

The auditory behaviour of primates: a neuroethological perspective

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The ethological approach has already provided rich insights into the auditory neurobiology of a number of different taxa (e.g. birds, frogs and insects). Understanding the ethology of primates is likely to yield similar insights into the specializations of this taxa's auditory system for processing species-specific vocalisations. Here, we review the recent advances made in our understanding of primate vocal perception and its neural basis.

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Abbreviations

A1	primary auditory cortex
AL	anterolateral belt area
CL	caudolateral belt area
FM	frequency-modulated
ML	middle lateral belt area
Tpt	temporoparietal area

Introduction

Animals have evolved to detect and process signals that are of particular relevance to their survival and reproductive success. For some species, the range of signals produced and perceived is narrow and typically restricted to the context of mating and alarm, for example most insects, whereas in other species, such as primates, a greater variety of signals are produced, allowing individuals to encode information about identity, species, sex, motivational state, size and referential target. Independent of such variations in repertoire size, biologists have gained considerable insights into both the design and underlying mechanisms of animal signals, by combining naturalistic studies with carefully controlled laboratory experiments. Of particular relevance to this review, studies of signal design have helped illuminate the role of specialized neural circuits in perceptual decoding.

In the auditory domain, neuroethological research has been crucial for our understanding of how the brain functions and how natural selection shapes brain design for complex behaviours. Echolocation in bats, song learning in birds, sound localization in barn owls, and mate choice in frogs continue to be robust models for auditory processing [1]. Even in humans, studies of our species-specific vocalization — speech — have been immensely successful in aiding our understanding of specialized neural function [2]. Oddly enough however, an ethological approach has generally not been adopted in studies of non-human primate

audition [3], with perhaps one exception, the squirrel monkey, *Saimiri sciureus* [4,5].

Following the lead of classical neuroethological studies of animal communication, we argue that, in order to understand the neural mechanisms underlying auditory processing in primates, it is necessary to understand how primates use their vocalizations during natural social interactions, and which features of a vocalization are critical to its functional classification. Here, we focus on the application of this approach to primate auditory behaviour and cortical function, placing an emphasis on two issues. First, are the design features of the primate's vocal communication system similar to that of other taxa? Second, how does the primate brain mediate call perception, and to what extent are such mechanisms similar to or different from those observed in other taxa?

The acoustic bases for vocal recognition

A primate's vocal repertoire contains a large variety of sounds that humans often perceive as a meaningless collection of screams, grunts, and barks. But how do the primates themselves perceive their species-specific vocalizations? Do they classify them in more subtle ways than we do? What acoustic cues do they use to distinguish different call types with different functions? Using both field playback experiments and psychophysical methods, ethologists are beginning to uncover the acoustic features that mediate call type classification and discrimination.

Different acoustic properties of communication signals potentially encode different kinds of biologically significant information [6]. In primates, differences in acoustic structure not only encode different call categories, but they also encode information about individual, sexual, and group identity [7–10], motivational state [11,12], body size and reproductive status [13,14]. Here, we focus on the acoustic cues associated with identity recognition and call type discrimination.

Recognition of individual, sexual and group identities

Individual and kin recognition have important implications for the evolution of social behaviour [15], and the behaviour of many species of primates suggests a capacity for such recognition on the basis of voice alone [16]. Field playback experiments on rhesus monkeys, *Macaca mulatta*, have tested the ability of females to distinguish kin from non-kin using the 'coo' vocalization [7,11]. On the basis of the latency and duration of head orienting responses towards the sound source, female rhesus monkeys respond quicker and for longer to the coos of their kin than to those of non-kin or distantly related kin [7]. In order to further explore this capacity to discriminate between kin based on acoustic cues alone, a habituation-discrimination paradigm

has been used, in which subjects were habituated to the 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 (increased duration of orienting response) to the coo call from the different relative. Thus, female rhesus monkeys are able to distinguish kin from non-kin, and different members of their kin group, on the basis of voice alone. What acoustic cues are they using to accomplish this? Acoustical analyses have revealed that the filtering effects of vocal tracts on the spectral structure of coo calls are critical for distinguishing individuals [8]. Rhesus monkeys call types that have less pronounced vocal tract filtering effects cannot be used as reliably as coo calls for identifying individuals [8].

