MECHANOSENSORY FEEDBACK FOR FLIGHT CONTROL AND PREY CAPTURE IN THE ECHOLOCATING BAT

by

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Abstract

Throughout the animal kingdom, organisms have evolved neural systems that process biologically relevant stimuli to guide a wide range of species-specific behaviors. Bats, comprising 25% of mammalian species, rely on diverse sensory modalities to carry out tasks such as foraging, obstacle avoidance and social communication. While it is well known that many bat species use echolocation to find food and steer around obstacles, they also depend on other senses. For instance, some bats predominantly use vision to navigate, and others use olfaction to find food sources. In addition, bats rely on airflow sensors to stabilize their flight, primarily through signals carried by microscopic hairs embedded in their wings and tail membranes. Studies have shown that bats performing an obstacle avoidance task show changes in their flight behavior when dorsal wing hairs are removed. Additionally, electrophysiological studies have shown that wing hairs are involved in airflow sensing, but little is known about the contribution of sensory hairs on the ventral surfaces of the wing and tail membranes to their flight control and other complex behaviors, such as prey handling. **Chapter 1** of my dissertation presents a general introduction to bat echolocation, flight kinematics, and airflow sensing for flight control. In **Chapter 2**, I review sensory hairs across the animal kingdom, from invertebrates to vertebrates. I discuss the role of sensory hairs for functions ranging from detection to locomotion and propose the use and benefit of mechanosensors in biologically-inspired technology. In **Chapter 3**, I devised an experiment to evaluate changes in capture success, as well changes in flight kinematics and adaptive sonar behavior, before and after depilation of sensory hairs in order to ascertain if these sensory

hairs have a functional role in both airflow sensing for flight control and tactile sensing for prey handling. In **Chapter 4**, I designed an experiment aimed at determining if firing patterns of S1 neurons change with airflow speed and angle of attack and if wing hair depilation affects S1 responses to whole wing stimulation. To answer these questions, I record neural activity in S1 of sedated big brown bats while the entire contralateral wing is systematically exposed to naturalistic airflow in a wind tunnel. Finally, in **Chapter 5**, I address open questions that remain, present experiments aimed at filling these gaps, and consider key points important for future work.

Advisor and first reader: Dr. Cynthia F. Moss
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לסבא וסבתא היקרים שלי, למרות שאתם חיים רחוק אני תמיד מרגישה שאני קרובה אליכם !תודה שתמיד הזכרתם לי לאכול ולהירגע !אתם אוהבים אותי ותומכים בי ללא תנאים !לשאר המשפחה הגדולה שלי, דודים, דודות וכל בני ובנות הדודים שלי שתומכים בי !תודה שאתם תמיד שם בשבילי !אני לא יכולה !מקווהו להיות בקרוב שוב ביחד אני אוהבת אותכם מאד !עוד לחכות

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"You must give up the life you planned in order to have the life that is waiting for you"

- Joseph Campbell

Dedication

This work is dedicated to all the women in science - past, present, and future.

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Chapter 1

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Introduction

With over 1400 species, bats comprise over one fifth of all mammals and can be found on every continent except Antarctica (Simmons, 2005). Bats are highly diverse and occupy a variety of habitats, from tropical forests to the desert, as well as a wide range of ecological niches, as they forage on insects, fruit, nectar, fish, meat, and blood. Whether foraging in cluttered or open-spaces or gleaning fruit and prey from trees or water, each bat species has evolved unique modifications to their behaviors that are dependent on their particular foraging strategy and environment (Schnitzler and Kalko, 2001). Some species of bats are specialized to fly fast and over long distances, whereas others are better equipped for slow or hovering flight. One adaptation in particular that has been thought to influence bat flight behavior are the microscopic sensory hairs located on the wing and tail membranes. Sensory hairs on the dorsal side of the wing membrane have been implicated in airflow sensing for flight control (Sterbing-D'Angelo et al., 2011; Sterbing-D'Angelo et al., 2017; Marshall et al., 2015). While bats fly and maneuver through their environment, they are not only receiving information from sensory hairs about airflow, but rather they receive multisensory information, including acoustic information, to guide their behavior.

The goal of this research is to investigate the role of sensory hairs in airflow sensing. Specifically, I investigated the effects of sensory hair removal from the wing and tail membranes of the big brown bat on flight control, prey handling, and adaptive sonar

behavior (Fig. 1.1). Below, I introduce the echolocating bat as the subject of all experiments in this thesis. I review echolocation, an active sensing system bats utilize to navigate, localize objects, and capture prey in a three-dimensional environment. Next, I generally introduce flight kinematics and review literature pertinent to airflow sensing for flight control in insects, birds, and bats. Finally, I present a brief description of each chapter in this thesis.

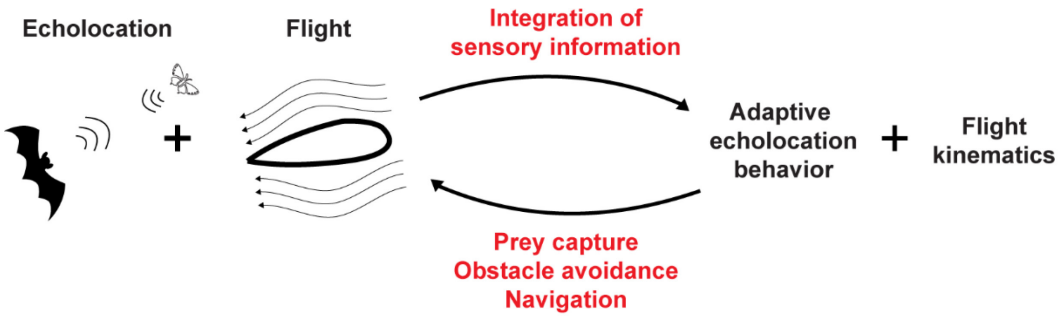

Fig. 1.1. Schematic of sensory integration for adaptive echolocation and flight behaviors.

Echolocation

Biological sonar, or echolocation, is a form of active sensing in which animals produce sounds that propagate through the environment and return as echoes from objects in the surroundings. Animals that rely on active sensing use information from the signals they produce to inspect and detect objects and features of a scene, and to inform their motor actions for relevant behaviors, such as navigation, obstacle avoidance, predator evasion, and prey capture. The echolocating bat produces intense ultrasonic calls and processes information in the returning echoes to localize and discriminate physical features of objects in their environment (Griffin, 1958). Most echolocating bats produce echolocation signals using their larynx. Sound is produced by passing air over

the vocal cords, causing them to vibrate. These vibrations are what generates the sound, similar to human sound production; but not all echolocating bats use the larynx to generate biosonar signals. For instance, bats of the genus *Rousettus* (suborder: *Pteropodidae*) produce ultrasonic tongue clicks to echolocate (Holland, Waters, and Rayner, 2004; Neuweiler, 2000).

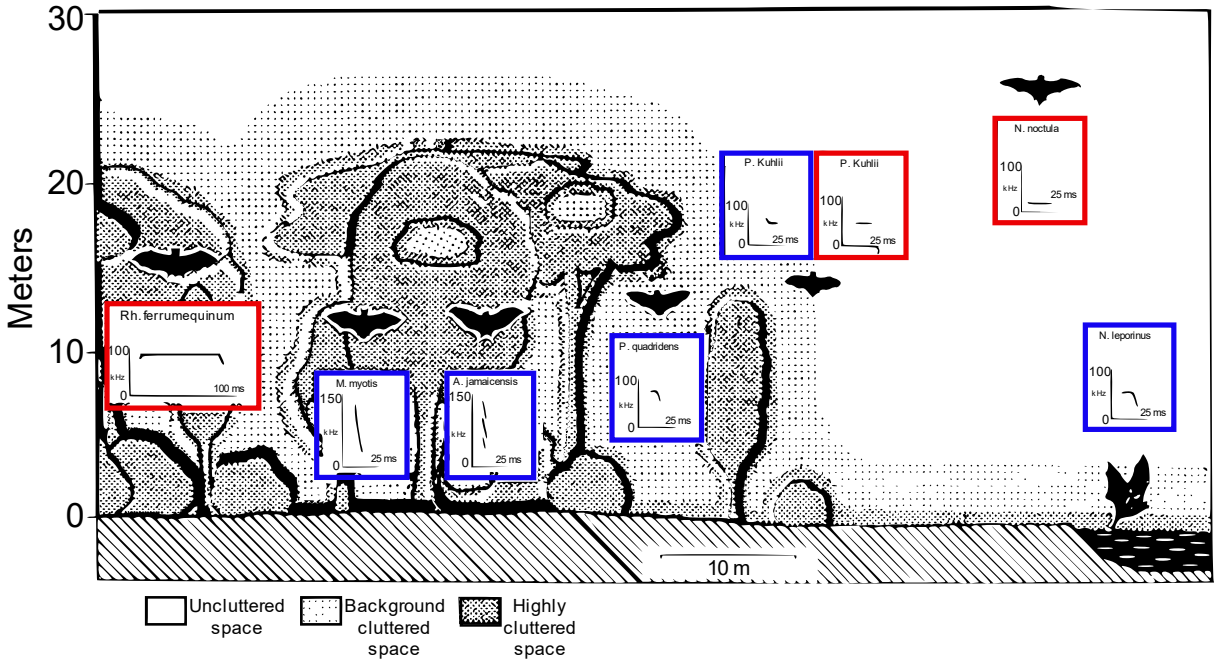

Fig. 1.2. Schematic of sonar signals from different bat species in their representative foraging habitats. Laryngeal echolocating bats produce two types of sonar signals: constant-frequency (CF; narrowband) or frequency-modulated (FM; broadband) signals. CF-FM (red) and FM (blue) bats adapt their sonar vocalizations as they detect, track, and intercept prey in a variety of habitats, in open space and in the presence of clutter (Figure adapted from Schnitzler and Kalko, 2001).

Depending on the species, there are two types of echolocation signals laryngeal echolocating bats produce, constant-frequency (CF) or frequency-modulated (FM) signals (Fig. 1.2). Echolocating bats use components of these two types of sonar sounds to forage in a wide variety of habitats. CF-FM bats produce long narrowband CF signals (10-100 ms), followed by an FM sweep component, whereas FM-bats produce broadband

sweeps that range in duration from 0.5 to 25 ms (Schnitzler and Kalko, 2001; Moss and Surlykke, 2010).

Previous findings have demonstrated that CF-FM and FM bats adapt their sonar vocalizations as they detect, track, and intercept prey in open space and in the presence of clutter. CF-FM bats have the ability to sense target motion from echo Doppler-shifts (Simmons, 1973). Specifically, bats that produce CF signals compensate for Doppler effects created by their own flight speed by adjusting the frequency of their sonar calls to ensure that echoes are received at the reference frequency, or the best frequency of the biological sonar receiver (Schnitzler et al. 1983; Moss and Surlykke, 2010), allowing for accurate discrimination of modulations of the CF signal component introduced by fluttering insect prey (Simmons 1973, 1979; Moss and Schnitzler, 1989, 1995; Moss and Surlykke, 2010). FM bats emit signals that are broadband, meaning that the signals sweep rapidly over a wider range of frequencies, providing exact time markers for the arrival time of echoes, which increases the accuracy of the signal for target localization (Simmons, 1973; Surlykke, Simmons, and Moss, 2016).

From these species-specific signals, echolocating bats organize complex patterns of echoes from objects in the environment by grouping and segregating the sounds from returning echoes into a perceptually informative representation of their environment (Bregman, 1990; Moss and Surlykke, 2001). Echolocating bats actively control and adapt the features of their sonar calls, including: the timing of calls, sonar beam aim, intensity, and spectro-temporal patterning of calls. These adaptations are believed to provide the bat with acoustic information regarding the three-dimensional position of a target or obstacle and information regarding the features of objects in the environment (e.g., depth,

structure, shape, and texture) (Simmons et al., 1974; Simmons et al., 1990; Moss and Surlykke, 2001; Aytekin, Mao, and Moss, 2010). Specifically, echolocating bats have the ability to identify and discriminate properties of physical objects based on the features of the returning echoes (Moss and Schnitzler, 1995; Moss and Surlykke, 2001). For instance, bats may discriminate the size of an object based on differences in the intensity of the returning echoes (Simmons and Vernon, 1971; Moss and Surlykke, 2001). Simmons and Vernon (1971) trained big brown bats (*Eptesicus fuscus*) to discriminate between two targets that differed in either size, shape, or distance using echolocation. Based on the properties of the targets, they observed that bats used differences in the overall intensity of the echoes to discriminate the size and shape of the objects (Simmons and Vernon, 1971).

In addition to discriminating physical properties of objects in space, echolocating bats must also have the ability to localize these objects in their environment. Acoustic information from the timing of emitted sonar calls and the respective returning echoes from the environment provide the bat with the necessary information to compute an object's position in elevation, azimuth, and depth. Echolocating bats can determine the vertical position, or elevation, of an object using monaural cues and spectral notches in echoes (Lawrence and Simmons, 1982; Wotton et al., 1996; Moss and Surlykke, 2001; Wohlgemuth, Luo, and Moss, 2016). Spectral notches are generated when the ridges and cavities of the outer ear, or pinnae alter the spectra of sounds entering the ear canal. In one experiment, Wotton and Simmons (1996) trained big brown bats to discriminate between vertical angles created by pairs of beads suspended from a fishing line and were rewarded for selecting the smaller angle. They found that bats used differences in the

location of spectral notches in the returning echoes to discriminate sound sources at different elevations, and that the location of the spectral notch increased in frequency with increasing elevation (Wotton et al., 1996).

Furthermore, echolocating bats compute the azimuthal position of objects using inter-aural differences in the arrival time, intensity and spectral content of the echoes at the two ears (Shimozowa et al., 1974; Simmons et al., 1983; Moss and Surlykke, 2001; Wohlgemuth, Luo, and Moss, 2016). Simmons et al. (1983) trained big brown bats to discriminate the angle between two arrays of rods in the horizontal (i.e., azimuthal) plane using echolocation and rewarded them for choosing the rods separated by the smallest angle. Surprisingly, they found that despite their small size, big brown bats were able to successfully discriminate the azimuthal position of objects with angles as small as 1.5º using interaural time cues (Simmons et al., 1983).

Echolocating bats can also estimate target distance, or depth by computing the time delay between the outgoing sonar signal they emit and the returning echo (i.e., pulse-echo delay) (Simmons, 1973; Simmons et al., 1974; Simmons et al., 1990; Moss and Surlykke, 2001; Schnitzler, Moss, and Denzinger, 2003; Wohlgemuth, Luo, and Moss, 2016). In a pioneering study, Simmons (1973) trained four different species of bats that produced different types of echolocation signals (i.e., FM, short CF-FM, and long CF-FM signals) to fly from a starting platform to the closer of two targets. He reported that all four species of bats could discriminate target range with high accuracy (Simmons, 1973).

For decades, researchers have investigated the ways bats adapt their echolocation behavior as they seek, track and intercept prey. In general, bats progress through three phases of echolocation in the pursuit of a target: the search phase,

approach phase, and capture phase (Schnitzler and Kalko, 2001; Moss and Surlykke, 2001; Moss and Surlykke, 2010; Moss, Chiu, and Surlykke, 2011) (Fig. 1.3). During these phases, echolocating bats adjust the call rate, duration, and bandwidth of their sonar signals as they approach a target. During the search phase, FM bats produce sonar calls at a low repetition rate that are long in duration, ranging from 8-25 ms. The bandwidth of search calls in FM bats are narrow and low in frequency (<30 kHz). Once bats detect and select a target, it enters the approach phase. The transition into the approach phase in FM bats is characterized by shorter, broadband sonar calls (2-6 ms) at a higher repetition rate, ranging in frequency from 30–120 kHz. In the final phase before prey capture, bats emit short duration sonar calls (0.5-1 ms) at a high repetition rate (150-200 Hz), also referred to as the terminal buzz phase (Schnitzler and Kalko, 2001; Moss and Surlykke,

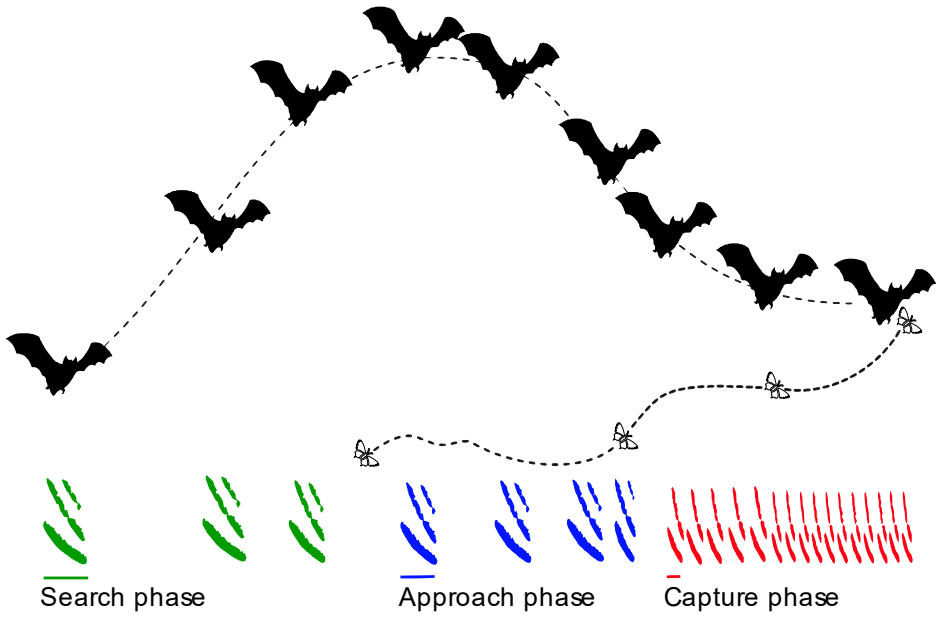

Fig. 1.3. Example of the three phases of echolocation in the big brown bat, *Eptesicus fuscus*. In the search phase (green), the big brown bat produces sonar calls that are long in duration (15-20 ms) at a call rate of 5-10 Hz. When the bat identifies its target and begins pursuit, it enters the approach phase (blue), which is characterized by sonar calls that are shorter in duration (2-5 ms) and a call rate of 20-80 Hz. During the final capture phase (red), also referred to as the terminal buzz phase, bats reduce the duration of sonar calls to 0.5-1 ms and increase the call rate to approximately 150 Hz (Figure adapted from Warnecke et al., 2015).

2001; Moss and Surlykke, 2010; Moss, Chiu, and Surlykke, 2011). While these adaptations vary across bat species, the overall pattern of increasing call rate and decreasing call duration as the distance to a target decreases is generally observed in both FM and CF-FM bats (Matsuta et al., 2013; Fawcett et al., 2015; Wohlgemuth, Luo, and Moss, 2016). Together, these adaptations to echolocation signal features allow echolocating bats to obtain the necessary information for localizing objects in three-dimensional space.

In summary, echolocating bats actively sample their environment and adapt the features of their sonar signals in order to obtain the acoustic information representing the location of objects in three-dimensional space. In addition to adapting their sonar signals, echolocating bats are simultaneously flying and navigating through their environment. Bats, as well as other flying animals, must also integrate sensory information from multiple modalities while maneuvering through complex habitats. In the next section, I review flight control and aerodynamics generally in flying animals and provide examples of specialized mechanosensors that contribute to their ability to alter their flight behaviors.

Flight control and kinematics: insects, birds, and bats

Insects, birds, and bats are the only living animals capable of powered flight. Flight kinematics, such as flight speed and maneuverability, rely on aerodynamic principles and are influenced by an animal's habitat and environmental conditions (i.e., clutter and wind conditions). Flying animals exploit these principles in order to adapt their flight behaviors, allowing them to navigate, hunt for prey, and evade obstacles and predators.

Level flight depends on the interaction and balance of aerodynamic forces (Fig.

1.4). Aerodynamic force can be defined by its components: lift, weight, thrust, and drag. The following equations define components of aerodynamic force:

(1) Lift = $C_L \rho V^2 S$

(2) Thrust = $C_T \rho V^2 S$

(3) Drag = $C_D \rho V^2 S$

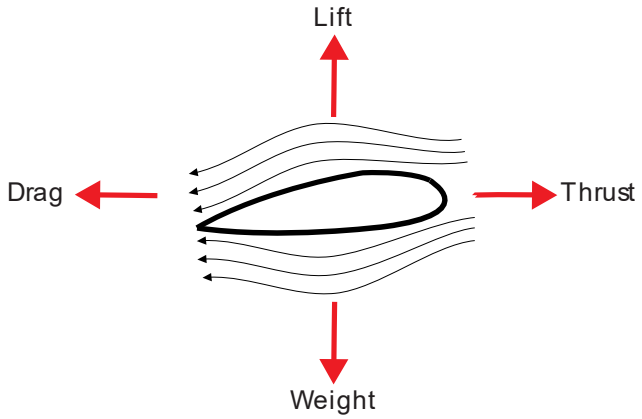

Fig. 1.4. Schematic of aerodynamic forces of flight.

Lift (eq. 1) is a force perpendicular to the direction of oncoming air and weight is a gravitational force that opposes lift. In order to remain airborne, an animal must generate enough lift to balance its weight. Thrust and drag are opposing forces that are parallel to the motion of the animal. Thrust (eq. 2) points in the same direction as the motion of the animal and is generated through the flapping of the wings. Drag (eq. 3) points in the opposite direction of the animal's motion and is experienced by the animal as it moves through the air during flight. In order for the animal to maintain forward motion, thrust must exceed drag. Other factors that also affect flight performance include air density (ρ), velocity (V), surface area of the wing (S), and angle of attack. Taken together, these factors determine the coefficients for lift (C_L), thrust (C_T), and drag (C_D).

The shape of the wing, and thus the surface area, change with respect to the angle of attack. The angle of attack is typically defined as the angle between the wing's line of reference and the oncoming airflow. When the angle of attack increases, the lift also increases until a maximum lift coefficient is reached. This is referred to as the critical angle of attack. The critical angle of attack depends on both the shape of the wing and the Reynolds number. The Reynolds number (eq. 4) is defined as the ratio of inertial forces to viscous forces within a fluid, in this case air, where ρ is the density of the fluid, V is the flow speed, D is the diameter of the tube, and μ is the dynamic viscosity of the fluid.

(4) $Re = \rho VD/\mu$

The Reynolds number is dimensionless and important for describing transport properties in microfluidics related to the size of the object (Rapp, 2017). For instance, small objects tend to little inertia and therefore have smaller Reynolds numbers, whereas larger objects have higher Reynolds numbers due to the increase in inertial forces (Rapp, 2017).

As the angle of attack increases beyond the critical angle, lift decreases and drag increases, resulting in increasingly turbulent airflow over the ventral surface of the wing and separation of airflow from the surface of the wing. When airflow is fully separated from the surface of the wing, this results in stall. A stall situation does not always result in a negative outcome, such as a crash, and can be advantageous for landing. The critical angle of attack for stall varies across aircrafts and animals, ranging from 15º to 20º in

fixed-wing aircrafts to 20º in large species of birds, and 30º to 50º in various species of insects (Vogel, 1967; Alexander, 2002).

Insect flight

Insects are one of the most abundant animal species on the planet. Some insects evolved the ability to fly over 350 million years ago and each of these insect species has evolved a distinct set of wings that are flexible and thin, ranging from 0.5 to just a few micrometers in thickness. Depending on the species, the forewings and hindwings of an insect vary in shape and size and can either be physically linked or operated independently of one another (Wootton, 1992). Similar to flying vertebrates (i.e., birds and bats), insects have flapping wings that dynamically change direction, angle, and shape during flight (Wootton, 1992).

Insect wingbeat frequency is inversely correlated with body size (Dickinson, 1990). During the downstroke of the flapping cycle, the wings are forced downwards and forwards. At the end of the downstroke, there is a deceleration of the wings' velocity, allowing the insect to rotate their wing into the upstroke position. The angle of the wing during the upstroke influences the magnitude of the aerodynamic forces, specifically the amount of lift and thrust generated by the insect. The downstroke kinematics are relatively consistent across insect species, whereas there are species-specific differences in the upstroke kinematics based on the size and anatomy of the wings (Dickinson, 1990; Dickinson, 2005; Wootton, 1992).

