

terms of motor commands — turned out to be wrong, the data were beautiful and for the first time put the motor system on the forefront of cognitive processes.

Do you have any strong views on journals and the peer review system? Yes. I think that the present review system is much less ‘honest’ and more biased than it was in the past. Twenty years ago, the reviewers cared about the results, checked carefully if the data had been collected correctly and whether appropriate controls had been carried out. The authors were free (within limits) to interpret them and to speculate on their significance. Now, reviewers most frequently jump on conclusions and evaluate positively only those studies that match their own favorite ideology or, worse, their own data — if they don’t, they reject the paper right away, even when the data are new and well collected. It seems that often the experiments under scrutiny are not read at all by the reviewer, or read only to find something that may justify their own *a priori* views. This behavior is probably the result of the present strong competition for grants and positions, as well as a lack of time.

What is the best advice you’ve been given? Probably that given me by John Eccles, who visited my lab at Parma in the eighties. I was studying the properties of the ventral premotor cortex in the monkey and, to my surprise, our data showed that most neurons coded a variety of motor acts — goal-directed movements, rather than simple joint displacements, as generally assumed at that time. I was tempted to propose that premotor cortex represents a ‘vocabulary of motor acts’, but I was afraid of the reaction of motor physiologists, at that time a very conservative bunch of people. Sir John told me. “Of course you have to propose it. When a scientist has the internal conviction that his idea is true, he must communicate it. Scientific conformism is the worst enemy of science progress”. I followed his advice on that occasion and later with mirror neurons.

I am convinced that a real scientist has a special, specific talent, like a director of an orchestra has for music. The difference is that talent in music

is easy to recognize; in science it is much more difficult. My advice to somebody starting their career in science is to be sure that they have this talent. Introspection, even more than opinions of others, should convince them. If a young researcher has this talent and is ready to sacrifice time and pleasures for using it, they should be encouraged to start a scientific career.

What is your greatest ambition? I think my major contribution to neuroscience has been to show that some high-order cognitive functions can be explained in neurophysiological terms. Understanding the actions and motor intentions of others is, however, just a small part of cognition. There are many other cognitive functions that allow us to understand others and enable social interaction. They are often referred to as ‘mentalizing’, and we know virtually nothing about them, apart from perhaps their approximate localization (the so-called ‘mentalizing network’). My greatest ambition is to start to break down this ignorance and to begin to elucidate the neurophysiological mechanisms underlying these cognitive functions.

What do you think is the biggest long-term challenge for the scientific community? The biggest challenge in my field is to come up with a neurophysiological model of ‘how the brain works’ that includes the acting individual with his thinking, emotions and capacity to interact with others. In the last few years, it has become clear that existing models of cognitive psychology are shallow and incomplete. As discussed by Eric Kandel (Am. J. Psychiatry (1999) 156, 505–524), the model of mental life proposed by Freud is still probably the most complete theory of the functioning of the human psyche. Some of Freud’s views are certainly updated, yet to interpret his model in the framework of modern neurophysiology will be an enormous intellectual achievement, and also an important step for understanding and, possibly, preventing and curing mental diseases.

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Quick guide

Bats

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What are bats? More than 1200 living species of bats constitute the Order Chiroptera (*Chiro* from the Greek for hand, and *Ptero* from the Latin for wing), the only mammals capable of powered flight (Figure 1). Today, bats occur in every terrestrial habitat except the high Arctic, the Antarctic, and some remote oceanic islands. Their diversity is greatest in the tropics and subtropics, with local faunas ranging from ~150 species at sites in Colombia to ~100 at sites in SE Asia and equatorial Africa. At the other extreme, Newfoundland, Canada, has just two species, the islands of Hawaii just one and there are none in French Polynesia. As adults, bats range in size from 2 g to 1.5 kg, with corresponding wingspans of 12 cm to 2 m; most species weigh less than 50 g.

Bats fill a number of trophic roles although most are predatory and eat mainly insects. Some predatory bats also eat other arthropods as well as vertebrates such as fish, frogs, reptiles, birds and mammals, even other bats. In tropical and subtropical areas many species of bats eat plant material, leaves, fruit, nectar and pollen. Vampire bats eat only the blood of living vertebrates; they have the most specialized diets. The three living species of vampire bats occur only in parts of Central and South America, and at least one, *Desmodus rotundus* (Phyllostomidae), sometimes drinks the blood of sleeping humans.

When did bats evolve? Bats were well established 52.5 million years ago during the Eocene and fossils from that time represent at least 11 families. The pectoral girdles (upper arms and shoulder joints) of exceptionally well-preserved Eocene bats from the Green River Shale in Wyoming and the Messel deposits in Germany indicate that these early bats could fly, suggesting that flight evolved just once in bats. We know of no fossils that are ‘almost bats’

and no living or fossil species that are flightless.