The capacity for individual recognition has also been explored in captive cotton-top tamarins, *Saguinus oedipus*, using the habituation-discrimination paradigm [10] as well as a novel phonotaxis procedure [9]. In these studies, 'long calls' were used as playback stimuli. Long calls in tamarins and other primates serve at least three different functions: territorial defense, mate attraction and pair formation, and maintenance of contact with visually isolated group members [17]. Results from both assays reveal that, like rhesus monkeys, cotton-top tamarins can identify individuals using only the acoustic cues of their long calls. The phonotaxis assay also revealed some interesting gender differences [9]. In this assay, subjects are placed in the middle of a T-shaped apparatus. Two different call types are played back sequentially from opposite sides, and the direction and duration of approaches by the subjects to either end of the T are measured. Under these conditions, males showed a bias to approach foreign females over familiar ones, whereas females approached cagemate and homeroom (i.e. familiar) males over foreign males. These results suggest that tamarins are able to distinguish between multiple levels of acoustic information encoded within a single vocal signal. Acoustic analyses of the tamarin long call suggest that there are multiple spectral and temporal parameters that tamarins can potentially use to make these discriminations and subsequent classifications [10].

In summary, when a primate vocalizes, receivers are provided with a range of acoustic information potentially concerning the signaler's body size, sex, individual identity, kinship and group membership. Variation in the acoustic structure of vocalizations among individuals within a group provides the basis for this type of discrimination.

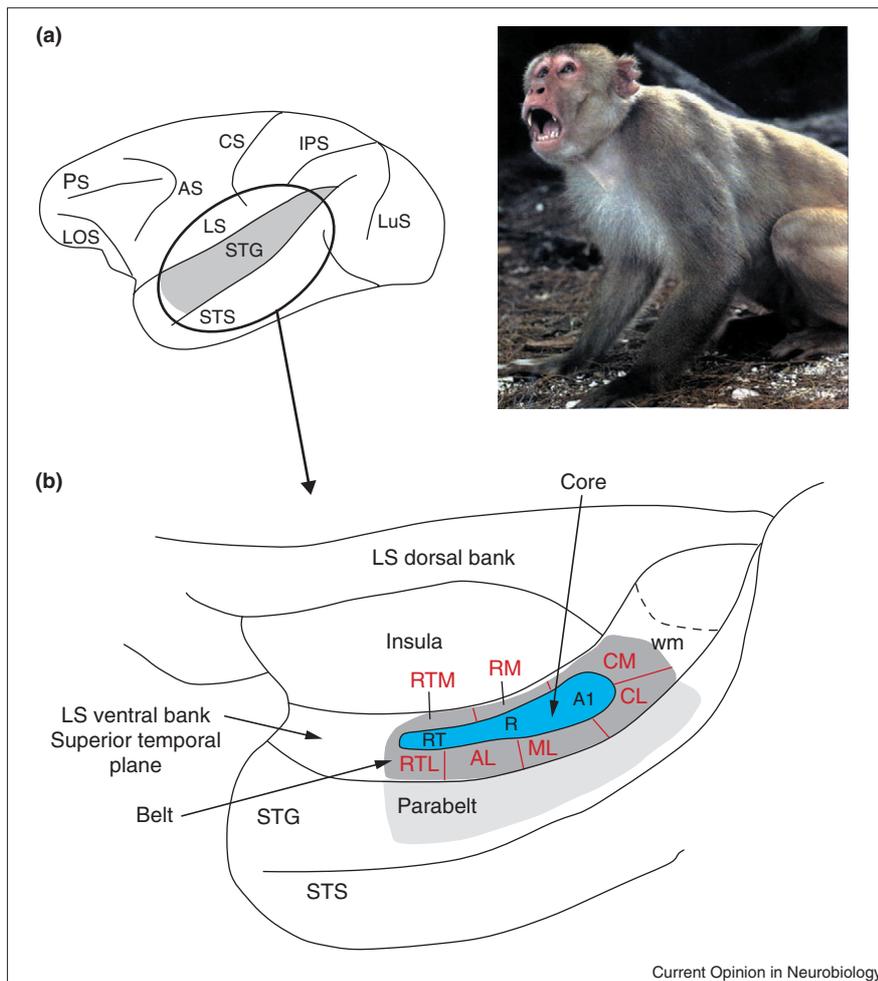
Call-type discrimination

Communication sounds across taxa are often complex, with time-varying spectral features. Animals commonly use multiple acoustic features to categorize the different types of vocal signals in their repertoire (e.g. [18]). Primates are no exception. Unfortunately, only a handful of studies have explored which acoustic cues are used to classify different conspecific vocalizations.

