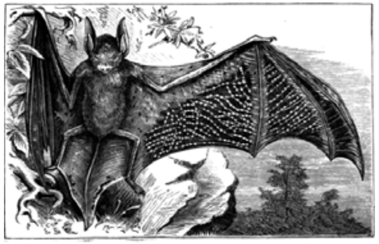


(Maxim,1912 : see ref. below)

# The neuroethology of touch in bats: cutaneous receptors of the bat wing.

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## Abstract

Although the wing is well represented in bat somatosensory cortex, surprisingly little is know of the nature and function of wing cutaneous receptors. Here we characterize two wing mechanoreceptor arrays and suggest some possible roles in bat flight and mid-air predation.

Frame A: Histology of wing membranes in the microchiropteran bats, *Antrozous pallidus* (shown in A) and *Eptesicus fuscus*, reveals regular arrays of raised-domes spaced across all wing surfaces.

Frame B: Bat domes resemble touch domes with epidermal concentrations of Merkel receptor cells (identified by quinacrine and Cytokeratin 20 antibody labeling).

Frame C: Unlike classic touch domes, each bat dome has a central hair with follicular concentrations of Merkel cells, free nerve endings and sebaceous glands, as typically found in mammalian tactile hairs. Hair-dome size and pattern vary by species, but are always found near wing bones or along intradermal elastin bands that span wing membranes.

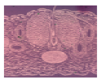
Frame D: Introduction to boundary layer air flow & lift. In primary afferent recordings, hair-domes show predominantly slow-adapting responses to direct contact, while dome hairs are most sensitive to turbulent airflow.

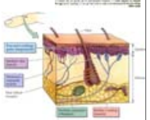
Frame E: Behavioral experiments show that after dome hair ablation bats have problems with complex flight maneuvers. Normal behavior resumes with hair re-growth. As the bat wing represents a highly adaptive airfoil, we hypothesize that dome hairs may provide feedback on boundary air turbulence necessary for estimations of lift during complex maneuvers.

Frame F: Primary afferent recordings also reveal separate arrays of fast-adapting stretch receptors located near limb joints and at points where elastin bands converge. Wing stretch receptors are highly sensitive to any membrane deformation but relatively insensitive to airflow. These receptors have large receptive fields that extend along elastin bands from an edge to the center of wing segments. Fields from opposite edges of a membrane often overlap within a central zone of enhanced tactile sensitivity. These wing zones may be important for midair predation. Behavioral experiments with bats trained to catch mealworms in midair indicate a strong preference for bats to catch airborne prey within these tactile sweet spots. *Support Contributed By: Ohio Univ.*


## Background:

To Right A late-19th C. illustration of a bat dome showing sebaceous & apocrine glands, hair follicle & indicating possible tactile receptors (ref. 1). Above is an early 20th C. illustration of bat-wing dome arrays as published in Scientific America by Sir Hiram Maxim. This illustration was used in support of Maxim's assertion that bats possessed a hypothetical (tactile-based) 6th-sense that could be used to model an early warning device that would allow ships to avoid icebergs (ref. 2). Middle right is Iggo's classic illustration of a mammalian Touch Dome (ref. 3). Lower right is a current textbook representation of the various tactile receptors found in human skin (ref. 4). The top right prey-catching photo was taken in the laboratory of Dr. H.-U. Schnitzler 1983.





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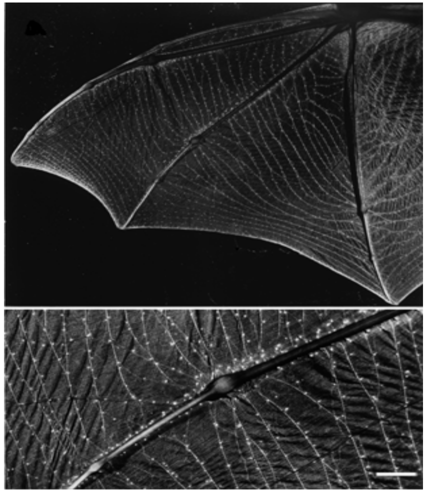
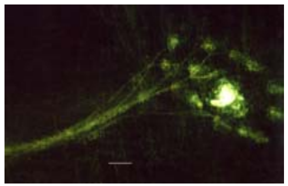


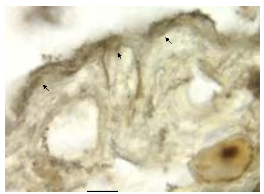
A. Above: all bat wing membranes show regular arrays of raised domes covering both ventral & dorsal surfaces. (*Antrozous pallidus* ventral surface, scale: 2 mm)

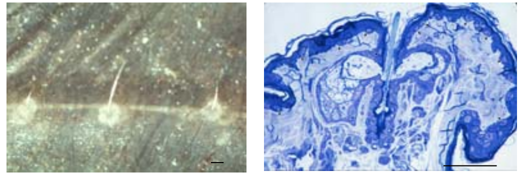
## B.