The oscillations and twisting of the wings result in changes of the aerodynamic forces experienced by the insect. While insects have some similarities to their flying

counterparts, they differ in the way they control the shape of their wings (Wootton, 1992). In contrast to birds and bats that have forelimbs and powerful muscles that allow them to control their wing camber, the musculature of insects does not extend beyond the axilla, where the thorax attaches to the wing. Instead, the camber of their wings is controlled locally by rigid structures on the wing itself, such as: veins, fold lines, flexion lines, scales, and spines. These components are engaged and operate together, offering both sensory feedback and structural support during flight.

Bird flight

Bird flight is one of the best studied forms of aerial locomotion. With approximately 10,000 species of flying avians, birds show tremendous diversity in wing morphology and size. An important defining feature of birds is their feathers. Flying birds have primary feathers on the lifting surface of their wings. These feathers are asymmetric in shape and are present on both the leading and trailing edge of the wings. The trailing edge feathers are long and flexible, whereas the leading-edge feathers are stiff, providing the wing with additional support against the forces from oncoming airflow.

Unlike insects, wing motion of birds is controlled by a symmetrical pair of pectoral muscles (Altshuler et al., 2015), which in turn directly influences their flight kinematics, such as wingbeat frequency and amplitude. In addition to controlling wing motion, birds can adjust the camber of their wings (Thomas, 1996; Lindhe Norberg, 2002; Lentink et al., 2007). Passive morphing of the wing occurs without engaging flight muscles, whereas active morphing recruits activity from the joints and intrinsic muscles of the wing in order to change its shape (Altshuler et al., 2015). Active morphing is defined by three variables:

wing twisting, wing folding, and wrist flexing. These variables affect the aerodynamic forces experienced during flight by changing the angle of incidence of the wing (Altshuler et al., 2015).

During flapping flight, birds generate lift and thrust by directing their wings downwards and forwards during the downstroke. During the upstroke, also referred to as the recovery stroke, birds actively morph their wings by flexing and twisting them in order to decrease wing area and reduce as much counterforce as possible. Throughout flight, birds dynamically modify the motion and shape of their wings to adjust flight kinematics and enhance flight control.

Bat flight

Bats are the only mammal capable of true powered flight, which evolved 65 million years ago. The anatomy of the oldest known bat fossils (*Onychonycteris finneyi* and *Icaronycteris index*), date back to approximately 52 million years ago and closely resemble that of modern-day bats (Hedenström and Johansson, 2015). With over 1,400 known species, bats comprise the second largest group of mammals on the planet, ranging in mass from approximately 2 g to 1.4 kg.

The size and shape of a bat's wings have evolved to support flight maneuvers in the environment they inhabit. For instance, bats that live in cluttered environments, such as densely packed forests, typically have short and broad wings, whereas bats that forage in open spaces tend to have wings that are longer and narrower. The size and shape of a bat's wings can serve as indicators of their preferred foraging strategy (Norberg and Rayner, 1987; Neuweiler, 2000). Frugivorous and carnivorous bats typically have large,

broad wings with increased musculature, which supports flight endurance and the strength to carry larger prey, whereas nectarivorous bats have short, broad wings that allow them to hover while feeding from flowers. Insectivorous bats have broad wings with a medium to wide wingspan which allow for high maneuverability when tracking insects.

The wing membrane extends across the forelimb and a set of elongated finger bones, homologous to the human hand, thus it is often referred to as a “hand-wing.” The bones of the hand-wing are less dense than the bones of the body, resulting in decreased mass and increased flexibility. A bat’s wing membrane is extraordinarily thin, ranging from 29 to 63 μm, depending on the species (Studier, 1972). Unlike the wings of birds and insects, which are made up of keratin feathers and chitin cuticle, the membrane of a bat wing is made of living skin that contain a variety of sensors, elastic fibers, vasculature, and specialized muscles (Hedenström and Johansson, 2015). Another unique feature of the bat wing membrane is its anisotropy, meaning that the physical and mechanical properties of the wing show chord-wise and span-wise differences (Hedenström and Johansson, 2015). The specialized anatomy of the bat wing allows for more precise control of the shape and angle of the wing (Wootton, 1992). Within the wing membrane, there are intrinsic muscles that are not connected to the wing bones and these muscles are involved in the control of wing camber and stiffness, which decrease the slack of the wing membrane and provide stabilization during flight (Neuweiler, 2000).

The distinctive anatomy of bat wings enables them to fly with high maneuverability, even at low velocities or turbulent conditions (Sterbing and Moss, 2018), and their flight kinematics are influenced by the shape and size of the wing. For example, wingbeat frequency is inversely proportional to wing size (i.e., surface area and chord length): Bats

with larger wings have a lower wingbeat frequency than bats with smaller wings. Further, the magnitude of lift produced during flight is directly influenced by various parameters of the wings, including surface area, camber, angle of attack, and flight speed. During the upstroke of the wingbeat cycle, thrust and lift are generated, but at the end of the upstroke, negative lift occurs as the bat transitions into the downstroke. This is compensated for by lift generation during the downstroke.

The surface area and camber of the wing are actively controlled by the bat throughout the wingbeat cycle. In particular, camber is controlled by the movement of the five fingers or digits and the legs of the bat. By manipulating particular digits and deflecting the legs, bats are able to stiffen and stabilize the leading edge of the wing and control the shape of the tail membrane, providing more support during flight. The tail membrane is connected to the hind legs in some bat species and can also contribute to flight control. The size and shape of a bat's tail membrane varies across species and offers an additional level of control for maneuverability. For example, bats can control the tautness of their tail membrane by spreading their legs. This can cause the membrane to parachute out, thus slowing the bat down and initiating a change in flight direction (Neuweiler, 2000).

Airflow sensing for flight control: insects, birds, and bats

Flying animals move swiftly through dynamic, three-dimensional environments. In order to maintain flight control while navigating through a complex environment, flying animals are equipped with an assortment of mechanoreceptors to sense changes in their surroundings.

Airflow sensing in winged insects

The sensory systems of insects comprise a wide range of sensors that have been implicated in flight control, including sensors that detect changes in optic flow, airflow, inertia, and wing load. Here I will focus on airflow sensors. Specifically, antennae and trichoid sensilla and their role in providing feedback to the flight control system.

Antennae

Antennal anatomy. All winged insects have a single pair of antennae that play an important role in mechano- chemo-, thermo-, and hydro-reception (Schneider, 1964). Antennal anatomy varies greatly across pterygotes, or winged insects, but basic structures are shared across species. Commonly, the antennae are composed of 2 basal segments (the scape and the pedicel) and a distal flagellum (Schneider, 1964; Taylor and Krapp, 2007). The first basal segment, the scape, is the most proximal segment of the antennae and articulates with the head capsule. The actuation of the head-scape joint is controlled by two to five tentorio-scapal muscles. The actuation of the head-scape joint and the number of tentorio-scapal muscles varies across insect orders. For example, Odonata (*Orthetrum*: Gewecke and Odendahl, 2004) and Orthoptera (*Locusta*: Gewecke, 1972b; Bauer and Gewecke, 1991; *Gryllus*: Honegger et al.,1990) have hinge-like antennal joints that are actuated by very few muscle units, whereas Lepidoptera (*Manduca*: Kloppenburg et al., 1997; Sane et al., 2007) and Hymenoptera (*Apis*: Snodgrass, 1956) have socket-like antennal joints with a greater number of tentorio-scapal muscles.

The second basal segment of the antennae, the pedicel, forms a hinge joint with

the scape under the actuation of two to four muscles within the scape itself (Taylor and Krapp, 2007). Additionally, the pedicel is covered with sensory bristles that are thought to aid in mechanosensation, but little is known about the exact function of these bristles. Lastly, the most distal segment of the antennae is the flagellum. The flagellum does not contain its own muscles and is passively articulated with the pedicel (Schneider, 1964; Taylor and Krapp, 2007). The structure of the flagellum and its range of motion are also highly variable across species. For instance, crickets typically have long whip-like flagella, whereas a housefly has a unique flagellar structure, where the first segment is an enlarged spheroid structure with the remaining segments containing fine feather-like projections called arista (Taylor and Krapp, 2007; Yeates et al., 2007; Chadha, 2014).

In addition to the scape, pedicel, and flagellum, there are two additional mechanoreceptors located at the pedicel-flagellar joint that contribute to the antennal sensory system. One is the Campaniform sensillum, which is located at the distal end of the pedicel segment. This disc shaped mechanoreceptor is sensitive to stresses applied to the exoskeleton of the insect (Taylor and Krapp, 2007). The second mechanoreceptor present within the antennae is the Johnston's organ, a type of scolopidia. This stretch-sensitive receptor is inserted at the pedicel-flagellar joint and is responsible for detecting motion of the flagellum (Taylor and Krapp, 2007).

Role of antennae in airflow sensing. Antennae have been implicated in insect flight control and are thought to be mechanoreceptors for maintaining stability during flight and for detecting changes in airflow direction and flight speed (Burkardt and Gewecke, 1965; Taylor and Krapp, 2007; Sane et al., 2007; Mamiya et al., 2011). Previous studies have shown that the flight speed of free-flying insects changes after amputation of the

antennae. Depending on the species of insect, flight speed has been shown to decrease (*Drosophila*: Campan, 1964; *Apis*: Neese, 1966; *Aglais*: Niehaus, 1981) or increase (*Locusta*: Gewecke, 1971, 1975; *Aedes*: Bässler, 1958) after antennal amputation. Furthermore, amputation studies have demonstrated that the antennae play a role in maintaining flight stability. For example, Sane et al. (2007) investigated whether the antennae in the hawk moth, *Manduca sexta*, conveys mechanosensory feedback for flight control. They found that removing the antennal flagellum reduced mechanical input to the Johnston's organ and severely disrupted moth flight stability, resulting in an increase in backward flight and collisions with walls (Sane et al., 2007).

In all species of insects studied to date, the antennae are protracted towards oncoming airflow in preparation for flight and the position of the antennae is further adjusted during flight. These adjustments are thought to be in reaction to changes in airflow and have been termed the antennal positioning reaction (Burkhardt and Gewecke, 1965; Gewecke, 1972a; Taylor and Krapp, 2007). As airspeed increases, the antennae rotate forward from the scape-pedicel joint in opposition to the movement of the pedicel-flagellum joint, reducing the drag present on the flagellum (Burkhardt & Gewecke, 1965; Taylor and Krapp, 2007). Additionally, studies have shown that the antennal positioning reaction is unaffected by the covering of compound eyes or changes in optic flow, but it is impeded when the pedicel-flagellum joint is immobilized (Burkhardt and Gewecke, 1965; Taylor and Krapp, 2007).

The research thus far has demonstrated that the antennae are essential components of the insect flight control system and the mechanoreceptors within the antennae are key for maintaining stability during flight and detecting airflow speed and

direction.

Wind-sensitive hairs

Trichoid sensilla are sensory structures located all over the body of insects. While there is speculation that these hair-like sensilla on other parts of the body, such as: the legs and wings, are involved in flight control, the only evidence of these sensilla playing a role in flight control comes from studies of sensilla on the head capsule, also referred to as cephalic hairs (Weis-Fogh, 1949; Taylor and Krapp, 2007; Chadha, 2014).

The first and most well-characterized trichoid sensilla were studied from locusts. In a pioneering experiment, Weis-Fogh (1949) found that they were able to induce flight in suspended insects when the sensilla located on the head capsule were stimulated by airflow. The role of cephalic sensilla in flight control was further confirmed when response to airflow was absent after obscuring the hairs from airflow with cellulose. Interestingly, studies have shown that mechanical stimulation of cephalic sensilla is not sufficient to induce flight (Boyd and Ewer, 1949; Weis-Fogh, 1956; Taylor and Krapp, 2007). Trichoid sensilla were not only found to be sensitive to airflow speed, but also to the direction of the airflow stimulus. Weis-Fogh first observed that locusts oriented towards the direction of the airflow stimulus (Weis-Fogh, 1949). Moreover, electrophysiological studies of isolated individual trichoid sensilla have shown that the maximal firing rate occurs when the airflow stimulus is aligned with the curvature of the hair (Camhi, 1969; Taylor and Krapp, 2007). Taken together, findings suggest that cephalic trichoid sensilla sensitivity to airflow speed and selectivity to airflow direction provide flying insects with crucial feedback for motor control during flight.

Airflow sensing in birds

In contrast to the abundant literature on the contribution of airflow sensing to flight control in insects, the literature on mechanosensory input to flight control in birds is more limited. Similar to mammals, birds have mechanoreceptors embedded in their skin. The four main types of mechanoreceptors are: Herbst corpuscles, Merkel cell receptors, Grandry corpuscles, and Ruffini endings (Necker, 1985; Necker, 2000). Here I will focus on mechanoreceptors that have been implicated in airflow sensing in birds.

Behavioral studies first indicated the presence of airflow sensors in the avian skin when researchers observed that tethered flight could be elicited and maintained when they directed continuous airflow at the animal (Woike, 1976; Gewecke and Woike, 1978). To further investigate this hypothesis, Gewecke and Woike (1978) analyzed various flight parameters before and after the breast feathers of birds were immobilized. They observed that birds were still able to maintain flight despite the immobilization of their feathers, but that their flight parameters were altered. For example, some animals increased their flight speed and wing beat frequency after feather immobilization (Gewecke and Woike, 1978).

Similar to the mechanoreceptors that are associated with hair follicles in mammals, mechanoreceptors in birds tend to aggregate around the feather follicles (Saxod, 1996). Merkel cells and Ruffini endings are slowly adapting receptors and in birds have been hypothesized to sense sustained deformations of the skin and feathers due to wind speed (Brown and Fedde, 1993; Altshuler et al., 2015). Herbst corpuscles, on the other hand, are only found in birds and are the most common receptors found in bird skin. These receptors are typically associated with secondary filoplume feathers and have both physiological and morphological similarities to mammalian Pacinian corpuscles (Hörster,

1990). These rapidly adapting receptors are sensitive to high-frequency vibrations (Hörster, 1990). Brown and Fedde (1993) stimulated the wings of a chicken while recording activity from the radial nerve. They found that directing airflow at the wing resulted in a discharge frequency that was correlated with the elevation of the feathers. Furthermore, they demonstrated that increasing the airflow velocity in turn increased the firing rate of these receptors. In summary, these findings suggest that mechanoreceptors associated with wing feathers in birds sense changes in airflow, providing feedback for flight control.

Airflow sensing in bats

Bats, like other mammals, have a variety of mechanoreceptors for somatosensation, such as Merkel cells, lanceolate endings, and Pacinian corpuscles. In addition to mechanoreceptors for touch, bats are equipped with microscopic sensory hairs on their tail, wings, and feet. Here, I will focus on sensory hairs that have been implicated in airflow sensing for flight control.

Bats do not possess glabrous skin, unlike other mammals (rat: Leem, Willis, and Chung, 1993; primate: Manfredi et al. 2012; human: Johansson and Vallbo, 1983). In addition to the fur or pelage hair found covering most of the bats' body, these animals have post-cranial hairs on various parts of their body, including the wings, tail, rump, and feet (Kang and Reep, 2013). One study examined post-cranial hairs on 66 species of bats and hypothesized that served sensory functions, based on their structure and placement. Furthermore, they suggested that these sensory hairs played different roles, depending on their placement, as well as life history traits of each species, such as: roost type, size

of roosting group, and diet. They found that the shape, length, and thickness of bat post-cranial hairs differed from those of the pelage hair, and that there was a correlation between placement of sensory hairs and function (Kang and Reep, 2013). For instance, hairs on the tail were thought to contribute to foraging and landing, whereas toe hairs were suspected to function mainly as a tool for grooming. While the functions of different types of post-cranial hairs are not fully understood, the hairs on the wings of bats were identified over one hundred years (Maxim, 1912), and more recently, have been investigated for their functional role as airflow sensors for flight control (Zook and Fowler 1986; Sterbing-D'Angelo et al. 2011).

The membrane of bat wings is sparsely lined with microscopic hairs. These hairs are associated with a variety of tactile receptors, including lanceolate receptors and Merkel cell neurite complexes (Marshall et al., 2015; Sterbing-D'Angelo et al., 2017). Empiricial studies have demonstrated that wing hairs act as airflow sensors (Sterbing-D'Angelo et al., 2011; Sterbing-D'Angelo et al., 2017; Marshall et al., 2015). Sterbing-D'Angelo et al. (2011) found that two different species of bats, *Eptesicus fuscus* (big brown bat) and *Carollia perspicillata* (short-tailed fruit bat), altered their flight behavior after depilation (i.e., hair removal) of different regions on the wing membrane. Using species-specific obstacle avoidance tasks, *Eptesicus fuscus* and *Carollia perspicillata* were observed to make wider turns around obstacles and increase their flight speed after depilation, respectively (Sterbing-D'Angelo et al., 2011).

Furthermore, electrophysiological studies have studied responses in primary somatosensory cortex (S1) to mechano-stimulation of the bat wing. Sterbing-D'Angelo et al. (2011) observed that neurons in S1 of the big brown bat responded to both light touch

and air puff stimulation, with a preference for reversed airflow. Moreover, Marshall et al. (2015) found that both air puff and tactile stimulation activated similar neural populations in bat S1 cortex. Interestingly, the firing rate of S1 neurons in response to air puff stimulation diminished after wing hair depilation but showed no decline in response magnitude to tactile stimulation in the same receptive field (Sterbing-D'Angelo et al., 2011), supporting the hypothesis that hairs on the wings of bats function as airflow sensors.

The current study: Goals and outline of thesis

First, in **Chapter 2** I review sensory hairs across the animal kingdom, from invertebrates to vertebrates. I discuss the role of sensory hairs in locomotion, exploration, and prey capture in a variety of animals from both land and sea. Additionally, I propose the use of mechanosensors in biologically-inspired technology.

While the Sterbing-D'Angelo et al. (2011) study reported quantitative changes in the flight behavior of the short-tailed fruit bat following wing hair depilation, only qualitative data on obstacle avoidance were reported for the insectivorous big brown bat. Obstacle avoidance is a necessary component in the behavioral repertoire of bats as they navigate through complex, three-dimensional environments, but bats must also perform goal-directed tasks, such as prey capture, where they must orient themselves towards a target of interest. How do sensory hairs on the bat wing and tail contribute to coordinating goal-directed flight? Does removal of airflow sensors on the wing and tail membranes affect adaptive sonar behavior? Do wing/tail membrane hair sensors support additional functions apart from monitoring airflow? Do the ventral and dorsal wing/tail membrane

hairs convey different information? To address these questions, in **Chapter 3**, I trained big brown bats to perform a goal-directed task where they captured a tethered insect on the wing in the laboratory flight room. I evaluated changes in capture success, as well changes in flight kinematics and adaptive sonar behavior, before and after depilation of sensory hairs (i.e., removal of hairs) in order to ascertain if these sensory hairs have a functional role in both airflow sensing for flight control and tactile sensing for prey handling.

Several electrophysiological studies have investigated the topographic organization of primary somatosensory cortex (S1) in the big brown bat and neural responses to artificial air puff and tactile stimulation of the wing (Chadha, Sterbing-D'Angelo, and Moss, 2011; Sterbing-D'Angelo et al., 2011; Marshall et al., 2015), but all of these experiments were conducted in anesthetized bats using a simple localized air puff or light touch stimulus delivered to a restricted region of the wing. Bat flight is dynamic and the sensory information they receive along the wing is not confined to an isolated location. One question that remains unanswered is how cortical responses are modulated by natural, whole wing stimulation. To answer this question, in **Chapter 4**, I recorded neural activity in S1 of sedated big brown bats while the entire contralateral wing was systematically exposed to naturalistic airflow in a wind tunnel. I present preliminary work aimed at determining if firing patterns of S1 neurons change with airflow speed and angle of attack and if wing hair depilation affects S1 responses to whole wing stimulation.

Finally, in **Chapter 5**, I discuss the results of all studies carried out for this thesis, address open questions that remain, and consider key points that are important for future work.

Chapter 2

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Mechanosensory hairs and hair-like structures in the animal kingdom: Specializations and shared functions serve to inspire technology applications

Brittney L. Boublil, Clarice A. Diebold, and Cynthia F. Moss, 2021 in review

Preamble: I review the diversity of biological hair and hair-like sensors across the animal kingdom in coordinated movement, orientation, and feeding and illustrate shared functional properties of hair and hair-like structures between invertebrates and vertebrates. By reviewing research on the role of biological hair and hair-like sensors, I aim to highlight how sensors inspired by biological systems could be of interest to the engineering community and contribute to the advancement of mechanosensing in artificial systems, such as robotics.

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Introduction

Across the animal kingdom, organisms have evolved specialized sensory systems to contend with complex environments and respond to new stimuli. Biological sensors

reveal high sensitivity, enable behavioral flexibility, and operate with energetic efficiency, providing powerful examples to inspire the design of artificial sensors.

Sensory hairs (i.e., vibrissae, tactile hairs, sinus hairs, or whiskers) have arisen throughout the animal kingdom to enable rapid and finely tuned tactile stimulus processing (Gaspard et al., 2017). While the architecture of tactile sensory hairs has been highly conserved over time (McGovern et al., 2015), animals have evolved species-specific specializations, based on their ecological niches and sensory adaptations, to support a multitude of complex behaviors.

Sensory hairs support species-specific behaviors, shaped by natural history, ecology, and niche. Here we review the role of mechanosensory hairs in coordinated movement, orientation, and feeding across the animal kingdom (see Table 2.1 and Fig. 2.1). We draw parallels between shared functions of mechanosensory hairs and hair-like structures and suggest ways this knowledge can be applied to new technological advances in robotic sensing.

Mechanosensory feedback for coordinated movement

Mechanosensory information is used to coordinate motion and navigate complex environments. Mechanosensory feedback also provides proprioceptive information about self-guided motion or spatial information about the environment when navigating small spaces. Many animals have evolved specialized hair and hair-like structures that provide mechanosensory feedback for coordinated movement.

Terrestrial invertebrates (Orthoptera, Diptera). Many insects, including stick insects and locusts, rely on proprioceptive input to coordinate movements like walking.

Table 2.1. Overview of features of hairs and hair-like structures.

