

PRIMATE BRAINS IN THE WILD: THE SENSORY BASES FOR SOCIAL INTERACTIONS

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Each organism in the animal kingdom has evolved to detect and process a specific set of stimuli in its environment. Studies of an animal's socioecology can help us to identify these stimuli, as well as the natural behavioural responses that they evoke and control. Primates are no exception, but many of our specializations are in the social domain. How did the human brain come to be so exquisitely tuned to social interactions? Only a comparative approach will provide the answer. Behavioural studies are shedding light on the sensory bases for non-human primate social interactions, and data from these studies are paving the way for investigations into the neural bases of sociality.

Unfortunately, neuroscientists cannot question non-human animals as they would a human subject. Instead, we must rely on an animal's natural responses to investigate which features of an animal's sensory world are relevant and why. Ultimately, understanding these crucial stimulus components will allow neuroscientists to formulate specific hypotheses about the design and function of brains. This ethological approach has already provided rich insights into the neurobiology of many species. Research into the natural behaviour of bats, for example, led scientists to discover that bats use the difference between the sound of an emitted vocalization and its subsequent echo to identify and localize a target¹. With this behavioural foundation, neuroscientists used the temporal and spectral attributes of echolocation signals to discern the specialized functional organization of the bat's auditory cortex². A similar story exists for studies of the electric fish. In the early 1960s, ethologists discovered that certain species of fish emit electrical discharges and can shift the frequency of these discharges away from the frequencies of interfering discharges of other fish. Once this species-specific 'jamming avoidance' behaviour was characterized in more detail, neuroscientists were able to map the neural circuitry that underlies it³.

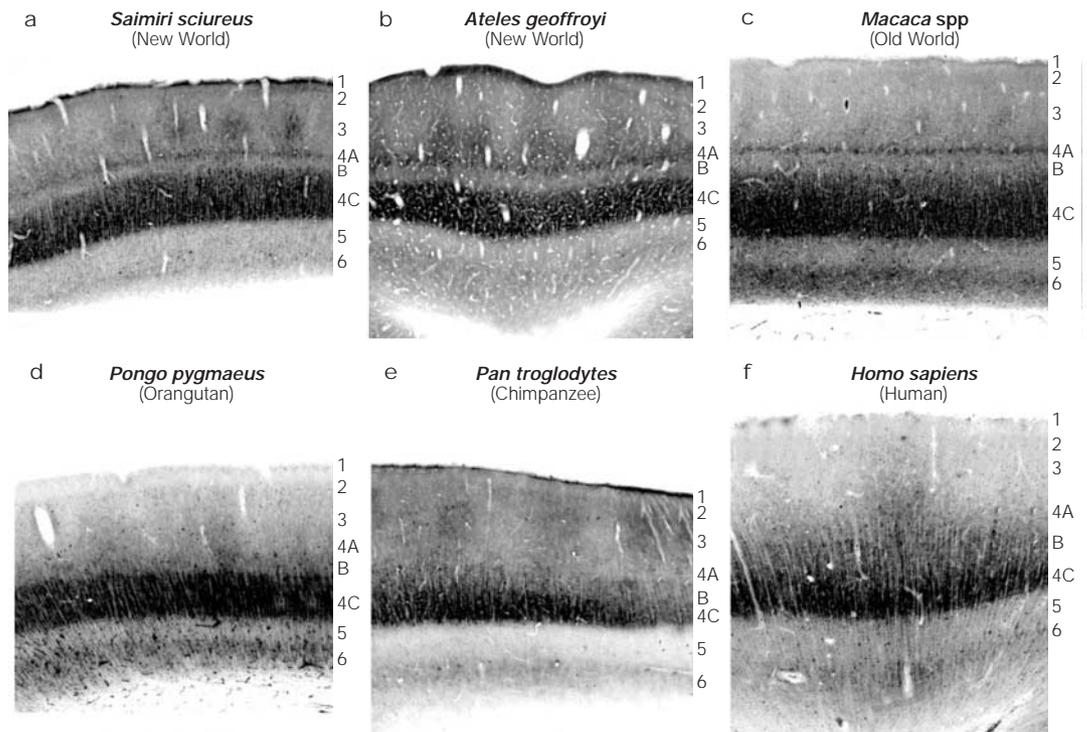
In these and other model systems (for example, songbirds⁴), neuroethological research has enhanced

our understanding of how natural selection shapes brain design for complex behaviours. Unfortunately, however, neuroscientists who investigate the function and structure of primate brains often focus on more general cognitive processes and neglect primates' species-typical behaviours. Ignoring the species-typical behaviour of animals leads to the erroneous idea that all mammalian brains are essentially different-sized versions of the same basic plan^{5,6} (BOX 1). There is no *a priori* reason why applying the neuroethological approach to primates should not yield similar insights into the species-specific design and function of their brains.

Primates are social beings. They constantly strive to improve their status. To selfishly operate within the structure of a social group or to secure appropriate mates, an individual must exploit and out-manoeuvre others. Primates, therefore, need to be calculating. They must be able to calculate the consequences of their own behaviour; to calculate the probable behaviour of other individuals; to calculate the balance of advantages and losses — and all this in a context that is constantly in flux (see, for example, REF 7). Such social skills require complex cognition: an ability to represent long, linear dominance hierarchies, to remember who is doing what to whom, and to manipulate this information to one's own advantage.

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Box 1 | The diversity of mammalian brains



Mammalian brains are as diverse as the species-typical behaviours they produce. Evolutionary divergence of brains can be revealed at several neuroanatomical levels, and includes variation in overall brain size (relative to body size), variation in the number of cortical areas, changes in connectivity between brain areas, and changes in cellular organization within an area. Here we provide just a sample of what is known.

Differences in overall brain size. The size of mammalian brains can vary a great deal, in both overall and relative terms. At a given body weight, brain weight can vary more than fivefold across species¹⁴⁰. For example, squirrel monkeys (*Saimiri* spp) weigh about 680 g, galagos (*Galago* spp) about 850 g and hedgehogs (*Erinaceus* spp) roughly 860 g. Although individuals of these species weigh roughly the same, their brain weights differ vastly: 22.0 g, 10.3 g and 3.4 g, respectively¹⁴¹.

Differences in the number of cortical areas. All mammals seem to have about 20 common cortical areas, but the number of areas has increased along certain branches of mammalian evolution¹⁴². Rhesus monkeys and other primates, for instance, have more visual, somatosensory and prefrontal areas than rats, hedgehogs or opossums^{142,143}. The Primate order might have unique cortical areas, such as the MIDDLE TEMPORAL VISUAL AREA, that are not homologous to cortical areas in non-primates¹⁴⁴.

Variation in connectivity between brain areas. Although certain brain areas are common to mammalian species, their connectivity patterns vary considerably. For example, in cats, the lateral geniculate nucleus (LGN) projects to visual areas 17 (the primary visual cortex, V1) and 18 (V2). However, in primates, the LGN projects almost exclusively to V1; the main input to V2 is from V1 (REF. 145). A similar shift from parallel thalamocortical projections to a serial processing pattern has occurred in the primate somatosensory system¹⁴⁶.

Variation in cellular organization. Comparative studies have revealed that the cellular structure of the cortical areas of different species can differ markedly. For example, relative to neighbouring pyramidal neurons in V1, MEYNERT CELLS are much larger in patas monkeys (*Erythrocebus patas*) and baboons (*Papio* spp.) than in humans and other primates¹⁴⁷. By contrast, human BETZ CELLS are much larger relative to neighbouring pyramidal neurons than those of other primates¹⁴⁷. Some cell types and laminar patterns seem to be unique to apes (including humans). The large 'spindle cells' of the cingulate cortex are found only in apes¹⁴⁸. Perhaps most surprising (given how often the macaque visual system is assumed to exactly replicate the human visual system) is that the primary visual cortex of Old and New World monkeys contains a dense cytochrome oxidase-containing band in layer 4A that is not evident in great apes (including humans)¹⁴⁹ (see figure).

