nature neuroscience

Species-specific calls activate homologs of Broca's and Wernicke's areas in the macaque

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The origin of brain mechanisms that support human language—whether these originated *de novo* in humans or evolved from a neural substrate that existed in a common ancestor—remains a controversial issue. Although the answer is not provided by the fossil record, it is possible to make inferences by studying living species of nonhuman primates. Here we identified neural systems associated with perceiving species-specific vocalizations in rhesus macaques using $H_2{}^{15}O$ positron emission tomography (PET). These vocalizations evoke distinct patterns of brain activity in homologs of the human perisylvian language areas. Rather than resulting from differences in elementary acoustic properties, this activity seems to reflect higher order auditory processing. Although parallel evolution within independent primate species is feasible, this finding suggests the possibility that the last common ancestor of macaques and humans, which lived 25–30 million years ago, possessed key neural mechanisms that were plausible candidates for exaptation during the evolution of language.

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The evolution of language is a challenging and controversial topic. A central, overarching question has been whether brain mechanisms that gave rise to language emerged in hominid species or developed from a functional substrate that existed in an extinct ancestral lineage common to both humans and nonhuman primates[1,2].

Although monkeys do not have language, they do possess a repertoire of species-specific vocalizations that—like human speech—seem to encode meaning in arbitrary sound patterns[3]. In nonhuman primates, this repertoire includes information that is crucial for survival, such as individual identity, emotional state and referential information about predators[1,3,4], food or an individual's size[5]. The calls that communicate this information must be shaped by several neural systems: sensory and motor systems that provide a substrate for perceiving and generating vocalizations, and a conceptual system that provides the substrate for representing the meaning of these vocalizations. These systems may in themselves support communication in a variety of nonhuman species[1]. Recent neuroimaging and electrophysiological studies in nonhuman primates provide evidence that these systems are activated when animals process conspecific (that is, species-specific) calls[6–10].

In humans, communication is enhanced by an additional system that supports the comprehension and production of language. The neural machinery that performs these core linguistic computations has, since the mid 19th century, been understood to be instantiated in perisylvian areas of the cerebral cortex, extending from Broca's area in the anterior Sylvian (lateral) fissure to Wernicke's area posteriorly[11]. Convergent clinical, electrophysiological and neuroimaging evidence has underscored the critical role of the anterior and posterior perisylvian areas in phonological, lexical and syntactic processes underlying both expressive and receptive language[11], which are not shared by nonhuman primate species.

But nonhuman primates are thought to possess structural homologs of these core perisylvian areas[12–20] (including homotypic portions of the contralateral hemisphere), as defined on the basis of similarities in cytoarchitectonics and neural connectivity. The functional significance of such homologies, however, is unclear, and whether the perisylvian regions are involved in processing species-specific calls in contemporary nonhuman primates—and, by implication, in a common ancestor—is not known. If they are, they may constitute a candidate for an antecedent neural system that was recruited for use during the emergence of language in humans. Understanding the role these regions play in living species of nonhuman primates might provide insights into how this may have occurred.

To address this issue, we presented auditory stimuli to awake rhesus macaques during acquisition of $H_2{}^{15}O$ positron emission tomography (PET) brain images to characterize patterns of activity in perisylvian cortices and their projection areas. Monkeys were trained to sit quietly in the scanner during presentation of acoustic stimuli. Sounds were broadcast from a speaker placed in front of the monkey, but hidden from view as were all other objects in the room. We presented two different classes of stimuli: species-specific macaque vocalizations ('coos' and 'screams'), and control stimuli ('nonbiological sounds'). Nonbiological sounds were selected to closely match the species-specific vocalizations in four acoustic parameters, frequency, rate,

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Received 8 May; accepted 26 June; published online 23 July 2006; doi:10.1038/nn1741