The abilities to fly and to echolocate may have been key to the origin and/or adaptive radiation of bats. If the ancestor of bats could echolocate, the combination of powered flight and echolocation would have allowed it access to nocturnal flying insects, a previously unexploited food supply. Some researchers believe bats evolved from an arboreal predecessor that glided from tree to tree using prey-generated sounds and/or echolocation to locate insects.

Flight or echolocation – which came first?

Although most researchers agree that bats are monophyletic, that is, that all species descended of a single common ancestor, there is no agreement about whether echolocation was an ancestral characteristic of bats. The classification of bats today recognizes two suborders (Yinpterochiroptera and Yangochiroptera), supported by a combination of morphological and genetic data (Figure 2). Even 10 years ago, bats had been arrayed in two different suborders (Megachiroptera and Microchiroptera). In the past, fruit bats of the Old World (Pteropodidae) were considered distinct from all other bats, but today they are grouped in the Yinpterochiroptera along with several other families that had been classified as Microchiroptera.

Bats using laryngeal echolocation include all those in the Yangochiroptera and most species in the Yinpterochiroptera, leaving open the question about the evolution of echolocation in bats. If laryngeal echolocation was ancestral in bats, then this trait was lost in the Pteropodidae, where a few species now echolocate with tongue clicks. If laryngeal echolocation was not ancestral, it may have evolved twice in bats, once in the ancestor of Yangchiroptera and again in the Yinpterochiroptera.

There are three schools of thought about the evolution of the key traits of bats: flight came first; echolocation came first; they evolved simultaneously. Contact between the stylohyal bone (part of the hyoid apparatus) and the tympanic bone (which surrounds the ear drum) is an unambiguous indicator of



Figure 1. Photos illustrating the diversity of bats.

Clockwise from top left: Macleany's moustached bat, *Pteronotus macleanyi* (Mormoopidae), here emerging from St. Clair cave in Jamaica; a common vampire bat, *Desmodus rotundus* (Phyllostomidae); an epauletted fruit bat, *Epomorphus wahlbergi* (Pteropodidae); a Brazilian free-tail bat, *Tadarida brasiliensis* (Molossidae); an Antillean ghost-faced bat, *Mormoops blainvillii* (Mormoopidae); and a group of Honduran white bats, *Ectophylla alba* (Phyllostomidae), roosting in a tent made from a *Heliconia* leaf.

laryngeal echolocation in extant bats, distinguishing them from all pteropodids. Unfortunately, both specimens of *Onychonycteris finneyi*, the oldest known fossil bat, are flattened and do not inform us about contact – or lack thereof – between these bones.

Thus, the single origin of laryngeal echolocation and its subsequent loss in the pteropodids is one plausible hypothesis, while the second proposes two origins of laryngeal echolocation: once in the Yinpterochiroptera and once in the Yangochiroptera. Both scenarios, at a minimum, need only require two evolutionary steps (Figure 2).

How social are bats? The social lives of bats are strongly influenced by the roosts they use during the day and by their reproductive behaviour. Some bats occupy huge roosts, for example the more than 10,000,000 Brazilian free-tailed bats (*Tadarida brasiliensis*, Molossidae) roosting together in single caves are the largest aggregations found among mammals. Colonies of bats numbering more than 1000 individuals are common in some species, but many others are solitary: in some species, a female and her one or two dependent young comprise the largest cohesive group. While most bats use naturally occurring

roosts, such as rock crevices and tree hollows or foliage, others make tents by biting through the veins of leaves so they fold down and protect the bats underneath them (Figure 1). Still others excavate roosts in termite nests. Some species, like the aforementioned Brazilian free-tailed bats, roost in human structures from buildings to mines to bridges.

Within some social units, bats coordinate and share information about the location of rich patches of food or ways to exploit novel food sources. Within a social unit, a common vampire bat that has had a blood meal will sometimes, when prodded, regurgitate blood into the mouth of a roost-mate that has not fed. This behaviour maximizes the chances of survival of individuals that did not successfully feed. Adult vampire bats miss a meal about once a month but for young it happens two or three times a week. Genetic data have shown that vampire bat social units are often mixtures of relatives and non-relatives, indicating that sharing information and food is reciprocally altruistic. Unlike other small mammals, individual bats from many species can live a long time (more than 10 years; in some species more than 30 years). Social learning and behavioural flexibility make them well suited to adapt to changing environmental conditions;