In summary, brains differ across mammalian species. Much more comparative and functional neuroanatomy is necessary to investigate differences between species, particularly between primate species, and far more attention to species-typical behaviours is required to make sense of the anatomical differences that come to light. For more in-depth coverage of these data, ideas and arguments, see the elegant work of Preuss and Kaas^{5,6,142,145,150}.

MIDDLE TEMPORAL VISUAL AREA

An extrastriate visual cortical area that is important for the analysis of visual motion.

MEYNERT CELLS

Specialized pyramidal neurons found in the primary visual cortex.

BETZ CELLS

Giant pyramidal neurons that are located in layer V of the primary motor cortex. Their axons project to the spinal cord, terminating directly on motor neurons.

In light of these abilities, Jolly⁸ and Humphrey⁹ proposed that sociality might have been the primary force driving the evolution of primate intelligence. This proposal is supported by studies of primates' natural behaviour^{10,11} (see below). There is tremendous variation in the social group sizes of different primate species. Logic dictates that, as social groups become larger, the ability to garner social knowledge by recognizing and remembering individuals and their relationships with other group members would be highly advantageous¹². Indeed, there is some indication that this ability might be related to primate brain evolution — social group size is correlated with neocortical volume in primates¹³ (a similar relationship exists for carnivores¹⁴). This finding, though popular, is controversial, as the statistical relationships between neocortex size and group size depend on the scaling methods that are applied¹⁵. With some methods, home range size and social group size are equally good predictors of neocortical size in primates.

A better way to examine the neural bases of primate social behaviour is to move beyond measures of brain size or neocortical size and to investigate how the anatomy and physiology of particular brain structures relate to species-typical social behaviours. For example, in the past few decades, a number of neuroscientists have investigated how the primate amygdala and medial temporal lobe are involved in general aspects of social cognition^{16–18}. However, the forces of evolution that shaped the primate social brain cannot have acted on a few neural structures in isolation — whole systems must have been shaped. A MACHIAVELLIAN AGENT must be able to receive and interpret sensory cues related to social situations. Here, we focus explicitly on visual and auditory cues that non-human primates use to guide their social behaviour, and on the neocortical structures involved in such sensory processing — particularly, the sensory cortical areas in the temporal lobe. By necessity, our review is biased towards investigations of a few semi-terrestrial Old World primate species. This is largely because much more is known about the social behaviour and neurobiology of these species than about arboreal primates. Where possible, we indicate where there might be interesting species differences within the Primate order.

The visual domain

Sexual colouration. Darwin¹⁹ noted over a century ago that primates are unique among mammals in that, in some species, there are marked differences in colouration between the sexes. Adult males of many Old World monkey species have particularly vivid displays, usually involving the face and anogenital regions ('sexual skins'). The functions of primate secondary sexual colouration are largely unknown. Associations between status and intensity of colouration have been reported in at least three species (vervet monkeys, *Cercopithecus aethiops*²⁰; gelada baboons, *Theropithecus gelada*²¹; and mandrills, *Mandrillus sphinx*²²). In mandrills, the rise and fall of males in the social hierarchy are accompanied by remarkable changes in visually conspicuous secondary

sexual characteristics²². When a male rises in rank, he experiences a large increase in testicular volume (from ~15 cm³ to ~30 cm³), an increase in circulating testosterone, and increased reddening of the sexual skins. When a male falls in rank, his testicles decrease in size (~30 cm³ to ~20 cm³) and, in some individuals, the sexual skin becomes less red.

Do individuals use these visual cues to guide their behaviour? In vervet monkeys, variability in the 'blueness' of scrotal colour seems to signal status within a colony²³. In support of this idea, intense agonistic and aggressive interactions among vervets often include genital displays such as the 'red, white and blue' display²⁴. During this display, dominant males encircle subordinates with their tails erect, exposing the red perianal region, the white tuft of hair between the scrotum and perineum, and the blue scrotum (FIG. 1a). To test whether male vervets use the blueness of a conspecific's scrotum to guide their behaviour, Gerald²⁰ paired captive vervet males with dark blue scrota with unfamiliar individuals with pale blue scrota. Individuals with dark scrota dominated those with pale scrota. Pairs of males with similarly coloured scrota (dark or pale) tended to be more aggressive towards each other than males whose scrotal colours were distinctly different. This indicates that males use this visual cue to assess the social status of other individuals. In a final test, males with pale scrota had their scrota painted dark blue before pairing. Remarkably, other individuals treated painted males according to the colour of their scrota — pale males were submissive towards dark-painted males. The dark-painted males, however, did not behave like dominant individuals, indicating that they were unaware of their own colour. These experiments unequivocally show a relationship between colour perception and social status in primates.

Secondary sex colouration might also be important for females' selection of a mate²⁵. During the mating season, the sexual skins of both female and male adult rhesus monkeys (*Macaca mulatta*) become redder (FIG. 1b). In males, testosterone induces reddening indirectly by being aromatized to oestrogen — the more testosterone a male has, the redder his sexual skins²⁶. As testosterone is linked to lowered immunocompetence, it has been proposed that a male's ability to display a costly testosterone-dependent trait (redness of sexual skins) might act as an 'honest' indicator of health and genetic quality²⁷. Do choosy females use the degree of redness as a criterion for judging the quality of a male?

Waite and colleagues²⁵ used an indirect measure of female choice — preferential looking — to address this question. They presented captive rhesus monkey females with two male faces, each with a different degree of redness, and measured how long the females looked at each face. The females looked longer at the redder faces than at the paler ones, indicating that they find redder faces more attractive. Similar looking-time measures in human infants and adults also correlate with attraction^{28,29}.

MACHIAVELLIAN AGENT
An agent that can make or
break alliances to serve his/her
selfish needs.

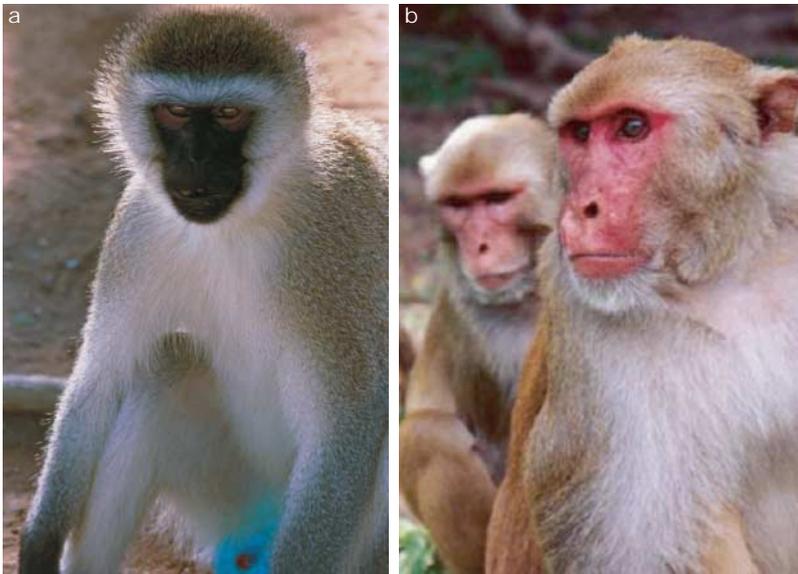


Figure 1 | Sexual colouration. **a** | A vervet male with blue ‘status symbol’ (photo copyright Ross Warner). The degree of scrotal ‘blueness’ can indicate male dominance — darker blue indicates greater fitness. Vervet males can use this indicator to assess the feasibility of physically challenging a male rival for resources. **b** | Male rhesus monkey with reddened face during the mating season (photo courtesy of Marc D. Hauser, with permission). Female rhesus monkeys prefer to look at males with redder faces. This indicates that the degree of redness indicates the fitness of the male.

