ORIGINAL PAPER

Organization of the primary somatosensory cortex and wing representation in the Big Brown Bat, *Eptesicus fuscus*

M. Chadha · C. F. Moss · S. J. Sterbing-D'Angelo

Abstract Bats are the only mammals capable of true powered flight. The bat wing exhibits specializations, allowing these animals to perform complicated flight maneuvers like landing upside-down, and hovering. The wing membrane contains various tactile receptors, including hair-associated Merkel receptors that might be involved in stabilizing bat flight. Here, we studied the neuronal representation of the wing membrane in the primary somatosensory cortex (S1) of the anesthetized Big Brown Bat, *Eptesicus fuscus*, using tactile stimulation with calibrated monofilaments (von Frey hairs) while recording from multi-neuron clusters. We also measured cortical response thresholds to tactile stimulation of the wings. The body surface is mapped topographically across the surface of S1, with the head, foot, and wing being overrepresented. The orientation of the wing representation is rotated compared to the hand representaion of terrestrial mammals, confirming results from other bat species. Although different wing membrane parts derive embryologically from different body parts, including the flank (plagiopatagium), the tactile sensitivity of the entire flight membrane (0.2–1.2 mN) is remarkably close or even higher (dactylopatagium) than the average tactile sensitivity of the human fingertip.

M. Chadha · C. F. Moss
Program in Neuroscience and Cognitive Science,
University of Maryland, College Park, MD, USA

M. Chadha · C. F. Moss
Department of Psychology, University of Maryland,
College Park, MD, USA

C. F. Moss · S. J. Sterbing-D'Angelo (✉)
Institute for Systems Research, University of Maryland,
A.V. Williams Building (115), College Park, MD 20742, USA
e-mail: ssterbin@umd.edu

Introduction

The Big Brown Bat is an insectivorous species that is widely distributed in North America. An aerial forager with an average weight of 16 g, a wing span of 32 cm and wing area of 166 cm^2 (Kurta and Baker 1990), *Eptesicus fuscus* has a favorable body mass to wing area ratio (i.e., low wing loading) for relatively slow flight (3–9 m/s) and high maneuverability (Norberg and Rayner 1987). It is an echolocating bat that has been traditionally classified under the suborder Microchiroptera. Relatively little is known about the somatosensory cortical organization in bats, with only two species of Microchiroptera (*Macroderma gigas* and *Antrozous pallidus*) and two species of Megachiroptera (*Pteropus poliocephalus* and *P. scapulatus*) studied to date (Calford et al. 1985; Wise et al. 1986; Zook and Fowler 1986; Krubitzer and Calford 1992). According to a new proposed phylogenetic classification based on molecular data, both *Pteropus* species and *M. gigas* belong to the same new suborder Yinpterochiroptera, and *E. fuscus* (this study) and *A. pallidus* to the new suborder Yangochiroptera (Teeling et al. 2005). This makes *A. pallidus* the only Yangochiropteran species whose somatosensory cortex has been studied to some extent. For a more complete understanding of the organization of somatosensory cortex in Yangochiroptera, we conducted mapping studies of the

somatosensory cortex of another species of this suborder, the Big Brown Bat.

The existence of orderly representations of the sensory surface in somatosensory cortex and other brain regions has long been known. Earliest observations of correspondence between peripheral tactile stimulation and cortical excitation were reported during the late 1930s and early 1940s (Marshall et al. 1938; Adrian 1941) in cats and monkeys. Since then, tremendous progress has been made in our understanding of the development and organization of representations of sensory surfaces in cortical and subcortical structures. Studies of animals with specialized sensory systems are especially useful, as they not only provide information on how particular sensory systems operate, but they also reveal the evolutionary forces that shape brain organization and function. Noteworthy examples of the importance of somatosensory surfaces in an animal's behavioral repertoire come from reports on their cortical representations, e.g., whisker representation in mice and rat "barrel" cortex (Woolsey and Van der Loos 1970; Petersen 2007), extreme magnification of the representation of two front teeth in naked-mole rats (Catania and Remple 2002), greatly expanded representation of the "tactile fovea" in star-nosed moles (Catania and Kaas 1997), and hand and lip representation in primates (Nelson et al. 1980).