Environment	Order	Species	Hair structure	Hair length (mm)	Location	Function	Reference
Terrestrial Invertebrates	Diptera	Brachycera (Fly)	Setae	0.0339 ±0.00471	Basal part of pulvillus	Attachment to surfaces	Gorb, 1998
	Blattodea	Periplaneta americana (Cockroach)	Sensilla of hair plates (short)	0.005-0.03	Leg joints	Limit detectors for coordinated movements	Wong and Pearson, 1975
	Blattodea	Periplaneta americana (Cockroach)	Sensilla of hair plates (long)	0.03-0.07	Leg joints	Limit detectors for coordinated movements	Wong and Pearson, 1975
	Araneae	Cupiennius salei (Wandering spider)	Trichobothria (filiform hairs)	0.1-1.4	Body and legs	Prey detection	Barth, 2000, 2002; 2004
	Hymenoptera	Odontomachus bauri (Trap jaw ant)	Hair-like sensilla and bristles	0.6-1.2	Mandibles	Prey detection	Gronenberg, 1994
Terrestrial Vertebrates	Carnivora	Felis catus (Domestic cat)	Mystacial vibrissae	40-70	Face	Detection for coordinated movement	Gottschaldt et al., 1973
	Carnivora	Felis catus (Domestic cat)	Carpal vibrissae	10-20	Forelimbs	Detection for coordinated movement	Nilsson and Skoglund, 1965
	Rodentia	Mus musculus (Mouse)	Mystacial vibrissae	30	Face	Detection, orientation, discrimination	Brecht et al., 1997
	Rodentia	Rattus norvegicus domestica (Rat)	Mystacial vibrissae	10-60	Face	Detection, orientation, discrimination, airflow sensing	Yu et al., 2016
Flying Invertebrates	Orthoptera	Locusts	Trichoid sensilla	0.03-0.35	Head capsule	Airflow sensing	Taylor and Krapp, 2007
	Orthoptera	Crickets	Cerci	0.03-1.5	Body	Airflow sensing	Chiba et al., 1992; Jacobs et al., 2008
Flying Vertebrates	Chiroptera	Eptesicus fuscus (Big brown bat)	Sensory hairs	0.08-1	Wings and tail	Airflow sensing, flight control	Sterbing and Moss, 2014; Sterbing et al., 2016
Aquatic Invertebrates	Decapoda	Astacus leptodactylus (Crayfish)	Conical hairs	0.4-0.8	Flagellum of antennae	Fluid sensing	Tautz et al., 1981
	Decapoda	Astacus leptodactylus (Crayfish)	Feathered hairs	0.9-1.2	Flagellum of antennae	Fluid sensing	Tautz et al., 1981
	Decapoda	Cherax destructor (Crayfish)	Sensory hairs	0.02	Chelae	Fluid sensing	Tautz and Sandeman, 1980
Aquatic Vertebrates	Cetacea	Balaena mysticetus (Bowhead whale)	Sensory hairs	3-46	Lips; caudal blowhole	Fluid sensing	Drake et al., 2015
	Carnivora	Mirounga angustirostris (Northern elephant seal)	Facial vibrissae	7.54-138.14	Face	Foraging	McGovern et al., 2015
	Sirenia	Trichechus manatus latirostris (Florida manatee)	Facial vibrissae and bristles	1-10	Face	Foraging, detection, discrimination, oripulation	Reep et al., 1998
	Sirenia	Trichechus manatus latirostris (Florida manatee)	Postcranial vibrissae	2-9	Body	Detection and localization of hydrodynamic stimuli	Reep et al., 2002

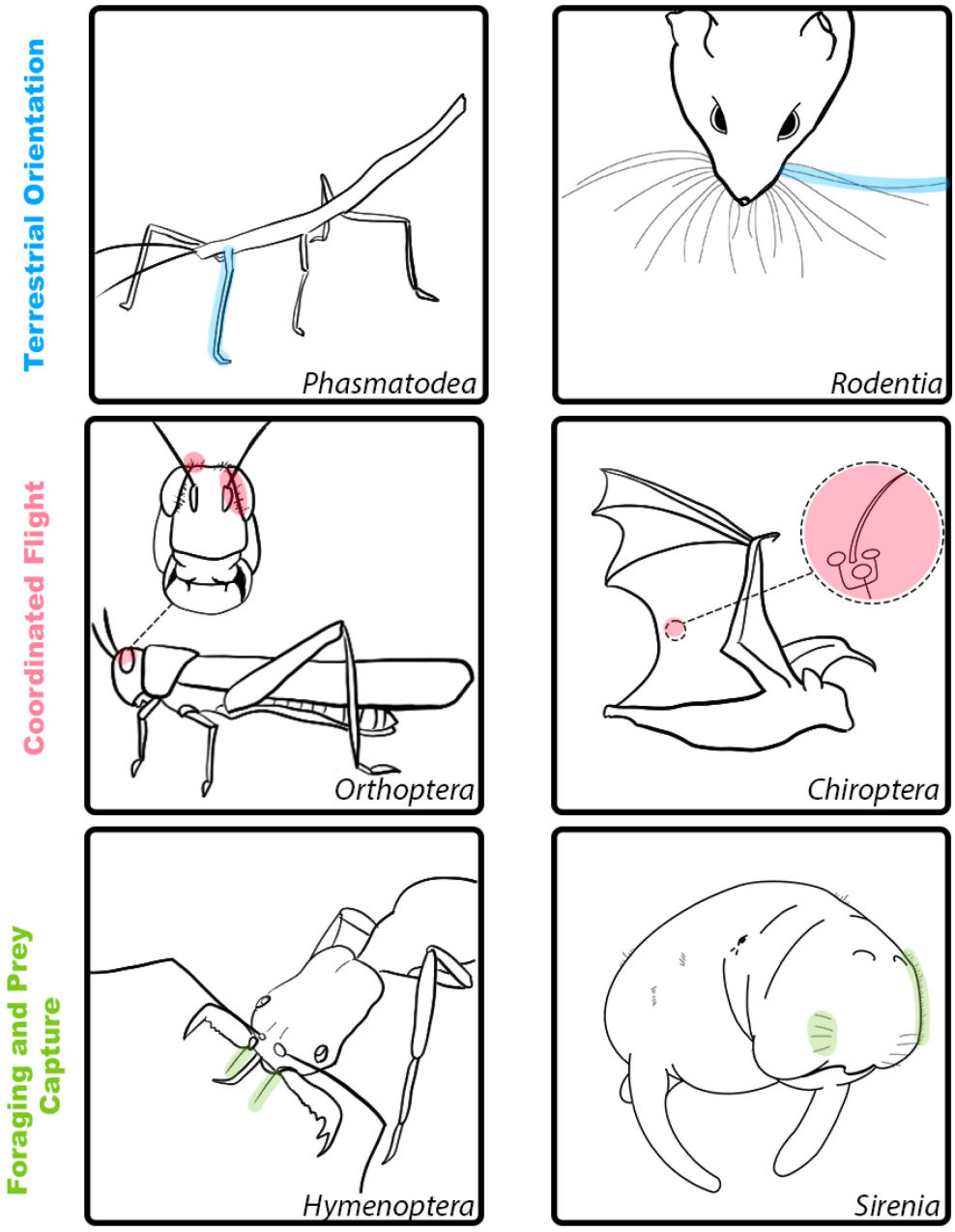

Fig. 2. 1. Illustrations of hair and hair-like structures with shared functional properties for select invertebrate and vertebrate species. *Top row (blue):* Examples of hair and hair-like structures for terrestrial locomotion in Phasmatodea (left) and Rodentia (right). These structures are involved in orientation and self-guided motion to support coordinated movement. *Middle row (red):* Examples of hair and hair-like structures for coordinated flight in Orthoptera (left) and Chiroptera (right). These structures detect airflow and support flight control. *Bottom row (green):* Examples of hair and hair-like structures for foraging and prey capture in Hymenoptera (left) and Sirenia (right). These structures are adapted to allow for species-specific foraging behaviors.

Hair plates are specialized proprioceptors composed of clusters of tactile hairs, with each individual sensillum innervated by a sensory neuron (Pringle, 1938; Tuthill and Wilson, 2016). These sensory neurons can adapt either slowly to maintained displacement or rapidly to transient hair movements (French and Wong 1977; Newland et al., 1995; Tuthill and Wilson 2016). Hair plates are often located in the folds of cuticles where they can be displaced during joint movements, providing proprioceptive information for movement (Pringle, 1938). This sensorimotor feedback is essential for many insects to coordinate walking movements. For instance, ablating hair plates located on the legs of many insects leads to uncoordinated movement and overstepping, where the back legs collide with front legs, suggesting the hair plates act as a sort of limit detector (Wong and Pearson, 1976; Dean and Wendler, 1983; Kuenzi and Burrows, 1995).

In addition to providing proprioceptive feedback to coordinate locomotion, hair-like structures can also aid in generating the necessary friction for movement itself. For many insects, including flies, hairy attachment pads are critical for providing the friction necessary to maintain attachment to a surface (Gorb et al., 2002; Bullock et al., 2008). Flies have pulvilli, adhesive pads covered by setae which have specialized ultrastructures to aid in the attachment and detachment of the fly to surfaces. Some setae on the distal part of the pulvillus secrete adhesive substances close to the contact area and the seta tip, while setae on the basal part of the pulvillus do not have a secretion mechanism (Gorb, 1998). These two ultrastructures on the distal and basal parts of the pulvillus aid in the fly's ability to attach to various surfaces. Navigation of these surfaces and environments provides important advantages to many invertebrates that have evolved to live in difficult environments. Organisms like caterpillars rely on sensory input to

coordinate the movement of their thoracic legs and prolegs to crawl and grip onto surfaces. For many species, rows of directionally sensitive stiff sensory hairs (plana hairs) on the lateral distal edge of the proleg project to the segmental ganglia which can directly control motor neurons for the coordination of leg movement (Weeks and Jacobs, 1987; Griethuijsen and Trimmer, 2014). Insects must often navigate surfaces with either horizontal orientation or little frictional support to adhere to, and specialized hair structures enable many organisms to occupy ecological spaces otherwise inaccessible.

Terrestrial vertebrates (Carnivora). The sensory hairs of cats (*Felis catus*) have been studied with respect to their role in transmitting sensory information from the external environment during locomotion, exploration, and orientation, particularly in low-light conditions (Schmidberger, 1932; Nilsson, 1972; Gottschaldt et al., 1973; Schultz et al., 1976). The facial vibrissae, or whiskers, of cats are large and possess a rich variety of mechanoreceptors (Gottschaldt et al., 1973; Schultz et al., 1976). In a classic behavioral study, Schmidberger (1932) compared blind cats navigating their environment with and without whiskers. They found that cats whose whiskers had been removed bumped into objects in their surroundings more frequently than cats with intact whiskers and their ability to locate small openings declined (Schmidberger, 1932). Furthermore, when walking down a corridor, cats without whiskers walked at slower speed and with impaired dexterity compared to cats with whiskers (Schmidberger, 1932). Interestingly, cats with intact whiskers not only successfully avoided obstacles, but were also able to stop in time to avoid collisions when their whiskers came into contact with an object (Schmidberger, 1932). In addition to facial vibrissae, cats possess carpal tactile hairs located on their forelimbs (Nilsson and Skoglund, 1965; Nilsson, 1969). These hairs are

located above the wrist on the volar side and are similar in structure and show properties resembling those of the facial vibrissae (Fitzgerald, 1940; Nilsson and Skoglund, 1965; Nilsson, 1969). These findings demonstrate that specialized hairs on the face and forelimbs of the cat play a critical role in sensing and transmitting tactile information while moving through the environment.

Flying invertebrates (Orthoptera, Hymenoptera, Blattodea). Generally, tactile hairs detect deflections and open mechanotransduction channels that provide sensory feedback. Tactile hairs can be directionally sensitive, as well as sensitive to changes in velocity, triggering an increase in spiking activity when deflected (Newland, 1990). Some insects have hairs that are specialized to detect airflow and can be deflected by slight changes in air motion, resulting in mechanosensory stimulation to receptor cells under the hair base (Shimozawa et al., 2003). The ability to detect airflow during flight is critical for producing rapid motor responses, particularly under windy conditions.

Many insects, including locusts, are covered with trichoid sensilla which can detect deflections produced through contact with objects in the environment or airflow, as described above. Some trichoid sensilla are located on the head capsule and are termed cephalic trichoid sensilla. Cephalic trichoid sensilla have explicitly been shown to be involved in flight control (Weis-Fogh, 1949; Taylor and Krapp, 2007). When tethered locusts were exposed to jets of air, hairs on the frons and vertex were stimulated and flight movements were induced (Weis-Fogh, 1949). When the air jets were removed, flight behavior stopped. Further, when hairs were covered with cellulose paint, sustained flight could no longer be induced by airflow stimulation (Weis-Fogh, 1949). This showed that stimulation of airflow detectors on the heads of locusts were sufficient to induce and

maintain flight in locusts (Weis-Fogh, 1949). Interestingly, static mechanical stimulation of the same hairs (as opposed to the dynamic deflection from airflow) was not sufficient to induce flight (Boyd and Ewer, 1949; Weis-Fogh and Pringle, 1956; Taylor and Krapp, 2007), indicating that airflow was necessary to elicit a behavioral response. Specialized hairs work in concert with motor systems in the locust to coordinate flight by detecting properties of airflow. Weis-Fogh (1949) first observed that locusts oriented towards the direction of airflow stimuli, suggesting that cephalic trichoid sensilla have directional tuning. When locusts detect a change in the angle of wind from deflections of their cephalic trichoid sensilla, this evokes a rudder like movement that stabilizes and adapts relative to the magnitude of the change in the wind angle (Camhi, 1970a). Locusts also orient their abdomen relative to changes in wind velocity as a potential response to avoid stall (Camhi, 1970b). In addition to locusts, trichoid sensilla on the compound eyes of honeybees have been implicated in correcting for wind drift (Neese, 1965; reviewed in Taylor and Krapp, 2007). Trichoid sensilla are important for detecting airflow patterns and changes to elicit rapid responses that maintain and coordinate flight behavior.

Some orthopterans, like crickets, have a cercal sensory structure which functions as both an extension of the auditory system and as a sensory mechanism capable of detecting and localizing changes in airflow (Boyan et al., 1986; Chiba et al., 1992; Landolfa and Jacobs, 1995; Jacobs et al., 2008). This structure consists of a pair of appendages on the rear abdomen of the orthopteran. These appendages are covered with 1000-2000 filiform receptor hairs whose movement innervates mechanosensory afferent neurons and projection interneurons (Chiba et al., 1992; Jacobs et al., 2008). The cercal system in orthopterans is highly directional (Landolfa and Jacobs, 1995), with a

hinge-like cuticle structure at the base of the hair (Gnatzy and Tautz, 1980). Cerci are key for detecting changes in an environment to allow for rapid behavioral reactions, as seen in escape responses in locusts (Boyan et al., 1986). The cercal system is also implicated in maintaining control during flight. For example, in cockroaches, ablation of one cerci causes asymmetrical flight (Fraser, 1977), suggesting bilateral cerci provide sensory feedback necessary to coordinate normal flight behavior.

Flying vertebrates (Chiroptera). Unlike other mammals in the animal kingdom (rat: Leem, Willis, and Chung, 1993; primate: Manfredi et al. 2012; human: Johansson and Vallbo, 1983), bats lack glabrous (i.e., hairless) skin (Sterbing-D'Angelo et al. 2011). In addition to the fur or pelage hair found covering most of the bat's body, they also have hairs on their wings, tail, rump, and feet (Kang and Reep, 2013). Kang and Reep (2013) examined postcranial hairs on 66 species of bats and hypothesized that these were sensory hairs based on their structure and placement. Furthermore, they suggested that these sensory hairs played different roles depending on their placement, as well as life history traits of each species, such as roost type, size of roosting group, and diet. They found that the shape, length, and thickness of postcranial hairs differed from those of pelage hairs, and they posited that bodily placement of sensory hairs is related to function (Kang and Reep, 2013). For instance, hairs on the tail were thought to contribute to foraging abilities and landing, whereas toe hairs were suspected to function mainly as a tool for grooming. The functions of these different types of postcranial hairs are not fully understood. It's noteworthy that hairs on the wings of bats were identified over one hundred years ago (Maxim, 1912), and many decades later have been implicated in airflow sensing for flight control (Zook and Fowler 1986; Sterbing-D'Angelo et al. 2011).

The membrane of bat wings is sparsely lined with microscopic hairs, which are associated with a variety of tactile receptors, including lanceolate receptors and Merkel cell neurite complexes (Marshall et al., 2015; Sterbing-D'Angelo et al., 2017). Sterbing-D'Angelo et al. (2011) found that two different species of bats, *Eptesicus fuscus* (big brown bat) and *Carollia perspicillata* (short-tailed fruit bat), altered their flight behavior after depilation (i.e., hair removal) of different regions on the wing membrane while performing an obstacle avoidance task. They found that *E. fuscus* and *C.perspicillata* made wider turns around obstacles and increased their flight speed after depilation, respectively (Sterbing-D'Angelo et al., 2011). These findings suggest that wing hairs act as airflow sensors that prevent stall (Sterbing-D'Angelo et al., 2011; Sterbing-D'Angelo et al., 2017).

Furthermore, extracellular recordings in bat primary somatosensory cortex (S1) show neural responses to light touch and air puff stimulation of the wing; S1 responses to air puffs showed directional selectivity, with a preference for reversed airflow (Sterbing-D'Angelo et al.; 2011). Marshall et al. (2015) found that both air puff and tactile stimulation activated overlapping regions in S1 of the big brown bat. The firing rate of S1 neurons in response to air puff stimulation diminished after wing hair depilation but showed no decline in response magnitude to light touch stimulation in the same receptive field (Sterbing-D'Angelo et al., 2011), supporting the hypothesis that hairs on the wings of bats function as airflow sensors.

Shared functional properties: Coordination of movement

Across the animal kingdom, organisms rely on rapid integration of mechanosensory signals to guide movement and navigation through natural environments. For small organisms like insects, the detection of self-movement aids in the coordination of their limb movements. Proprioceptive feedback from hair plates near the legs proves essential to locomotion in many species of insects. The facial vibrissae and tactile hairs on the forelimbs of cats share a similar function, aiding in effective navigation. Despite morphological and physiological differences across taxa, feedback from sensory hairs and hair-like structures enables common functions for locomotion and navigation. Ablation of sensory hairs in stick insects and cats lead to uncoordinated movements, demonstrating that despite structural differences in the size and placement of these hairs, they contribute to the same function of maintaining successful coordinated motion.

Hairs and hair-like structures also ensure that organisms can navigate environments that fit their ecological and behavioral needs. Small insects like flies and caterpillars rely on strong adhesive gripping to navigate difficult terrain and adhere to vertical surfaces, which is enabled through specialized hair pads. Similarly, cats navigate small openings they detect using sensory hairs to monitor the external environment. In diverse organisms, traversing natural environments is enabled by the presence of specialized sensory hairs and hair-like structures.

From flying insects, like locusts to the only flying mammals, bats, sensory hairs also play an important role in effectively detecting airflow to rapidly adapt to environmental changes (e.g., wind) and enable coordinated flight. The specific placement and structure of hairs and hair-like structures allows for directional selectivity and plays a key role in

their functions. For example, locusts have sensory hairs on their head capsules that provide information about wind speed and direction that can evoke behavioral responses to maintain flight while bats are equipped with microscopic wing hairs that serve as airflow sensors that signal unsteady conditions and prevent stall. These examples serve to illustrate that both invertebrate and vertebrate animals rely on mechanosensory hairs to sense airflow for flight control.

Detection and orientation

Specialized sensory hairs enable efficient detection and orientation to stimuli in the environment, from obstacles to potential predators or prey. Animals that possess hair and hair-like structures can detect small mechanical disturbances in their surroundings, allowing for adaptive and rapid behavioral responses.

Aquatic invertebrates (Decapoda). Crustaceans are arthropods that have developed specialized sensory hairs to detect changes in water flow in their environments. Water disturbances produced by other animals in a fluid environment cause flow patterns that can be detected by mechanoreceptors to enable rapid behavioral responses. These hydrodynamic cues are vital for detecting the presence of a predator, mate, or even a potential meal. While mechanosensory hairs operating in air and water serve similar functions, the comparatively high density and small kinematic viscosity of water (Casas et al., 2012) have placed evolutionary pressures on aquatic animals.

Some crustaceans, such as crayfish, are corpuscular and use non-visual cues to navigate and orient effectively. Many species rely on tactile input from the antennae to detect changes in the environment as they search for prey. Antennae can consist of short

proximal segments that support multi-segmented flagellum (Sanderman, 1985). Two types of sensory hairs have been described in the crayfish species, *Astacus leptodactylus*, smooth conical hairs and feathered hairs which are evenly distributed along the flagellum. Both hairs are sensitive to low amplitude vibrations, with smooth hairs being stimulated directly by motion in the water, whereas feathered hairs are driven by the bending of the flagellum caused by the water movement (Tautz et al., 1981). These two types of hairs on the flagellum may aid in the localization of moving objects in the crayfish's environment. This possibility is supported by findings that show crayfish in T-mazes with one denervated antenna turn towards their unaltered side, which suggests that bilateral comparisons of antenna signals are used to localize the source of water motion (McMahon et al., 2005). In addition to specialized appendages equipped with sensory hairs, crayfishes have mechanoreceptive hairs distributed over most of their bodies that respond to hydrodynamic disturbances (Tazaki and Ohnishi, 1974). In *Cherax destructor*, sensory hairs grouped together in pits found on the chelae are most sensitive to water vibration frequencies between 150-300 Hz (Tautz and Sandeman, 1980). Highly sensitive detectors can identify changes in the crayfish's environment quickly, such as approaching predators from further distances. This can enable a faster behavioral response to change course or avoid potential predators, ultimately being a key sensory mechanism for survival.

Terrestrial vertebrates (Rodentia). Mice (*Mus musculus*) and rats (*Rattus norvegicus*) have served as conventional animal models for studying the role of vibrissae in orienting and foraging under low light conditions (Vincent, 1912). Vibrissae located on the mystacial pad of the face are arranged in a grid-like pattern, consisting of rows and

columns, where each individual whisker can be identified by a unique set of coordinates (Brecht et al., 1997; Diamond et al., 2008; Yu et al., 2016). Rodent mystacial vibrissae are involved in both passive and active sensing (Yu et al., 2016). Rodents interact with their environment when their whiskers contact an object or are displaced. Rodents also employ the use of their whiskers to detect and identify objects and surfaces of different shapes and textures by actively and rhythmically moving their whiskers (Diamond et al., 2008). This behavior is referred to as 'whisking' (Welker, 1964; Carvell and Simons, 1990; Yu et al., 2016), and is used during a wide range of behaviors, including navigation and foraging.

While whiskers provide tactile information, allowing rodents to successfully interact with objects and navigate in their environment, recent studies have demonstrated that vibrissae also signal displacement caused by airflow. Yu et al. (2016) investigated the role of rat facial vibrissae in airflow sensing and characterized the mechanical responses to airflow. Individual whiskers were plucked and secured to an experimental setup to measure whisker movement. Two high-speed video cameras recorded movement of the whisker driven by naturalistic airflow stimuli. They found that whiskers bend in the direction of the airflow stimulus and that the bending magnitude is positively correlated with airflow speed (Yu et al., 2016). More recent work has further examined vibrissal airflow sensing and found that the direction and magnitude of the whisker's deflection changes as a function of airflow speed (Yu et al., 2019). In addition, they performed recordings in primary sensory trigeminal ganglion neurons to vibrissal stimulation and report that the firing rate of these neurons increased with airspeed (Yu et al., 2019), suggesting that rodent facial vibrissae can mediate tactile and anemotaxic behavior.

Other rodent species, such as hamsters, gerbils, chinchillas, and naked mole-rats also possess sensory hairs that function as mechanosensors for tactile-guided orienting and foraging (Wineski, 1982; Crish et al., 2003; Mitchinson et al., 2011; Crish et al., 2016). While a majority of rodent mechanosensory research has focused on cranial or facial vibrissae, some rodent species have postcranial vibrissae, such as the naked mole-rat (*Heterocephalus glaber*) (Crish et al., 2003; Crish et al., 2016). Naked mole-rats are subterranean rodents with poor visual and auditory acuity (Crish et al., 2016). To navigate elaborate underground burrows, forage for food, and care for their young, naked mole-rats must rely on mechanosensors to guide their behavior. Like other underground mammals, the naked mole-rat has a highly specialized somatosensory system designed to aid in navigation in low light conditions. In addition to an array of facial vibrissae, naked mole-rats are equipped with a unique array of approximately 40 postcranial vibrissae along the body (Crish et al., 2003; Crish et al., 2016). These body vibrissae are sparsely and systematically distributed in a grid-like pattern from the torso, all the way to the tail. Previous work has shown that the body vibrissae play a role in tactile guided sensing. Crish et al. (2003) found that the deflection of a single body vibrissa of an unrestrained naked mole-rat elicited orienting behaviors. Specifically, stimulation of the body vibrissa caused the animal to orient its snout in the direction of the stimulation, revealing that the body vibrissae enable the animal to accurately localize and orient to stimuli in the environment. As part of this study, two additional experiments were conducted to examine responses to stimulation of other tactile receptors in the skin and facial vibrissae. In the first experiment, the skin between body vibrissae was stimulated. They observed that skin stimulation was less reliable in eliciting orienting responses and did not always evoke the

animal's orientation towards the site of stimulation. In the second experiment they found that when the facial vibrissae were deflected, the animal exhibited a snapping movement, which was not present during body vibrissae stimulation. Taken together, these findings demonstrate that body vibrissae of the naked mole-rat, much like facial vibrissae in other animals, serve as key mechanosensors and support the role of these sensory hairs in tactile guided detection and orientation.

Aquatic vertebrates (Cetacea, Sirenia, Carnivora). Much like their terrestrial counterparts, aquatic mammals possess sensory hairs on their face and body. The distribution of these hairs on the body and face varies across species, depending on their primary function. For example, Bowhead whales (*Balaena mysticetus*) have patches of hairs on their lips and caudal to their blowholes, which are thought to act as a passive sensory system to detect flow of water and air (Drake et al., 2015). Another example is the harbor seal (*Phoca vitulina*) that uses facial vibrissae to detect water movements created by prey (Dehnhardt et al., 1998; 2001).