Visual recognition of conspecifics. The ability to identify individual group members and their relationships can minimize the time and expense associated with testing social relations repeatedly. Primates, therefore, spend much of their time watching others, and are highly motivated to attend to visual stimuli involving conspecifics. Macaque monkeys, for example, consistently favour looking at slides or movies of conspecific individuals over non-conspecific animals or objects^{30–32}. Looking at social stimuli is so rewarding for some species that it can be used as an incentive for learning tasks³³. Furthermore, once rhesus and long-tailed (*Macaca fascicularis*) macaques learn to discriminate between faces, alterations in posture, orientation, colour, size and illumination have little effect on face-discrimination performance³⁴. Monkeys trained in this way can even use body parts other than the face to discriminate known individuals³⁵. So, macaques seem to recognize conspecific individuals from these two-dimensional images, not just arbitrary complex visual patterns.

Many primate species also pay selective attention to different types of conspecifics in different dyadic relationships. Female stump-tailed macaques (*Macaca arctoides*) prefer to look at slides of other females with infants than at lone females³⁰. Long-tailed macaques can discriminate between mother–offspring dyads and other types of pairing³⁶. A subject trained on a simultaneous discrimination task where the positive slide was a mother–offspring pair and the negative slide was an ‘other–offspring’ pair could generalize to 14 novel pairs of slides. She correctly chose the mother–offspring slides even though she’d never seen the slides before. Dasser³⁶

suggests that visual experience with the real counterparts contributed to this ability to discriminate mother–offspring pairs — matrilineal kin associate at much higher rates than non-kin.

Their patterns of visual observation can also reveal what monkeys know about the social hierarchy. Rhesus monkeys vary their patterns of looking according to the rank of stimulus animals³⁷. They show a remarkably linear pattern in which the duration that they spend observing an animal is inversely related to the linear dominance hierarchy — an individual will spend significantly less time observing higher-ranking members than lower-ranking ones.

Eyes, actions and mind. When primates observe conspecifics, what are they usually looking for? Primates spend much of their time looking at the faces of other individuals and, in particular, at their eyes. Rhesus macaques, for example, naturally attend to the eyes when viewing human and conspecific faces^{38–40}. The attention directed at the eyes often seems to be used to assess where an individual is looking. Many primate species will spontaneously orient to where other individuals are looking. Macaques follow the gaze of both conspecifics^{41–44} and humans^{45,46}. When the image of a rhesus monkey (stimulus monkey) looking to one side is flashed in front of rhesus monkeys or humans, both species covertly shift their attention (as measured by microsaccades) to match that of the stimulus monkey, even though it does not predict where a target stimulus will appear⁴¹. When the stimulus monkey’s direction of gaze and the target location matched (again, unpredictably), reaction times were significantly less than in the conflicting conditions⁴¹ (FIG. 2a). Chimpanzees (*Pan troglodytes*) also follow the gaze of human experimenters^{46–49} and conspecifics⁴⁴ and, more interestingly, can successfully follow an individual’s line of regard past barriers and distractors to a target object^{48–50}.

The ability of primates to follow and react to gaze raises the question of what different primate species understand about the eyes. Do primates simply attend and orient to where others are looking, or do they understand that where another individual is looking is psychologically significant? Santos and Hauser⁵¹ used an expectancy violation paradigm to examine whether cotton-top tamarins (*Saguinus oedipus*) understand that where an individual looks often predicts where that individual is likely to act. The logic behind the expectancy violation paradigm is that subjects will look longer at events that violate their expectations than at more consistent control events. In this study, when tamarins watched a human experimenter reach for one of two objects, they looked significantly longer when the experimenter looked towards one object but reached for the other. There are two possible interpretations: (i) tamarins know that eye gaze/head orientation indicates where an individual is attending; and/or (ii) tamarins have learned to associate head cues and reaching cues and, when those cues are incongruent with their experience, it looks unusual.

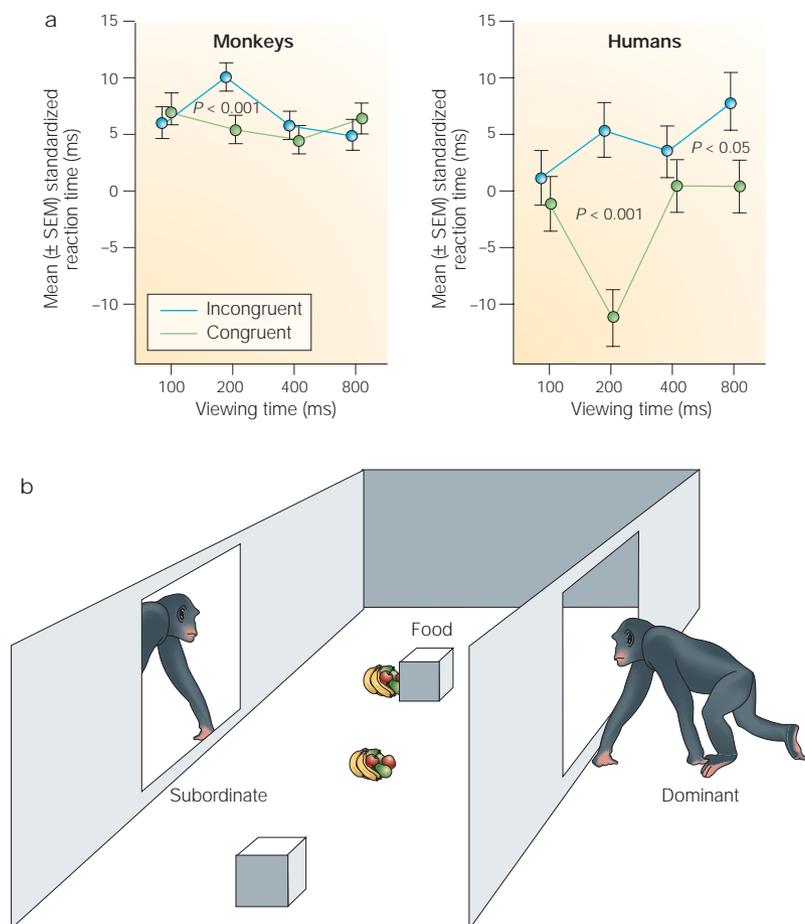


Figure 2 | The eyes have it. a | The effects of social cues on reaction times in monkeys and humans. Mean (\pm SEM) standardized reaction times for congruent (green lines) and incongruent (blue lines) trials. Humans and monkeys were trained to move their eyes towards one of two peripheral targets. A monkey face, with eyes directed to one side or the other, was presented centrally but did not predict the side on which the peripheral target would appear. Nevertheless, both humans and monkeys had faster reactions times when the presented monkey's eye direction was congruent with peripheral target location. Reproduced, with permission, from REF. 41 © (2003) Elsevier Science. **b** | Competitive paradigm for testing what chimpanzees understand when they see conspecifics. A subordinate and a dominant chimpanzee face each other across a room. Between them is a highly valued piece of food that both can see. Off to the side is the same type of food hidden behind a barrier so that only the subordinate chimpanzee can see it. If the subordinate chimpanzee understands what the dominant chimpanzee can and cannot see, then he should always go after the hidden food to avoid conflict. Modified, with permission, from REF. 64 © (2001) Academic Press.

Researchers have also explored whether primates understand that looking at an object leads to knowing about that object. Early work on this question seemed to indicate that, when tested in controlled laboratory situations, most primates have little understanding that seeing leads to knowing^{52–54}. For example, chimpanzees and other primates do not spontaneously use information about another individual's direction of gaze when searching for hidden food^{48,55–61}. In a typical study, an experimenter attempts to communicate the location of a piece of hidden food by looking at or gesturing towards one of two possible hiding locations. Without direct training, relatively few non-human primates succeed in this task.