Field observations of Japanese macaques, *Macaca fuscata*, [19] have provided some of the earliest insights into the importance of distinctive cues in call-type discrimination. Green [19] observed that Japanese macaques produce different types of coo calls that vary morphologically and as a function of socioecological context. More detailed analyses of two coo types has revealed a key discriminating feature: the temporal position of the peak frequency. In captivity, psychophysical experiments have confirmed that Japanese macaques can use this temporal cue to perceptually classify their coo vocalizations [20,21]. These studies have also demonstrated a left hemisphere bias (i.e. a right ear advantage) for discriminating species-specific vocalizations. Recently, Le Prell and Moody [22*] have directly tested the hypothesis that the temporal position of the peak frequency is a sufficient cue for call-type discrimination, by presenting coos that were temporally reversed, but with all other acoustic features (e.g. the amplitude envelope) held constant. They hypothesised that if the temporal position of the peak frequency was the sole cue used for classification by Japanese macaques, then the animals would be 'tricked' into classifying all reversed versions in the opposite manner to the one in which they had originally classified the forward coo exemplars. However, the results showed that for many exemplars, Japanese macaques still performed the classification of reversed coos correctly, by using other cues present in the signals. The authors conclude that single-cue categorization schemes alone fail to predict the perceived similarity of coo calls by Japanese macaques.

In support of the Japanese macaque findings, field playback studies of rhesus monkeys also show that vocal recognition relies upon multiple acoustic cues. These studies were built upon the initial findings by Hauser and Andersson [23] who demonstrated that wild rhesus monkeys orient to the right upon hearing conspecific vocalizations played back from directly behind them, whereas they orient to the left upon hearing heterospecific signals. Using this orienting response asymmetry as an assay, Hauser *et al.* [24] tested the role of inter-pulse interval on call recognition. Rhesus monkeys produce several vocal signals composed of short, repeated bursts of acoustic energy ('pulses') separated by brief periods of silence ('inter-pulse intervals'). Playback experiments, using temporally manipulated exemplars of a subset of these calls — shrill barks, grunts and copulation screams — demonstrated that expanding or contracting the inter-pulse interval, beyond the species-typical range, eliminated the right-ear orienting bias normally seen for shrill barks and grunts, but not for copulation screams [24]. Thus, the inter-pulse interval is an important temporal cue for distinguishing shrill barks and grunts from non-conspecific sounds. Building upon this finding, the role of other temporal features was tested by conducting playbacks of time-reversed calls [25]. By using time-reversed calls, the role of time-based cues, such as the amplitude envelope shape, can be tested in isolation, keeping the overall spectral content of the call constant. Reversed exemplars of shrill barks and harmonic arches caused rhesus monkeys to shift

Figure 1



Auditory responsive regions in the rhesus monkey cerebral cortex. **(a)** The shaded region of the brain corresponds to the approximate location of auditory-responsive areas on the exposed surface of the superior temporal gyrus. **(b)** A closer view of the superior temporal plane shows the 'core' and 'belt' areas of auditory cortex. In this figure, the overlying dorsal bank of the lateral sulcus is graphically reflected upwards to reveal the ventral bank. AS, arcuate sulcus; CM, caudomedial; CS, central sulcus; IPS, intraparietal sulcus; LS, lateral sulcus; LOS, lateral orbital sulcus; LuS, lunate sulcus; PS, principal sulcus; R, rostral; RM, rostromedial; RT, rostromedial; RTL, lateral rostromedial; RTM, medial rostromedial; STG, superior temporal gyrus; STS, superior temporal sulcus; wm, white matter.

their orienting bias from right to left, suggesting that these signals are classified as something other than 'conspecific sounds'. These results underscore the importance of multiple temporal cues in rhesus monkey vocal recognition.

Neural bases for vocal recognition

What are the underlying neural mechanisms for primate vocal recognition? Although we currently lack definitive answers, a growing body of work suggests some exciting avenues for future research. In fact, as we argue, current work on the cortical physiology of auditory processing of macaques holds out the hope of doing for hearing what studies of macaque visual cortex have already done for seeing. Here, we present the state of knowledge in a top-down fashion.