As the only mammals with true powered flight, bats combine remarkable flight capabilities including hovering, mid-air predation, and high maneuverability, with high efficiency (Winter and von Helversen 1998). The bat wing is essentially made of all the elements of a typical mammalian forelimb, with the metacarpals greatly elongated, except for the thumb, which is not embedded in the wing membrane and is used for food handling, grooming, and climbing. The wing membrane or patagium, stretches from the side of the body to cover the entire forelimb, and the hindlimb, except the foot (Fig. 1). Part of the membrane lies between the shoulder and wrist, and is called propatagium. The wing section between the body and the fifth digit is called the plagiopatagium, and that between fingers 2 and 5, the dactylopatagium. The uropatagium or the interfemoral membrane (IFM) is the part of wing that stretches between the tail and the hindlimb. The wing membrane, besides being anisotropic and highly compliant (Swartz et al. 1996), is covered by an array of tactile sensory receptors in the form of domed, microscopic hairs (Zook and Fowler 1986). It has been hypothesized that these wing receptors might provide a continuous stream of information about air-flow patterns over the wing surface and help a flying bat optimize its wing shape, position and camber, in order to achieve and sustain complex flight maneuvers (Zook 2005, 2006).

By comparing the present findings with previously published reports, we can shed light on inter-species differences in cortical organization among flying and non-flying mammals, echolocating versus non-echolocating bats, and across the new taxonomical suborders of bats. Magnified cortical representations generally correspond to high innervation density and/or the behavioral importance of the sensory surface to the animal. If indeed the unique wing hairs and their associated tactile receptors (Merkel cells and others) as well as stretch receptors embedded in the membrane are important for sensing air-flow around the wing membrane and the membrane shape, one might expect to find an expanded representation of the wing in the somatosensory cortex, and low tactile thresholds.

Materials and methods

Experimental animals

Five adult insectivorous bats (*E. fuscus*; three males and two females) weighing between 15 and 21 g were used for this study. Bats were wild-caught in Maryland and housed in a vivarium at the University of Maryland. Bats were housed under reversed 12 h light/dark conditions and given food and water ad libitum. All experimental procedures followed National Institute of Health guidelines and were approved by the University of Maryland Institutional Animal Care and Use Committee (IACUC).

Surgical preparation

At least 1 day prior to surgery the selected bat had the fur over its scalp removed with commercially available depilatory cream (e.g., Veet). On the day of the surgery, each animal was initially anesthetized with 3% isoflurane (700 ml/min O$_2$) and anesthesia was maintained at 1–3% level during surgery and cortical recordings. Breathing was monitored visually and body temperature was maintained at about 37°C by placing the animal on a heating pad. Standard sterile surgical procedures were followed throughout the experiment. Once the animal was anesthetized, a midline incision exposing the skull was made and muscles of mastication deflected from the midline. A custom-made stainless steel head-post was then glued close to Bregma using cyanoacrylate glue (Loctite 4161). The bats were allowed to recover for 2–3 days before physiological recordings were initiated.

Electrophysiological recordings

On the day of neural recordings the bat was first anesthetized at 3% and maintained on 1–3% Isoflurane (700 ml/min O$_2$) during the entire session. The head-post was used to secure the head with a set screw to a vibration isolation

table (Kinetic Systems). A craniotomy measuring approximately 2 mm by 2 mm was performed over the somatosensory cortical region (the dura mater was left intact) and sterile saline/silicone oil (Fluka Analytical, DC 200) was used to prevent the exposed cortex from desiccation. A low impedance (~1 MΩ) tungsten reference electrode was inserted into a non-somatosensory region e.g., the visual cortex, of the opposite hemisphere through a 100 μm hole in the skull made with a polished needle. A high impedance recording electrode (15–20 MΩ tungsten, FHC Inc.) was used to record extracellularly from multiple units. The electrode was attached to a micromanipulator, oriented perpendicular to the cortical surface and lowered using a hydraulic microdrive (FHC Inc.). Recordings were made from multiple electrode penetrations, spaced 100–250 μm apart from depths of 50–250 μm, ensuring that electrode remained mostly within the supragranular layers of the cortex. The overall thickness of the somatosensory cortex varies from 800 to 1200 μm (Covey, unpublished). Each recording session lasted about 4–6 h, and each animal underwent 2–6 recording sessions spread over a period of 1–4 weeks.