Florida manatees (*Trichechus manatus latirostris*) are obligate aquatic mammals that inhabit warm, shallow waters with low visibility. Manatees have a poorly developed visual system and lack the ability to echolocate (Mass et al., 2012; Bauer et al., 2003). To successfully navigate their environments, they rely largely on sensory input from an array of facial hairs and bristles, as well as a system of postcranial hairs distributed over their bodies (Reep et al., 2001, 2002; Gaspard et al., 2013, 2017). Through anatomical studies, these sensory hairs have been shown to share attributes with vibrissae found in other terrestrial species, which include prominent blood sinus complex, a capsule of dense connective tissue, and substantial innervation (Reep et al., 2001; 2002). Research

findings also suggest that the facial vibrissae of manatees are used in active touch, such as tactile exploration and feeding (Marshall et al., 1998), whereas sensory hairs along the body of manatees have been hypothesized to play a role in passive detection of the environment via perturbations of the water (Sarko et al., 2007; Gaspard et al., 2017).

Recent behavioral studies of manatees have further investigated the hypothesis that postcranial hairs are involved in detection of hydrodynamic stimuli. Gaspard et al. (2017) conducted a series of experiments in which manatees were trained on a go/no-go task, where the goal was to correctly discriminate the directional flow of hydrodynamic stimuli. Manatees were trained to indicate the direction of a stimulus by withdrawing from a stationing bar and touching a response target with their muzzle on the side where a stimulus was presented. These experiments were conducted with postcranial hairs either intact or trimmed. Researchers observed that the manatee's ability to detect and discriminate hydrodynamic stimuli was significantly attenuated after postcranial hairs were trimmed (Gaspard et al., 2017). These findings implicate this array of sensory hairs on the body of the manatee in the detection and localization of hydrodynamic stimuli, suggesting that these hairs can aid in exploration and navigation.

Shared functional properties: Detection and orientation

Specialized sensory hairs have also evolved to suit environmental constraints. Aquatic organisms often have shorter hairs with larger diameters to better suit the kinetics of water compared to hairs primarily in air. In manatees, the postcranial hairs are shorter and wider compared to the facial vibrissae (Gaspard et al., 2017). All of the organisms discussed in this section possess highly sensitive hairs or hair-like structures that enable

them to explore and navigate novel environments, while avoiding potential threats. For example, crayfish are equipped with two different types of hairs that provide separate mechanosensory signals to guide behavior. Similarly, the naked mole-rat possessed both facial and postcranial vibrissae that enables them to accurately detect their surroundings and orient in low light conditions. Despite differences in the structure and location of hairs in species as diverse as crustacea, rodents and manatees, the function of mechanosensory hairs appears largely conserved across organisms.

Prey capture and feeding

Many organisms have evolved species-specific adaptations for searching, capturing, and consuming their prey. Hair and hair-like structures provide sensory feedback during foraging, as well as during the manipulation of food or prey.

Terrestrial invertebrates (Araneae, Hymenoptera). With the vast diversity of invertebrates, specializations of hair and hair-like structures can provide key sensory and mechanical feedback that enables a wide variety of behaviors, including foraging, prey capture and feeding. Many species of spiders that do not establish webs and instead roam to hunt their prey have particularly numerous hair sensilla that can support highly sensitive detection. For example, the nocturnal wandering spider, *Cupiennius salei,* waits for prey and then rapidly strikes to capture its target. Using sensory cues from substrate vibrations caused by creatures walking on the ground or air movements like those produced by flight, *C. salei* can detect their prey and then rapidly strike within a few hundred milliseconds (Seyfarth, 1980; Barth, 1998; Barth, 2002). Specialized hair-like structures called trichobothria (filiform hairs, similar to those described in the section

Flying invertebrates), support prey capture behavior in *C. salei*. The hairs are approximately 0.1 to 1.4 mm in length, with frequency responses ranging between about 40 Hz to 600 Hz, exhibiting among the highest sensitivities of a biological sensor currently known (Barth, 2000; Barth, 2002; Barth, 2004). Interneurons receive sensory input from trichobothria on the walking legs of *C. salei*, with individual interneurons showing different response characteristics, suggesting parallel processing of different parameters of the sensory signal across populations of neurons (Friedel and Barth, 1997). The phasic response characteristics of the receptor cells of the trichobothria and interneurons are particularly suited for detecting behaviorally relevant pulse-like air flow, such as those caused by small prey flying by (Barth, 1995; Friedel and Barth, 1997; Barth and Höller, 1999). Specifically, pulse-like airflow can be distinguished from background noise and low velocity airflow with relatively small fluctuations (Barth et al., 1995; Friedel and Barth, 1997), making the sensitivities and response patterns of trichobothria specialized for detecting and locating prey.

The sensitivity and rapid sensory feedback carried by specialized sensory hairs supports diverse behaviors in many terrestrial insects. The trap jaw ant (genus *Odontomachus*), for instance, has mandibles that can strike in less than 0.5 ms, with the entire reflex from sensory stimulation to strike taking between 3-10 ms (Gronenberg et al., 1993; Just and Gronenberg, 1999). In one species of trap jaw ants, *Odontomachus bauri,* predatory strikes close at speeds between 35 and 64 m/s, making it one of the fastest ballistic predatory appendages in the animal kingdom (Patek et al., 2006). Two very long bristles (600-1200 μm) located on each mandible act as mechanosensory triggers that release the trap jaw mechanism, leading to the rapid mandible strike

(Gronenberg, 1994). These long bristles have large afferent axons that rapidly provide sensory feedback indicating an object is within striking range and coordinate a synchronized closure of the mandibles (Just and Gronenberg, 1998). Interestingly, this hair trigger requires sufficient behavioral context to snap the mandibles closed. The mandible strike response is inhibited in the presence of conspecifics (Jaffe and Marcuse, 1983; Gronenberg and Tautz, 1994), indicating this behavior is not simply triggered by the stimulation of these hairs alone and instead requires proper sensory and behavioral conditions to elicit this powerful strike.

In addition to predation, the trap jaw ant's remarkable mandibles can also be used for propulsion. These ants can orient their mandibles against substrates to launch themselves into the air, a mechanism that improves likelihood of survival when escaping from predators (Larabee and Suarez, 2015; Mohan and Spagna, 2015). Escape jumps can reach vertical heights of 6-8 cm, and defensive jumps reach horizontal distances of 5-40 cm (Patek et al., 2006). Various sizes of hairs and hair-like structures provide necessary sensory information to coordinate the rapid movements of these mandibles. Specifically, in addition to the long bristles (i.e., trigger hairs), the mandibles also possess very small hair-like sensilla and a row of smaller hairs that likely provide proprioceptive information about the positioning of the mandibles (Gronenberg, 1994).

Aquatic vertebrates (Carnivora, Sirenia). The sensory hairs or vibrissae of marine mammals serve as mechanosensors and show species-specific specializations for navigation and foraging. These specializations depend on a variety of factors, including: the animal's environment, diet, and morphology. For example, the northern elephant seal (*Mirounga angustirostris*) forages in deep waters, both during the day and

at night and feeds primarily on vertically migrating prey, such as: plankton, fish, and squid (McGovern et al., 2015). While the northern elephant seal has high visual sensitivity, it is limited by the time of day in which it forages. In low light conditions, the northern elephant seal must rely on multimodal sensing and use both vision and mechanosensation via its facial vibrissae to navigate and forage for prey (McGovern et al., 2015).

Another aquatic mammal that utilizes sensory hairs to forage and feed is the Pacific walrus (*Odobenus rosmarus divergens*) (Fay, 1982; Kastelein, Stevens, and Mosterd, 1990; reviewed in Gaspard et al., 2017). The Pacific walrus forages at night in deep water with low visibility and preys on benthic organisms such as clams, oysters, and mussels (Fay, 1982; Kastelein, Stevens, and Mosterd, 1990). Due to the position of its eyes and the width of its snout, the Pacific walrus has reduced visibility in front of its face (Kastelein, Stevens, and Mosterd, 1990) and therefore takes advantage of sensory hairs located on the face for tactile information from the surroundings. The Pacific walrus has approximately 400 to 700 vibrissae organized into 13 to 18 rows on their mystacial pads (Fay, 1982). These vibrissae are extremely mobile and have been observed to be active and move rapidly during the exploration of objects or during feeding (Fay, 1982). Early research hypothesized that these vibrissae in Pacific walruses serve a sensorimotor function and were responsible for providing crucial tactual information for foraging and feeding. One study demonstrated that even when blindfolded, a walrus could discriminate objects of different shapes and sizes using the mystacial vibrissae (Kastelein, Stevens, and Mosterd, 1990). Additionally, they found that vibrissae on different parts of the mystacium served different roles, where the lateral vibrissae functioned primarily for

detection and the more central vibrissae for discrimination (Kastelein, Stevens, and Mosterd, 1990).

In addition to tactile sensing, vibrissae have also been shown to be involved in the handling of objects and food. Sirenians are the only mammals known to use mystacial vibrissae for tactile exploration and handling of objects. As noted above, the Florida manatee utilizes facial vibrissae, also referred to as perioral bristles, for tactile exploration and feeding, as well as oripulation, or the handling of objects and food with facial musculature (Marshall et al., 1998; Reep et al., 2001; Bauer et al., 2018). This behavior was first described in 1875 by Chapman and has since been studied in order to define the range of control of the facial vibrissae. Marshall et al. (1998) studied how Florida manatees used their perioral bristles to interact with and oripulate objects and food. In this study, manatees were given a variety of vegetation and inanimate objects during feeding trials. The researchers observed that manatees primarily relied on tactile information from their bristles to guide their behavior. Specifically, they reported that manatees tended to close their eyes while foraging and feeding and thought it may be a protective measure to avoid damaging their eyes when foraging in vegetation (Marshall et al., 1998). Moreover, they found that the use of the bristles varied depending on whether the presented vegetation was submerged or floating and could independently reverse the direction of specific bristles when presented with a food item or object that they disliked. The vibrissal-muscular complex enables coordinated and rhythmic movements of the lips, bristles, and jaw, allowing for dexterous exploration and manipulation of objects in the environment. These findings support the role of perioral bristles in both tactile discrimination and prehensile control for foraging and feeding.

Shared functional properties: Prey capture and feeding

Species-specific adaptations of sensory hairs can enable highly specialized natural behaviors. In some of the examples we have discussed in this section, the function of mechanosensory hairs is to enable highly specialized foraging and feeding strategies. The trichobothria of *Cupiennius salei* is an interesting biological model for detecting behaviorally relevant sensory inputs because they have the highest sensitivities of any biological sensor currently known (Barth, 2000; Barth, 2002; Barth, 2004). Trap-jaw ants like *Odontomachus bauri* rely on trigger hairs to execute one of the fastest ballistic predatory motions in the animal kingdom. Both examples of insects presented here rely on rapid response, with *O. bauri* receiving sensory input from specialized trigger hairs that directly innervates muscles in the jaw and the trichobothria of *C. salei* detecting pulse-like air flow produce by small flying prey. Compared to the highly sensitive hairs and hair-like structures of invertebrates, sensory hairs of vertebrates can provide similar mechanosensory signals during foraging and feeding. In aquatic mammals, such as walruses and manatees, facial vibrissae or bristles are engaged during foraging behaviors to provide sensory feedback, enabling the animal to detect and discriminate prey from their surroundings.

Engineering applications of biologically inspired hair sensing

Mechanosensors are essential for the survival of all living animals, including humans. Many technological advances have been influenced by scientific knowledge of biological mechanosensors throughout the animal kingdom, from invertebrates to mammals, including the development and implementation of biomimetic hair and hair-like

sensors. As discussed in this review, animals utilize sensory hairs to navigate, forage, and interact with their environment. Many bio-inspired robots have been developed based on the unique functional properties of sensory hairs in these behaviors. In this section, we present some examples in which natural hair and hair-like sensors have inspired technology thus far and propose new applications.

In 2007, Pearson et al. designed the Whiskerbot, a biologically inspired robot that focused on the implementation of the rodent whisker sensory system for exploration. The Whiskerbot is made of a “head” sensory unit with two rows of three whiskers on each side, and a two-wheeled “body” (Pearson et al., 2007). To mimic the whisking behavior of rodents, each whisker shaft can sweep forward and backward, and the angle of each shaft can be measured with respect to the head unit using optical shaft encoders. The Whiskerbot is equipped with three types of actions: dead reckoning, exploring the environment, and orienting to the stimulus. While the action of dead reckoning is based on conventional path integration and exploring the environment is hard-wired into the robot to mimic the exploratory strategy of rodents, the orienting to the stimulus is achieved by contacts made on the whisker shaft.

Previous work on the rodent whisker sensory system has demonstrated that animals can extract spatial information, as well as textural characteristics from objects in the environment by whisking (Welker, 1964). Additionally, rodents do not require a well-illuminated environment to function; rather they can operate under small, low-light conditions by using their whiskers to sense their surroundings. These functions of the rodent whisker system have been implemented in sensory robotics (Pearson et al., 2007; Takei et al., 2014; reviewed in Amoli et al., 2019).

Biomimetic sensors inspired by other characteristics and functional properties of rodent whiskers have been developed. In 2014, Takei et al. developed electronic whiskers, also referred to as e-whiskers. These whiskers were designed to detect changes in pressure and strain and were constructed from carbon nanotube (CNT) to provide flexibility and silver nanoparticles (AgNPs) to enhance conductivity. Testing revealed that an array of e-whisker sensors successfully mapped air flow in two and three dimensions (Takei et al., 2014; reviewed in Amoli et al., 2019).

Hair-like sensors found in arthropods have served as inspiration for technology, because of their high sensitivity, small size, and role in detecting changes in fluid (i.e., air and water) dynamics. For example, Ko et al. (2015) designed an acceleration sensor inspired by insect filiform hairs. They attached a rigid metal rod to a piezoresistive membrane that detects changes in electrical resistance when applied with physical force, acting as a strain sensor. Numerous groups have also developed highly sensitive artificial hair-like sensors capable of detecting changes in flow velocity, direction, and strength (Maschmann et al., 2014; Ko et al., 2015; reviewed in Han et al., 2018).

Future applications. Now we turn to bioinspired technology that does not yet utilize artificial hair-like sensors but could benefit from their application. Developed in 1975, robotic grippers are tasked with securely grasping objects, a common operation for robotic manipulators. A gripper can be defined as a tool that is mounted at the end of a piece of equipment to grasp, carry, and place objects. While grasping objects may appear to be executed with ease by many animals, including humans, this operation has proven difficult for robots. In addition to grasping an object, robotic grippers must also have the ability to sense the characteristics of the object (i.e., shape, size, texture) and interact

with the environment in order to adapt their grasp to prevent crushing an object and to avoid dropping it (Brown et al., 2010; Syed et al., 2019; reviewed in Zhang et al., 2020). Various sensors, including tactile, visual, and hearing sensors have been integrated into robotic grippers to enhance sensitivity and stability. We propose that robotic grippers could benefit from an artificial hair-like sensor, a variation on tactile sensing, to enhance performance. Specifically, the application of hair-like sensors to robotic grippers could allow for earlier detection of an object's position, as well as changes to the surrounding environment (i.e., fluid dynamics and vibrations). Moreover, hair-like sensors could also contribute as an additional layer for monitoring the strength and effectiveness of the grasp.

As discussed in this review, there are many animal behaviors that rely heavily on sensory feedback from hairs on their face and body, and a wider range of biologically inspired technology could implement this knowledge in robotic systems. For example, Colorado et al. (2012) designed a micro aerial vehicle with morphing wings inspired by bat anatomy and flight. The robot was constructed from shape memory alloys, or SMAs, which act as muscle-like actuators, providing the motions of a bat's wingbeat, as well as mimicking the flexible nature of the bat's bone structure. The goal of this study was to develop the first autonomously flying bat-like robot. While many features of bat anatomy and physiology were applied in the development of this flying robot, Colorado et al. omitted a key sensor. Bats have microscopic sensory hairs on their wings that have been shown to sense changes in airflow and have been implicated in flight control (Sterbing-D'Angelo et al. 2011). The implementation of artificial hair-like sensors to their flying bat-like robot could enhance aerodynamic performance. Another example of robotic systems

that could benefit from hair-like sensors are small-scale drones. Many advancements have been made in developing the technology for small-scale drones that allow them to be used for a range of applications, from photography to environmental monitoring and mapping (Di Luca et al., 2020). One limitation of small-scale drones is poor flight control in turbulent conditions (Di Luca et al., 2020). Wind gusts and turbulence can lead to stall, which both drones and flying animals alike experience. As discussed above, bats have a specialized way to detect changes in airflow through specialized hairs on their wings. The incorporation of bio-inspired hair-like sensors could allow for increased sensitivity for airflow detection, and in turn result in enhanced flight control in small-scale drones.

While there have been significant strides in the advancement of bioinspired hair sensor technology, the field still must overcome many challenges and limitations. One limitation is the materials and fabrication techniques used to construct the artificial sensors. Natural hairs and hair-like structures are small, even microscopic in some animals. In addition to their size, these structures are highly sensitive, flexible, and strong. Implementation of all these properties into a single sensor or array of sensors poses a challenge for engineers. Depending on the material, it may not be feasible to construct a sensor that has the exact same size and sensitivity as the biological one. For instance, there is often a hysteresis effect, or lag, when using polymers to design hair-like sensors (Han et al., 2018). Another limitation of artificial hair-like sensors is their durability. Animals encounter dramatic changes to their environmental conditions, such as extreme winds and fluctuations in temperature and weather conditions, and the sensory hairs and hair-like structures they possess must also endure these changes. Designing an artificial sensor that is both sensitive and durable under a wide range of conditions has proven

difficult, with many of the artificial sensors becoming damaged during testing. Lastly, the biological mechanoreceptors tend to outperform the artificial sensors. While many inherent specializations of biological systems have yet to be uncovered, new discoveries of biological sensory systems continue to motivate and innovate bio-inspired technologies.

Conclusions

Our review aims to highlight the diversity of sensory hair and hair-like structures in the animal kingdom and their functions in supporting a rich repertoire of behaviors, which can inform and inspire advances in sensory technology. By better understanding natural mechanosensory hairs and the feedback they provide to actuators, we can develop sensors with enhanced sensitivity and multifunctionality. The biological and artificial systems can also reciprocally advance science and engineering, whereby detailed understanding of biological systems can inform technology, and artificial systems can reveal gaps in knowledge of biological systems. Together, these two fields can synergistically inform future advances in sensory-guided actions.

Chapter 3

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Sensory hairs for flight control and prey capture in the big brown bat, *Eptesicus fuscus*

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Preamble: I investigated the role of ventral and dorsal sensory hairs in flight control and prey capture using a goal-directed task. Five echolocating bats (Eptesicus fuscus) were trained to capture a tethered insect in flight. I analyzed each bat's prey capture performance, as well as flight kinematics (flight speed, wingbeat frequency, and turn rate) and adaptive echolocation behaviors (sonar call interval and duration, and the terminal buzz duration), before and after depilation of sensory hairs.

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Abstract

Echolocating bats are equipped with sensory hairs on their wings and tail membranes. Studies have shown that bats performing an obstacle avoidance task adapt

their flight behavior when dorsal wing hairs are removed. Additionally, electrophysiological studies have shown that wing hairs are involved in airflow sensing, but little is known about the contribution of sensory hairs on the ventral surfaces of the wing and tail membranes to their flight control and other natural behaviors, such as prey handling. Here, we investigated the role of ventral and dorsal sensory hairs in flight control and prey capture using a goal-directed task. Five echolocating bats (*Eptesicus fuscus*) were trained to capture a tethered insect in flight. We analyzed each bat's prey capture performance, as well as flight kinematics (flight speed, wingbeat frequency, and turn rate) and adaptive echolocation behaviors (sonar call interval and duration, and the terminal buzz duration), before and after depilation of sensory hairs. We found that depilation of sensory hairs resulted in significant changes to insect capture performance, flight kinematics, and adaptive echolocation behavior. Additional analyses revealed that these behaviors differ when bats are depilated on a single surface, as compared to symmetric depilation (i.e., both ventral and dorsal sides). These findings advance our understanding of sensorimotor feedback for flight control and insect capture behavior in bats.

Introduction

As animals maneuver and navigate through their natural environments, they must integrate external sensory stimuli from their surroundings with signals from self-generated motion in order to quickly and effectively adapt motor commands to steer around obstacles and intercept targets. Past research on sensorimotor integration has focused largely on species that rely primarily on vision to guide their actions (rodents: Terrazas et al., 2005; primates: Killian et al., 2012; humans: Zhao and Warren, 2015). However, the

animal kingdom is rich with animals that utilize a wide range of sensory modalities to guide their behaviors: barn owl (hearing and vision, Wagner et al., 2013), zebrafish (mechanoreception, Stewart et al., 2013), pigs (olfaction, Brunjes, et al., 2016, star nosed mole (mechanoreception, Catania and Kaas, 1995), and knife fish (electroreception, Heiligenberg, 1973). The echolocating bat relies primarily on active hearing to navigate through the environment. It also receives sensory information through other modalities, including mechanosensory signals from microscopic hairs on the tail and wings, making the echolocating bat an excellent model for studying multimodal sensing and sensorimotor integration. Sensory hairs on the bat's dorsal wings have been implicated in airflow sensing (Sterbing-D'Angelo et al., 2011; Sterbing-D'Angelo et al., 2017; Marshall et al., 2015), but it remains unknown whether sensory hairs on the ventral surface of the wing contribute to flight control and other behaviors, such as prey handling. We investigated effects of sensory hair removal from the ventral and dorsal wing and tail membranes on flight kinematics, prey capture and adaptive echolocation behaviors.

Echolocating bats emit sonar calls, listen to the returning echoes from objects, and compute the distance and direction to targets from the features of echoes (Simmons, 1973), all while rapidly flying through the environment. The echolocation behavior of *Eptesicus fuscus*, an aerial hawking insectivore, is comprised of well-characterized phases of foraging: search, approach, and capture of prey. When *E. fuscus* searches for an insect, it produces sonar calls that are long in duration (15-20 ms) at a repetition rate of 5-10 Hz (Surlykke and Moss, 2000; Moss and Surlykke, 2010; Moss et al., 2011). Once the bat detects and selects a target, it adapts its echolocation behavior and enters the approach phase. The approach phase is characterized by shorter sonar calls (2-5 ms) at

a repetition rate of 20-80 Hz (Surlykke and Moss, 2000; Moss and Surlykke, 2010; Moss et al., 2011). As the bat prepares to capture the insect, it reduces the duration of sonar pulses (0.5-1 ms) and increases the repetition rate to about 150 Hz, resulting in what is commonly referred to as the terminal buzz phase (Surlykke and Moss, 2000; Moss and Surlykke, 2010; Moss et al., 2011).

While echolocation behavior has been well characterized in many bat species, these animals have access to somatosensory information that may contribute to the planning and execution of prey capture. The bat's hand-wing consists of five digits extended across a thin, flexible membrane. Unlike other mammals that contain glabrous skin (rat: Leem, Willis, and Chung, 1993; primate: Manfredi et al. 2012; human: Johansson and Vallbo, 1983), the membrane of the bat wing, as well as the tail, are sparsely lined with microscopic hairs. These hairs are associated with a variety of tactile receptors, including lanceolate endings and Merkel cell neurite complexes (Sterbing-D'Angelo et al., 2017), and have been implicated in airflow sensing (Sterbing-D'Angelo et al., 2011; Sterbing-D'Angelo et al., 2017; Marshall et al., 2015).

Evidence from a behavioral study in two species of bats, *Eptesicus fuscus* and *Carollia perspicillata*, suggests that microscopic hairs embedded in the dorsal wing membrane contribute to flight control. Flight behavior was compared in intact and dorsal wing hair depilated bats while they performed an obstacle avoidance task. Both species showed alterations in flight behavior after depilation of the dorsal wing membrane. Quantitative data from *C. perspicillata* showed that depilated bats flew faster as they approached an obstacle and made wider turns to steer around the obstacle, compared to trials in which wing hairs were intact (Sterbing-D'Angelo et al., 2011), suggesting that the

dorsal wing hairs are involved in airflow sensing and convey information about flight speed and turbulence, allowing the bat to make adjustments in flight to avoid stall. Qualitative data from *E. fuscus* suggest that wing hair depilation induces wider turns around obstacles, but quantitative analysis of flight kinematics in this species was not conducted. Further, past studies of the effects of wing hair depilation have focused on obstacle avoidance tasks, rather than goal-directed flight.