Hemispheric asymmetries

As alluded to in the previous section, behavioural experiments under laboratory and field conditions reveal that at least two Old World monkey species exhibit asymmetries in their perception of conspecific vocalizations. Psychophysical studies of coo calls in Japanese macaques reveal a right ear

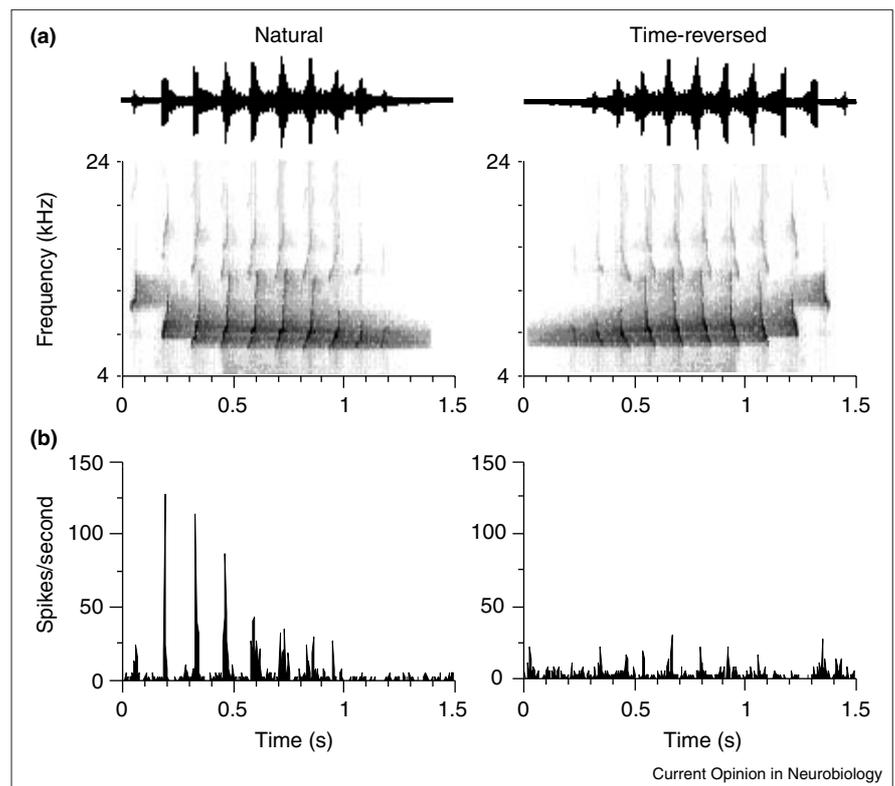
advantage [20,26]. Field playback studies of rhesus macaques demonstrate a right ear orienting bias in response to conspecific vocalizations [23–25]. Finally, recent psychophysical experiments with rhesus macaques show a right-ear advantage when discriminating between species-specific 'scream' vocalizations [27]. These behavioural/perceptual asymmetries suggest an underlying neural asymmetry.

Neuroanatomical and experimental lesion studies in macaques strongly support the studies of behavioural lateralization. For instance, the length of the left Sylvian fissure, which is adjacent to auditory association cortex, has been found to be significantly greater than the right Sylvian fissure in macaques (*M. fascicularis* and *M. mulatta*) [28,29]. Volumetric measurements of the temporoparietal area (Tpt) in macaques, an auditory region equivalent to the planum temporale in humans and pongids, indicate that the left area Tpt is significantly larger than the right [30].

Auditory cortical lesions in Japanese macaques trained to discriminate their coo vocalizations also lend strong support to a large-scale neural specialization [26]. Unilateral

Figure 2

Neural selectivity to marmoset twitter calls. **(a)** Waveforms (top) and spectrograms (bottom) of both a natural and a reversed version of a marmoset twitter call. **(b)** Responses of A1 neurons to the stimuli shown in (a). Responses shown as a compound post-stimulus time histogram generated by summing individual post-stimulus time histograms derived from 14 single units from A1 of a marmoset. Figure courtesy of X Wang [37].



lesions of the left (but not the right) auditory cortex in Japanese macaques result in a transient impairment in the discrimination of species-specific vocalizations but not other types of auditory stimuli. Bilateral lesions result in a complete and permanent inability of Japanese macaques to discriminate coos—a deficit not due to hearing loss associated with auditory cortical lesions [31]. A recent follow-up to these studies has demonstrated that bilaterally lesioned Japanese macaques can discriminate sounds of different frequencies but cannot determine whether a sound changes frequency (a temporal cue characteristic of the coo vocalization) [32].