Tactile stimulation

Once the electrode was mounted and set into position, the contralateral wing was spread and taped by the tip to the recording table. Subsequently, the electrode was advanced into the cortex and the wing and body surface stimulated using a set of calibrated monofilaments (von Frey hairs, North Coast). The von Frey hairs are available in sets of 20 with discrete, fixed weights. The hairs are calibrated in a logarithmic scale from 0.008 to 300 g (0.08–2943 mN), within a 5% standard deviation. Stimulation consisted of pressing the monofilaments at right angles against the skin until they bend and subsequently are released. Progressively thinner filaments were used to determine the neural thresholds. We applied the same method for determining the threshold as has been done in clinical studies, established by Johansson et al. (1980). Both wing surfaces were tested. Mapping was based solely on tactile stimulation with the calibrated von Frey hairs. Borders and center of receptive fields could not be determined with air puff stimulation, because it is not spatially confined enough and the direction of force is variable. Neurons responded always to stimulation of both wing surfaces, because the wing membrane is remarkably thin (Studier 1972). However, the thresholds were sometimes lower when the ventral side was stimulated leading to the conclusion that this side was preferred. Preference of ventral or dorsal side were not mapped separately on the cortical surface, but rather random, most likely module (column) by module (column). Therefore, we did not include this information in the graphs.

Data collection and analysis

The neural responses were amplified using a differential amplifier (Bak Electronics, MDA-4I), band-pass filtered (500–5000 Hz, Stanford Research Systems, Model SR650), monitored on an oscilloscope and played through a speaker. Receptive fields were defined on the basis of a neural activity clearly distinguishable from baseline response as monitored on the oscilloscope and the speaker. For each electrode penetration that elicited neuronal responses to tactile stimulation, receptive fields were drawn on pictures of the bat. To document and reconstruct the recording sites, drawings of the craniotomy including the vasculature were made and electrode positions marked as noted off the digital micromanipulator (Mitutoyo) using a benchmark for reference. Receptive field data from four bats was used to construct cortical surface maps of the body surface and wings. Neuronal threshold data were collected from five bats. At the end of the recording sessions, bats were given a lethal dose (0.05 ml) of sodium pentobarbital (390 mg/ml) via intraperitoneal injection.

Results

In the present study, a total of 221 electrode penetrations were made in five animals to define the organization of the primary somatosensory cortex (S1). Recording depths ranged from 50 to 250 μm relative to the onset of neuronal activity at the cortical surface. Hence, the recording sites were located mostly in the supragranular cortical layers II/III, a few possibly in layer IV. While the electrode was advanced into the cortex, the body surface of the bat, including the wing membrane, was stimulated using von Frey monofilaments to locate a region that elicited neural activity. Receptive fields mapped using this method of stimulation, were used to determine somatotopic organization of S1.