More recent work indicates that primates might understand more about the nature of the eyes than previously thought. If primates understand the psychological importance of the eyes, then they should use this information when vying with other individuals in competitive social situations^{11,62}. Hare and colleagues⁶³ set up a situation in which chimpanzees could compete over access to hidden pieces of food. A subordinate and a dominant chimpanzee were positioned on alternate sides of a middle cage that contained two pieces of food (FIG. 2b). In some cases, the food was placed so that the dominant individual could see only one of the two pieces. If the subordinate individual was sensitive to what the dominant chimpanzee could and could not see, then the subordinate chimpanzee should have attempted to retrieve only those foods that the dominant individual could not see. Across a number of conditions and replications^{64,65} (but see REF. 66), subordinate chimpanzees selected food pieces that the dominant individual could not see, indicating that some primate species might understand that seeing leads to knowing.

Neural correlates of visual behaviour. Few visual neurobiological studies focus on how socially relevant stimuli and stimulus features are processed by the brain. Studies of primate colour vision, for example, have focused solely on the relationship between the number, and spectral characteristics, of different retinal cone photoreceptors and the ability to detect coloured fruit among foliage⁶⁷. In this domain, there are interesting species differences — primates are unique among mammals in possessing trichromatic colour vision, but not all primates are trichromatic. All Old World monkey and ape species are trichromatic, but many New World monkeys (for example, squirrel monkeys) are polymorphic — different members of the same species have different types of colour vision⁶⁷. So far, no study has examined the relationship between colour vision and sexual colouration at the level of photoreceptors or the neocortex.

The strongest evidence for a link between visual socioecology and neurobiology are the 'face cells' of the temporal cortex^{68–70}. These neurons respond selectively to the presentation of faces. That is, although they can respond to other complex visual stimuli, these neurons respond at least twice as vigorously to faces or components of faces (such as eyes or mouths). Face cells are primarily found in the temporal cortex, specifically in the inferior temporal (IT) cortex^{69,71} and in the superior temporal sulcus (STS)^{68,70,71} (FIG. 3a).

The IT cortex and STS seem to have different roles in face processing. The IT cortex is more important for processing facial identity, whereas the STS is more involved in processing facial expressions (including eye gaze direction) and other 'biological motion' inputs. Hasselmo *et al.*⁷¹ presented rhesus monkeys with images of the faces of three individual macaques with three expressions representing two emotional categories (a calm face, a slightly open-mouthed threat, and a fully open-mouthed threat). The researchers measured neural responses in the IT cortex and STS across identities and expressions. They found that neurons had differential

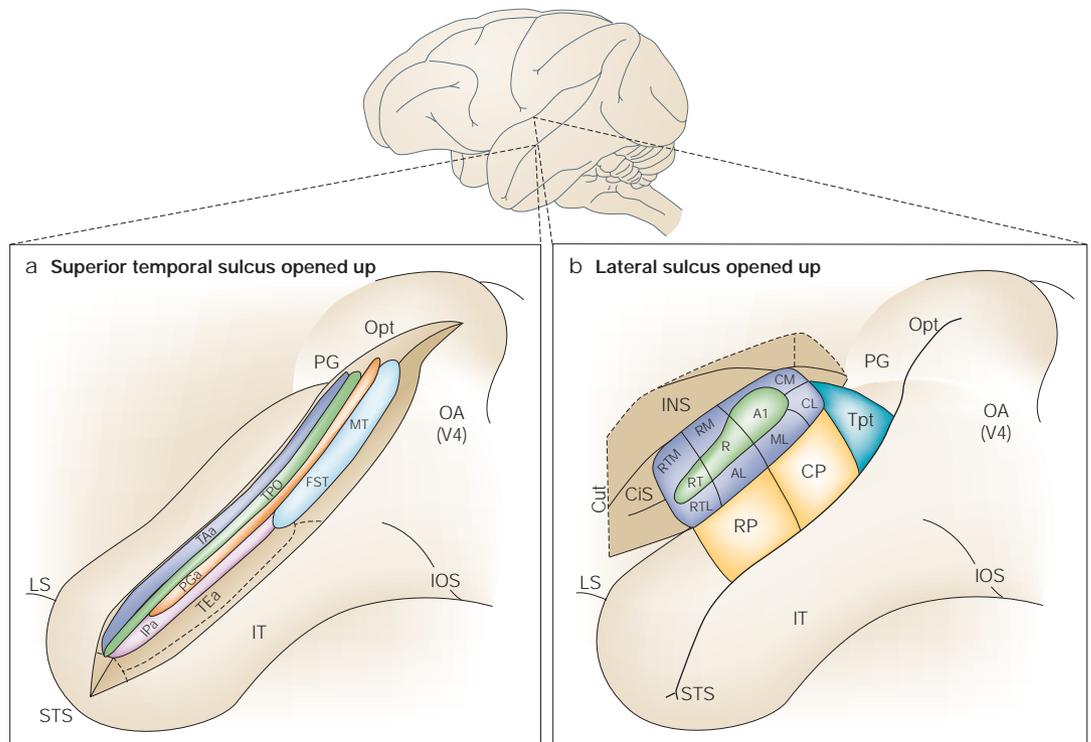


Figure 3 | Current models of temporal lobe cortical anatomy. **a** | Visual and multisensory areas in the superior temporal sulcus (STS). Neurons in the STS are more responsive to facial expressions and different viewing angles than neurons in the inferior temporal (IT) cortex. IT cortical neurons are more sensitive to facial identity. LS, lateral sulcus; IOS, inferior occipital sulcus; other labels refer to cytoarchitectonic areal designations. Modified, with permission, from REF. 138 © (1994) John Wiley & Sons, Ltd. **b** | Auditory areas within and around the LS. The core region (A1, R and RT) are thought to be ‘primary-like’ areas, responding best to pure tones, while the surrounding lateral belt areas (CL, ML and AL) are more response to complex sounds. The response properties of other areas have not been systematically investigated. A1, auditory area 1; AL, anterior lateral belt; CIS, circular sulcus; CL, caudolateral belt; CM, caudomedial belt; CP, caudal parabelt; INS, insula; ML, middle lateral belt; R, rostral area; RM, rostromedial belt; RP, rostral parabelt; RT, rostrottemporal area; RTL, rostrottemporolateral belt; RTM, rostrottemporomedial area; Tpt, temporoparietal area. Modified, with permission, from REF. 139 © (2001) John Wiley & Sons, Ltd.

sensitivity to different identities, independent of facial expression, and vice versa. Also, neurons that were sensitive to facial identity were mostly located in the IT cortex, and neurons that were sensitive to facial expression were found primarily in the STS.

The IT cortex and STS have extensive reciprocal connections and probably share face-specific information. Recording in both regions, Sugase *et al.*⁷² found that information about both the stimulus category (object versus human versus monkey) and its identity or expression was available in a single neuron’s response. The expressions used were open-mouthed threats, yawns, neutral faces and ‘coo’ faces (lips protruding while producing an affiliative coo call). For 37% of face-responsive neurons, category information was encoded in the early part of the response and, on average, information about identity or expression was encoded later in the response.

Most studies of face cells have used passive viewing. More recently, Ono and colleagues⁷³ examined the roles of the STS and IT cortex during a face-identification task. Japanese macaques (*Macaca fuscata*) were required to perform a delayed match-to-sample task in which the sample was a frontal view of a human face and test faces

were one of seven viewed from one of seven different angles. Under these conditions, face-sensitive neurons in the STS seemed to encode viewing angle independent of facial identity. By contrast, IT neurons encoded facial identity, not viewing angle. A small subpopulation of IT neurons had very long latencies — greater than 150 ms — that were strongly correlated with behavioural reaction times. Larger changes in viewing angles of the match face elicited longer reaction times and longer neural response latencies⁷³ (FIG. 4).