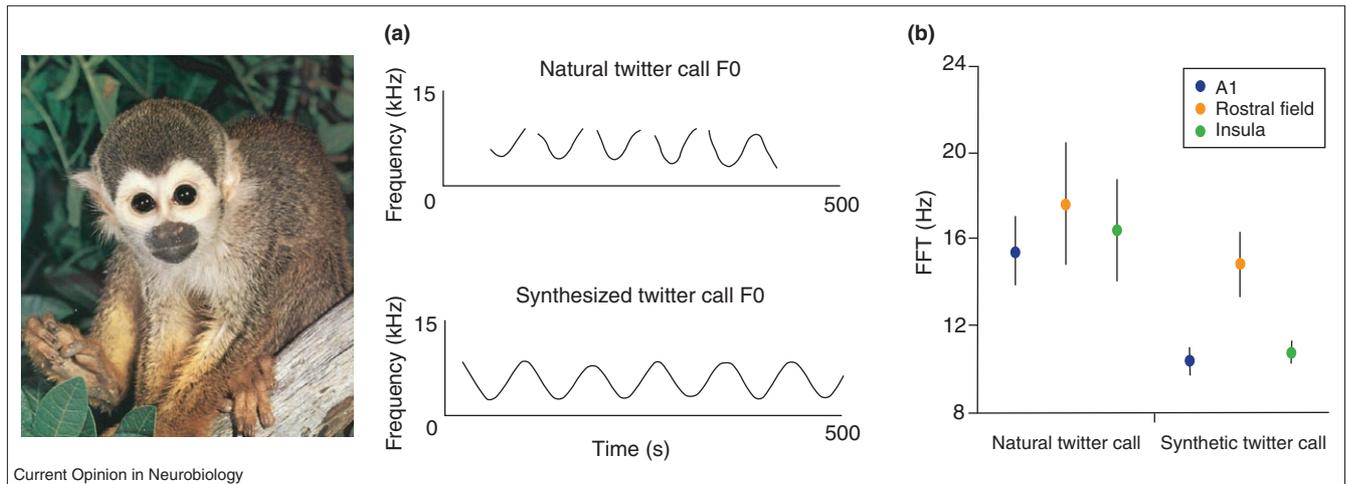
Call selectivity at the single unit level

Despite the importance of vocal communication in the lives of primates, we lack a complete understanding of how biologically relevant features of complex sounds are processed at the level of single neurons or small populations of neurons. In other taxa, studies of the neural representation of species-specific vocalizations have revealed neurons that respond selectively to communication sounds [34,35]. For example, in songbirds, neurons in the forebrain are highly selective to a bird's own song: responses to the bird's own song are more robust when compared to responses to conspecific songs or time-reversed versions of the bird's own song [34]. In light of studies like these, the extent to which conspecific vocalizations are represented in the primate auditory cortex has received renewed interest.

Until recently, the squirrel monkey was the only primate model for investigating the role of auditory cortex in processing species-specific vocalizations. Studies of this species have found that most cells in the superior temporal gyrus respond to species-specific vocalizations [4,5]. However, one of the drawbacks of these studies was that recordings were made across the superior temporal gyrus without reference to any cytoarchitectural or functional subdivisions therein. More recent studies have recorded from identified locations within the auditory cortex [35], and have broadened the range of species tested [36,37,38•,39•].

In the anesthetized rhesus monkey, electrophysiological mapping has delineated three cochleotopic areas along the superior temporal gyrus (Figure 1) [36]. They have been labelled the caudolateral (CL), middle lateral (ML), and anterolateral (AL) belt areas. Unlike the primary auditory cortex (A1), neurons in these areas respond best to complex sounds, such as band-passed noise and species-specific vocalizations. In fact, neurons in all three lateral belt areas prefer rhesus monkey calls to energy-matched pure tone stimuli. Furthermore, among the seven call exemplars tested, 90% of lateral belt neurons respond better to certain call types over others. Tian *et al.* [38•] have tested whether functional differences across lateral belt areas exist at the single neuron level; in particular, these authors were interested in whether certain belt areas were better suited to processing vocalizations as opposed to spatial location than

Figure 3



Neural selectivity to squirrel monkey twitter calls. **(a)** Spectrographic representation of a squirrel monkey twitter call and a synthetic FM sound with similar frequency sweeps and period repetition rates to the natural call. **(b)** Average neural responses from three cortical areas to a natural twitter call and a synthesized sound with similar FM modulation and a period repetition of 16 Hz. The mean values of neural responses

are derived from a Fast Fourier Transform (FFT) of the post-stimulus time histograms, which represent a quantitative measure of the degree of phase-locking of neurons with the stimulus. The results show that neurons in all the areas studied (A1, insula and rostral field) phase-lock to FM elements of the natural call. Vertical lines indicate standard deviations. Figure redrawn from Bieser [35].

others, and vice versa. In a cleverly designed experiment, anesthetized rhesus monkeys were presented with seven different conspecific call types from seven different azimuthal positions. On the basis of recordings from all three lateral belt areas, it appears that the AL belt area is highly 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 ML area has response properties that are intermediate between AL and CL. These data suggest that different lateral belt areas may have unique functions, possibly related to their distinct connections with the prefrontal cortex [40–42].