The present study quantified the flight kinematics, adaptive echolocation behaviors, and capture performance of intact and depilated big brown bats*, Eptesicus fuscus*, engaged in a goal-directed prey capture task. Bats were studied before and after depilation of their ventral tail and wing membranes, and a subset of animals also underwent subsequent dorsal wing-tail depilation. Using high-speed video and audio recordings, we monitored the bats' sonar behavior and approach to the target, as well as their ability to handle and capture the target. We hypothesized that bats with ventral hair depilation would show a drop in insect capture performance relative to baseline, as well as changes in flight kinematics (i.e., increased flight speed and decreased turn rate). We also hypothesized that sensory hair depilation would affect echolocation behaviors. Specifically, we predicted that bats would decrease the duration of their terminal buzz phase following ventral depilation, resulting from a loss of information about their flight speed. We further hypothesized that there would be differences between the ventral and dorsal depilation conditions. Studies have shown that both the ventral and dorsal surface of the bat wing have leading edge vortices (LEVs) (Muijres et al., 2014). Based on these findings, we hypothesized that asymmetric depilation of a single surface (i.e., ventral or dorsal side) would produce larger behavioral changes than symmetric depilation (i.e.,

both ventral and dorsal sides). We predicted that symmetric depilation would revert changes in insect capture behavior, flight kinematics, and echolocation behavior back to baseline levels.

Materials and Methods

Animals

Five wild-caught insectivorous bats [*Eptesicus fuscus* (Palisot de Beauvois, 1796); 2 males and 3 females)] weighing between 14 and 21 g served as subjects for this study. All bats were collected in the State of Maryland under permit number 55440. Bats were fed mealworms (*Tenebrio molitor* larvae) daily to maintain their individual weights throughout training and experimental testing. Bats were housed in two group cages in the animal facilities at the Johns Hopkins University under a reversed light/dark cycle (12 h: 12 h dark: light). All experimental procedures were approved by the Institutional Animal Care and Use Committee (IACUC) at Johns Hopkins University.

Apparatus and data acquisition

The experiment was conducted in a large laboratory flight room (7 x 6 x 2.5 m) with the walls and ceiling lined with acoustic foam (Sonex Classic, Sonex Acoustics, San Jose, USA) and shielded from external electrical noise. Dim, long-wavelength lighting was used during data acquisition to ensure bats relied on echolocation to complete the task rather than visual cues (Hope and Bhatnagar, 1979). Three high-speed Miro cameras (Phantom M310, Vision Research Inc., New Jersey, USA), operating at a frame rate of 300 Hz, were mounted to the ceiling of the flight room. Two cameras had wide-angle lenses and were

positioned to allow for coverage of the entire flight room. The third camera was focused on the tethered insect and zoomed in closely to allow for behavioral scoring. Video footage was used to record and reconstruct the bats' 3D flight trajectories, as well as to confirm the outcome of each trial and calculate the bats' flight kinematics. Additionally, we measured the time each bat took to initiate a capture attempt using a stopwatch.

We used two ultrasonic capacitor microphones (NEUmic, Ultra Sound Advice, UK) placed below the target to record the bat's adaptive echolocation behavior during prey capture attempts. Signals from each microphone were filtered between 10 kHz and 100 kHz (USBPBP-S1, Alligator Technology, Costa Mesa, CA, USA) and sampled at 250 kHz (NI PXI-6143, National Instruments, Austin, TX, USA). We used an end-trigger to capture

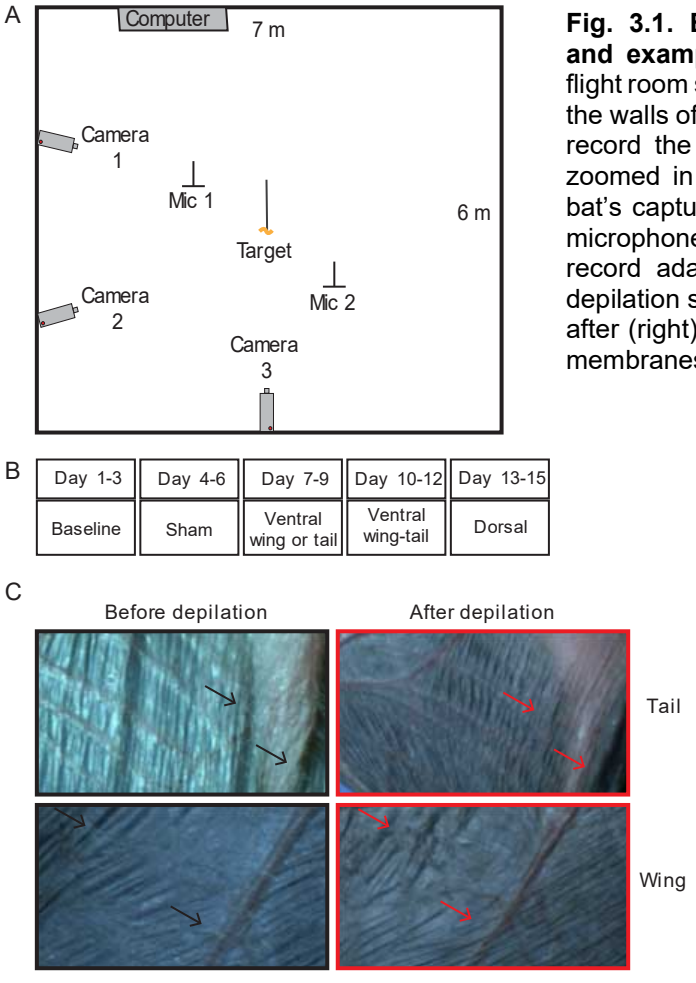

Fig. 3.1. Experimental setup, depilation schedule, and example depilation. (A) Schematic of laboratory flight room setup. Three high-speed cameras mounted on the walls of the flight room, two with wide-angle lenses to record the trajectory of the bat to the target and one zoomed in closely to the tethered insect to record the bat's capture strategy and performance. Two ultrasonic microphones positioned around the tethered insect to record adaptive echolocation behavior. (B) Outline of depilation schedule. (C) Sample images before (left) and after (right) depilation of the tail (top) and wing (bottom) membranes.

five seconds of audio data and 1.67 seconds of video data as the bats made capture attempts. The video cameras and microphones were synchronized using a common Transistor-Transistor Logic (TTL) trigger signal. Schematics of the experimental setup are presented in Fig. 3.1A.

Experimental procedures

Five bats were trained in an open room to capture a tethered mealworm that was hanging from the ceiling in the center of the room by a monofilament fishing line (Berkley Trilene, 0.9 kg test, 0.13 mm diameter). Bats were allowed to fly freely around the room and approach the tethered insect from any direction. To prevent bats from attempting to capture in between trials, a second experimenter covered the insect until the initiation of the next trial. We began data collection once bats learned to capture the insect for a minimum of seven days. At the beginning of each day of data collection, water-soluble glue (Grimas Mastix Water Soluble, Heemstede, Holland) was used to secure on the bat two reflective hemispheres (diameter: 9 mm) to the back and one reflective sticker (diameter: 8 mm) to the head between the ears of each bat in order to make it easier to localize the bats' position in the video recordings. The total weight of all of the reflective markers was 0.54 g. At the end of each day, the head and body markers were carefully removed, and the bats were returned to their home cages. All bats performed the insect capture task for 3 to 4 days for each condition (as described below).

Each bat began in the baseline intact condition, where they performed the insect capture task without any manipulation to wing or tail hairs, followed by a sham manipulation. In the sham depilation treatment, water was applied to the ventral wing

and/or tail membranes using a cotton tipped applicator. The membranes were then rinsed off after two minutes with lukewarm water and gently patted dry. Each bat then underwent a series of depilation treatments (Fig. 3.1B), where the microscopic hairs from their tail and/or wing membrane were removed using a commercial depilatory cream (Veet Sensitive Skin formula). Three of the five bats (one male, two female) were depilated on the ventral tail membrane first; we refer to this group as the ventral **tail-first** group. The other two bats (one male, one female) were depilated on the ventral wing membrane first; we refer to this group as the ventral **wing-first** group. Next, the ventral wing or ventral tail was depilated for the tail-first and wing-first groups, respectively; we refer to this as **wing-tail** depilation. Following complete depilation of the ventral wing and tail, three bats (one male, two female) were depilated on the dorsal membranes. Two of three bats (one each from the tail-first and wing-first groups) underwent complete dorsal wing and tail depilation. The third bat showed a skin reaction when the depilatory cream was applied to the dorsal tail membrane, and therefore only the dorsal tail membrane was depilated. Due to this animal's reaction to the depilatory cream, data from this bat was excluded from all analyses for the dorsal condition. All treatments were conducted 18 to 20 hours before data collection. We confirmed that all hairs were removed following depilation treatments by placing the depilated membrane under a microscope (Fig. 3.1C). If any hairs remained, a spot depilation was performed immediately following the initial depilation to remove them. Regrowth of wing and tail hairs takes 9 to 12 months (unpublished), far beyond the data collection period of this study. An outline of the depilation schedule is presented in Fig. 3.1B.

Behavioral analysis

For each trial, we analyzed the time to attempt prey capture, target interception strategy, and performance across all depilation conditions relative to the baseline condition. A summary of the total number of trials and number of trials by bat for each parameter are presented in Table 3.1. We measured the time it took the bat to attempt to capture the insect from the start of a trial, until it produced a terminal buzz, the high repetition call rate produced before initiating prey interception. Time measurements were taken for four of the five bats. A one-way ANOVA was used to analyze the log-transformed time to attempt insect capture (time to attempt x condition). Capture strategy for each trial was determined based on the first part of the bats' body that contacted the tethered insect and categorized as either a tail-scoop or wing-reach. Chi-square tests were used to test whether observed fractions of tail-scoop and wing-reach strategies differed from the expected fractions across conditions.

Next, we categorized each trial as one of the following: capture, fumble, tap, or miss. A capture was defined as an attempt that resulted in the bat successfully taking the worm from the tether and eating it. A fumble was defined as an attempt by the bat to take the worm into its possession but failure to transfer it to the mouth, resulting in the worm dropping to the floor. A tap was an attempt in which the bat contacted the worm without ever taking it into possession. A miss was categorized as an attempt in which the bat positioned its wing or tail membrane to intercept the worm but did not contact it. We further organized trials depending on whether or not the bat successfully intercepted the target as either a success trial (i.e., capture) or a failure trial (i.e., fumble, tap, or miss). Capture

performance was calculated as the percentage of success trials relative to the total number of trials for each bat and condition. Chi-square tests were used to test whether

Table 3.1. Summary of the total number of trials and number of trials by bat for each parameter.

Parameter	Bat	N trials by bat	N trials total
Time to attempt prey capture	1	226	
	2	193	
	3	274	
	4	188	***881***
Prey interception strategy	1	276	
	2	243	
	3	312	
	4	290	
	5	240	***1361***
Capture performance	1	314	
	2	284	
	3	350	
	4	270	
	5	270	***1488***
Flight speed	1	285	
	2	284	
	3	341	
	4	269	***1179***
Wingbeat frequency	1	147	
	2	133	
	3	181	
	4	103	***564***
Turn rate	1	285	
	2	284	
	3	341	
	4	269	***1179***
Pulse interval (PI)	1	251	
	2	283	
	3	330	
	4	258	***1122***
Call duration	1	255	
	2	284	
	3	343	
	4	268	***1150***
Buzz duration	1	210	
	2	233	
	3	294	
	4	226	***963***

observed fractions of successful and failure trials differed from the expected fractions across conditions. The *p*-values were adjusted for each parameter to account for multiple comparisons using the Bonferroni-based false discovery rate method, resulting in a *p*-value threshold of 0.01.

Video analysis

For each trial, the position of the bat, wing tips, target and microphone were manually labeled using video recordings from two high-speed Phantom Miro cameras (M310 model) running at 300 frames per second. These data were digitized using the DLTdv digitizing tool software (Hedrick, 2008) in MATLAB. Data from one of the five bats were collected a year prior using different data acquisition equipment and arrangements, and therefore were not included in these analyses, and only performance data are reported for this animal. Parameters of flight kinematics were analyzed using customized programs written in MATLAB. The marker on the bat's head was used to determine the bat's position. Once position data for each trial was obtained, we interpolated and smoothed the labeled marker trajectories using the spline and smooth function in MATLAB, respectively. Gaps longer than 15 frames or 50 ms were not interpolated and were excluded from further analyses. Position values were binned into 25 cm bins with respect to target distance. We calculated flight speed using the distance travelled by the bat between each frame divided by the time lapse between frames. We then z-score normalized the flight speed to each bat's own baseline flight speed. Wingbeat frequency was calculated by first locating the wingbeat peaks and troughs using the *findpeaks* function in MATLAB, and then calculating the instantaneous phase of the wingbeat from

the analytic signal. We then fit the flight speed and wingbeat frequency variables to a generalized linear model (GLM) using a backward stepwise procedure (eq. 1). The bat's distance to the target was set as a continuous predictor variable. The treatment condition was categorized as a nominal predictor in the GLM. In addition, we also assessed the interaction between distance and condition. Turn rate was calculated along the xy-plane using the difference in angular flight direction between each frame and smoothed using a 60-frame moving average. To statistically quantify differences in turn rate with respect to condition, we performed nonparametric comparisons across conditions using the Wilcoxon method. The *p*-values were adjusted for each parameter to account for multiple comparisons using the Bonferroni-based false discovery rate method, resulting in a *p*-value threshold of 0.01.

(1) Predicted value = $\beta_0 + \beta_1$(distance) + β_2(condition) + β_3(distance x condition)

Audio analysis

Audio data were processed and analyzed using custom MATLAB programs. Data from one of the five bats were collected a year prior using different equipment and settings, and therefore were not included in these analyses. We found that a low-pass corrected waveform from the floor microphone yielded the best signal-to-noise ratio, and we manually labeled the onset and offset of each sonar vocalization for each trial by drawing an amplitude threshold. The timing of the onsets and offsets were corrected for the travel time of the bat to floor microphone positioned below the target. Sonar call duration was calculated as the difference in time between the onset and offset of a single

sonar vocalization. Pulse interval (PI), a metric used to quantify the sonar call rate of the bat, was calculated as the time interval between the onsets of two consecutive sonar vocalizations. Audio data values (i.e., PI and call duration) were binned into 25 cm bins with respect to target distance. We then fit sonar pulse duration and PI to a GLM using a backward stepwise procedure (eq. 1). The treatment condition was categorized as a nominal predictor in the GLM for all response variables. The bat's distance to the target was set as a continuous predictor variable. In addition, we also assessed the interaction between distance and condition. The terminal buzz phase consists of two parts, buzz I and buzz II, with PIs of approximately 9 to 15 ms and 6 to 8 ms, respectively (Surlykke and Moss, 2000). We identified the terminal buzz phase (i.e., buzz I and buzz II combined) as the first time point when the PI was below 12 ms, and buzz II as the first time point when the PI was below 8 ms. The buzz duration was defined as the time between the first and last sonar pulse within these segments of the buzz phase. A one-way ANOVA was used to analyze the buzz duration (buzz duration x condition). The *p*-values were adjusted for each parameter to account for multiple comparisons using the Bonferroni-based false discovery rate method, resulting in a *p*-value threshold of 0.01.

Results

Insect capture behavior

In the prey capture experiment, bats were trained to take a tethered insect (mealworm) in the laboratory flight room. For each trial, we measured the time it took each bat to make a capture attempt across conditions (Fig. 3.2). There was a significant effect of condition on the average time to attempt prey capture ($F(5,34)=9.50$, $p<0.0001$; Fig

3.2). *Post hoc* Student's *t*-tests (with Bonferroni corrections) revealed that there were no significant differences between the sham and tail-first depilation conditions relative to baseline. There was a significant increase in the time to attempt prey capture for the wing-first (t=2.7, p<0.01), wing-tail (t=2.89, p<0.01), and dorsal (t=6.34, p<0.0001) depilation conditions compared to baseline. These observations were not driven by a single bat and are consistent across bats within the same condition.

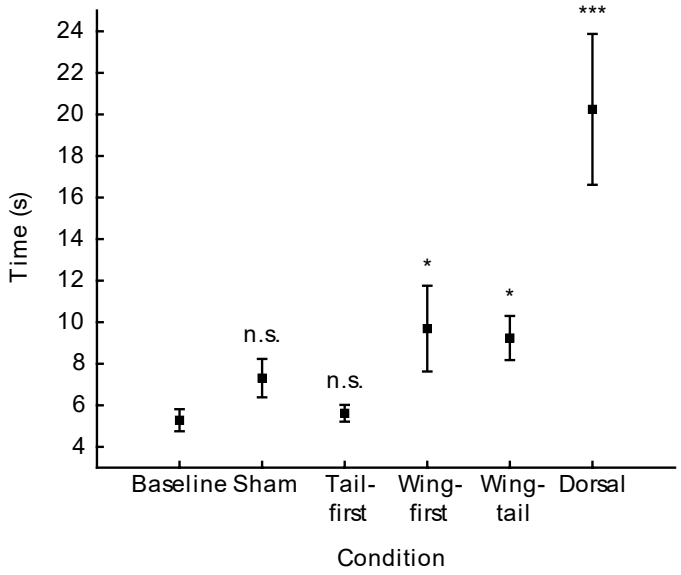

Fig. 3.2. Time to attempt insect capture following sensory hair depilation. Mean time to attempt insect capture (in seconds) across conditions. Error bars indicate ±s.e.m. Bats showed a significant increase in the average time to attempt insect capture following ventral wing-first (t=2.7, p<0.01), wing-tail (t=2.89, p<0.01), and dorsal (t=6.34, p<0.0001) depilation conditions compared to baseline. There was no significant difference in the average time to attempt insect capture for the sham and tail-first conditions. Asterisks indicate the overall significance of each condition compared to the baseline condition (n.s., not significant; *p<0.01; **p<0.001; ***p<0.0001).

Next, we categorized the bat's target interception strategy as a tail-scoop, wing-reach, or mouth for each attempted capture (Fig. 3.3A). In the wild, insectivorous bats frequently use their tail membrane to intercept prey (Webster and Griffin, 1962). In this experiment, we observed that bats use the tail-scoop strategy 87.44% of the time, whereas they use the wing-reach and mouth capture strategy 12.42% and 0.15% of the time, respectively. There was a significant effect of condition on capture strategy (χ^2(5,

N=1359)=20.18, p<0.01; Fig. 3.3A). A chi-square test of proportions revealed that there were no significant differences between the sham, tail-first, and dorsal depilation conditions relative to baseline. There was a significant increase in wing-reach strategy for the wing-first (χ^2(1,N=303)=10.45, p<0.01) and wing-tail (χ^2(1,N=684)=13.42, p<0.001) depilation conditions compared to baseline. The majority of bats exhibited an increase in wing-reach strategy (four of five bats) following ventral wing depilation. One bat demonstrated a strong preference for the tail-scoop strategy and did not modify their insect capture strategy following depilation.

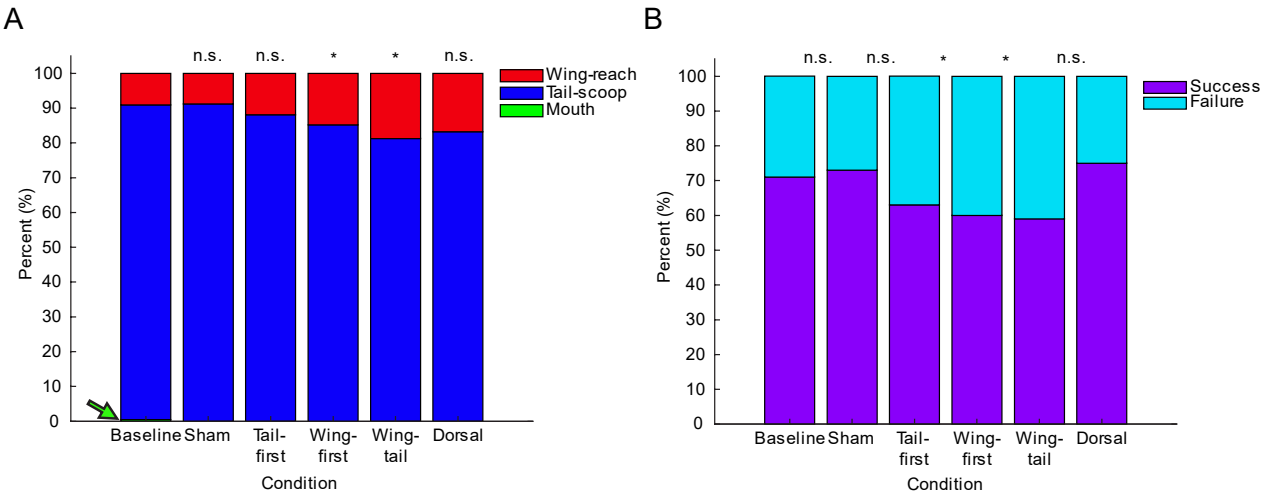

Fig. 3.3. Insect capture strategy and performance following sensory hair depilation. (A) Percent of each capture strategy across conditions: wing-reach (red), tail-scoop (blue), and mouth (green). For all trials and conditions bats predominantly used the tail-scoop strategy (87.44%), followed by the wing-reach strategy (12.42%) and the mouth capture strategy (0.15%). Bats showed no significant differences in capture strategy between the sham, tail-first, and dorsal depilation conditions relative to baseline. Bats increased the use of the wing-reach strategy for the wing-first (χ^2(1,N=303)=10.45, p<0.01) and wing-tail (χ^2(1,N=684)=13.42, p<0.001) depilation conditions relative to baseline. (B) Percent of success (purple) and failure (aqua) trials by condition. Bats showed no significant differences in capture performance for the sham, tail-first, and dorsal depilation conditions relative to baseline. Bats significantly decreased capture performance (i.e., decrease in success trials) compared to baseline for the wing-first (χ^2(1)=11.24, p<0.001) and wing-tail (χ^2(1)=13.76, p<0.001) depilation conditions. Asterisks indicate the overall significance of each condition compared to the baseline condition (n.s., not significant; *p<0.01; **p<0.001; ***p<0.0001).

We then evaluated capture performance, calculated as $N_{success}/N_{total}$, across all depilation conditions (Fig. 3.3B). There was a significant difference in capture performance with depilation (χ^2(5, N=1488)=26.44, p<0.0001). A chi-square test of

proportions revealed that there were no significant differences between the sham, tail-first, and dorsal depilation conditions relative to baseline. We observed a significant decrease in capture performance relative to baseline for the wing-first ($\chi^2(1)=11.24$, $p<0.001$) and wing-tail ($\chi^2(1)=13.76$, $p<0.001$) depilation conditions. The majority of bats exhibited a decrease in capture performance (four of five bats) following ventral wing depilation. One bat consistently captured the tethered insect regardless of condition. It could be possible that this bat was able to adapt its behavior in such a way that allowed for it to compensate for the effects of the depilation (i.e., adapting capture strategy).

Flight kinematics

We calculated the flight speed using 3D reconstructions of the bats' position during each recorded frame and normalized the bats' flight speed to its own baseline flight speed. We compared across conditions the overall average normalized flight speed (Fig. 3.4A) and flight speed as a function of bat-target distance in 25 cm bins (Fig. 3.4B). There was a significant main effect of condition ($F(5)=52.47$, $p<0.0001$; Fig. 3.4A) and distance ($F(1)=46.84$, $p<0.0001$; Fig. 3.4B) on flight speed. No interaction effect was observed. *Post hoc* Student's *t*-tests (with Bonferroni corrections) revealed that there was a significant increase in mean flight speed relative to baseline in the sham ($t=4.27$, $p<0.0001$), wing-first ($t=11.78$, $p<0.0001$), and wing-tail ($t=10.69$, $p<0.0001$) depilation conditions. There were no significant differences in the mean flight speed for the tail-first and dorsal depilation conditions relative to baseline. These observations were not driven by a single bat and are consistent across bats within the same condition. A summary of raw (i.e., not normalized) flight speeds for *E. fuscus* across conditions at various distances

from the target are presented in Table 3.2.