The ability to detect where another individual is looking is highly adaptive because the gaze direction of an individual can be used to predict that individual’s movements or actions (see above). To investigate the putative neural bases for the perception of gaze following, Perrett and co-workers⁷⁴ searched for neurons in the temporal cortex that responded to such cues. They reasoned that as neurons in the STS are often tuned to many views of the head — more views than are needed for recognition purposes — these neurons might be involved in coding social intention. In other words, these cells might signal where another individual is attending by encoding the combination of head orientation and gaze direction. The investigators found that many of the

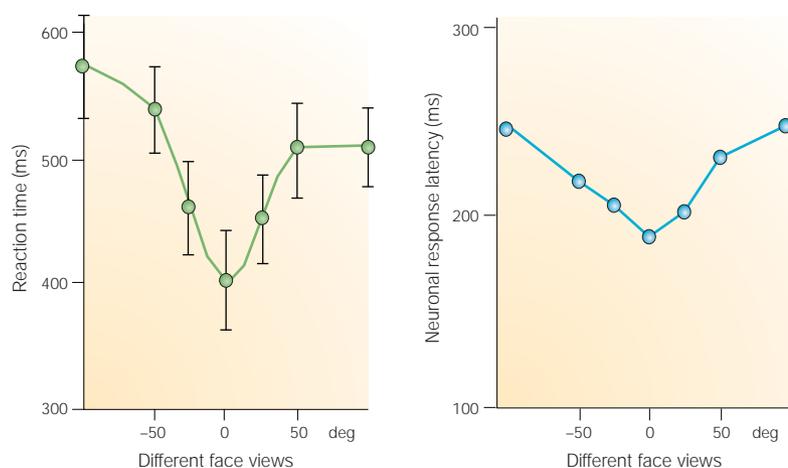


Figure 4 | Relationship between reaction times and the latency of one neuron in the inferior temporal gyrus of a monkey performing a delayed match-to-sample task. The stimuli were human faces seen at different viewing angles. The x axes represent the seven different facial views. The y axes depict time in milliseconds. The correlation between reaction time and neuronal latency was significant ($r = 0.85$, $P < 0.05$). Modified, with permission, from REF. 73 © (2004) American Physiological Society.

cells that responded to head view were equally (if not more) sensitive to gaze direction. The cells responded most robustly if head orientation and gaze direction were congruent; that is, if the cell was selective for a head turned laterally away from the monkey (to the right, for example), then that cell gave a greater response to the stimulus if the eyes were also laterally oriented (eyes looking to the right). This finding is also supported by lesion experiments. Rhesus monkeys trained to identify different faces and objects showed no behavioural deficits after bilateral STS lesions. However, such lesions significantly impaired discrimination of eye gaze direction^{75,76}. Note that such deficits might reflect impairment of a more general recognition process rather than one specific to eye gaze⁷⁷.

Can such gaze-sensitive neural responses be linked to the intentional action? Jellema *et al.*⁷⁸ have argued that the STS might also be involved in linking visual attention and action of others. They described a small population of neurons that respond when the monkey sees an actor making a reaching movement and simultaneously looking towards the target position of the reach. If the actor makes the same movement, but looks in an arbitrary direction, the neurons respond less vigorously. The authors suggest that such selectivity can arise through the convergence of more numerous gaze/face-selective neurons⁷⁴ and neurons that respond to body movements⁷⁹. This might be the neural equivalent of the demonstration (described above) that tamarins are surprised when humans look in one direction while reaching in another⁵¹.

Each of these neurophysiological studies has drawbacks when viewed in the light of ethological relevance. Studies examining facial expressions often use only a limited set of facial expressions from the experimental species and do not encompass more than a few emotional categories (neutral, aggressive, fearful, affiliative).

For example, a systematic investigation of the representation of different emotional categories embodied by different facial expressions (for example, yawns, fear grimace, lip smacking, teeth grinding and so on) might reveal that threatening faces are overrepresented in the temporal lobe compared to fear grimaces.

Many studies also mix human faces with conspecific faces or sometimes only use human faces. It would be interesting to know whether reaction times, rate of learning face discriminations and neural representations differ if conspecific, instead of human faces, are used. A comparative study is necessary to test whether neural specializations are specifically tuned to conspecific faces or expressions (see REFS 80,81 for work in rhesus monkey infants that indicates a possible innate component), to primate faces in general, or are simply part of a general mechanism for representing visual categories. After all, sheep have 'face' cells in their temporal lobes that are selective for human faces⁸², but we would be hard-pressed to argue that they evolved a specialized circuit for this purpose.

It would also be enormously informative if the presence or absence of face-selective neurons was investigated in primate species other than macaques. Do arboreal species or New World monkeys have as many face cells as macaques? One prediction is that the presence of face cells is correlated with the degree to which a species relies on visual communication. In addition, the facial musculature of primates has undergone considerable divergence. For example, the musculature involved in moving facial whiskers in prosimians was co-opted for use in making other facial movements in monkeys and apes^{83,84}. This is paralleled by increased use of visual communication in the latter species⁸⁵.

The auditory domain

Individual voice recognition. As described above, primates can use visual cues to identify individuals, but in the natural world such visual cues are often compromised by distance, vegetation, other individuals and/or poor lighting. As such, we might expect primates to process information about others using other modalities as well. Unlike visual signals, acoustic signals can transmit information over large distances and usually without catastrophic interference from objects in the environment.

When a primate vocalizes, listeners are provided with a range of potential acoustic information about the signaller's body size, reproductive status, individual identity, kinship and group membership⁸⁶⁻⁹⁰. For example, the cotton-top tamarin produces long, multi-syllabic calls that contain a number of acoustic cues that are used to identify different individuals⁹⁰ (FIG. 5a). These include the start frequency of the first syllable and its duration. Similarly, rhesus monkeys produce coo and grunt calls with formant structures (the spectral patterning that results from vocal tract filtering) that reliably encode individual identity⁹¹. Primates could use variation in the acoustic structure of different individuals' vocalizations to determine who is nearby and who is calling (FIG. 5b).

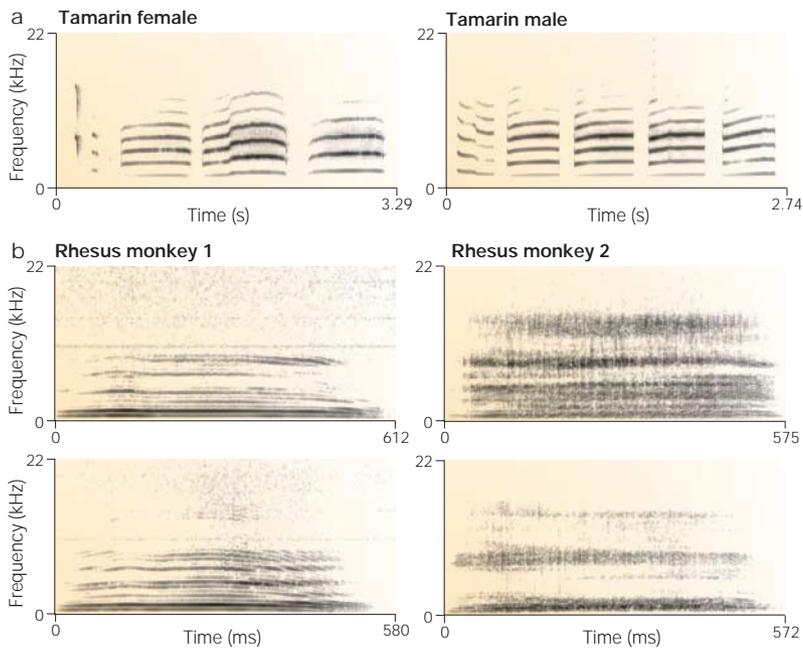


Figure 5 | Individual variation in vocalizations. **a** | Spectrograms of long calls produced by male and female cotton-top tamarins. These calls are often produced when individuals are visually isolated from members of their group. Differences in several acoustic features distinguish the long calls of male tamarins from those of females. These differences allow the calls to be distinguished by listeners. **b** | Spectrograms of two coo calls from two rhesus monkeys. Coo calls are produced in many contexts including isolation, presentation of food and during group movement. There is considerable variation between the coo calls of different individuals, but not as much variation between two calls of the same individual. So, rhesus monkeys can identify individuals simply by listening to their coos.