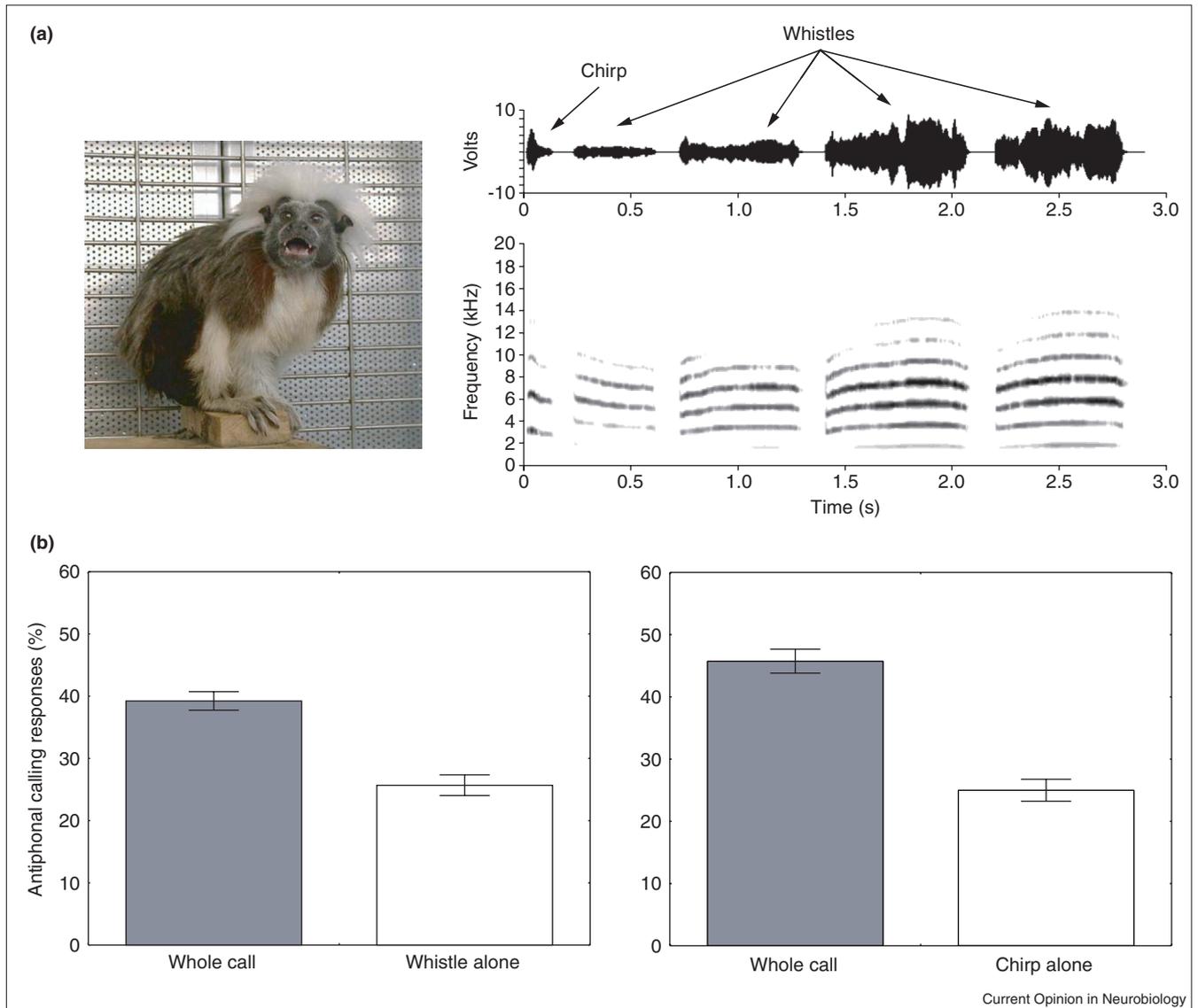
The lateral belt areas are not the only regions with neurons selectively responsive to species-specific vocalizations. Although neurons in primate A1 respond more robustly to pure tones than neurons in other higher order auditory areas, recent studies reveal that A1 neurons can also be selective to complex time-varying stimuli. In common marmosets, *Callithrix jacchus*, and squirrel monkeys, A1 neurons can even be selective for conspecific calls [35,37,39**]. In both species, A1 neuronal firing patterns appear to phase-lock to the temporal envelope of the species-specific vocalizations used as stimuli.