Figure 1 (lower panels) outlines the findings from two animals. The overall topography that emerges from the combined results from four animals was that of a complete and ordered representation of the contralateral body surface. The most medial part of S1 represented the hind limb, with the distal parts of the foot placed rostrally. However, for most locations that represented the foot, we made no attempt to further distinguish between representation of the single toes or phalanges, because these structures are so small in the Big Brown Bat that stimulation with von Frey hairs could not be accurately performed. The tail, including the IFM was represented lateral to the distal hindlimb. The back of the animal was represented caudo-medially. The head and face of the animal were represented in the most rostro-lateral area of S1. The receptive fields of the head
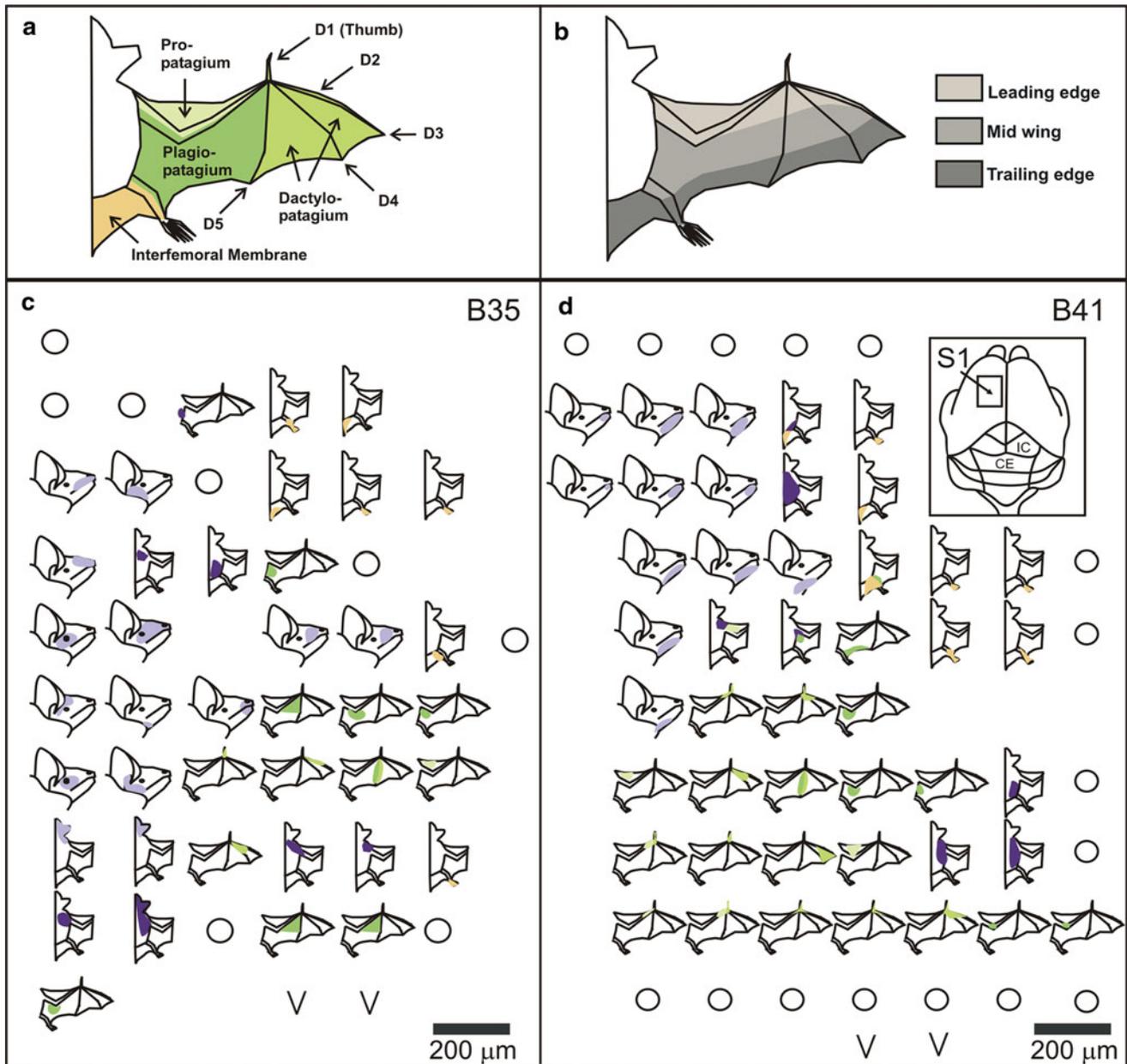
Fig. 1 *Top panels* The organization of the bat wing (**a**) and its functional areas (**b**). *D1–5* indicate digits 1–5 with *D1* being the thumb. Results of the somatosensory cortical mapping from two bats (**c**, **d**). *Colored areas* indicate receptive fields close to neuronal threshold, obtained from electrode penetrations regularly spaced within a rectangular craniotomy covering S1 (*inset panel* **d**). *Open circles* indicate penetrations with no observed somatosensory activity, and *V* indicates regions exhibiting visual activity

were very small compared to other parts of the body, and often only several millimeters in diameter. Different parts of the face including the upper lip, snout with the vibrissae, the lower lip, chin, pinna including the tragus, and the forehead had separate/non-overlapping receptive fields i.e., electrode penetrations placed only 150–250 μm apart resulted in receptive fields on distinct regions of the face.

The forelimb, along with the wing membrane, was represented centrally and caudally. The distal forelimb, including the digits and the associated membrane, were represented at the caudal border of the area. Digit 1 (D1) had small receptive fields, as compared to other regions on the body. Digits 2 and 3 (D2 and 3) had overlapping receptive fields and were situated medial to D1. Digits 4 and 5 (D4 and D5) and the associated wing membrane were located most medially in the forelimb representation. The propatagium, or the pro-wing, was represented laterally, adjacent to D1.