Several experiments have explored whether primates can identify members of their own group or other groups through voice alone^{87,90,92–96}. Female rhesus monkeys listening to recorded coo vocalizations responded more quickly and for a longer duration to the coos of their kin than to the coos of non-kin or distantly related kin⁸⁷. In a habituation–discrimination paradigm, subjects were habituated to successive presentations of coo calls from one relative and then tested with the presentation of a coo call from a different relative. Subjects showed a rebound in their responsiveness (duration of orienting response) to the coo call from the different relative⁸⁷. These results indicate that female rhesus monkeys can distinguish kin from non-kin using voice alone. In a further study, acoustical analyses revealed that the filtering effects of vocal tracts on the spectral structure of coo calls might be crucial for distinguishing individuals⁹¹.

Vervet mothers can also recognize close relatives using voice alone. These terrestrial primates live in large multi-male, multi-female groups. Because of constant predation, most vervet monkeys do not live to see their first birthday. Female vervet monkeys are therefore highly motivated to protect their infants during the first few years of life. Cheney and Seyfarth found that mothers pay special attention to the screams of their infants⁹². On hearing playbacks of their offspring's screams, vervet mothers react more quickly and are more likely to approach the sound source (a hidden speaker) than when they hear the screams of unrelated offspring in the group.

The most convincing evidence for individual vocal recognition is that, upon hearing two call types produced by one individual, vervet monkeys know that it is the same individual. When vervets see an individual from a neighbouring social group approaching, they produce one of two acoustically distinct calls — the 'wrr' and the 'chutter'. The two intergroup calls are functionally equivalent — both elicit vigilance in listeners. A clever playback experiment mimicked such an intergroup encounter by playing an individual's (Vervet A) wrr vocalization through a hidden speaker⁹⁴. After hearing repeated presentations of Vervet A's wrr calls without any other vervet groups in the vicinity, group members began to ignore him — he became an unreliable signaller. However, they responded appropriately to a wrr call from a different vervet. What happened when group members heard Vervet A's functionally equivalent, but acoustically distinct, chutter call? They continued to ignore Vervet A; that is, they knew, by voice alone, that it was the same unreliable individual.

Many other primate species, in addition to the semi-terrestrial species described above, have some capacity to recognize individuals by voice. For arboreal species, individual recognition by voice is obligatory, as group members are often out of sight. In support of this notion, cotton-top tamarins can distinguish individuals by their long calls⁹⁰, as can other arboreal New World species such as spider monkeys (*Ateles geoffroyi*)⁹⁷ and titi monkeys (*Callicebus moloch*)⁹⁸. Primates can also use vocal cues to determine whether a calling individual is a group-mate or a foreigner. Male grey-cheeked mangabeys (*Cercocebus albigena*), an arboreal Old World species, produce a loud, long call dubbed the 'whoopgobble' that is used to maintain spacing between adjacent mangabey groups. For this call to function as a spacing signal, males must be able to distinguish the whoopgobbles of their own group from those of adjacent groups. Waser's⁹⁶ playback experiments showed that mangabeys move away from the source when they hear the calls of neighbouring males, but move towards the source when they hear calls from their own group members.

We do not know whether different species use different acoustic cues to recognize individuals. For the coos of rhesus monkey and the grunts of chacma baboons, it has been argued that vocal tract resonances/formants are statistically the most robust cues for recognizing individuals⁹⁹. This might or might not be the case for other call types produced by these species. Other species might use different cues, such as the sequential organization of syllables in a long call⁹⁸. For mangabeys, the acoustic differences that mediate individual recognition seem to be in the tonal structure of the 'whoop' portion of the call and/or the tonal structure, duration and temporal patterning of the 'gobble' portion⁹⁶. In all likelihood, all primates use multiple acoustic cues to identify individuals, but some cues might be more reliable than others. Specific tests to determine which cues are important have not been conducted in any species.

Vocal advertising for sex. Although recognizing individuals and attending to foreigners are essential tasks for survival, a primate must ultimately find high-quality mates to ensure reproductive success. In many non-primate mating systems, mate choice is based on an assessment of auditory signals that are presumed to correlate with fitness. For example, females of a particular frog species (*Physalaemus pustulosus*) use the fundamental frequency of the male advertisement call (which correlates negatively with body size) to select the biggest male as a mate¹⁰⁰.

Copulation calls are produced immediately before, immediately after, or during copulation and can serve as auditory indicators of reproductive status. Whether primates produce copulation calls or not varies considerably according to species¹⁰¹. For example, among prosimians, female lemurs (*Lemur catta*) do not produce copulation calls, but females of one species of loris (*Nycticebus coucang*) do. Among New World monkeys, spider monkey females (*Ateles fusciceps*) do not produce copulation calls, but capuchin females (*Cebus apella*) do. In many Old World monkey and ape species, particularly those with multi-male mating systems, individuals (males, females or both sexes) produce copulation calls^{101,102}. Semple^{102,103} has studied the function of female copulation calls in Barbary macaques (*Macaca sylvanus*). Barbary macaque females were mated sooner after playbacks of their copulation calls than after a control female's playback. Playbacks to male dyads revealed that only the higher-ranking of the two would approach the sound source, while the other male stayed behind. These results indicate that the copulation calls of Barbary macaques are an indirect mechanism of female mate choice, because females more frequently mate with the higher-ranking male. The data also indicate that these calls promote competition between sperm by reducing the interval between matings¹⁰². Of course, a male Barbary macaque seeking a suitable mate would be wise to select, and fight for, a female that is in the peak stage of fertility. Indeed, male Barbary macaques can distinguish the reproductive states of conspecific females on the basis of voice alone¹⁰³. Playbacks of female copulation calls produced during late oestrus (when they are most likely to ovulate) elicited stronger responses from males than calls produced during early oestrus. So, the copulation calls of Barbary macaques influence their reproductive success.

Male long-tailed macaques also respond to female copulation calls, and their responses vary according to the stage of the female's ovarian cycle during which the calls are produced¹⁰⁴. In rhesus monkeys, only males produce copulation calls and always during copulation¹⁰⁵. It is not clear what role these vocalizations have, but there is some evidence that females regard the calls as true indicators of male quality¹⁰⁵ (but see REF 106 for an alternative account). Female copulation calls are also related to the dominance rank of the vocalizer and thus could also be a form of intrasexual competition between females. For instance, female pig-tailed macaques (*Macaca nemestrina*) and sooty

mangabeys (*Cercocebus torquatus atys*) vary their rate of copulation calling according to their rank in the dominance hierarchy — low-ranking females call more frequently and for longer than high-ranking ones¹⁰⁷. It is not known why copulation calls are evident sporadically throughout the primate lineage, or why one sex only or both produces them.

The sound of dominance. Male primates can expend a considerable amount of time and energy in elaborate displays that involve repeated vocalizations. These displays generally serve two functions: to intimidate rivals and to attract mates. The acoustic structure and number of vocalizations can allow listeners to assess the health of the vocalizer. Like copulation calls, if the production of such vocalizations is more costly or difficult for individuals in poor condition than for those in good condition, they provide listeners with accurate information about the vocalizers' relative competitive abilities. Primates can use this information for mate selection (as discussed above for copulation calls) and to choose rival males that are worth fighting. Primates (especially males) spend much of their time vying for status in a dominance hierarchy. To limit the cost of potential competitions, males must accurately assess whether a physical confrontation is likely to have a favourable outcome; that is, whether they can win. As such, honest acoustic cues about another individual's size and status might help males to determine whom to fight and when.