In an exquisite study of the cortical representation of the marmoset's 'twitter' call, Wang *et al.* [37,39**] have correlated the spectral and temporal firing patterns of A1 neurons with the acoustic features of the twitter call. They find that, instead of being phase-locked to the rapidly changing spectral features of the twitter call, A1 firing patterns are phase-locked only to the pulses of the call (i.e. the peaks in

the amplitude envelope; Figure 2a,b). Across the A1 cortical field, neurons responding to the twitter call are synchronized not only to stimulus features but also to each other. Furthermore, twitter calls from different individual marmosets evoked unique but overlapping patterns of neural responses, suggesting, perhaps, the existence of a neural pathway for individual recognition. In order to test the selectivity of these responses to conspecific calls, Wang *et al.* [37] used time-reversed versions of the twitter call as stimuli and found that neuronal responses decreased dramatically (Figure 2a,b). This pattern parallels Margoliash's [33] finding that neurons in the song system of white-crowned sparrows respond best to the bird's own song compared to reversed versions of the song. From these data alone, it is unclear whether differences in the neural responses to normal versus reversed twitter calls are solely due to differences between the acoustic structures of the two stimuli, or whether they also result from differences in the behavioural relevance of normal versus reversed calls. To test for the latter possibility, a comparative study of A1 neural responses to identical natural and time-reversed marmoset twitter calls was conducted in cats and marmosets [39**]. Unlike in the marmoset, cat A1 neurons exhibited no preference for natural marmoset twitter calls over their reversed counterparts. Thus, at the level of A1, it appears that the neural circuitry of marmosets is specialized to process its own species-specific calls.

Bieser [35] has compared neural responses of auditory cortical neurons in the squirrel monkey to periodic frequency-modulated (FM) elements constructed on the basis of this species' 'twitter' calls (Figure 3a). As in the marmoset, neurons in A1, the rostral auditory field, and the insula (see

Figure 4



Units of perception in cotton-top tamarin long calls. (a) Cotton-top tamarin combination long call. The time-amplitude waveform (top) and spectrogram (bottom) of a representative combination long call are shown with labeled chirps and whistles. (b) Antiphonal calling

responses to playbacks of whole long calls versus single syllables (whistles and chirps). Responses were greater to whole calls than to single whistles or chirps. Error bars show 1 SEM. Figure modified from [47].

Figure 1) responded by phase-locking to either the up or down FM sweeps within the synthesized stimuli (up to period repetition rates of 16 Hz). Interestingly, a comparison of neural responses to synthesized versus natural twitter calls, with matched period repetition rates, has revealed that neurons responded more faithfully (in terms of phase-locking) to natural conspecific twitter calls than to synthetic calls (Figure 3b). This was true for all three cortical areas. The primary difference between the two stimuli was the presence of a strong amplitude modulation in the natural calls, which divided the U-shaped FM contours into separate units (Figure 3a). Bieser [35] suggests that the better encoding of the natural twitter call by auditory neurons can be

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

On the basis of these studies on the marmoset and squirrel monkey auditory cortex, it appears that even in early stages of cortical processing, selectivity for species-specific communication sounds exists and may be founded on experience-dependent and/or species-specific neural mechanisms.

The units of perception and combination-sensitive neurons: an hypothesis

Many primate species produce bouts of vocalizations containing sequences of either similar or dissimilar acoustic

units. Ethologists studying primate communication systems are faced with the daunting task of dividing the vocal repertoire into different types of meaningful acoustic units (e.g. bouts, vocalizations, syllables, etc.). How does one determine whether a sequence of temporally distinct units emitted by an animal represents a single functional unit (e.g. meaningless syllables put together to form a word in speech), a string of functionally independent units (e.g. a sentence in speech), or something more urbane such as the simple repetition of one small unit (e.g. a bout of laughter, 'ha, ha, ha!')? A true understanding of how vocal signals are parsed must be derived from the animal's perspective: vocal signals must be segregated into those acoustic units that elicit meaningful responses from intended receivers — the units of perception [3,17].