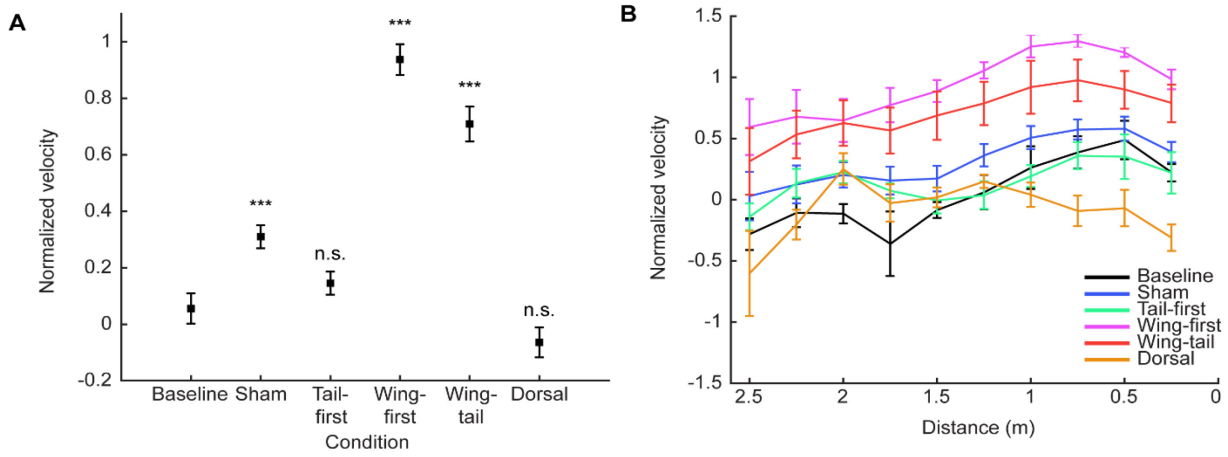

Fig. 3.4. Flight speed following sensory hair depilation. There was a significant main effect of condition ($F(5)=52.47$, $p<0.0001$) and distance ($F(1)=46.84$, $p<0.0001$) on flight speed. No interaction effect was observed. Error bars indicate ±s.e.m. (A) Mean flight speed by condition, normalized to each bat's baseline. Bats showed no significant differences in mean flight speed for the tail-first and dorsal depilation conditions relative to baseline. Bats significantly increased flight speed in the sham ($t=4.27$, $p<0.0001$), wing-first ($t=11.78$, $p<0.0001$), and wing-tail ($t=10.69$, $p<0.0001$) depilation conditions. (B) Mean flight speed plotted as a function of bat-target distance (bin size: 25 cm). Asterisks indicate the overall significance of each condition compared to the baseline condition (n.s., not significant; *$p<0.01$; **$p<0.001$; ***$p<0.0001$).

Table 3.2. Summary of flight speeds of Eptesicus fuscus across conditions at varying distances from the target.

Condition	Distance from target (m)	Minimum flight speed (ms^{-1})	Maximum flight speed (ms^{-1})	Mean flight speed (ms^{-1})
Baseline	0.25	1.72	3.80	2.76
Baseline	1	1.98	4.81	3.21
Baseline	2	1.83	5.16	3.63
Sham	0.25	1.81	3.73	2.79
Sham	1	2.56	4.52	3.42
Sham	2	2.62	5.51	3.94
Tail-first	0.25	1.79	3.81	2.87
Tail-first	1	2.48	4.00	3.16
Tail-first	2	2.30	4.70	3.59
Wing-first	0.25	2.09	4.01	2.94
Wing-first	1	2.39	5.07	3.81
Wing-first	2	2.73	5.26	4.45
Wing-tail	0.25	1.75	4.05	2.97
Wing-tail	1	1.86	4.71	3.58
Wing-tail	2	2.77	5.33	4.20
Dorsal	0.25	1.76	3.77	2.39
Dorsal	1	1.98	3.97	3.03
Dorsal	2	2.87	5.04	3.76

Next, we calculated wingbeat frequency using the instantaneous phase of the wingbeat from the analytic signal. We compared the average wingbeat frequency across conditions, as well as with respect to bats' distance from the target using 25 cm distance bins (Fig. 3.5). There was a significant main effect of condition ($F(5)=10.94$, $p<0.0001$; Fig. 3.5A) and distance ($F(1)=11.54$, $p<0.001$; Fig. 3.5B) on wingbeat frequency. Additionally, there was a significant interaction effect between condition and distance ($F(5)=6.60$, $p<0.0001$). *Post hoc* Student's *t*-tests (with Bonferroni corrections) revealed that there was a significant increase in mean wingbeat frequency relative to baseline in the tail-first ($t=3.15$, $p<0.001$), wing-first ($t=3.44$, $p<0.001$), and wing-tail ($t=5.92$, $p<0.0001$) depilation conditions. There were no significant differences in the mean wingbeat frequency for the sham and dorsal depilation conditions. These observations were not driven by a single bat and are consistent across bats within the same condition.

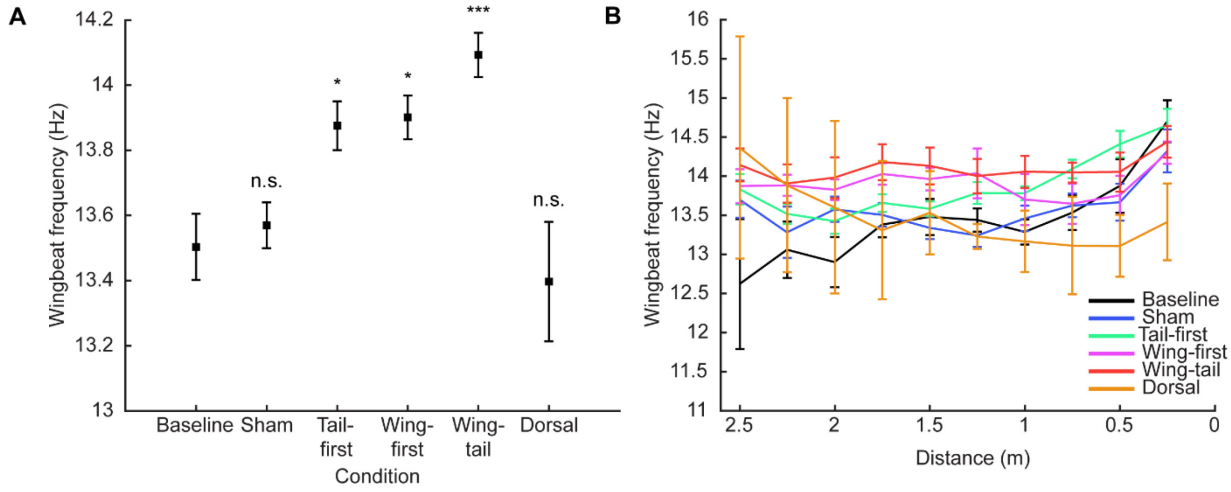

Fig. 3.5. Wingbeat frequency following sensory hair depilation. There was a significant main effect of condition ($F(5)=10.94$, $p<0.0001$) and distance ($F(1)=11.54$, $p<0.001$) on flight speed. There was a significant interaction effect between condition and distance ($F(5)=6.60$, $p<0.0001$). Error bars indicate ±s.e.m. (A) Mean wingbeat frequency by condition. Bats showed no significant differences in mean wingbeat frequency for the sham and dorsal depilation conditions. Bats significantly increased mean wingbeat frequency in the tail-first ($t=3.15$, $p<0.001$), wing-first ($t=3.44$, $p<0.001$), and wing-tail ($t=5.92$, $p<0.0001$) depilation conditions relative to baseline. (B) Mean wingbeat frequency plotted as a function of bat-target distance (bin size: 25 cm). Asterisks indicate the overall significance of each condition compared to the baseline condition (n.s., not significant; *$p<0.01$; **$p<0.001$; ***$p<0.0001$).

We also analyzed turn rate as bats approached the target. We calculated turn rate along the xy-plane using the difference in angular flight direction between each frame. We compared changes in turn rate across conditions with Wilcoxon rank sums tests using a one-way chi-square approximation. We found a significant effect of condition on turn rate ($\chi^2(5)=101.63$, $p<0.0001$; Fig. 3.6). There was a significant decrease in turn rate relative to baseline for the sham ($z=-3.28$, $p=0.001$), wing-first ($z=-6.61$, $p<0.0001$), wing-tail ($z=-4.41$, $p<0.0001$), and dorsal ($z=-5.32$, $p<0.0001$) depilation conditions. There was an increase in turn rate for the tail-first depilation condition, but this comparison was not statistically significant ($z=1.77$, $p=0.078$). All bats exhibited a decrease in turn rate following ventral wing depilation. Following dorsal depilation, the two bats exhibited opposite trends, one further decreased their turn rate relative to baseline and the other increased their turn rate back to baseline levels. The bat that increased their turn rate

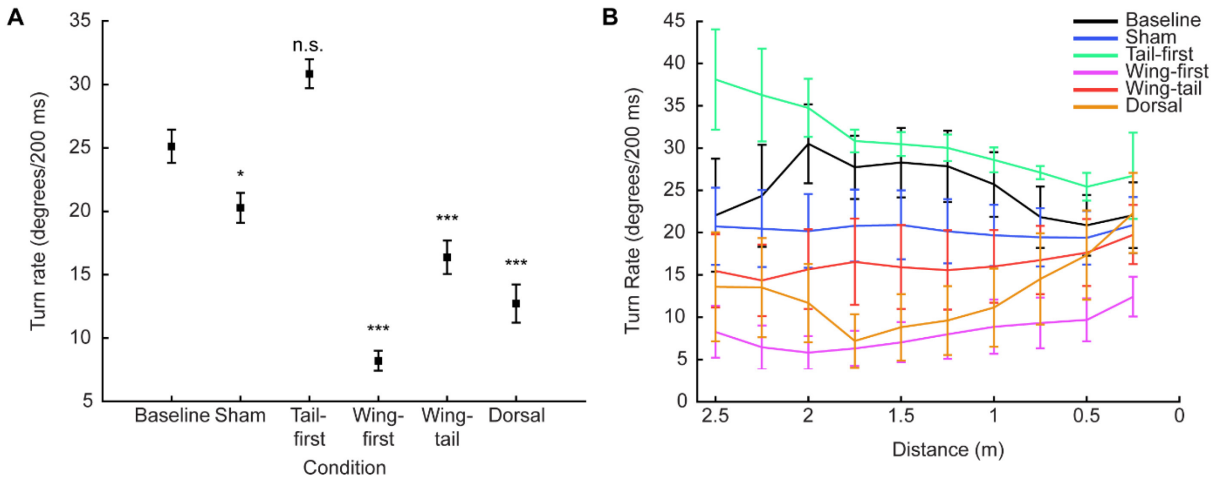

Fig. 3.6. Turn rate following sensory hair depilation. (A) Mean turn rate by condition. Bats showed significant differences in turn rate across depilation conditions ($\chi^2(5)=101.63$, $p<0.0001$). Bats significantly decreased turn rate relative to baseline for sham ($z=-3.28$, $p<0.01$), wing-first ($z=-6.61$, $p<0.0001$), wing-tail ($z=-4.41$, $p<0.0001$), and dorsal ($z=-5.32$, $p<0.0001$) depilation conditions. Bats showed an increase in turn rate for the tail-first depilation condition, but this comparison was not statistically reliable (n.s., $p=0.078$). (B) Mean turn rate plotted as a function of bat-target distance (bin size: 25 cm). Error bars indicate ±s.e.m. Asterisks indicate the overall significance of each condition compared to the baseline condition (n.s., not significant; *$p<0.01$; **$p<0.001$; ***$p<0.0001$).

tended to take the same trajectory as it approached the target, which could have contributed to the return to baseline levels following dorsal depilation.

Adaptive echolocation behavior

We analyzed the bats' adaptive echolocation behaviors as they approached the target (Fig. 3.7). We compared the average pulse interval (PI) across conditions (Fig. 3.7A), as well as changes in PI with respect to the distance from the target using 25 cm distance bins. There was a significant main effect of distance on PI ($F(1)=452.34$, $p<0.0001$), but there was no significant effect of condition. Additionally, there was no significant interaction effect between condition and distance for PI. These observations were not driven by a single bat and are consistent across bats within the same condition.

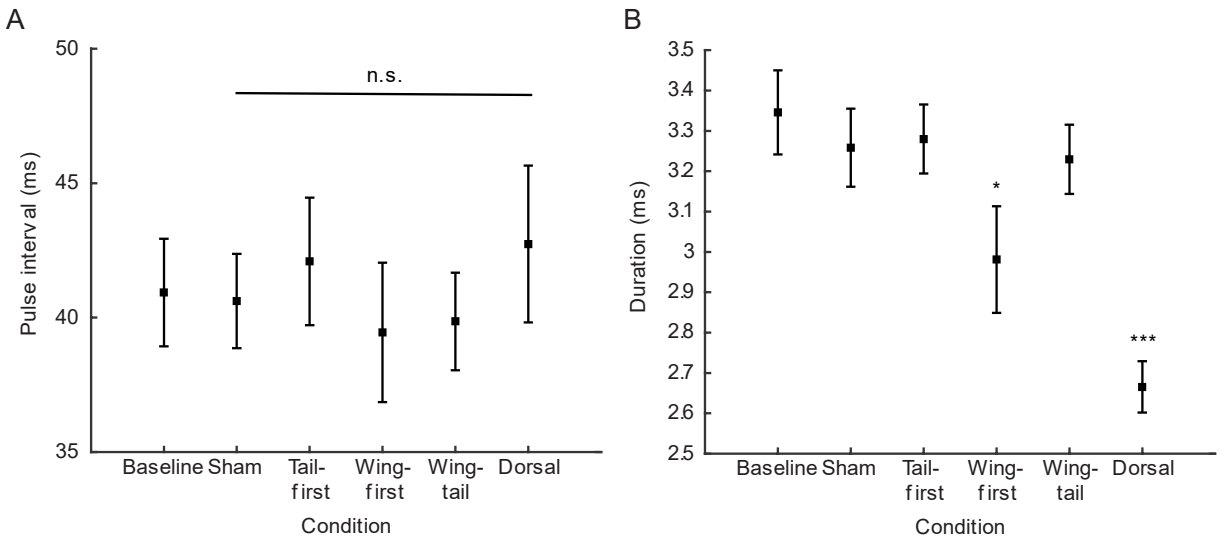

Fig. 3.7. Adaptive echolocation behavior following sensory hair depilation. (A) Mean sonar pulse interval (PI) by condition. There was a significant main effect of distance on PI ($F(1)=452.34$, $p<0.0001$), with bats decreasing PI as they approached the target. There was no significant main effect of condition or interaction effect between condition and distance on PI. (B) Mean sonar call duration by condition. There was a significant main effect of condition ($F(5)=6.09$, $p<0.0001$) and distance ($F(1)=63.81$, $p<0.0001$) on sonar call duration, but no interaction effect. Bats significantly decreased sonar call duration in the wing-first ($t=-2.82$, $p<0.01$) and dorsal ($t=-4.97$, $p<0.0001$) depilation conditions relative to baseline. Error bars indicate ±s.e.m. Asterisks indicate the overall significance of each condition compared to the baseline condition (n.s., not significant; *$p<0.01$; **$p<0.001$; ***$p<0.0001$).

We also compared the average sonar call duration across conditions (Fig. 3.7B), as well as changes in sonar call duration with respect to the distance from the target using 25 cm distance bins. There was a significant main effect of condition ($F(5)=6.09$, $p<0.0001$) and distance ($F(1)=63.81$, $p<0.0001$) on sonar pulse duration. There was no significant interaction effect. *Post hoc* Student's *t*-tests (with Bonferroni corrections) revealed that there was only a significant decrease in sonar call duration in the wing-first ($t=-2.82$, $p<0.01$) and dorsal ($t=-4.97$, $p<0.0001$) depilation conditions relative to baseline.

Lastly, we analyzed the duration of the terminal buzz phase across conditions (Fig. 3.8), which was defined as the time between the first and last sonar pulse within the terminal buzz phase. We analyzed the duration of the terminal buzz phase with both segments (i.e., buzz I and buzz II) combined (Fig. 3.8A), as well as the buzz II segment individually (Fig. 3.9). There was no significant effect of condition on buzz duration when evaluating buzz I and buzz II segments combined. There was a significant effect of

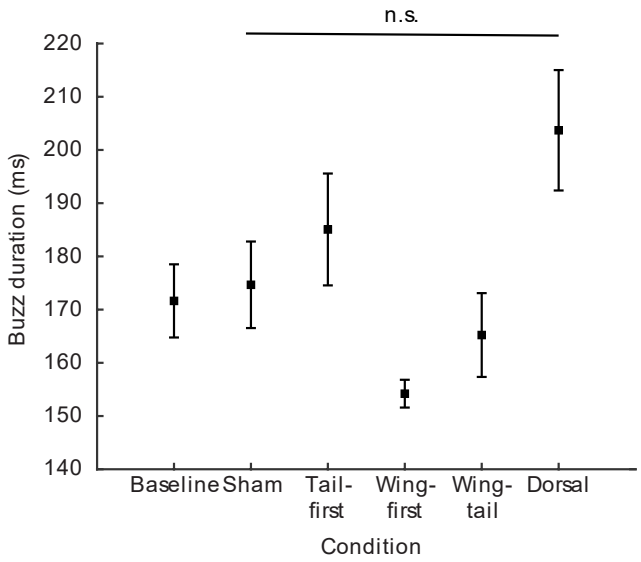

Fig. 3.8. Duration of temporal buzz phase following sensory hair depilation. Mean buzz duration by condition, buzz I and buzz II segments combined. Bats showed no differences in buzz duration following sensory hair depilation. Error bars indicate ±s.e.m. Asterisks indicate the overall significance of each condition compared to the baseline condition (n.s., not significant; *$p<0.01$; **$p<0.001$; ***$p<0.0001$).

condition on the duration of the buzz II segment ($F(5)=21.14$, $p<0.0001$; Fig. 3.9). *Post hoc* Student's *t*-tests (with Bonferroni corrections) revealed that there was only a significant difference in the wing-first ($t=-3.00$, $p<0.01$) and dorsal ($t=8.74$, $p<0.0001$) depilation conditions relative to baseline (Fig. 3.9.).

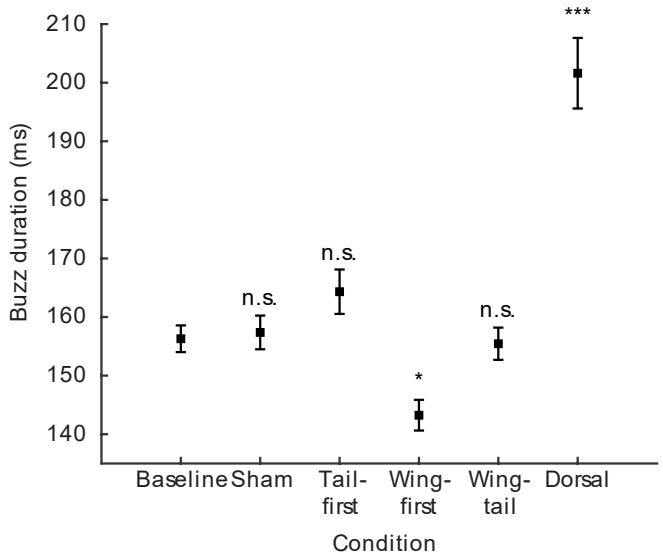

Fig. 3.9. Duration of buzz II segment of the temporal buzz phase following sensory hair depilation. Mean duration by condition, buzz II segment only. There was a significant effect of condition on the duration of buzz II ($F(5)=21.14$, $p<0.0001$). Bats significantly decreased buzz II duration in the wing-first depilation condition ($t=-3.00$, $p<0.01$) and increased buzz II duration in the dorsal depilation condition ($t=8.74$, $p<0.0001$), compared to baseline. Error bars indicate ±s.e.m. Asterisks indicate the overall significance of each condition compared to the baseline condition (n.s., not significant; *$p<0.01$; **$p<0.001$; ***$p<0.0001$).

Discussion

The goal of this study was to investigate the contribution of microscopic hairs on the ventral and dorsal surfaces of the bat wing and tail membrane to prey handling, flight kinematics, and adaptive sonar in a goal-directed insect capture task. We trained five echolocating big brown bats, *E. fuscus*, to capture a tethered insect on the wing, before and after depilation of the wing and tail membranes. Our behavioral data show that ventral tail depilation (i.e., tail-first) alone does not result in changes in flight speed or turn rate,

insect capture performance or adaptive echolocation behavior. By contrast, ventral wing depilation (i.e., wing-first or wing-tail depilation) results in an increase in the time to attempt prey interception, as well as an increase in a wing-reach strategy, a decrease in capture performance, and changes in flight kinematics. Following ventral wing depilation, bats flew faster and made wider turns compared to baseline. Changes in capture strategy and the time to attempt prey interception persisted with the addition of dorsal depilation, while capture performance improved. Following dorsal depilation, flight velocity returned to baseline values, whereas turn angle remained low. Bats that underwent wing-first or dorsal depilation showed the only statistically reliable changes in echolocation behavior. Namely, bats that received ventral wing-first depilation showed a decrease in call and buzz II duration relative to baseline, whereas bats that also received dorsal depilation showed a decrease in call duration and an increase in the duration of the buzz II segment, compared with the baseline condition. These findings are discussed below.

Previous worked showed that dorsal wing depilation affects flight control in two species of echolocating bats, *C. perspicillata* and *E. fuscus* (Sterbing-D'Angelo et al., 2011). While quantitative data from *C. perspicillata* were presented, no quantitative analyses of flight kinematics were reported for *E. fuscus*. Here, we provide a quantitative analysis of flight kinematics in a different bat species, *E. fuscus*, using a goal-directed (i.e., prey capture) task, along with quantitative analyses of adaptive echolocation behavior and insect capture performance. Additionally, data for these parameters are presented from both single membrane (i.e., tail-first and wing-first) and double-membrane depilation (i.e., wing-tail), as well as ventral and dorsal membrane depilation.

Does sensory hair depilation affect prey handling and/or insect capture performance?

Our analyses revealed significant changes in insect capture behaviors following depilation of sensory hairs. Specifically, we found statistically reliable increases in the time to attempt prey capture in the wing-reach strategy, and a decrease in insect capture performance for ventral wing-first and wing-tail depilation. Webster and Griffin (1962) documented the insect capture behaviors of several bat species and found that the most common strategy used by insectivorous bats to intercept prey was a tail-scoop, followed by a wing-reach strategy. Similar to our findings, a mouth capture strategy was rarely utilized, presumably due to the small size of the bat's mouth. Moreover, Webster and Griffin reported that when the target prey item was detected late or was outside of the bats' direct intercept trajectory, bats tended to deploy a wing-reach strategy. These observations are consistent with our findings that sensory hair depilation affects insect capture behaviors. Specifically, we find an increase in the use of the wing-reach capture strategy following ventral wing-first and wing-tail depilation, which could be a result of the changes in flight kinematics (i.e., an increase in flight speed and wingbeat frequency and a decrease in turn rate). For instance, bats that are flying faster following depilation may mis-calculate their arrival time at the target, resulting in bats reaching out at the last moment with their wing, which can then lead to an increase failed capture attempts (i.e., decrease in capture performance). Moreover, the coupling between the changes in flight speed and turn rate may render the animals unable to make tight maneuvers to position the tail membrane in line with the prey. This chain of events from the changes in flight kinematics to the changes observed in the capture strategy may all contribute to an increase in the bats' failure to accurately align themselves with respect to the target, thus

resulting in an increase in the time to attempt prey capture, changes in capture strategy, and decreased success following ventral wing depilation.

Does sensory hair depilation produce similar quantitative effects on flight kinematics across bat species? Does ventral membrane depilation produce similar effects as dorsal depilation?