Dome Merkel cells labeled in the bat *Antrozous pallidus* with quinacrine fluorescence. (central bright spot is the hair follicle, 50 µm, ref. 5)



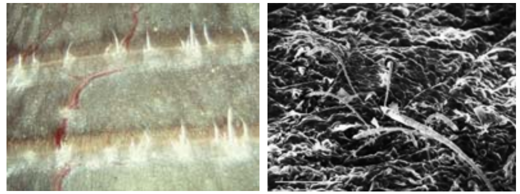
Dome Merkel cells labeled in the bat *Eptesicus fuscus* with a Cytokeratin 20 monoclonal antibody (Dako, ref. 6).





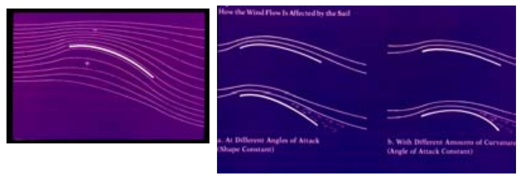
C. Above: Unlike classic touch domes, wing-membrane domes show a single, projecting hair (*Antrozous pallidus, 50 µm*).

Below: In certain wing areas (between legs), domes are often clustered together. (right, scanning electron micrograph, 100 *µm*)



## D. What do the Merkel cells/tactile hairs signal?

Below: Airfoil lift properties depend upon smooth air flow in the boundary layer next to the wing (below left). Turbulent air flow in the boundary layer often results from a mismatch between air speed & airfoil curvature/angle of attack (below right). Preliminary physiological recordings suggest that tactile hairs are specifically sensitive to turbulent air flow.




## E. Flying Bats With and Without Their Dome Tactile Hairs.

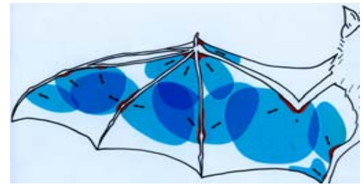
Below, left & right: Average patterns of flight elevation changes for two individual bats (Eptesicus fuscus) navigating a sharp, 90 degree corner (vertical green bar) videotaped in an enclosed room. In each figure, the orange trace indicates average flight elevations for 10 flight trials immediately after dome tactile-hair removal. The green trace in each figure represent the average elevation plots from 20 flight paths with hairs in place: 10 trials before hairs were removed and 10 trials after hairs grew back.

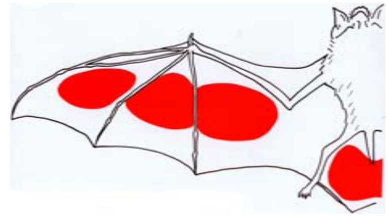
## F. Wing Stretch Receptors & Airborne Prey-Capture

Above: For mid-flight prey capture, bats rely on the wing & wing membranes as ready-made "catchers' mitts".

Below: Preliminary recordings of primary afferents (*Eptesicus fuscus & Pteronotus parnellii*) suggest the concentration of a second set of tactile receptors at strategic points near finger joints (red areas, first figure below). These receptors are insensitive to airflow, but extremely sensitive to stretching of the wing membrane. Receptive fields (light blue) often overlap (dark blue). These overlapping "sweet spots" coincide with membrane areas where flying bats prefer to gather airborne prey in mid-flight (red areas in bottom figure).

(Bats trained for mid-air capture of mealworms shot into the air).



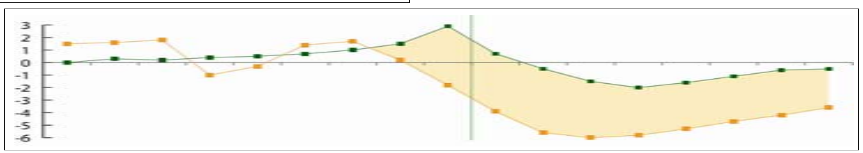


## Conclusions:

1) As the bat wing represents a highly adaptive airfoil, we hypothesize that dome hairs & Merkel cell receptors may provide necessary feedback of boundary-layer air flow. Such feedback may be important for accurate estimations of lift during complex flight maneuvers.

2) Wing stretch receptors may be important for providing tactile feedback for efficient midair capture of insect prey.

**Bat 1:**
Plots of elevation changes during a 90° turn (vertical bar)
Green trace= Wings with hairs
Orange trace= Wings without hairs




**Bat 2:**
Plots of elevation changes during a 90° turn (vertical bar)
Green trace= Wings with hairs
Orange trace= Wings without hairs