Understanding the order of units within primate long calls and then experimentally changing the order of such units in playback experiments can provide insights into the units of perception. In titi monkeys, *Callicebus moloch*, and gibbons, *Hylobates lar*, males produce long calls, in which the arrangement of units is fairly consistent for a particular individual [43,44]. In order to determine whether these primates are sensitive to the order of units within their species-typical long call, playback experiments have been conducted using both normal and manipulated calls involving unit rearrangements. Both titi monkeys and gibbons responded with an increased rate of aggressive/territorial calls. These results suggest that at least some primate species are sensitive to the order of units within a call, a pattern that has been demonstrated for several Passerine songbirds [45].

By exploiting the rich species-typical vocal behaviour expressed by cotton-top tamarins in captivity, Ghazanfar *et al.* [46••] have investigated the units of perception in this species' long call. In response to social isolation, tamarins will emit a long call beginning with 1–2 chirp units and ending with 2–5 whistle units (Figure 4a) [47]. Upon hearing such vocalizations, conspecifics often respond with their own antiphonal long calls, that is, they respond to a long call by producing their own long call. Although tamarins can produce chirps and whistles independently, the authors hypothesized that the combination of both syllable types functions as a more effective stimulus (i.e. the unit of perception) for eliciting antiphonal long calls than either unit alone. Playback experiments using whole long calls, isolated chirps and isolated whistles confirmed this hypothesis. Whole calls were much more effective in eliciting antiphonal long calls than either single whistles or single chirps (Figure 4b). These data suggest that the whole call is the most meaningful unit from the perspective of socially isolated receivers.

What are the neural mechanisms that could process such vocal sequences and subsequently release species-typical vocal responses? One candidate neuronal mechanism is the non-linear response of neurons to the combined elements of a signal, as compared to the individual elements alone.

Combination-sensitive neurons have been described extensively in the auditory systems of bats [34,48], frogs [49], and songbirds [50] using species-specific vocalizations as stimuli. We predict that, like these taxa, primates with long, multi-element vocalizations will have neurons that are combination-sensitive, particularly when the unit of perception is the whole sequence of units. For example, the central auditory system of tamarins may contain neuronal populations that are combination-sensitive to both temporal and spectral components of the chirp-whistle sequence present in their long calls.

There is some evidence for combination-sensitive neurons in the owl monkey, *Aotus trivirgatus*, and the long-tailed macaque, *M. fascicularis* [51,52]. Primary auditory cortical neurons in both species respond non-linearly to combinations of pure tones. In the owl monkey, when stimuli are constructed to match a neuron's spectrotemporal receptive field, these stimuli can elicit robust responses from auditory cortical neurons [51]. When these stimuli deviate spectrally or temporally from the neuron's receptive field, however, they elicit weaker responses. Brosch *et al.* [52] have investigated the relationship between combination sensitivity and the spectrotemporal tuning properties of cortical neurons in A1 and the caudomedial area of auditory cortex in anesthetized macaques. They found that the majority of multi- and single-units showed response enhancement to sequences of two tones. In other words, compared to the presentation of a single tone in isolation, the response to the two tones in succession elicited a significantly enhanced response. Although such response enhancement occurred for a variety of tone frequencies and a wide range of inter-tone intervals, a given neuron fired best to a two-tone sequence if each of the tones were within a specific frequency range and separated by a specific inter-tone time interval. Thus, A1 neurons of the owl monkey and the long-tailed macaque exhibit combination selectivity to tone stimuli. It remains to be seen whether such selectivity is present when vocalizations such as long calls are used as stimuli.

Conclusions and future directions

Although much progress has been made in our understanding of how primates use their vocalizations and how such signals are represented in the auditory cortex, we still lack a paradigm that can address both of these facets of communication simultaneously. For example, manipulations of vocal signals that are used to probe neurophysiological responses are divorced from how primates might perceive such signals, and vice versa. In the future, it will also be worthwhile to use awake behaving primates for neurophysiological investigations. There are many functions of vocalizations in the wild that can be adapted to the laboratory setting (e.g. individual recognition through vocalizations). Finally, future research will benefit from further investigation into cross-modal perception, using the interplay between vocal production and perception, as has been studied in birdsong [53,54]. In particular, primate species that readily vocalize in the laboratory

environment (e.g. squirrel monkeys, marmosets and tamarins) [46^{**},55], and respond to synthetic versions of their vocalizations, provide an excellent tool for the study of the functional connectivity between vocal and auditory systems during call perception and production.

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