Fig. 2 Average cortical surface map or "homunculus" obtained from pooling data from four bats. The *left panel* shows the matched positions of recording sites in each of the four bats. Matching was done using anatomical landmarks such as median suture, bregma, and major vessels. The color scheme matches Fig. 1. *Bk* back, *D* digit, *Dac* dactylopatagium, *Ft* foot, *IFM* interfemoral membrane, *Pin* pinna, *Pla* plagiopatagium, *Pro* propatagium, *Sh* shoulder, *Tr* tragus, *V* ventrum
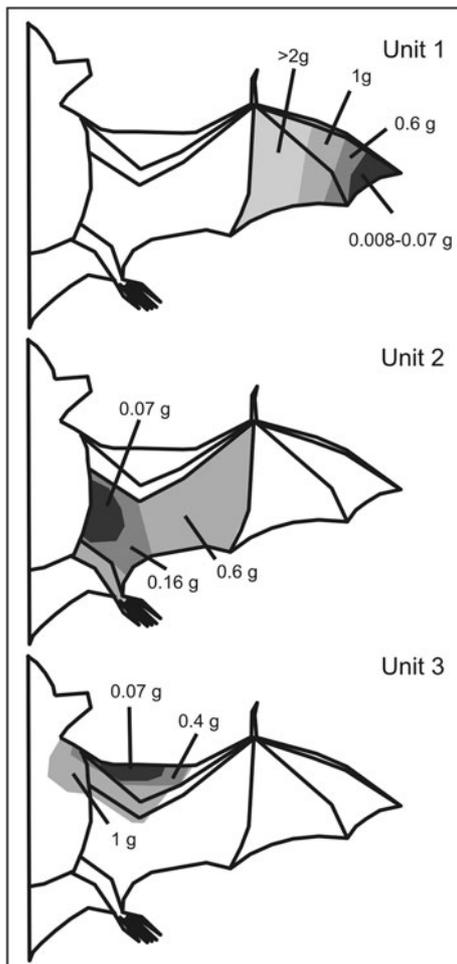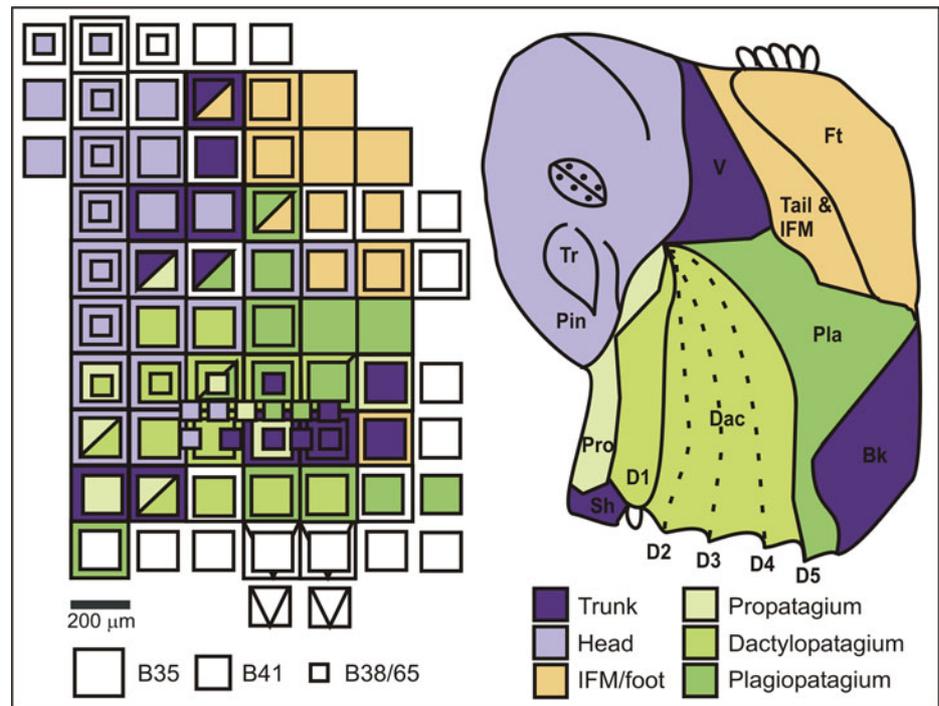
The representation of distal forelimb and the wing in S1 is reverse of the representation in all walking mammals, including primates, carnivores and rodents, where the digits are oriented rostrally with the palm placed caudally. Consequently, in the bat, the representations of D5 and plagiopatagium are adjacent to the representations of the flank and back instead of the hindlimb, and the representation of the thumb is close to the representations of the shoulder and pinna instead of the lower jaw in walking mammals. In most of our cases, D5 marked the border of receptive fields that were centered in the dactylopatagium, and was excluded from receptive fields that were centered in the plagiopatagium. In only a few cases and only at suprathreshold stimulus intensities, receptive fields crossed the D5 border. Results of somatosensory mapping from four animals were pooled to generate the cortical surface map as shown in Fig. 2.

