PRIMATE-LIKE RETINOTECTAL DECUSSION IN AN ECHOLOCATING MEGABAT, ROUSETTUS AEGYPTIACUS

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Abstract—The current study was designed to reveal the retinotectal pathway in the brain of the echolocating megabat Rousettus aegyptiacus. The retinotectal pathway of other species of megabats shows the primate-like pattern of decussation in the retina; however, it has been reported that the echolocating Rousettus did not share this feature. To test this prior result we injected fluorescent dextran tracers into the right (fluororuby) and left (fluoroemerald) superior colliculi of three adult Rousettus. After a 2-week survival period the animals were killed, fixed via transcardial perfusion, and the retinas whole mounted and examined under fluorescent excitation to reveal the pattern of retrograde transport. Red and green labeled retinotectal ganglion cells were found in side-by-side patches on either side of a vertical decussation line in the temporal retina of all six retinas. The Rousettus examined thus exhibited the same pattern of retinal decussation as reported previously for other megabats and primates, but unlike that seen in other mammals. The current result indicates that the prior study appears to have suffered technical problems leading to an incorrect conclusion. The results of our study indicate that, as may be expected, all megabats share the derived retinotectal pathway once thought to be the exclusive domain of primates. The current study provides additional support for the diphyletic origin of the Chiroptera and aligns the megabats phylogenetically as a sister group to primates. © 2008 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: evolution, Mammalia, vision, flying primate, Chiroptera, midbrain connectivity.

Bats present an interesting evolutionary dilemma that has not been settled despite accumulating evidence and strong statements from sides supporting either a mono- or diphyletic origin of the Chiroptera. The prevailing view, supported by DNA evidence, is that megabats and microbats are monophyletic and therefore have a common flying ancestor (Murphy et al., 2001). This same DNA evidence also aligns megabats and rhinolophoids microbats, the two different kinds of bats, in an arrangement called “paraphyly of microbats” (Teeling et al., 2002). Rhinolophoids have a complex nose leaf combined with the most sophisticated, Doppler-shift compensated laryngeal echo-location; they have microchromosomes in their karyotype; and they have a relatively simple brain organization (excluding the auditory system) resembling that of insectivores (Manger et al., 2001; Maseko and Manger, 2007). In contrast, megabats have no nose leaf or laryngeal echo-location, a normal karyotype, a unique papillated retina and a complex brain (Rosa, 1999; Manger and Rosa, 2005; Maseko et al., 2007) with visual connections akin to the pattern found otherwise only in primates (Allman 1977; Pettigrew, 1986). Molecular evidence from serum proteins (Schreiber et al., 1989), alpha-crystallin (Jaworski, 1995) and other proteins contradict the DNA evidence that aligns rhinolophoids with the very different megabats, as does morphological analysis (Jones et al., 2002).

The alternate view is the “flying primate” hypothesis, which has a long history beginning with Linnaeus (1758), who placed a megabat with primates, championed by Smith (1980) and revived in a modern version which stresses the large number of derived features shared between primates and megabats and not found in the microbats (Pettigrew et al., 1989; Maseko et al., 2007). In this thesis, the characters used to link megabats and microbats are all flight-related, including the DNA sequences which seem to have undergone similar convergent changes in base composition as a result of mutational biases heightened by the intense metabolic demands of flight (Pettigrew, 1994; Pettigrew and Kirsch, 1998). Although considered unlikely by some, convergence of nucleotide sequences is supported by the close similarity in BLAST searches of COI DNA sequences in rhinolophoids and birds! Convergence of sequence structure is also well described in lysozyme of leaf-eating colobus monkey and cow, which associate closely and anomalously in molecular trees if no other information is provided (Hammer et al., 1987). The importance of the “flying primate” hypothesis, if correct, is that it would indicate that flight has evolved twice in mammals. It would also offer a new sister group, with as many taxa as the primates themselves, with which to help understand primate evolution. This approach to bat phylogeny would also offer a new model for the effect of high metabolic rate on the genome and the evolution of isochores discovered by Bernardi and colleagues (e.g. Sabeur et al., 1993).