Consistent with the previously published findings in *C. perspicillata*, we found an increase in flight speed and a decrease in turn rate in *E. fuscus* following depilation of sensory hairs. Specifically, we found that bats with ventral wing depilation (i.e., wing-first or wing-tail depilation) increased their flight speed and reduced their turn rate (i.e., made wider turns) compared to the baseline condition, whereas ventral tail depilation (i.e., tail-first) alone did not result in significant changes to either measure. Additionally, we found that flight speed returned to baseline levels following dorsal depilation, while turn rate remained low relative to the baseline condition. Findings from the dorsal depilation condition are discussed further below.

Unexpectedly, we observed significant differences between the baseline and sham conditions for both flight speed and turn rate. It is possible that the sham procedure of stroking with the cotton swap and rinsing with water (mimicking depilation procedures but without hair removal) introduced additional stress or stimulation to the sensory hairs and other receptors on the wing and tail membranes. This difference appears to be temporary, as flight speed and turn angle returned to baseline following the tail-first depilation, three days later.

Depilation also produces changes in wingbeat frequency. Our data show that ventral tail-first, wing-first, and wing-tail depilation results in an increase in wingbeat frequency. Furthermore, wingbeat frequency returns to baseline levels following dorsal depilation (discussed below). Past work has shown that five different species vespertilionid bats actively control and adapt the shape of their tail membrane in order to generate thrust and lift (Adams et al., 2012). Additionally, they report a coordination between the flapping of the wings and tail membrane (Adams et al., 2012), demonstrating that the wingbeat cycle and movement of the tail membrane are closely related. Interestingly, our data show an increase in the wingbeat frequency of *E. fuscus* even when only the ventral tail membrane is depilated (i.e., tail-first depilation), suggesting that the interactions between the wing and tail membrane have been disrupted by depilation of the sensory hairs. Unfortunately, our video recordings did not allow for close examination of camber changes of the tail membrane. Additional studies are needed to disentangle how the wing and tail membranes and the sensory hairs on each of these membranes interact and contribute to sensorimotor feedback that supports coordinated flight.

Does sensory hair depilation affect adaptive echolocation behavior?

Past research has quantified adaptive echolocation behaviors of *E. fuscus* taking insects in laboratory and field settings (Surlykke and Moss, 2000; Sändig, Schnitzler, and Denzinger, 2014; Corcoran and Moss, 2017; Jones and Conner, 2019). When bats localize a prey item, they decrease their sonar call duration and PI as they move closer to the target until they enter the terminal buzz phase. The terminal buzz phase is

characterized by PIs of approximately 9 to 15 ms in buzz I and 6 to 8 ms in buzz II (Surlykke and Moss, 2000; Moss and Surlykke, 2010; Moss et al., 2011). We find no effect of depilation condition on PI, but bats do show a decrease in sonar call duration following the wing-first and dorsal depilation conditions. Furthermore, bats show a decrease in buzz II duration in the wing-first depilation condition and an increase in buzz II duration in the dorsal depilation condition. The changes in both call duration and buzz II duration following wing-first and dorsal depilated bats suggest that depilation disrupts the natural coordination between flight and echolocation behaviors. For example, bats that are flying faster after depilation may not accurately monitor their own flight speed. Depilated bats may therefore misjudge their arrival time at the target, resulting in a shorter buzz II segment, the portion of the terminal buzz phase that occurs immediately before insect capture. With the exception of the terminal buzz phase duration, we observe little effect of depilation on echolocation behaviors, suggesting that the reliability of this active sensing system allows bats to successfully navigate their environment and capture prey, even with disrupted airflow sensing to the wing and tail membranes.

Is there a difference between asymmetrical (i.e., ventral) and symmetrical (i.e., ventral and dorsal) depilation?

Our findings further support the hypothesis proposed by Sterbing-D'Angelo et al. (2011) that wing membrane hairs provide sensorimotor feedback and function as airflow sensors, and perhaps more specifically flight speed sensors. Neurons in the primary somatosensory cortex (S1) representing the wing respond to air puff stimulation with sparse, temporal onset firing patterns. S1 neurons that represent the wing membrane

also preferentially fired in response to reversed airflow, i.e., airflow from the trailing edge to leading edge of the wing (Sterbing-D'Angelo et al., 2011). The neural responses to air puff stimulation disappeared after depilation of dorsal wing hairs, but depilation did not interfere with responses to light touch stimulation of the wing membrane, indicating that other tactile receptors remained intact. In our study, we found that depilation of the ventral wing (i.e., wing-first or wing-tail conditions) resulted in decreased capture success, as well as significant changes in the flight kinematics (i.e., flight speed, turn rate, and wingbeat frequency). Interestingly, we found that the capture performance, flight speed, and wingbeat frequency in bats that received dorsal depilation returned to baseline levels. This suggests that when only one side of the wings are depilated; an imbalance or asymmetry in signaling is created, resulting in changes to sensorimotor feedback guiding flight kinematics and prey capture. Work on the aerodynamics of bat flight proposed that wing hairs could provide sensorimotor feedback to monitor the leading-edge vortex (LEV), which generates lift (Muijres et al., 2014). Muijres et al. (2014) has shown that there are two simultaneous LEVs of opposite spin on different sides of the wings during the upstroke, one on the dorsal side and one on the ventral side, in the lesser long-nosed bat (*Leptonycteris yerbabuenae*) during free flight (Muijres et al., 2014). Notably, when the LEV is attached to the wing, the air flows from the trailing edge to the leading edge, which coincides with the preferred direction of airflow by the sensory hairs (Muijres et al., 2014; Sterbing-D'Angelo et al., 2011).

While insect capture performance, flight speed, and wingbeat frequency return to baseline levels following dorsal treatment (i.e., symmetric depilation), other aspects of the bats' behavior did not, such as time to attempt insect capture, turn rate, call duration, and

buzz phase duration. These changes could potentially be due to changes in the bats' motivation and flight path selection to the target. These findings are preliminary due to the small sample size and more experiments are needed to better understand differences between asymmetrical and symmetrical wing membrane depilation on behavior.

Taken together, our data show that the specialized hairs on the wings of the big brown bat play an important role in sensorimotor feedback for flight control and insect capture behavior. Furthermore, these findings support our hypothesis that depilation of one side of the wing results in an asymmetry of sensory input that is largely resolved with depilation of the opposite side. Thus, future experiments that focus on disentangling the sensory inputs from sensory hairs on the ventral and dorsal sides of the wings can enhance our understanding of the aerodynamics and sensorimotor feedback systems of bat flight.

Chapter 4
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Cortical responses to dynamic mechanosensory signals on the bat wing under naturalistic airflow conditions

Introduction

Animals have evolved diverse somatosensory systems that are specific to their behaviors and environment, allowing them to successfully navigate and forage (Catania and Henry, 2006). For example, rodents' facial vibrissae enable foraging and maneuvering through tight, dark spaces (Prescott, Mitchinson, and Grant, 2011). Star-nosed moles have poorly developed eyes and instead rely on 22 unique appendages surrounding their nostrils that serve as a sensory organ for touch in order to navigate and forage (Catania, 2011). While the somatosensory system has been widely studied in diverse animal species for decades, the bat offers distinct opportunities to advance knowledge. Bats are the only mammal capable of true, powered flight (Sterbing-D'Angelo et al., 2011; Sterbing-D'Angelo et al., 2017; Marshall et al., 2015; Chadha, Moss, and Sterbing-D'Angelo, 2011). Their remarkable ability to fly can be attributed to the specialized anatomy of their wings. Each bat wing consists of five digits extended across a thin, flexible membrane. It is noteworthy that the bat wing is sparsely covered with microscopic hairs on both the dorsal and ventral side of the wing membrane. These microscopic hairs, distinct from body fur, project from dome-like structures and are associated with various tactile receptors, including lanceolate receptors and Merkel cell neurite complexes (Sterbing-D'Angelo et al., 2017).

Behavioral studies provide evidence that bat wing hairs contribute to airflow sensing and flight control. Sterbing-D'Angelo et al. (2011) investigated the role of wing hairs in the flight behavior of two different species of bats, *Eptesicus fuscus* (big brown bat) and *Carollia perspicillata* (short-tailed fruit bat), in obstacle avoidance tasks. They found that the flight behavior was altered after depilation of different regions on the wing membrane. Specifically, *E. fuscus* and *C. perspicillata* made wider turns around obstacles and increased their flight speed after depilation, respectively.

Previous neurophysiological findings implicate bat wing hairs in airflow sensing (Sterbing-D'Angelo et al., 2011; Sterbing-D'Angelo et al., 2017; Marshall et al., 2015). Sterbing-D'Angelo et al. (2011) report that neurons in the primary somatosensory cortex (S1) of *E. fuscus* respond to air puff stimulation of the wing. Specifically, neurons in the wing region of S1 show directionally selective responses, with many neurons firing preferentially to reverse airflow stimulation. Furthermore, neurons in bat S1 are activated by both air puff and tactile stimulation with sparse, temporal onset firing patterns (Marshall et al., 2015). Interestingly, responses to air puff stimulation declined after depilation (i.e., hair removal) of dorsal wing hairs, whereas responses to tactile stimulation remained intact (Sterbing-D'Angelo et al., 2011). These findings support the role of these wing hairs as sensors for airflow.

While previous neurophysiological data provide evidence for the role of these microscopic wing hairs in airflow sensing, experiments were conducted using artificial stimuli that do not lend themselves to simulating natural conditions experienced during flight. Here, I examine S1 cortical responses to whole wing airflow stimulation in the sedated big brown bat. The contralateral wing is systematically exposed to naturalistic

airflow across the entire wing, with varying wind speeds, and changes in the wing angle, in a wind tunnel. To determine the contribution of wing hairs to S1 responses, I perform S1 recordings with and without wing hairs. I hypothesize that higher wing angles and airflow velocities increase stimulation of mechanosensory hairs on the wing membrane, resulting in an increase in the firing rate of S1 neurons. I predict a decrease in response magnitude of S1 neurons that represent the wing after wing hairs are removed.

Materials and methods

Animals

Wild-caught insectivorous bats (*Eptesicus fuscus*) weighing between 17 and 21 g serve as the initial subjects for this study. All bats are collected in the State of Maryland under permit number 55440. Bats are fed mealworms (*Tenebrio molitor* larvae) daily to maintain their individual weights throughout experimental testing. Bats are housed individually in the animal facilities at the Johns Hopkins University under a reversed light/dark cycle (12 h: 12 h dark: light). All experimental procedures are approved by the Institutional Animal Care and Use Committee (IACUC) at the Johns Hopkins University.

Experimental apparatus and setup

The experiment is conducted in a customized closed-loop wind tunnel with a 0.3 x 0.3 x 1 m transparent test section. Two high-speed Miro cameras (sampling 200 Hz; Phantom M310, Vision Research Inc., New Jersey, USA) are used to record the wing's camber as the angle of the wing and airflow velocities were systematically changed. The wind tunnel is calibrated with an anemometer (McMaster-Carr, New Jersey, USA) based

on methods described in Barlow et al. (1999). We use an end-trigger to capture five seconds of video and neural data, synchronized by a TTL pulse. The experimental setup is presented in Fig. 4.1A,B.

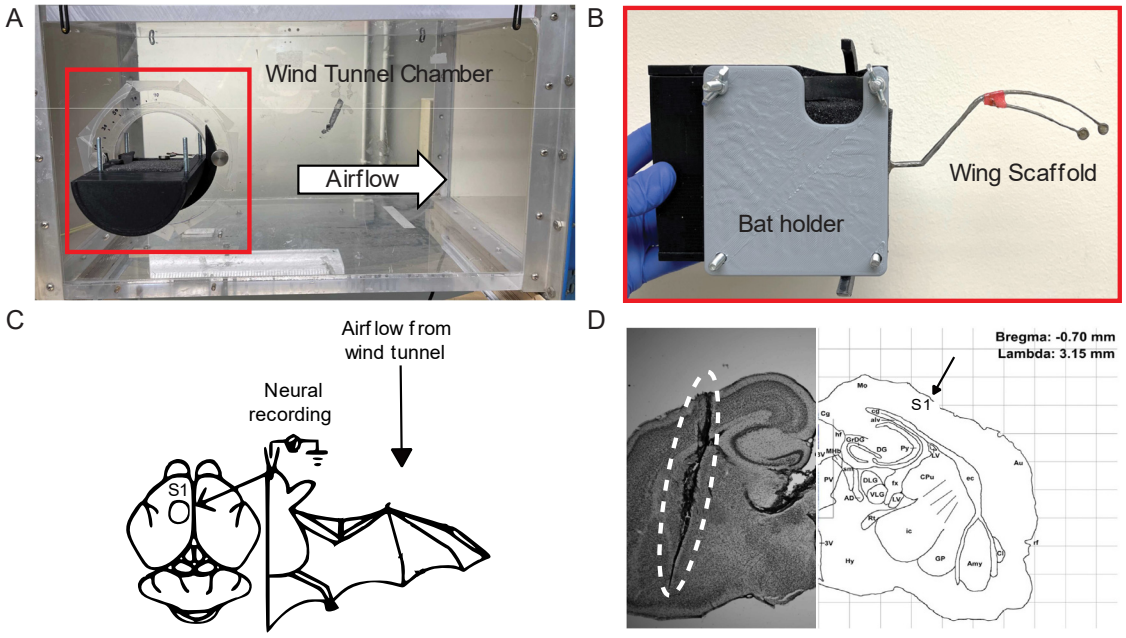

Fig. 4.1. Experimental setup for neural recordings in the closed wind tunnel. (A) Image of wind tunnel chamber setup for neural recordings. Direction of airflow is indicated by a labeled white arrow. The location of the bat holder is outlined with a red square. (B) Image of bat holder/restraint with customized wing scaffold. (C) Schematic of *in vivo* electrophysiological recordings (Figure adapted from Marshall et al., 2015). (D) Cresyl-stained coronal section from brain of big brown bat. Location of electrode penetration is indicated by a dashed white line (left) and a schematic of a coronal section from the big brown bat (right). The location of S1 is marked with a black arrow. Note: depth of electrode track is not representative of the depth during recordings.

Surgical preparation

The surgical preparation and implantation of the silicon probe follows a three-day protocol. For all surgical procedures described below, the bat's body temperature is maintained at 37°C by placing it on a heating pad and their respiratory rate is monitored visually and recorded every 20 minutes. On day 1, the bat is anesthetized with 4% Isoflurane (800 mL/min O_2) until they reach the surgical plane, and then maintained at 1 to 3% during the surgery. The fur over the scalp is removed with a depilatory cream (Veet

Sensitive Skin formula), the scalp is washed and disinfected with iodine, and a midline incision is made to expose the skull and muscles of mastication. The muscles are retracted and a custom stainless steel head post is secured to the bat's skull using an adhesive cement (C&B Metabond, Parkell Inc., New York, USA), which stabilizes the bat's head during the mapping process and the implantation of the silicon probe. The bat is placed back into their home cage to recover overnight. The next day, the bat is placed into a custom holder and head-fixed, then a small craniotomy is made over primary somatosensory cortex (S1). Using a 16-channel silicon probe (1x16 channels, A16, 5 mm shank length, 100 µm between adjacent sites, Neuronexus, Michigan, USA), the area that represents the right wing membrane is mapped by manually stimulating the wing with a cotton-tipped applicator. Lastly, on day 3, a 16-channel silicon probe (4x4 channels, HS16, 3 mm shank length, 100 µm between adjacent sites, 125 µm between shanks, Neuronexus, Michigan, USA) is inserted into mapped region of S1. The probe is mounted onto a miniaturized microdrive and is secured in place using an adhesive cement (C&B Metabond). The bats are allowed one to two days to recover from surgery before physiological recordings begin. Each bat's weight and activity are monitored throughout this recovery period.

Electrophysiological recordings and experimental procedures

On each recording day, the bat is sedated using a subcutaneous injection of 80 mg/kg ketamine hydrochloride solution (100 mg/mL Zetamine, VetOne, Idaho, USA) and 10 mg/kg xylazine solution (20 mg/mL AnaSed Injection, Akorn Inc., Illinois, USA). The bat's respiration rate is monitored and recorded throughout the recording session. The

bat is placed on a heating pad and the contralateral wing is spread open and fixed onto a custom scaffold using a water-soluble glue (Grimas Mastix Water Soluble, Heemstede, Holland). The scaffold is then secured to the wind tunnel, with the contralateral wing inside the wind tunnel's test section.

Multiunit extracellular activity is recorded for up to one hour in each recording session over the course of one to two weeks (typically 3 days/week). Recording probes are advanced approximately 100 µm between recording sessions to allow the tissue at least 24 hours to settle before the next recording. Neural activity is recorded while the contralateral wing is exposed to uniform airflow at varying speeds (0 to 7 ms^{-1}) and incidence angles (0° to 30°) (Fig. 4.1C). Due to limitations of the wind tunnel controls, the lowest airflow velocity is 1.6 ms^{-1}, therefore measurements at airflow velocities between zero and 1.6 ms^{-1} cannot be obtained. The airflow velocity and incidence angle of the wing are systematically adjusted throughout each recording session. Video recordings of the wing are synchronized to the neural recordings to correlate changes in the firing activity of S1 neurons with changes in airflow conditions.

For each bat, recordings are initially taken with wing hairs intact. After three to four recording sessions, the hairs from the dorsal side of the wing are removed using a depilatory cream (Veet Sensitive Skin formula), following the protocol outlined in Boublil et al. (in prep). Briefly, the depilatory cream is applied to the wing and then rinsed off after 90 seconds with lukewarm water and gently patted dry. We confirm that all hairs are removed microscopically. If any hairs remain, a spot depilation is performed to remove them. All recordings under the depilated wing hair condition are performed 24 hours later to allow time for the wing to dry and for any irritation to settle.

At the conclusion of the experiment, bats are transcardially perfused. They are first anesthetized in a chamber that is filled with isoflurane (4%) and subsequently deeply anesthetized by an intraperitoneal injection of sodium pentobarbital (0.1 mL, 390 mg/mL, Beuthanasia-D, USA). The perfusion is performed with 50 mL of phosphate buffered saline (PBS) followed by 100 mL of 4% paraformaldehyde (PFA) in PBS. The brains are extracted and then post-fixed in 4% PFA in PBS at 4°C until further processing. Prior to sectioning, brains are cryoprotected using a 30% sucrose in PBS solution and stored at 4°C until they sank to the bottom of the tube. The brains are sectioned coronally with a freezing cryostat at −20 °C at a thickness of 50 μm. Free floating sections are collected and mounted on Fisher SuperFrost Plus slides and stained with Cresyl violet. Final recording positions of the silicon probe in S1 are located and verified (Fig. 4.1D) using a bat brain atlas (Big Brown Bat Stereotaxic Brain Atlas, unpublished, E. Covey, University of Washington).

Neural data analysis

Using both the local field potential (LFP) from multiunit recordings and spike waveforms from individual neurons, I examine changes in neural activity in the wing region of S1 in response to alterations in airflow conditions, in the presence and absence of microscopic wing hairs that have been previously implicated in airflow sensing (Sterbing-D'Angelo et al., 2011; Sterbing-D'Angelo et al., 2017; Marshall et al., 2015). Spike waveforms and timestamps of extracellular potentials are extracted using an offline sorting software (Offline Sorter v3, Plexon Inc., USA). Extracellular waveforms are

classified as either individual neurons or multiunit activity using principal component analysis (PCA) and template matching algorithms.

To determine if S1 firing patterns change as a function of airflow velocity, angle of attack, or a combination of both, I compare the average firing rate of individual S1 neurons for all combinations of airflow velocities (0 to 7 ms^{-1}, in 0.5 ms^{-1} increments) and incidence angles (0° to 30°, in 5° increments). Next, I compare the average firing rate of these neurons with and without dorsal wing hairs to test whether these microscopic hairs provide sensory feedback regarding changes in airflow to S1. Furthermore, I analyze the LFP under the previously mentioned conditions by computing power spectra densities (PSDs) of the signals in order to determine if signals from S1 are tuned to a particular frequency of wing vibration resulting from changes in the airflow conditions.

Predicted results

Wing camber and movement changes with angle

Qualitative observations showed that the camber of the wing changed as a function of wing angle. I plan to quantify changes in the camber of the wing by calculating the maximum height of the wing membrane based on the chord line and compare those measurements across all conditions. Further, airflow velocity also affects the frequency at which the wing membrane flutters. I plan to digitize the high-speed videos to calculate the flutter frequency of the wing in the wind tunnel and correlate the movement with changes in firings patterns of S1 neurons. I observe an increase in the amount of turbulence of the wing membrane at lower angles and higher velocities. I predict that the changes in neural activity described in previous sections will be correlated with changes

in the fluttering of the wing membrane. Particularly, larger quantities of turbulence on the wing membrane would lead to more activation of wing hairs and other tactile receptors, resulting in an overall higher firing rate of corresponding S1 neurons.

Changes in neural activity under naturalistic airflow conditions

Due to errors in the calibration of the wind tunnel, the airflow velocities used were higher than intended. Future experiments will conduct recordings are naturalistic airflow speeds, ranging from 0 to 7 ms^{-1}. Preliminary neural recordings in the wing region of S1 show clear changes in the LFP and multiunit firing patterns with varying airflow velocities (0 ms^{-1}, 6.25 ms^{-1}, 10 ms^{-1}, and 14 ms^{-1}) and angles of attack (0°, 10°, 20°, and 30°). For example, there is an increase in firing at the largest angle of attack (i.e., 30°). Neural activity was compared to an airflow velocity of 0 ms^{-1} and an angle of attack of 0° as a control.

Effects of wing hair depilation on S1 firing patterns

Neural recordings of S1 with and without intact wing hairs are currently planned. Based on previous findings using air puff and tactile stimuli, I predict that the average firing rate will decrease after depilation of the dorsal wing hairs. Analysis of changes in the wing kinetics and morphology are currently in progress.

Discussion

At present, we are unable to dissociate the contributions of the wing hairs from other tactile receptors (e.g., stretch receptors, Merkel cells, Meissner corpuscles,

Pacinian corpuscles) embedded in the wing and tail membranes. One question that remains is how these other receptors contribute to sensorimotor integration and feedback for flight control. Another question that we are unable to address with our current experiments is how this information is integrated and represented in the brain of an awake, behaving bat. Is the flow on a flapping wing the same as the flow on a fixed wing? How might these differ, and what could be the implications for inference (i.e., what kind of frequencies might dominate in each condition)? Data collection and analysis for the S1 neural recordings are still in progress and I plan to record at least two additional bats. I will focus on comparisons on S1 responses before and after dorsal wing hair depilation treatments.

Chapter 5
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General conclusions and future directions

My thesis examined the role of sensory hairs, with a focus on airflow sensing in the big brown bat. Chapter 2 reviews hair and hair-like structures across the animal kingdom and considers the sensory signals they provide to guide animal behaviors, such as coordinated movement, orientation, object detection, foraging, and prey capture. In Chapter 3, I report on the contribution of microscopic hairs on the ventral and dorsal surfaces of the bat wing and tail membrane to prey handling, flight kinematics, and adaptive sonar in a goal-directed insect capture task. My results show that sensory hair depilation disrupts the natural coordination between flight and echolocation behaviors, as well as changes to bats' capture strategy and decreased capture success. These findings support the hypothesis that wing membrane hairs provide sensorimotor feedback and function as airflow sensors, and perhaps more specifically flight speed sensors. In Chapter 4, using sedated big brown bats, I present an experimental plan to study S1 cortical responses to contralateral wing stimulation in a wind tunnel, where I can control air speed and wing angle. I will compare S1 responses in baseline recordings and in wing hair depilated bats. The work presented in my dissertation advances our knowledge of mechanosensory feedback for coordinating movement and adapting behavior, but many questions still remain unanswered. Below I discuss open questions and present experiments designed to address them.

Experiment 1: Contribution of dorsal and ventral wing hairs to flight control

As discussed in Chapter 3, depilation of specialized sensory hairs on the wings of big brown bats resulted in significant changes to flight kinematics and insect capture behaviors, indicating that wing membrane hairs serve as airflow (i.e., flight speed) sensors and play a critical role in sensorimotor feedback. Interestingly, we found differences in the bats' behavior when both sides of the wings were depilated (i.e., ventral and dorsal) compared to when only one side was depilated (i.e., ventral), suggesting that when only one side of the wings are depilated, an imbalance or asymmetry in sensory feedback is created.

