopter [6,7]. On arrival at a flower,



Current Biology

Figure 1. Tuning functions of directionselective neurons in the pretectum/AOS

(A) A generic direction tuning function plotting spike rate against direction. The solid red line depicts the increased spike rate above the spontaneous rate for a range of rightward motions, while the dashed line shows the level of inhibition relative to ongoing spontaneous activity for leftward image motion. (B) Typical directional tuning functions for LM (red) and nBOR (black) in non-hovering birds. (C) The black arrow shows the actual direction of motion, which generates 50% of the maximum spike rate in both LM (vertical red line) and nBOR (horizontal black line). By comparing these spike rates, it is possible to deduce the direction of motion.

they insert their beak into the nectar reservoir and remain stationary, locked onto the visual target despite disturbances in airflow. It is only



Figure 2. Directional tuning in the hummingbird LM.

(A) Diagrammatic illustration of the directional tuning of cells in hummingbird LM. These tuning functions are depicted as being narrow to assist in visualizing the tuning of the population. The cell shown in black signals motion up and to the right at 45° . (B) In fact, neurons in hummingbird LM have broad tuning functions and closely spaced preferred directions. Tuning functions from three cells are shown, with preferred directions 10° apart.

necessary to watch hummingbirds do this for a few minutes to realize the precision — and beauty — of their actions.

It may be the increased need for precision that leads to an increased number of directional channels in hummingbird LM. Why evolution selectively pushed pretectal LM along this route, rather than recruiting the AOS nuclei as a whole, remains an intriguing mystery. Mechanistically, the existence of many directional channels in LM may be a form of line labeling. In this scenario, each direction of unintentional body movement would be detected via a small group of directionselective cells (Figure 2A, black tuning function). These cells would then initiate the appropriate directional motor

response to counteract deviations from the hover. Line labeling in the periphery is an established method for transferring sensory information to the brain, as in the sense of taste for example [8]. But for line labeling to work well in hummingbirds, we would predict narrow directional tuning functions, as depicted in Figure 2A. In fact, tuning functions in hummingbird LM are quite broad, with closely spaced preferred directions [2] (Figure 2B).

How could the system interpret outputs from cells with broadly tuned directional functions? Color vision mechanisms may give clues towards a mechanism. Humans have three broadly tuned color channels in the electromagnetic wavelength spectrum short, medium and long wavelengths with the medium and long wavelength channels not only having broad, overlapping bell-shaped absorption spectra, but also similar peak wavelengths [9]. Despite this, humans can discriminate between many hues, although only about twelve hues can be distinguished when requiring 'absolutely identifiable differences' [10]. Perceived color can be modeled by extracting the unique combination of response amplitudes for a given stimulus across all color channels [11]. Similarly, it is likely that unique directions are extracted from hummingbird LM by pooling across cells with similar preferred directions. The next step in working out the mechanism would be to record the responses of many LM neurons simultaneously and model the potential fidelity for directional discrimination using decoding and information theory methods at the cell population level [12,13]. These approaches have been applied to compare line labeling and pooling mechanisms in the encoding of stimulus orientation in the visual cortex [14].

Another thing that makes hummingbird LM unique is its preference for high image speeds. When flying very close to visual structures, even the slightest body movement will translate into high-speed image motion across the retina. In other birds and mammals pretectal neurons can be classed as being sensitive to either fast or slow image speeds [15–17]. In hummingbirds, only the fast cells exist. It is likely that their habit of flying close to flowers in dense vegetation has tuned the

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hummingbird LM to its specific visual environment.

The pretectum and AOS have long been regarded as a highly conserved design across vertebrates. The new work by Gaede *et al.* [2] has revealed a variation in the pretectum of the hummingbird that may be a specific adaptation for hovering.

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Evolution: Selfing Takes Species Down Stebbins's Blind Alley

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Shifts from outcrossing to selfing have occurred thousands of times across the tree of life. By reducing the size of the gene pool, selfing should limit adaptive potential. A refreshing empirical experiment with snails supports this long-standing hypothesis.

Reproduction is an essential part of life, and many biologists are rightly obsessed with it. For one, we are all part of an uninterrupted stream of successful reproductive events that connect our parents to us, and perhaps ourselves to our children. While biparental sex (i.e., mating between two individuals, or outcrossing) is the rule for humans, this is not the only possibility in nature. In groups such as flowering plants and invertebrates, hermaphrodites are common and these individuals are capable of mating with themselves - a process known as 'selfing' (Figure 1). Upon comparing outcrossing and selfing plant species, George Ledyard Stebbins famously proposed selfing to be an evolutionary "blind alley" that constrains adaptation: "self fertilization [...] would reduce markedly the evolutionary potentialities of those lines which adopted it" [1]. The possibility of reduced adaptive potential in selfing organisms has inspired a great number of theoretical [2-5] and empirical studies on the effects of mating systems on neutral and quantitative genetic variation in nature [6-8]. However, no empirical selection experiment has yet directly put to the test a central tenet of the blind alley hypothesis - that selfing limits the rate of adaptive evolution. Now, in a

new paper in this issue of Current Biology, Noël *et al.* [9] test this prediction in snails.

The experimental approach was straightforward. Noël et al. [9] experimentally evolved snail (Physa acuta) populations. At the outset, replicate populations were established with one of two mating systems for 30 generations: 100% outcrossing each generation, or switching between 100% selfing and 100% outcrossing every other generation. Partial selfing causes a reduction in the effective population size and the efficacy of recombination in comparison to the fully outcrossing lines [10]. Indeed, the partially selfing lines lost 42% more of their quantitative genetic variation, which is the raw material of adaptation. After 30 generations, all of the snail populations were then subjected to artificial selection on shell shape, a trait that varies considerably within and among snail species. Individuals with the most round shells were selected under two mating regimes: 100% outcrossing or 100% selfing. This experimental design permits a decoupling of the effects of immediate selfing and a history of selfing on the rate of adaptive evolution, allowing the effects of both to be experimentally determined.

Challenging the blind alley hypothesis is a tricky business. The effects of selfing

and selection are notoriously difficult to isolate, as evidenced by Fisher's famous line, "either inbreeding or selection, never both at the same time" [11]. This issue arises because 'adaptive potential' is not the same for outcrossing and partially selfing populations. In outcrossing populations, additive genetic variance is the key quantity determining the response to natural selection. With selfing, however, non-additive components of genetic variation can contribute to the response to selection [12]. It is possible to compare the



Figure 1. The flower of a primarily selffertilizing plant species, *Mimulus laciniatus*. The evolution of selfing commonly occurs, yet its influence on adaptive potential has been difficult to test empirically. Photo: D. Grossenbacher.