The echolocating megabat, Rousettus aegyptiacus, presently stands apart in the debate, since there was a failure to demonstrate in this species the primate-like retinotectal pathway (Thiele et al., 1991) that had been previously documented in various species of the megabat...
genera *Pteropus* and *Rousettus* in two other studies (Pettigrew, 1986; Pettigrew et al., 1989; Rosa and Schmid, 1994). If this represented a real difference within the sub-order of megabats, it would mean that the evolution of a different form of tongue-clicking echolocation in *Rousettus* was also accompanied by visual changes, indicating that intraordinal changes in major pathways of the brain could take place more rapidly than commonly observed (Manger, 2005). On the other hand, the possibility of a technical flaw has been raised (Rosa and Schmid, 1994). Megabats fly with the rostrum of the skull inclined markedly downwards, yet the rostrum was placed horizontally in the study by Thiele and colleagues (1991), thus elevating the visual axes and resulting in their electrophysiological exploration being confined to the far inferior visual field, where even primates lack the sharp decussation between the visual fields of the midbrain that is seen on axis.

The present study was designed to resolve this confounding issue in the mono- vs. di-phyletic origin of bats debate using anatomical tracing techniques that would unequivocally determine whether the visual system of *Rousettus* is primate-like or not. We placed a red fluorescent tracer (fluororuby) into the right midbrain and a green fluorescent tracer (fluoroemerald) into the left midbrain and examined the pattern of retrograde transport to the retinas. We found the primate-like pattern of retinal decussation, with fluorescently labeled retinotectal ganglion cells in two opposite-colored distributions on either side of the vertical meridian, exactly as found in primates but not other mammals. Thus, all members of the sub-order Megachiroptera are likely to possess primate-like retinotectal pathways, including the tongue-click echolocating genus *Rousettus*. This intraordinal uniformity helps to reaffirm the value of using brain traits in determining interordinal phylogenetic relations as well as providing added support for the flying primate hypothesis.

**EXPERIMENTAL PROCEDURES**

Two adult females and one adult male Egyptian rousette (*Rousettus aegyptiacus*) weighing around 120 g were used in the current study. The megabats were captured in a cave adjacent to Lega-manteetse Nature Reserve in Limpopo Province, South Africa under the permission and supervision of the Limpopo Provincial Nature Conservation Directorate. All animals were treated and used according to the guidelines of the University of the Witwatersrand Animal Ethics Committee, which parallel those of the National Institutes of Health for the care and use of animals in scientific experimentation. The number of animals used in the current study was the minimum required to obtain a reliable result and the experiments were conducted in such a way as to alleviate any undue suffering.

For injection of tracer into the superior colliculus the animals were initially anesthetized with i.m. doses of ketamine hydrochloride (40 mg/kg, Aneket-V diluted in sterile water) and xylazine (2 mg/kg, Chanazine diluted in sterile water) and placed in a stereotaxic frame. Anesthetic level was monitored using the eye blink and withdrawal reflexes in combination with measurement of the heart rate and tissue oxygenation level. If extra anesthesia was required a dose equal to half the initial dose was administered. The occipital cortex was exposed under aseptic conditions and aspirated to expose the dorsal surface of the midbrain allowing direct visual identification of the superior colliculus. Following this approximately 5 μl of tracer was delivered into the anterior pole of superior colliculus using a glass micropipette glued to the end of a 10 μl Hamilton microsyringe to minimize damage to the midbrain in these small brains. We injected two fluorescent dextran tracers, fluororuby and fluoroemerald (5% in 0.1 M phosphate buffer (PB), Molecular Probes), into the left and right superior colliculi respectively. After completion of the injections, a soft contact lens was cut to fit over the exposed cerebral cortex and region of aspersion, the retracted dura pulled over the contact lens, and the excised portion of bone repositioned and held in place with dental acrylic. The temporal muscles were reattached using surgical glue and the midline incision of the skin sutured. Following surgery antibiotics were administered as a single dose in all cases (0.1 ml/kg, Peni-la, a long acting penicillin-based antibiotic) and atipamezole hydrochloride (Antisedan, 0.5 mg) was given to reverse the effects of xylazine.

Following a 2-week recovery period the megabats were placed under deep barbiturate anesthesia (Euthanize, 200 mg sodium pentobarbital/kg, i.p.), then perfused intracardially upon cessation of respiration. The perfusion was initially done with a rinse of 0.9% saline solution at 4 °C, followed by a solution of 4% paraformaldehyde in 0.1 M phosphate buffer (PB) (approximately 1 ml/kg of each solution). The bats were dark-adapted and the eyes covered during perfusion to reduce adherence of the pigment epithelium to the retina. Brains were then removed from the skull and post-fixed overnight in 4% paraformaldehyde in 0.1 M PB, and then allowed to equilibrate in 30% sucrose in PB. For each brain the midbrain and diencephalon was dissected away from the remainder of the brain in a single block and sectioned in a coronal plane as a one in three series of 50 μm thick sections and stained for Nissl substance, reacted for cytochrome oxidase, or directly mounted onto 0.5% gelatin-coated slides for observation under fluorescent excitation. The eyes were dissected free from the head and the retinas dissected from the eye and manually flattened. The retinas were mounted on gel-coated slides, covered in glycerol and coverslipped. Images were collected using 10× objective on a Zeiss CSM 510 Meta confocal microscope, whose custom software allowed the automatic compilation of two superimposed montages, for rhodamine and FITC excitation respectively. The montages were later merged in the “Channels” (RGB) option of Photoshop.