Neurons in S1 were highly sensitive to tactile stimulation and responded to monofilament stimulation, light brushing of the skin with cotton-tipped applicators, blunt objects, and stimulation by air puffs. Receptive field size varied with location, with D1, foot, and the face region showing the smallest sizes compared to all other regions on the body. Receptive field size also varied with stimulation intensity, with greater monofilament weight resulting in bigger areas. Figure 3 shows

◄ **Fig. 3** The size of the receptive fields increases with stimulus intensity (von Frey hairs of different filament weight). Results for three cortical locations that respond to stimulation of different parts of the wing are shown. *Different shading* indicates the expansion of the receptive fields under stimulation with different filament weights
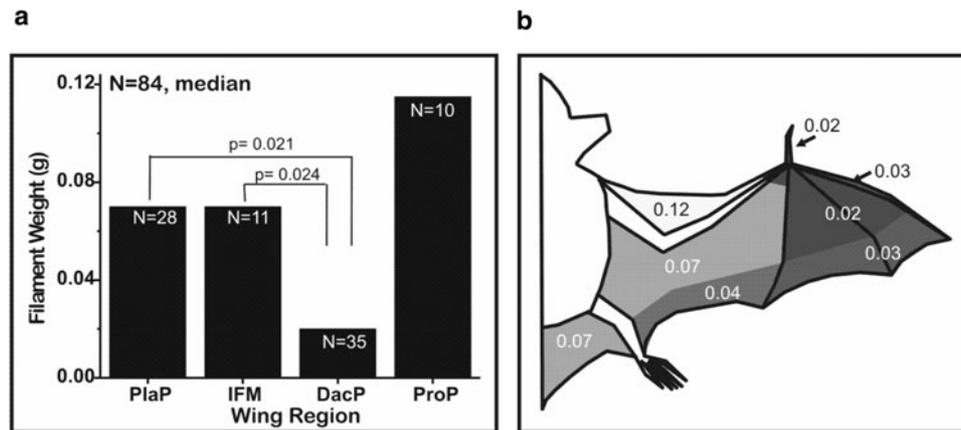
Fig. 4 Tactile response threshold as determined using calibrated monofilaments (von Frey hairs). **a** data from four parts of the wing of five bats were pooled, the plagiopatagium (*PlaP*, see Fig. 1, *N* = 28), the interfemoral membrane (*IFM*, *N* = 11), the dactylopatagium (*DacP*, *N* = 35), and the propatagium (*ProP*, *N* = 10). The thresholds of the dactylopatagium were significantly different from the IFM, and

PlaP (Mood's Median Test *p* = 0.024 and 0.021, respectively). **b** Median thresholds in gram filament weight for different functional regions. The weight in g is equivalent to a ten-fold value in mN (e.g., 0.02 g equals 0.2 mN). *Darker shading* indicates lower thresholds. Note that, e.g., the trailing edge of the PlaP, is more sensitive than the remainder of the PlaP

examples of the change in receptive field size, recorded from three different S1 locations responding to stimulation of the wing, including the trailing edge and wing tip, the mid-wing, and the leading edge, respectively.

Reducing stimulus intensity by choosing successively lighter monofilaments allowed us to determine the response thresholds of different parts of the wing in five animals. Figure 4 summarizes the results. The tactile thresholds of the plagiopatagium and the IFM were significantly higher than those of the dactylopatagium (a), with the trailing edge of the wing (including the wing-tip), and most parts of the dactylopatagium including the thumb showing a response to lowest weighted monofilaments (0.02–0.04 g = 0.2–0.4 mN), as compared to other mid-wing areas, the IFM, and the propatagium (0.07–0.12 g = 0.7–1.2 mN) (b).

Discussion

In the present study, we investigated the organization of S1 in the Big Brown Bat, *E. fuscus*. We also characterized tactile response thresholds of different regions of the bat's wings. Our findings show a complete and orderly representation of the contralateral body surface in S1 (Figs. 1, 2), consistent with the findings from other mammalian species. However, there were features of this somatotopic map that stood out. The most noticeable aspect was the overrepresentation of the wing (including the IFM), with almost a third of S1 occupied by it. This enlarged hand and wing representation is also evident in other reports on bat somatotopic maps (Calford et al. 1985; Wise et al. 1986; Zook and Fowler 1986; Krubitzer and Calford 1992). These

findings suggest that bat hand-wings have a particularly high innervation supplying the tactile mechanoreceptors. Another possibility is that flight induced mechanosensory cortical activity is influencing the size of cortical representation of the hand-wing. In either case, it remains to be established how bats might be using this stream of sensory information during flight or other behaviors. A second feature that *Eptesicus* shares with other bat species is the disproportionate increase of D1 representation, the only free digit, which is used for food handling, climbing, and grooming.