These honest acoustic cues seem to be particularly important for intrasexual competition between male savannah baboons (*Papio cynocephalus ursinus*). Savannah baboons live in large multi-male, multi-female groups. The dominance hierarchy of the males is linear, and is driven by competition for access to receptive females¹⁰⁸. Males produce a loud, two-syllable vocalization — called the 'wahoo' — in many contexts, including alarm, loss of contact, as part of pre-dawn choruses, and during contests with other males in the group. Although the different calls sound similar to human ears, each has unique acoustic features¹⁰⁹. Playback experiments show that savannah baboons can readily distinguish wahoos used in the context of alarm from those used during sexual contests¹¹⁰.

The production of extremely loud contest wahoos is often accompanied by aggressive chases and arboreal displays that can last for more than an hour. These displays are energetically very costly. As such, it has been proposed that wahoos serve as honest indicators of a male's dominance status or competitive ability. There are four lines of evidence that support this hypothesis¹¹¹. First, high-ranking males are more likely than low-ranking ones to participate in a contest wahoo exchange. Second, high-ranking males produce wahoo calls at a greater rate and their call bouts last longer. Third, males are more likely to participate vocally if a contest is initiated by an opponent of similar rank, and these contests more frequently develop into a physical fight (the auditory equivalent of scrotal colouration in vervets; see above). Finally, wahoo exchanges between individuals of different rank are more likely to be terminated by the subordinate

individual. Importantly, it is the rate of calls, the duration of bouts and so on that indicate the status of a male, rather than particular acoustic features related to his body size¹¹¹. So, baboons use auditory displays, in addition to visual ones, to signify their status during intra-group contests.

Auditory cues might be even more important during contests between males from different groups, as these encounters typically require males to assess the probability of beating rivals without being able to see them. Howler monkeys (*Alouatta pigra*) listen to the loud calls of potentially interloping neighbouring males and assess the 'numeric odds' that a confrontation will have an advantageous outcome¹¹². When listening to the loud calls of one or three foreign howler males, the alpha male of the resident group will respond more quickly, and with a longer duration, with his own loud calls if the odds are even or favour his group. That is, he assesses how many foreign males are calling and compares that number to the number of male members in his group. Given the high levels of background noise and attenuation of such long distance signals in the rainforest, this is auditory stream segregation *par excellence*.

Vocal exchanges and social structure. Primates in general seem to have an excellent ability to identify individuals on the basis of voice alone. Can they also understand the relationships between individuals on the basis of a vocal exchange, as they do in the visual domain⁹⁹? In the study described above⁹², Cheney and Seyfarth used playback experiments to show that female vervet monkeys can reveal what they understand about third-party relationships by their responses to certain vocalizations. When the investigators played back the screams of a juvenile to a group of three females, all of whom had offspring in the troop, only the mother of the screaming infant rapidly looked towards the source (as described above). But the other two females usually looked towards the mother of the juvenile without any other apparent cues. So, vervets associate specific screams with specific individuals, and specific individuals with their mothers.

There is also evidence that some species use auditory information alone to determine which individuals belong to different social groups. Old World monkey social groups, for example, are composed of strict hierarchies. Although the hierarchy of males is dynamic, the hierarchy of females tends to be stable. Related females form a hierarchical social structure called a 'matriline'. All of the females within a matriline are dominant or subordinate to all the members of another matriline. So, there is a hierarchy within and between matriline. Changes in rank can occur between two females within a matriline or, more rarely, between two matriline. The latter type of 'rank reversal' is an important change for the entire group, whereas a rank change within a matriline does not really affect the lives of those outside that matrilineal group.

Playback of simulated vocal exchanges to wild baboons was used to investigate whether monkeys have knowledge of these hierarchies¹¹³. Using threat grunts and submissive screams, anomalous vocal exchanges

were created in which a subordinate individual threat-grunted towards a dominant individual who screamed. These simulated exchanges mimicked a rank reversal within a matriline (X2 threat versus X1 scream) or between two matriline (Z1 threat versus Y1 scream). Baboons responded more intensely to playbacks of between-matriline rank changes than to playbacks of within-matriline reversals. This indicates that baboons can simultaneously classify group members according to their individual attributes and their membership in higher order groups.

Neural correlates of auditory behaviour. Auditory communication is vital in the lives of primates, but we are only beginning to understand how biologically relevant features of primate calls are processed at the levels of single neurons or small populations of neurons (see REFS 114,115 for recent reviews). This might be because there is a persistent tendency to think of auditory systems as generic (the same across all mammals except bats, for instance) and linear processors of sounds (see REF 116 for an excellent critique).

For many years, the squirrel monkey was the only primate model for investigating the role of the auditory cortex in processing species-specific vocalizations (see REF 117 for review). Studies of this species found that most cells in the superior temporal gyrus respond to species-specific vocalizations, but not selectively^{118,119}. However, these recordings were made across the superior temporal gyrus, usually without reference to any cytoarchitectural or functional subdivisions (FIG. 3b; see REF 120 for review of the current model of auditory cortical organization). Also, sophisticated digital signal processing techniques were not available at the time. Nevertheless, some interesting findings emerged from these investigations. For example, in squirrel monkey primary auditory cortex (A1), and the cortical region lateral to it, time-reversed calls elicited responses as strong as those elicited by normal conspecific calls¹²¹. Multiple exemplars of the same call type (the 'isolation peep') elicit similar temporal discharge patterns in a subpopulation of auditory cortical neurons, but unique discharge patterns per exemplar in a smaller subpopulation¹²². The latter could be used to process individual recognition.

More recently, recordings were made from identified locations in the auditory cortex of squirrel monkeys. Bieser¹²³ compared the responses of auditory cortical neurons in the squirrel monkey to periodic frequency-modulated (FM) elements that were based on the structure of this species' 'twitter' calls. Neurons in A1, the rostral auditory field and the insula responded by phase-locking to either the up or down FM sweeps within the synthesized stimuli (up to period repetition rates of 16 Hz). However, neurons in all three areas responded more reliably (in terms of phase-locking) to natural conspecific twitter calls than to synthesized calls with matched repetition rates. The main difference between the two stimuli was the strong amplitude modulation of the natural calls, which divided the U-shaped FM contours into separate units. Bieser¹²³ suggested that the better encoding of the natural twitter call by auditory

neurons could be attributed to this amplitude modulation dividing the call into syllable-like elements.

Temporal features also seem to have an important role in driving responses to vocalizations in the auditory cortex of marmosets (*Callithrix jacchus*). Wang and colleagues¹²⁴ investigated the responses of A1 neurons to normal, time-compressed, time-expanded and reversed versions of the marmoset's twitter call. Instead of being phase-locked to the rapidly changing spectral features of the twitter call, firing patterns in A1 were phase-locked only to the pulses of the call (the peaks in the amplitude envelope). Compressing, expanding or reversing the call reduced the population response in A1. Neural responses to time-reversed calls were particularly reduced. Furthermore, twitter calls from two different individuals (with different spectrotemporal characteristics) evoked unique but overlapping patterns of neural responses — perhaps a step along the neural pathway for recognition of individuals by voice. Another study revealed that degrading the temporal envelope of the twitter call reduced its effectiveness in driving marmoset A1 neurons, but degrading the spectral envelope had less influence on response magnitudes¹²⁵.

In anaesthetized rhesus monkeys, electrophysiological mapping using band-passed noise as stimuli delineated three cochleotopic areas along the superior temporal gyrus: the caudolateral (CL), middle lateral (ML) and anterolateral (AL) belt areas¹²⁶ (FIG. 3b). Unlike neurons in A1, neurons in these areas responded best to complex sounds, including species-specific vocalizations. Neurons in all three lateral belt areas responded preferentially to rhesus monkey calls compared with energy-matched pure tone stimuli. For the seven call exemplars tested, 90% of lateral belt neurons responded better to certain call types than to others. In a related study, Tian and colleagues¹²⁷ argued that the AL belt area is more selective for call type but not for sound-source location, whereas the CL belt area is less selective for call type but highly selective for sound-source location. The response properties of the ML area are intermediate between those of AL and CL.