**RESULTS**

Reconstruction of the midbrain injection sites showed that they were localized to the anterior pole of the superior colliculus in all six injections (Fig. 1). The core of each injection site was less than 1 mm in diameter and in all cases spanned the superficial to deep layers of the colliculus. Neither fluororuby nor fluoroemerald label crossed the midline of the midbrain in any of the three bats. In keeping with the localized injection sites there was a corresponding, highly-specific pattern of labeling in the retina. The ipsilateral retina always had labeling in a temporal crescent with a sharply defined vertical boundary on the nasal side in all six cases (two different labels in three bats; fluororuby-labeled, ipsilateral retinotectal neurons in a temporal crescent of the three left retinas and fluoroemerald, ipsilateral retinotectal neurons in a temporal crescent of the three right retinas). The contralateral retinotectal ganglion cells were labeled in the nasal retina, with a vertical temporal boundary which was slightly more diffuse compared with the ipsilateral projection (Fig. 1) and which aligned with the nasal boundary of the ipsilateral retinotectal ganglion cells having the opposite fluorescent tag. Be-
Fig. 1. Retinotectal decussation in *Rousettus*. Montage of the ganglion cells on each side of the naso-temporal decussation showing a sharper transition for the ipsilateral retinal ganglion cells (IPSI) than for the contralateral-projecting ganglion cells (CONTRA), which are found weakly scattered 1–2 mm on the temporal side of the decussation (A). The small white rectangle in the fully reconstructed right retina of case three (left column) shows the approximate location from which the montage was reconstructed. In all three cases (case 1, case 2, case 3), retrograde label showed a naso-temporal decussation, with right retinas showing rhodamine-labeled ganglion cells on the nasal side of the decussation and an adjacent patch of fluorescein-labeled ganglion cells on the temporal side. In left retinas there was a complementary pattern of labeling. In all three cases the left superior colliculus was injected with fluororuby (rhodamine) and the right superior colliculus was injected with fluoroemerald (fluorescein) (B) and 2 weeks were allowed for retrograde transport to the retina. Sections through the midbrain showed that the label had been confined to the superior colliculus in all three cases (fluororuby and fluoroemerald injection sites). The injection sites for case one are shown in B, as well as immediately adjacent sections reacted for cytochrome oxidase (C) and stained for Nissl substance (D). The scale bar~1 mm in D and applies to B, C, and D. The variation in the size of the temporal crescent of ipsilateral label was due to unavoidable, variable loss of small amounts of peripheral retinal tissue during transection of the eyeball and dissection.

cause there were two labels, one for each retina, this pattern could be double-checked in each retina, where the naso-temporal decussation pattern had opposite colors in each retina (Fig. 1). We thus had a robust internal control for any leakage of label to the other side that might have compromised the decussation pattern and given the false impression that retrograde label involved the whole retina.

Retinotectal ganglion cells are the most diverse of any population, including the very largest and the smallest in the retina. This diversity was evident in the population that was labeled following injection (Fig. 1).