Another feature of the somatotopy in *Eptesicus* was the reversed orientation of the distal forelimb, including the wing membrane. In other words, the bat hand-wing is represented and oriented in a manner such that the digits are directed caudally. This is in contrast to the hand representation in all walking mammals examined to date (Kaas 1983), where the digits point rostrally. First noted by Calford et al. (1985) in the gray-headed flying fox, *Pteropus policephalus*, this reversed forelimb orientation has since been reported in the other bat species examined as well (Zook and Fowler 1986, Wise et al. 1986). This finding of reversed wing representation was further explored in subcortical structures in two other studies. Martin (1993) examined the dorsal column nuclei (gracile, cuneate, and spinal trigeminal nuclei, first order synaptic stop of ascending somatosensory fibers) of *Pteropus scapulatus* (little red flying fox) and did not find any evidence of a clear topography, but instead observed the body surface representation as a series of dorsomedially to ventromedially oriented bands. In a later study, Manger et al. (2001) examined the thalamus of the gray-headed flying fox to address the locus

of this reversed wing representation. Their findings revealed an inverted wing representation in the ventrobasal and posterior thalamic complexes, with the implication that ascending somatosensory fibers were getting reorganized in the medial lemniscus, between the dorsal column nuclei and the thalamus.

The significance of this inverted representation remains unknown. Calford et al. (1985) proposed that normal posturing of the bat wing, which is opposite to that of the hand orientation in walking mammals, serves as a constraint for the observed bat cortical somatotopy. The increase of wing surface by addition of the plagiopatagium, which derives from the flank (Cretekos et al. 2005), and attaches to D5, might have been the evolutionary force for the rotation of the hand representation. The caudal representation of the distal digits might just be a byproduct of this rotation, because the dactylopatagium is a product of blocked apoptosis of the embryonal interdigital webbing (Weatherbee et al. 2006).

Despite the unusual representation of the distal forelimb and wing, the basic somatotopic representation of *E. fuscus* is similar to mammalian cortical maps (Kaas 1983). Nevertheless, when compared to the findings from flying fox (Calford et al. 1985), differences relating to the phylogeny and natural behaviors of the two bat species become evident. Compared to the flying fox (*Pteropus* sp.), a non-echolocating Yinpterochiropteran bat, *Eptesicus* has a much larger pinna representation, relating to the relatively larger pinna size and its importance in echolocation behavior. Another noticeable difference relates to the foot representation in the two species. Whereas receptive fields generally encompassed more than one digit, or the entire foot of *Eptesicus*, *Pteropus* exhibits an enlarged and well-defined foot representation, with individual digits clearly discernible. Similar differences in cortical somatotopy were also highlighted by Wise et al. (1986), between their findings from the Australian ghost bat, *M. gigas*, (a Microchiropteran and Yinpterochiropteran) and the flying fox, also a Yinpterochiropteran, (Calford et al. 1985) which might be attributable to the difference in the overall size of the foot.

In addition to investigating the somatotopic organization of S1 in *E. fuscus*, we also measured the tactile response thresholds of different regions of its wings using von Frey monofilaments. Thresholds were generally low on all wing locations, matching or exceeding the average sensitivity of the human finger tip (Johansson et al. 1980).

The findings presented here raise a number of important questions with regards to the central representation of the somatosensory periphery, and its importance in the behavioral repertoire of bats. The findings of a large wing representation in S1, and extremely low thresholds for tactile sensitivity, point to the importance of the sensory feedback offered by the bat hand-wing. From a neuroetho-logical perspective, how bats use this stream of sensory information during flight, or the tactile feedback provided while utilizing the wings and/or the tail membrane for swooping prey in mid-air, is yet unknown. It would be of great interest to unravel the underlying sensorimotor circuits, and the details of the neurohistology of the chiropteran wings. Recent experiments using quantitative flow visualization techniques have revealed that flying bats generate complex wake patterns, with inverted vortex loops that are shed near the wing tip (Hedenström et al. 2007), and the presence of leading edge vortices during mid-downstroke (Muijres et al. 2008). By noting cortical thresholds to tactile stimulation intensity at different wing regions, we get indirect evidence of the importance of these regions in sensing air-flow patterns to provide sensory feedback for optimal flight control. Hence, micro-air vehicles and air probes for aviation could be improved by implementing biomimetic version of the bat's wing sensor array.