Two important caveats of these recent studies are that only one exemplar per call category was used (see variation within call category in FIG. 5) and no other, behaviourally relevant complex sounds were used. So, it is not possible to ascertain whether auditory belt neurons are vocalization-selective (in the same manner that face neurons are selective for faces) or simply vocalization-sensitive. Aside from showing sensitivity to conspecific vocalizations, all of these neurophysiological studies lack behavioural relevance. It is entirely possible, for example, that although time-reversing calls affects neural responses, reversed calls might have no effect at the behavioural level. If the primate auditory system is as specialized for vocal processing as the human or bat auditory systems¹²⁸, one must first identify the acoustic features that are relevant to particular adaptive problems and then use this information to examine how neural mechanisms can extract such cues¹¹⁴. Naturalistic behavioural studies of cotton-top tamarins illustrate how this can be achieved.

Like many primates, including marmosets, cotton-top tamarins produce loud, multi-syllabic calls dubbed 'long calls'¹²⁹. On hearing long calls, conspecifics reliably respond with their own antiphonal long calls. Which acoustic features of the long call can elicit an antiphonal call from a conspecific? Playback experiments using a combination of normal and experimentally manipulated long calls as stimuli, and the antiphonal calls of isolated individuals as the dependent measure, were set up to identify the relevant acoustic features^{130,131}. Tamarins preferentially produced antiphonal calls in response to whole calls rather than to signals composed of one of the two syllable types that comprise long calls¹³⁰. Interestingly, tamarins did not distinguish between normal long calls and time-reversed or pitch-shifted long calls, but the species-typical amplitude envelope was required to elicit normal response rates¹³¹.

These behavioural experiments allow us to generate meaningful hypotheses for the neural mechanisms that underlie primate communication. For example, in the case of the cotton-top tamarin, one might predict that neurons in the auditory cortex are sensitive to the combination of syllables in the long call, but insensitive to the order of syllables within the call. The behavioural sensitivity of tamarins to temporal cues embedded in the amplitude envelope, and their insensitivity to spectral cues¹³¹, is in remarkable concordance with the neural sensitivities of the closely related marmoset^{124,125}.

Visual–auditory interactions

As described above, primates have large and diverse repertoires of visual and auditory communication signals. Although we have treated the two modalities separately, this division is, of course, artificial. Many of these signals are produced concomitantly. Rhesus monkeys, for example, assume different facial expressions when producing particular vocalizations^{132,133}. Threat calls are accompanied by an open mouth and staring, whereas coo calls are produced while lips are protruded for an extended time (FIG. 6a). Such bimodal signals are advantageous for detection, discrimination and learning, as has been shown for multimodal signals in other domains, modalities and taxonomic groups¹³⁴. For 'higher' cognitive processes such as developing knowledge of kinship and rank^{7,113}, learning to recognize an individual's voice must include a process by which individuals match their visual observations of others to the others' voices — perhaps creating conceptual representations rather than representations in one sensory modality or the other.

We know little about the perceptual and neural bases of multimodal integration of communication signals in primates. However, some progress has recently been made in assessing whether primates understand the correspondence between the auditory and visual components of their signals. In a preferential looking paradigm, rhesus monkeys can match the auditory components of threat and affiliative (coo) calls with the appropriate facial expressions without any explicit

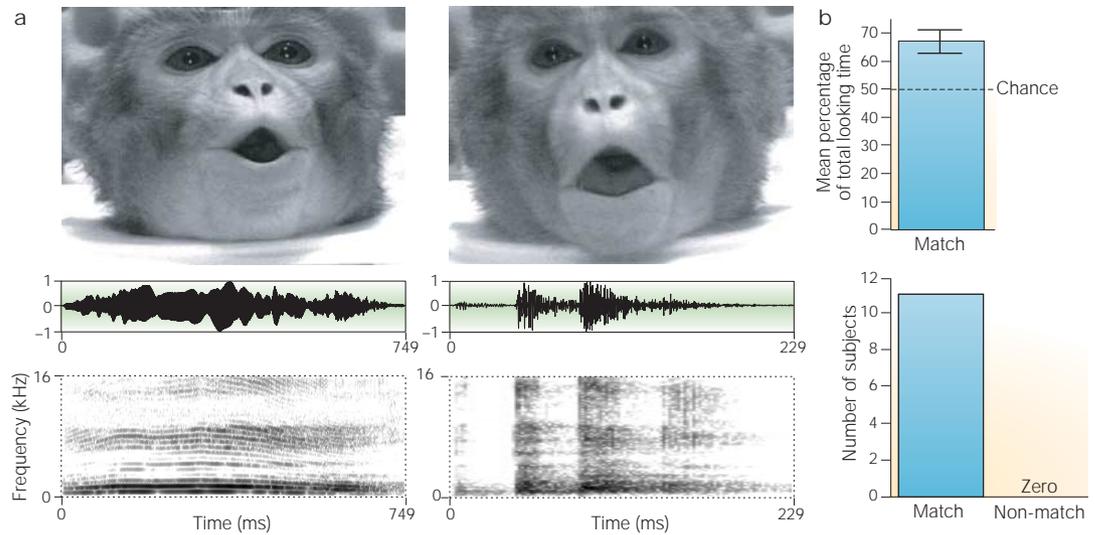


Figure 6 | **Multimodal vocalizations.** **a** | Single video frames of coo (left) and threat (right) vocalizations made by a rhesus monkey. The vocalizations' oscillograms (middle panels) and spectrograms (lower panels) are also shown. Frames were extracted at the point of maximal mouth opening during the vocalization. Rhesus monkeys produce unique facial expressions when they vocalize different call types. **b** | Mean percentage of total looking time to the face that matched the heard vocalization (upper panel) and proportion of subjects who looked longer at the match screen (lower panel). All subjects looked longer at the screen that matched the vocalization heard through the hidden speaker. The ability of monkeys to match facial expressions with vocalizations could represent an evolutionary precursor for human speech-reading. Reproduced, with permission, from *Nature* REF. 135 © (2003) Macmillan Magazines Ltd.

training or reward¹³⁵ (FIG. 6b). One drawback of this study is that the monkeys could use simple amodal cues (such as sound duration and duration of mouth opening) to make a match. Two other studies of chimpanzees have avoided this problem by using match-to-sample paradigms to show how chimpanzees integrate visual and auditory signals^{136,137}. Izumi and Kojima¹³⁶ showed that a chimpanzee could match facial postures to voice for some vocalizations. Parr¹³⁷ showed that chimpanzees have preferences for either the auditory or visual modalities depending on which expression was perceived; these biases were consistent with the importance of that modality during natural experience.

Socioecologically sensible neuroscience

In his monumental book, *The Evolution of Communication*, Hauser¹⁰¹ concluded with a section entitled 'A socioecologically sensible neuroscience'. He

argued that there is abundant evidence from throughout the animal kingdom that the design of an animal's brain is exquisitely suited to the particular socioecological problems faced by that species. He noted that this fact had escaped the attention of most mammalian neuroscientists. We have tried to bridge this chasm between ethology and sensory neuroscience for primates by highlighting and reviewing what we know about the sensory cues that are used by primates to operate in their special niche — societies. Much work — interesting work — lies ahead of us. A true Darwinian approach would compare primates not only with non-primates, but also with other primates that occupy different niches, such as those that live in smaller versus larger social groups or those that are more terrestrial than arboreal. In general, though, we are confident that studying how primate brains work in the wild will give us greater insights into their design and relationship to our human brains.

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Competing interests statement

The authors declare no competing financial interests.

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