**DISCUSSION**

The question raised about the status of the visual pathways in Rousettus aegyptiacus was affirmatively settled by this study: i.e. Rousettus has the primate-like pattern of retinotectal connections (Fig. 2). This suggests that the previous electrophysiological investigation of Rousettus was technically flawed by the use of an inappropriate head orientation, as pointed out previously by Rosa and Schmid (1994). The earlier anatomical study of Thiele et al. (1991) lacked the strong controls we used against spread of label to the opposite side. The very large amount of tracer that they used was not credibly confined to one side by the straight midline edge that they show (their Fig. 4, R23). This edge suggests a septum that is restraining diffusion across the midline, in contrast to the widespread pattern of diffusion in all other directions, even though there is no such septum in the midbrain. This interpretation is supported by the fact that Thiele et al. (1991) actually obtained part of the "primate-like result" that they claimed was absent, in the form of a sharply decussated pattern of retinotectal ganglion cells in the ipsilateral retina (their Fig. 6). If this ipsilateral representation were not matched by a corresponding decussation in the contralateral retina, it would be entirely unphysiological, with huge convergent binocular disparities measured in tens of degrees, instead of the slightly divergent binocular disparities that they actually observed. So we can presume that the apparent absence of a contralateral decussation is due to technical problems, most likely a result of spread of label. Contamination of the anterior pole of the opposite superior colliculus via the injected pretectum would label, and so eliminate, the expected, unstained, temporal crescent of the contralateral retina, thus creating the whole field distribution that was observed in the contralateral retina. The pattern of anterograde label that they claim to be partially incompatible with the primate pattern has a small anterior defect in the ipsilateral retinotectal input that is consistent with damage to the temporal retina precisely where the needle, without a mitigating micropipette, was inserted in this comparably small eye (their Fig. 8, left). Other anterograde studies in Rousettus have verified that the retinotectal projection is consistent with the primate-like pattern, with an input to the anterior pole of both superior colliculi from the same eye (Pettigrew et al., 1989). The presence of this anterior pole input, representing the binocular field of the ipsilateral eye, can be inferred in the bats of the Thiele et al. (1991) study from the strong decussated labeling that they observed in the ipsilateral temporal hemiretina of Rousettus.

In summary, many of the primate-like features that are claimed to be absent are inconsistent with other features that they found in Rousettus, such as the ipsilateral decussation, which cannot be reconciled with the absence of a corresponding decussation in the contralateral retina, nor can it be reconciled with an absent projection to the anterior pole of the superior colliculus where the temporal retina is represented. These inconsistencies can readily be

**Fig. 2.** Schematic diagrams of the retinotectal and retinogeniculate pathways in a generalized mammal in comparison to that seen in the megabats and primates that share a common organization of the retinotectal pathway to the exclusion of all other mammals including microbats. In contrast to the generalized mammalian plan, primates and megabats achieve binocular integration at the level of the superior colliculus, whose anterior pole has superimposed maps of the ipsilateral (4, 5 in the megabat diagram, middle) and contralateral (1, 2 in the megabat diagram) eyes' contralateral hemifield. The numbering shown on the megabat diagram applies equally to the primate diagram, with the proviso that "higher" primates, such as anthropoids and apes, would have a higher proportion of the representation concerned with the region of binocular overlap. This arrangement is like that achieved in all mammals at the level of the lateral geniculate nucleus, but is unknown at the midbrain level except for megabats and primates. The generalized mammalian plan, at left, represents the complete contralateral retina and therefore both hemifields. This arrangement is unlike that achieved at the level of the lateral geniculate nucleus in the same mammals and conforms to the ancestral retinotectal pattern found generally in vertebrates.
explained technically by problems with head orientation, by diffusion of tracer to the opposite side and by a small amount of local damage to the temporal retina of the small eye.

Phylogeny estimated from brain traits

In the continuing debate over the origins of bats, DNA sequence data has come up against conflicting brain data, with a common view being to discredit the value of brain data for phylogeny, a view that was reinforced by the apparent failure of the visual pathways of Roussettus to conform to the pattern observed in other megabats and primates. This issue can be revisited now that this failure has been corrected and ordinal classifications are being shown to have stability and validity from other kinds of brain data (Maseko and Manger, 2007; Maseko et al., 2007), not to mention the visual connections apart from the retinotectal projections, such as the primate-like lamination pattern of lateral geniculate nucleus in megabats (Pettigrew et al., 1989), their primate-like, highly elaborated visual cortex, which is the largest relative to total cortical area of any mammal (Rosa et al., 1993) and their early-maturing, temporal visual area whose organization and position is like the unique primate area MT (Rosa, 1999). In fact there are many reasons for discounting the DNA data on bats rather than the brain data, including a number of molecular studies using protein sequence data that conflict with DNA and support the inferences from the brain. For example, using more than 20 different monoclonal antibodies against serum protein epitopes, Schreiber et al. (1994) showed that the nearest sister group to the primates was megabats, with microbats being only distantly related. Similarly, other protein sequence data, such as hemoglobin, alpha-crystallin and opsin, all split the bats (Pettigrew et al., 1989; Jaworski, 1995; Wang et al., 2004). Recent work on substitutions in the highly conservative FoxP2 gene also shows no support whatever for the extraordinary pairing of megabats and rhinolophid microbats nor any support for monophyly of megabats and microbats (Li et al., 2007).