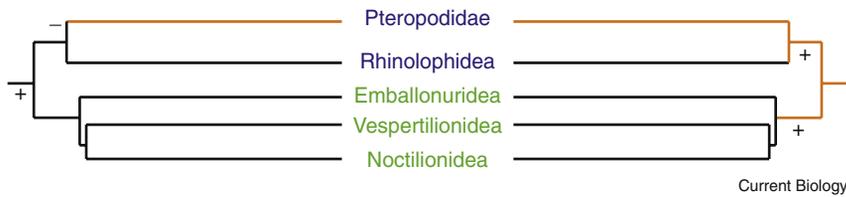


Figure 2. Two equally parsimonious views on the evolution of echolocation in bats. Black lines indicate those lineages containing the extant laryngeal echolocators. Names in blue constitute the Yinpterochiroptera, those in green the Yangochiroptera. According to an old and now defunct hypothesis, the Pteropodidae were a distinct sub-Order (the Megachiroptera) with all other bats forming a single monophyletic group, the Microchiroptera (after Teeling 2009).

however, low rates of reproduction make their populations vulnerable to catastrophic change.

Reproduction underlies social organization in bats, most of which have a single mating season each year. Social organization associated with reproductive behaviour in bats ranges from putative monogamy to polygyny and promiscuity. Bats typically have one, sometimes two, young per litter and neonates are huge, weighing 25% to 30% of the mother's postpartum body mass. Many species, particularly of plain-nosed bats (Vespertilionidae), use delayed fertilization to ensure that both mating and parturition occur at the most favourable times of year. Other bats use delayed development to achieve the same end. Some tropical species that have more than one litter a year use a postpartum oestrus and delayed development to time birth when food is plentiful; for example, Seba's short-tailed bats, *Carollia perspicillata* (Phyllostomidae) can delay development at the primitive streak stage for more than 50 days.

What of white noses and windmills? Two recent environmental changes threaten the survival of bats: the emergence of white nose syndrome, and the proliferation of wind turbines. To date, white nose syndrome, which is caused by a fungus, has posed the greatest threat to bats hibernating underground in NE North America (the USA and Canada). In February and March 2006, white nose syndrome first appeared in little brown bats (*Myotis lucifugus*, Vespertilionidae) hibernating in six underground sites near Albany, New York. In bats, successful hibernation means long periods of uninterrupted torpor. White nose syndrome

interferes with the pattern of arousal of bats from hibernation, causing them to burn up and exhaust their stores of body fat well before the end of winter. By 2010, literally millions of little brown bats had succumbed to the effects of white nose syndrome, which by then had spread widely to almost 100 underground sites to the north, south, east and west of the original locations. The population of little brown bats in the NE United States is estimated to have been 6.5 million in 2005, but the dire prediction is that this species will have been locally extirpated within 10 years.

Meanwhile, the quest for 'green energy' has led to the erection of turbines at so-called wind farms. Bats, particularly those that migrate, are much more vulnerable to death at turbines than birds. Most bat mortality is caused by embolisms arising from the difference between pressures outside the body and those inside the lungs. This situation develops near the rotating blades of wind turbines that also kill bats in collisions. Mortality caused by white nose syndrome or wind turbines is not sustainable by slow-reproducing animals such as bats. To date we have no viable solutions for mitigating the spread of white nose syndrome or reducing bat mortality at wind turbines.

Why bats and Dracula? Bats in many Western societies are commonly associated with filth and insanity, achieving dubious celebrity status due to their association with the undead, but often well-dressed, bloodsuckers of human folklore. Yet, it was not until Bela Lugosi's 1930s portrayal of Dracula in the movie based on the Bram Stoker novel that the link between bats and vampires was first made. Bats are said to

be involved in the epidemiology of diseases such as rabies, histoplasmosis, Ebola, Nipah and SARS, casting an even darker shadow on these all too often maligned mammals. True, diseases like rabies are uniformly lethal to people (and bats), but public apprehension is based on the outcome of contraction rather than the chances of being exposed. Happily, in many non-Western societies, bats are positive symbols of fertility, long life and prosperity. Proponents of bat conservation worldwide correctly emphasize the vital roles bats play as predators of insects, pollinators and dispersers of seeds.

The diversity of bats provides biologists with an embarrassment of riches across topics from ecology and evolution to physiology, morphology, and behaviour. Their connections to human folklore are intriguing, but whether viewed as good luck or bad, we pose a much greater threat to them than they do to us. As mobile, long-lived mammals that fill a number of trophic roles, bats are excellent candidates for alerting us to the impact of global climate change and habitat destruction. The discoveries of cryptic species of bats, for example the soprano pipistrelle in England in 1995, reveal them as valuable indicators of biodiversity.

Where can I find out more?

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