References

Adrian ED (1941) Afferent discharges to the cerebral cortex from peripheral sense organs. J Physiol 100:159–191

Calford MB, Graydon ML, Huerta MF, Kaas JH, Pettigrew JD (1985) A variant of the mammalian somatotopic map in a bat. Nature 313:477–479

Catania KC, Kaas JH (1997) Somatosensory fovea in the star-nosed mole: behavioral use of the star in relation to innervation patterns and cortical representation. J Comp Neurol 387:215–233

Catania KC, Remple MS (2002) Somatosensory cortex dominated by the representation of teeth in the naked mole-rat brain. Proc Natl Acad Sci 99:5692–5697

Covey E (unpublished) A stereotaxic brain atlas of the Big Brown Bat, *Eptesicus fuscus*. University of Washington

Cretekos CJ, Weatherbee SD, Chen CH, Badwaik NK, Niswander L, Behringer RR, Rasweiler JJ (2005) Embryonic staging system for the short-tailed fruit bat, *Carollia perspicillata*, a model organism for the mammalian order Chiroptera, based upon timed pregnancies in captive-bred animals. Dev Dyn 233:721–738

Hedenström A, Johansson LC, Wolf M, von Busse R, Winter Y, Spedding GR (2007) Bat flight generates complex aerodynamic tracks. Science 316:894–897

Johansson RS, Vallbo ÅB, Westling G (1980) Thresholds of mechano-sensitive afferents in the human hand as measured with von Frey hairs. Brain Res 84:343–351

Kaas JH (1983) What, if anything, is SI? Organization of first somato-sensory area of cortex. Physiol Rev 63:206–231

Krubitzer LA, Calford MB (1992) Five topographically organized fields in the somatosensory cortex of the flying fox: microelectrode maps, myeloarchitecture, and cortical modules. J Comp Neurol 317:1–30

Kurta A, Baker RH (1990) *Eptesicus fuscus*. Mammalian Species 356:1–10

Manger PR, Rosa MG, Collins R (2001) Somatotopic organization and cortical projections of the ventrobasal complex of the flying fox: an "inverted" wing representation in the thalamus. Somatosens Mot Res 18:19–30

Marshall WH, Woolsey CN, Bard P (1938) Cortical representation of tactile sensibility as indicated by cortical potentials. Science 85:388–390

Martin RL (1993) Representation of the body surface in the gracile, cuneate, and spinal trigeminal nuclei of the little red flying fox (*Pteropus scapulatus*). J Comp Neurol 335:334–342

Muijres FT, Johansson LC, Barfield R, Wolf M, Spedding GR, Hedenström A (2008) Leading-edge vortex improves lift in slow-flying bats. Science 319:1250–1253

Nelson RJ, Sur M, Felleman DJ, Kaas JH (1980) Representations of the body surface in postcentral parietal cortex of *Macaca fascicularis*. J Comp Neurol 192:611–643

Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Phil Trans Royal Soc Lond 316:335–427

Petersen CCH (2007) The functional organization of the barrel cortex. Neuron 56:339–355

Studier EH (1972) Some physical properties of the wing membrane of bats. J Mammal 53:623–625

Swartz SM, Groves MS, Kim HD, Walsh WR (1996) Mechanical properties of bat wing membrane skin. J Zool 239:357–378

Teeling EC, Springer MS, Madsen O, Bates P, O'Brien SJ, Murphy WJ (2005) A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307:580–584

Weatherbee SD, Behringer RR, Rasweiler JJ, Niswander LA (2006) Interdigital webbing retention in bat wings illustrates genetic changes underlying amniote limb diversification. Proc Natl Acad Sci USA 103:15103–15107

Winter Y, von Helversen O (1998) The energy cost of flight: do small bats fly more cheaply than birds? J Comp Physiol B 168:105–111

Wise LZ, Pettigrew JD, Calford MB (1986) Somatosensory cortical representation in the Australian ghost bat, *Macroderma gigas*. J Comp Neurol 248:257–262

Woolsey TA, Van der Loos HV (1970) The structural organization of layer IV in the somatosensory region (SI) of mouse cerebral cortex. The description of a cortical field composed of discrete cytoarchitectonic units. Brain Res 17:205–242

Zook JM (2005) The neuroethology of touch in bats: cutaneous receptors of the wing. Soc Neurosci Abstr 78:21

Zook JM (2006) Somatosensory adaptations of flying mammals. In: Kaas JH (ed) Evolution of Nervous Systems, vol 3. Academic Press, Oxford, pp 215–226

Zook JM, Fowler BC (1986) A specialized mechanosensory array of the bat wing. Myotis 23–24:31–36