How then to explain the overwhelming bootstrap support for bat monophyly from DNA sequences, not to mention the extraordinary grouping of megabats with rhinolophoids? Molecular convergence between these two different groups of bats is one possible explanation, like the convergent sequences of lysozyme in leaf-eating monkeys and the cow, which are placed together on a phylogenetic tree based on these sequences (Hammer et al., 1987). Moreover, DNA errors are not unprecedented, with the eukaryote, Dictyostelium, being strongly placed by DNA in the prokaryotes (Loomis and Smith, 1995) and the cephalochordate, Amphioxus, firmly placed by DNA outside the chordates (Naylor and Brown, 1998). In both these cases, the error in DNA sequences was corrected by using protein sequence data. The likely source of error in the case of bat DNA is well described (Pettigrew, 1994; Pettigrew and Kirsch, 1998), although largely ignored by recent studies (Teeling et al., 2002, 2005). Both microbats and megabats have unusually high AT levels in their DNA, with megabats having the highest level in vertebrates (75%) (Arrighi et al., 1972). Because of the isochore phenomenon, where long tracts of DNA tend to have a uniform AT content, even in non-coding sequences (Sabeur et al., 1993), the same gene can have a highly similar sequence in unrelated bats because of the AT bias. Due to this bias, tree-building algorithms anomalously associate unrelated bats whose similarity in DNA sequence has arisen independently, not as a result of common ancestry. A dramatic example of this association by convergent DNA is the proposed megabat-rhinolophid link (Teeling et al., 2002), a probable result of the fact that megabats and rhinolophid microbats have the most modified genomes among mammals, these independent genomic modifications having occurred independently because of the high metabolic demands of flight (Pettigrew and Kirsch, 1998). In these terms, the DNA data on bats are those requiring skepticism and caution in phylogeny, not the brain data, which are consistent when compared with such widely divergent data as the protein sequence data already mentioned, reproductive characters such as menstruation (present in megabats and primates; Zhang et al., 2007), the structure of the penis (Smith, 1980), allometry of the forelimb (Pettigrew et al., 1989), and cranium (Hill and Smith, 1984).

Click echolocation and the brain

The recently proposed phylogeny of bats describing megabats and rhinolophoids as sister taxa has provoked some unwarranted speculation about the evolution of echolocation, whose laryngeal version is supposed to have disappeared in the megabats, only to be resurrected in a far inferior tongue-clicking form in Roussettus. A recent MRI study has concluded, based on this scenario, that the larger inferior colliculus of Roussettus supports a link with microbats, which have a very large inferior colliculus indeed (Hu et al., 2006). We agree that Roussettus has a slightly larger inferior colliculus than other non-echolocating megabats, but note that this is still a far cry from the greatly enlarged microbat inferior colliculus. It should be emphasized that the tongue-clicking echolocation of Roussettus has no physiological or evolutionary connection to the laryngeal type of echolocation of microbats. This was a well-accepted fact until the new paraphyly of microbats was proposed. We think that a more likely evolutionary scenario (in fact the prevailing one until recently) is that Roussettus tongue-click echolocation is a derived feature and that the enlarged inferior colliculi are also a derived feature of Roussettus that arose as a response to the needs of detecting echoes of tongue clicks, a scenario with exactly the opposite polarity to that proposed by Hu et al. (2006) in which Roussettus is primitive and linked to microbats.

The “flying primate” hypothesis is thus capable of illuminating and rationalizing many current problems in phylogeny. An example of a problem that could be solved in this way is the mechanism of the evolution of the primate lateral geniculate nucleus, which undergoes a rotation from prosimians to anthropoids, perhaps driven by the development of the adjacent pulvinar, whose early stages
might be represented by the least-rotated, dorsolateral position of the megabat and dermopteran geniculates (Pet-
tigrew et al., 1989). These and many other problems in
brain evolution could be tackled under the rubric of the
“flying primate” hypothesis.

Acknowledgments—The authors would like to thank Mr. Stan
Rogers of the Limpopo Province Biodiversity Unit and Mr. Adhil
Bhagwandin and Dr. Oleg Lyamin for assistance with capture
of the animals studied. We would also like to thank the staff of
the Central Animal Facility, University of the Witwatersrand for
their assistance with animal care and surgical procedures. This work
was funded by the Department of Education South Africa research
incentive scheme and the National Research Foundation of South
Africa.

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(Submitted 5 February 2008)

Please cite this article in press as: Pettigrew JD, et al., Primate-like retinotectal decussation in an echolocating megabat, ROUSET-

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