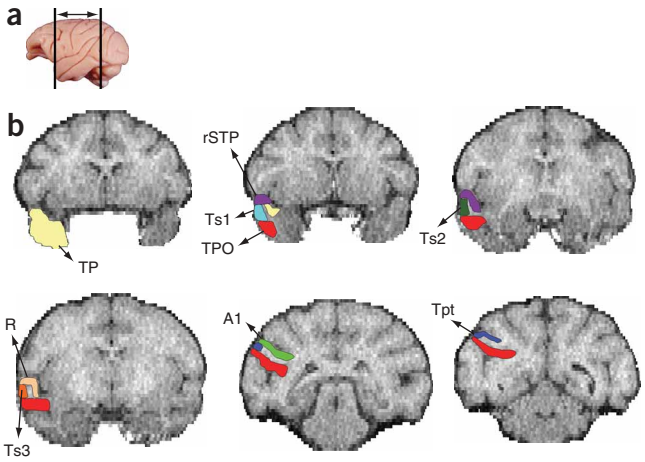

Figure 1 MRI-based anatomically segmented STG atlas. (**a**) Lateral view of a rhesus monkey brain illustrating approximate locations of the most anterior and the most posterior coronal sections shown in **b**. (**b**) MRI coronal slices, from anterior (top left) to posterior (bottom right), indicating the nine areas into which the STG was subdivided (illustrated in the left hemisphere): temporal pole (TP), rostral supratemporal plane (rSTP), STG gyral surface (Ts1, Ts2 and Ts3), TPO, auditory core (R and A1) and temporoparietal (Tpt).

scale and duration (see Methods), thus mitigating the possibility that differential brain responses were due to low-level acoustic features of these stimuli. Each monkey participated in multiple PET scanning sessions, resulting in the acquisition of 16 scans in each of the three stimulus conditions (coos, screams and nonbiological sounds).

To map activations in the superior temporal gyrus (STG) and in additional perisylvian areas, we performed voxelwise comparisons between the three stimulus conditions (Methods). We first evaluated each monkey individually. Here we report significant differences in regional cerebral blood flow (rCBF) between conditions only when these differences were detected in the same location in all three monkeys. To confirm the consistency of findings across monkeys, we extracted normalized regional cerebral blood flow (rCBF) values from the activation clusters and performed a repeated-measures analysis of variance (ANOVA) on these data. To establish the location of activation clusters within the STG, we used a magnetic resonance imaging (MRI)-based anatomically segmented atlas in which the STG was subdivided into nine areas in each hemisphere and modified to conform to each monkey's anatomy (**Fig. 1** and Methods; see also **Supplementary Note** online and **Supplementary Table 1** online). In addition, we extracted rCBF values from these regions for use in correlation analyses (**Supplementary Note**).

RESULTS

Acoustic analysis

The two classes of sounds, species-specific calls (coos and screams; **Fig. 2a** and **2b**, respectively) and nonbiological sounds (**Fig. 2c**), were analyzed along three parameters—frequency, rate and scale (Methods). The mean frequency was 2,316.8 ± 46.5 Hz (mean ± s.d.) and 2,138.7 ± 50.6 Hz for species-specific vocalizations and nonbiological sounds, respectively; the mean rate was 8.0 ± 2.8 Hz and 9.2 ± 3.0 Hz, respectively; and the mean scale was 2.0 ± 1.4 and 2.4 ± 1.5 cycles per octave, respectively. We computed a probability density function for each parameter (Methods) and obtained interpolated graphs of these functions for species-specific calls and nonbiological sounds (**Fig. 2d–f**).

To quantitatively compare species-specific and nonbiological stimuli with respect to these acoustic features, we performed permutation analyses (Methods). These acoustic analyses confirmed the desired match between species-specific vocalizations and nonbiological sounds for the frequency, rate and scale parameters (**Fig. 2** and Methods).