This study and previous work have only investigated the effects of sensory hair depilation in two species of bats, the big brown bat (*Eptesicus fuscus*) and short-tailed fruit bat (*Carollia perspicillata*). Therefore, additional work should be conducted to investigate sensory hair depilation in a larger variety of bat species to obtain a comprehensive understanding of the role of sensory hairs in species-specific behaviors. Moreover, our findings on the effects of dorsal versus ventral wing membrane depilation are preliminary due to the small sample size, thus, it is important to further examine the differences between asymmetrical and symmetrical wing membrane depilation to fully understand the contribution of dorsal and ventral wing hairs on the behavior of the big brown bat.

Open questions:

(1) Is there a difference between ventral and dorsal asymmetrical wing hair depilation on the flight and insect capture behaviors of the big brown bat?

(2) Do flight and insect capture behaviors return to baseline levels following symmetrical (i.e., ventral and dorsal) wing hair depilation?

Hypothesis:

Asymmetrical depilation of a single wing surface (i.e., ventral or dorsal side) results in larger behavioral changes than symmetrical depilation (i.e., both ventral and dorsal sides). Additionally, flight and insect capture behaviors in the symmetrical depilation condition will not be significantly different from the baseline condition.

Experimental design:

Big brown bats will be trained in an open room to capture a tethered mealworm. Each bat will begin in the baseline intact condition, where they perform the insect capture task prior to any manipulation to wing hairs, followed by a sham manipulation (see Chapter 3 for sham depilation protocol). Each bat will then receive either complete dorsal or ventral wing hair depilation following the depilation protocol described in Chapter 3. This will be referred to as the **asymmetric depilation condition**. Following the asymmetric depilation, bats will receive complete depilation of the remaining side of the wing membranes. This will be referred to as the symmetric depilation condition. An outline of the depilation schedule is presented in Fig. 5.1.

For each condition, bats' flight kinematics (i.e., flight speed, wingbeat frequency,

and turn rate) and insect capture behaviors (i.e., interception strategy and capture performance) will be measured and compared to the baseline condition.

Day 1-3	Day 4-6	Day 7-9	Day 10-12
Baseline	Sham depilation	Asymmetrical depilation (dorsal or ventral)	Symmetrical depilation (dorsal and ventral)

Fig. 5.1. Outline of depilation schedule for experiment proposed in Experiment 1. Examining the differences between asymmetrical and symmetrical wing hair depilation.

Experiment 2: Neural recordings in S1 of the big brown bat

A number of previous studies have recorded neural activity in S1 of anesthetized big brown bats (Sterbing-D'Angelo et al., 2011; Sterbing-D'Angelo et al., 2017; Marshall et al., 2015). S1 neurons that represent the wing membrane have been shown to respond to air puff stimulation and fire preferentially to reversed airflow stimuli (i.e., airflow from the trailing edge to the leading edge of the wing). Further, depilation of dorsal wing hairs resulted in the loss of neural responses to air puff stimulation, whereas removal of dorsal sensory hairs did not affect neural responses to light touch stimulation, indicating that other tactile receptors in the wing membrane remained intact.

As discussed in Chapter 4, past experiments were conducted using artificial stimuli that were not able to capture the natural airflow conditions produced during flight. Furthermore, S1 neural responses were recorded with only the removal of dorsal wing hairs, but past findings from studies on the aerodynamics of bat flight have shown that leading edge vortices (LEVs) are simultaneously present on both the dorsal and ventral side of the wing in the lesser long-nosed bat (*Leptonycteris yerbabuenae*) during free

flight (Muijres et al., 2014). Therefore, additional studies are necessary in order to understand the changes in S1 neural responses under naturalistic airflow conditions, and to determine the contribution of sensory feedback from dorsal and ventral wing hairs.

Open questions:

(1) How does S1 neural activity of sedated big brown bats change with naturalistic airflow stimulation of the entire wing?

(2) How do cortical responses in the brain of awake, freely flying bats differ from those recorded under sedation in the wind tunnel?

(3) How does asymmetrical (i.e., dorsal or ventral) versus symmetrical (i.e., dorsal and ventral) depilation of wing hairs affect cortical responses in the experiments designed to answer questions (1) and (2)?

Hypothesis:

Neural recordings in S1 in sedated big brown bats

Under whole wing stimulation using a closed wind tunnel, S1 neural activity will increase at higher airflow velocities and wing angles due to the increase in stimulation of mechanosensory hairs on the wing membrane. Additionally, the response magnitude of S1 neurons will decrease following asymmetrical depilation of wing hairs and remain unchanged with subsequent depilation treatments.

Neural recordings in S1 of free-flying big brown bat

Under natural flying conditions, S1 neural activity will dynamically change with the

wingbeat. Specifically, S1 cortical responses will increase during the upstroke, when LEVs are present on both the dorsal and ventral sides of the wing membrane. Furthermore, depilation of sensory wing hairs will result in a substantial decline in cortical responses. Lastly, changes in flight kinematics will follow similar patterns as those reported in Chapter 3.

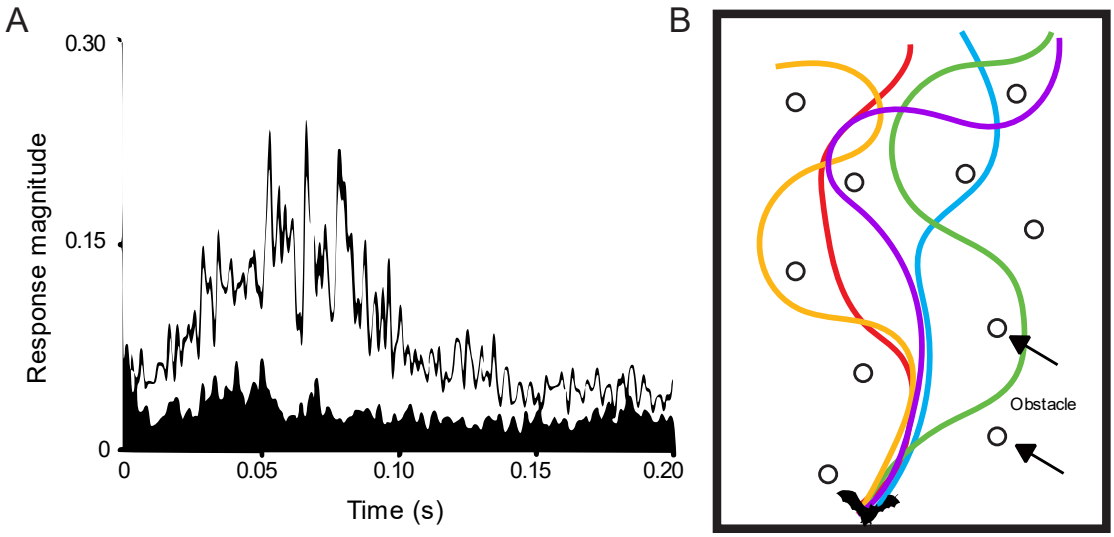

Fig. 5.2. Schematics for proposed experiments in sedated and free-flying big brown bats. (A) An example of S1 neural activity before (open line) and after (filled area) wing hair depilation (Figure adapted from Sterbing et al., 2011). (B) Schematic of obstacle avoidance task. Circles represent obstacles and examples are marked with black arrows. Illustrative examples of trajectories a bat might take around the obstacles are represented by different colored lines (orange, red, purple, blue, and green).

Experimental design:

<u>Neural recordings in S1 in sedated big brown bats</u>

Multiunit extracellular activity from S1 will be recorded in sedated big brown bats while the contralateral wing is exposed to uniform airflow at varying speeds (0 to 7 ms^{-1}) and incidence angles (0° to 30°). The airflow velocity and incidence angle of the wing will be systematically adjusted throughout each recording session. For each bat, recordings will begin with wing hairs intact, followed by asymmetrical and symmetrical depilation of

sensory wing hairs, using the depilation protocol outlined in Chapter 3. Cortical responses will be measured and compared across air speeds and angles, before and after sensory hair depilation (Fig. 5.2A).

Neural recordings in S1 of free-flying big brown bat

Briefly, multiunit extracellular activity from S1 will be recorded from awake, free-flying big brown bats while they engage in an obstacle avoidance task (Fig. 5.2B). Recordings will begin with wing hairs intact, followed by asymmetrical and symmetrical depilation of sensory wing hairs, using the depilation protocol outlined in Chapter 3. Cortical responses will be measured and compared before and after sensory hair depilation, as well as changes in flight kinematics (i.e., flight speed, wingbeat frequency, and turn rate).

Conclusion

Bats have evolved a repertoire of dynamic behaviors that have allowed them to contend with the complexity of their environments. From their diverse ecological niches to being the only mammal capable of powered flight to their wide range of adaptive sonar behaviors, bats serve as a powerful model for investigating sensorimotor integration in animals performing naturalistic behaviors. By recording aspects of bat flight and echolocation behaviors, we can gain insight into the signals used to guide their actions. In addition to their wide range of behaviors, bats navigate through three-dimensional space, offering a unique perspective into the brain that will allow us to obtain a more complete picture of how sensory signals from the environment are integrated during

naturalistic behaviors. I hope the research and findings presented in my thesis inspires further investigation of mechanosensory feedback, in both the echolocating bat and other freely behaving animals. I hope this work motivates researchers to design experiments that tap into each animal's specialized set of behaviors, to deepen our understanding of how the brain integrates information and the functional relationships between behavior and the environment.

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Curriculum vitae

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EDUCATION

Fall 2021	**POSTDOCTORAL FELLOW, ANATOMY AND NEUROBIOLOGY** University of California, Irvine | Irvine, CA Advisor: Dr. Laura Ewell, PhD
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Spring 2018	**M.A.**, **PSYCHOLOGICAL AND BRAIN SCIENCES** Johns Hopkins University | Baltimore, MD Advisor: Dr. Cynthia F. Moss, PhD
Spring 2013	**B.S., HUMAN BIOLOGY** University of California, San Diego | La Jolla, CA

RESEARCH EXPERIENCE

2014 – 2016	**STAFF RESEARCH ASSOCIATE** University of California, San Diego | La Jolla, CA Department of Biology, Section of Neurobiology Advisor: Dr. Stefan Leutgeb, PhD
2013 – 2016	**LABORATORY MANAGER** University of California, San Diego | La Jolla, CA Department of Biology, Section of Neurobiology Advisors: Dr. Stefan Leutgeb, PhD and Dr. Jill Leutgeb, PhD
2012 – 2014	**UNDERGRADUATE RESEARCH ASSISTANT** University of California, San Diego | La Jolla, CA Department of Biology, Section of Neurobiology Advisor: Dr. Stefan Leutgeb, PhD

GRANTS, FELLOWSHIPS, AND AWARDS

2021 **EPILEPSY RESEARCH TRAINING PROGRAM (NIH T32)**
T32 grant provides support to institutions to develop or enhance research training opportunities for postdoctoral fellows to be trained in epilepsy research.
Granting Agency: National Institutes of Health
Institution: University of California, Irvine | Irvine, CA
Principal Investigator: Laura Ewell

2019, 2021 **WALTER L. CLARK SERVICE AWARD**
Johns Hopkins University award recognizing a graduate student who has demonstrated an excellent record of service to the department, including active committee involvement, mentorship, and community outreach.

2019 **EXCELLENCE IN TEACHING AWARD FOR KRIEGER SCHOOL OF ARTS AND SCIENCES - FINALIST**
This award honors the best graduate teaching assistants in the School of Arts and Sciences. These teaching assistants are commended for the care and concern they take with their subject and their students.

2018 **WALTER L. CLARK TEACHING AWARD**
Johns Hopkins University award recognizing a graduate student who has demonstrated an aptitude for instruction in the classroom, leveraging their knowledge and communication skills to enhance the undergraduate education experience.

PUBLICATIONS

Sabariego, M., Schönwald, A., **Boublil, B. L.**, Zimmerman, D. T., Ahmadi, S., Gonzalez, N., ... & Leutgeb, S. (2019). Time Cells in the Hippocampus Are Neither Dependent on Medial Entorhinal Cortex Inputs nor Necessary for Spatial Working Memory. *Neuron*.

Schlesiger, M. I., **Boublil, B. L.,** Hales, J. B., Leutgeb, J. K., & Leutgeb, S. (2018). Hippocampal global remapping can occur without input from the medial entorhinal cortex. *Cell reports*, 22(12), 3152-3159.

Schlesiger, M.I., Cannova C.C., **Boublil B.L.**, Hales J.B., Mankin E.A., Brandon M.P., Leutgeb J.K., Leibold C., Leutgeb S. (2015). The medial entorhinal cortex is necessary for temporal organization of hippocampal neuronal activity. *Nature Neuroscience*, 18(8), 1123–1132.

Schlesiger, M.I., Cressey, J.C., **Boublil, B.L.**, Koenig, J., Melvin, N.R., Leutgeb, J.K., & Leutgeb, S. (2013). Hippocampal activation during the recall of remote spatial memories in radial maze tasks. *Neurobiology of Learning and Memory*, 106, 324-333.

IN PREPARATION

Boublil, B.L., Yu, C., Shewmaker, G., Sterbing, S., & Moss, C.F. (submitted). Sensory hairs for flight control and prey capture in the big brown bat, *Eptesicus fuscus*.

POSTER PRESENTATIONS

B.L. Boublil, M.J. Wohlgemuth, C.F. Moss. 2018. Inactivation of the superior colliculus alters orienting behaviors in the echolocating bat. Society for Neuroscience Abstract. Poster Presentation San Diego. November 2018.

M. Sabariego, D. Zimmerman, A. Schonwald, V. Alluri, N. Gonzalez, C. Luong, **B.L. Boublil**, J.K. Leutgeb, S. Leutgeb. 2018. Hippocampal sequential firing during delay intervals is not required for working memory performance. Society for Neuroscience Abstract. Poster Presentation San Diego. November 2018.

M. Sabariego, A. Schonwald, **B.L. Boublil**, S. Ahmadi, D. Zimmerman, N. Gonzalez, J.K. Leutgeb, S. Leutgeb. 2017. CA3 cells remain informative about the current spatial location in medial entorhinal cortex lesioned rats. Society for Neuroscience Abstract. Poster Presentation Washington D.C. November 2017.

M. Sabariego, **B.L. Boublil**, S. Ahmadi, A. Schonwald, S. Acosta, J.K. Leutgeb, R.E. Clark, S. Leutgeb. 2016. Bridging Discontinuous Events without Hippocampus and Medial Entorhinal Cortex: A Behavioral and a Physiological Evaluation. Society for Neuroscience Abstract. Poster Presentation San Diego. November 2016.

M.I. Schlesiger Maclaren, **B.L. Boublil**, J.B. Hales, J.K. Leutgeb, S. Leutgeb. 2016. Distinct hippocampal maps emerge without inputs from the spatial mapping system in the medial entorhinal cortex. Society for Neuroscience Abstract. Poster Presentation San Diego. November 2016.

S. Viana Da Silva, K. Gaur, **B.L. Boublil**, E. Lee, J.K. Leutgeb, E. Koo, S. Leutgeb. 2016. Impairments of hippocampus-dependent memory in mice with targeted expression of APP to CA3 principal neurons. Society for Neuroscience Abstract. Poster Presentation San Diego. November 2016.

M. Sabariego, S. Ahmadi, **B.L. Boublil**, J.K. Leutgeb, R.E. Clark, S. Leutgeb. 2016. Spatial Working Memory Without Hippocampus and Medial Entorhinal Cortex: A Behavioral and Physiological Evaluation. Federation of European Neurosciences Societies Abstract. Poster Presentation Copenhagen. July 2016.

S. Viana Da Silva, **B.L. Boublil**, J.K. Leutgeb, E. Koo, S. Leutgeb. 2016. Neuronal dysfunction in mice overexpressing hAPP in hippocampal CA3 principal neurons. Federation of European Neurosciences Societies Abstract. Poster Presentation Copenhagen. July 2016.

M. Sabariego, **B. L. Boublil**, G. De Guia, J. K. Leutgeb, R. E. Clark, S. Leutgeb. 2015. Hippocampal and medial entorhinal cortex lesions result in only a transient

impairment in delayed spatial alternation: Physiological evaluation of the functional recovery. Society for Neuroscience Abstract. Poster Presentation Chicago. October 2015.

B. L. Boublil, M. P. Brandon, M. Gallagher, J. K. Leutgeb, and S. Leutgeb. 2014. Hippocampal spatial coding in aged rats is altered by septal inactivation. Society for Neuroscience Abstract. Poster Presentation Washington D.C. November 2014.

M.I. Schlesiger, C.C. Cannova, E.A. Mankin, **B.L. Boublil**, J.B. Hales, J.K. Leutgeb, C. Leibold, S. Leutgeb. 2013. The medial entorhinal cortex is required for hippocampal phase precession. Society for Neuroscience Abstract. Poster Presentation San Diego. November 2013.

INVITED TALKS

Boublil, B.L., Sterbing, S., and Moss, C.F. 2019. Tactile sensing in the big brown bat, Eptesicus fuscus. Talk presented at the monthly Global SOAR/NIFTI Telecon in Baltimore, MD. May 2019.

TEACHING EXPERIENCE

GUEST LECTURES

Fall 2020 — **COMPARATIVE NEURAL SYSTEMS AND BEHAVIOR RESEARCH DISCUSSIONS**
Title: “Introduction to Animal Research”
Johns Hopkins University | Baltimore, MD
Undergraduate Course
Professor: Cynthia Moss, Ph.D.

Summer 2020 — **COMPARATIVE NEURAL SYSTEMS AND BEHAVIOR RESEARCH DISCUSSIONS**
Title: “Introduction to Bats and Biodiversity”
Johns Hopkins University | Baltimore, MD
Undergraduate Course
Professor: Cynthia Moss, Ph.D.

Fall 2017 — **INTRODUCTION TO PSYCHOLOGY**
Title: “What Drives Us: Food”
Johns Hopkins University | Baltimore, MD
Undergraduate Course
Professor: Dr. Chaz Firestone, Ph.D.

TEACHING ASSISTANTSHIPS

Spring 2019 — **BEHAVIORAL ENDOCRINOLOGY**
Johns Hopkins University | Baltimore, MD

Undergraduate Course
Professor: Dr. Kisi Bohn, Ph.D.

Fall 2018 **RESEARCH METHODS IN EXPERIMENTAL PSYCHOLOGY**
Johns Hopkins University | Baltimore, MD
Undergraduate Course
Professor: Dr. Jeff Bowen, Ph.D.

Spring 2018 **INTRODUCTION TO SOCIAL PSYCHOLOGY**
Johns Hopkins University | Baltimore, MD
Undergraduate Course
Professor: Dr. Stephen Drigotas, Ph.D.

Fall 2017 **INTRODUCTION TO PSYCHOLOGY**
Johns Hopkins University | Baltimore, MD
Undergraduate Course
Professor: Dr. Chaz Firestone, Ph.D.

2008 – 2014 **ANATOMY AND PHYSIOLOGY**
El Camino High School | Oceanside, CA
High School Course
Instructor: George Griffin

COMMUNITY ENGAGEMENT

2020 – 2021 **PSYCHOLOGICAL AND BRAIN SCIENCES OUTREACH COMMITTEE**
Departmental committee comprised of researchers, postdoctoral fellows, students, and staff whose mission is to promote equitable access to science education in our community.

2017 – 2019 **BATS AND BARCLAY ELEMENTARY - ORGANIZER**
Introduced first and fourth grade students from Barclay Elementary School to my research with bats. Used actual field recordings to teach students about sound physics, acoustics, and echolocation. Specifically, how bats use echolocation to navigate through their environment and to catch prey.

Fall 2018 **RETHINK EDUCATION PROJECT - STUDYING ECHOLOCATING BATS**
Guided lab tour and talk about studying echolocating bats for middle school students within the “Rethink Education” project.

Fall 2017 **BRYN MAWR SCHOOL – INVITED SPEAKER**
Lectured to high school students from Bryn Mawr, an all-girls private school, about my graduate research, pursuing a career in neuroscience from a woman’s perspective and answered questions regarding college and pursuing a career in STEM.

Fall 2017	**PATTERSON HIGH SCHOOL BALTIMORE CITY – INVITED SPEAKER** Lectured to high school students from Patterson High School during a visit to Johns Hopkins University about neuroscience, my current research studies, and answered questions regarding pursuing an education and career in STEM.
2016 – 2017	**STEM ACHIEVEMENT IN BALTIMORE ELEMENTARY SCHOOLS (SABES)** NSF-funded after-school program. Volunteer mentorship focused on enhancing STEM curriculum and improve the learning experience of the students.
2010 – 2012	**CLINICAL CAREER EXTENDER INTERNSHIP (CCE)** Volunteer internship focused on enhancing the quality of patient care while educating interns interested in pursuing a career in the medical field.

ACADEMIC SERVICE

2020 – 2021	**BRAIN-RELATED INDUSTRIAL, ACADEMIC, AND CONSULTATION CAREERS (BRAINIAC) COMMITTEE – CO-FOUNDER** Collaborative committee between the Psychological and Brain Sciences, Cognitive Science, and Neuroscience department. This committee was awarded the PhD Professional Development Innovation Initiative award. The PhD Professional Development Innovation Initiative is intended to ensure that Johns Hopkins PhD students, while immersed in their training, can learn about, have exposure to, and begin to explore a range of career options relevant for their field, and for their lives**.**
2018 – 2020	**ALUMNI NETWORKING HAPPY HOUR – ORGANIZER** Co-sponsored event between Psychological and Brain Sciences, Cognitive Science, Mind Brain Institute, and Neuroscience departments aimed to provide information to graduate students and postdoctoral fellows regarding non-academic careers. Responsible for inviting Johns Hopkins University alumni, reserving travel, room and board, event venue and catering.
2016 – 2021	**PSYCHOLOGICAL AND BRAIN SCIENCES GRADUATE STEERING COMMITTEE – REPRESENTATIVE** Responsible for relaying concerns, ideas, and upcoming activities to the faculty and staff, then communicating this information to other graduate students in my cohort.
2019	**HOW TO FIND A RESEARCH EXPERIENCE – INVITED PANELIST**

Discussed ways to gain research experience. Answered questions from undergraduates at Johns Hopkins University regarding how to search for the right lab, what qualities research labs are looking for, and how to contact the lab for a position.

2017 – 2019 **PSYCHOLOGICAL AND BRAIN SCIENCES COLLOQUIUM SERIES - ORGANIZER**
Responsible for inviting guest speakers, as well as organizing and coordinating their visit to our department. Organize meetings with faculty members and students.

MENTORSHIP

UNDERGRADUATE RESEARCH ASSISTANTS

2020 – 2021	David Gauthier, Johns Hopkins University
2020 – 2021	Leigh Kinsler, Johns Hopkins University
2020 – 2021	Jessie Gallegos, Johns Hopkins University
2020 – 2021	Katherine Armenta, Johns Hopkins University
2020	Kristen Chao, Johns Hopkins University
2020	Isaac Lee, Johns Hopkins University
2020	Mya Thomas, Johns Hopkins University
2020	Adriana Pereira, Johns Hopkins University
2017 – 2020	Cory Silver, Johns Hopkins University
2019	Brooke Stanicki, Johns Hopkins University
2017 – 2019	Sarah Huh, Johns Hopkins University
2019	Daniela Zapata, Johns Hopkins University
2018 – 2019	Rogelio Schouten-Hernandez, Johns Hopkins University
2017 – 2019	Sage Otterson, Johns Hopkins University
2017 – 2018	Ellie Clawson, Johns Hopkins University
2016 – 2017	Grant Shewmaker, Johns Hopkins University
2017	Omar Cardona, Johns Hopkins University
2017	Diego Gonzalez, Johns Hopkins University
2015 – 2016	Antonia Schonwald, University of California, San Diego
2015 – 2016	Stefany Acosta, University of California, San Diego
2013 – 2014	Alesha Foster, University of California, San Diego

PROFESSIONAL MEMBERSHIPS

2013 – Present ***Society for Neuroscience (SfN)***