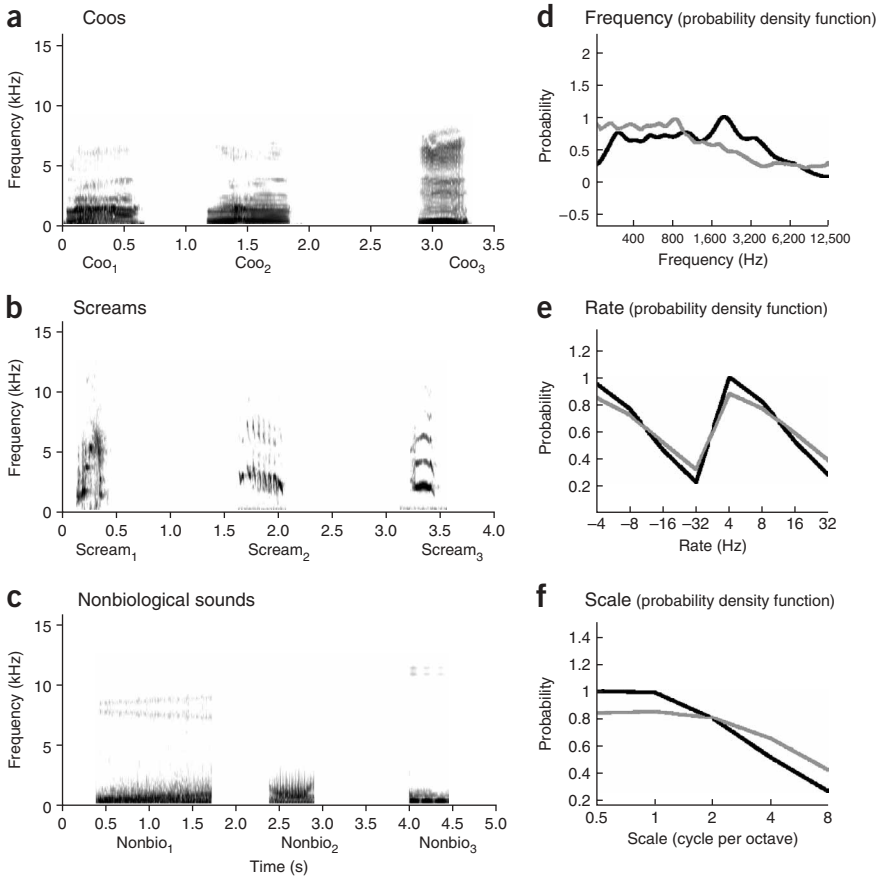

Figure 2 Illustration of acoustic analysis. (**a–c**) Spectrograms of exemplars of the different classes of stimuli are illustrated for (**a**) coos, (**b**) screams and (**c**) nonbiological sounds. (**d–f**) Interpolated graphs depicting species-specific calls (black) and nonbiological sounds (gray) for probability density functions are illustrated individually for frequency, rate and scale. Permutation analysis (Methods) confirmed that species-specific calls and nonbiological stimuli did not differ significantly with respect to frequency ($P = 0.51$) or rate ($P = 0.36$) and differed only marginally with respect to scale, or sound density ($P = 0.04$).

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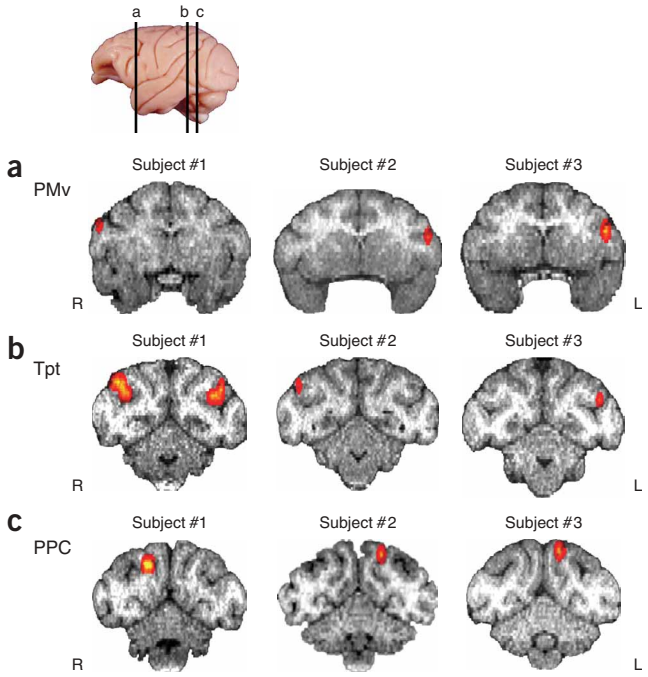

Figure 3 Selective activation elicited by species-specific vocalizations in the macaque. (**a**–**c**) Significant clusters derived from SPM analyses illustrated for ventral premotor cortex (PMv), area Tpt and posterior parietal cortex (PPC). The lateral view of the macaque brain (top) indicates the approximate location of these coronal sections. R, right hemisphere; L, left hemisphere.

Responses to species-specific calls and nonbiological stimuli

Both species-specific calls and nonbiological stimuli were associated with similar patterns of activity in the STG: increasing rCBF along the anterior-posterior axis with greater overall activity in the right hemisphere (**Supplementary Note** and **Supplementary Fig. 1** online). However, voxelwise contrasts revealed significant differences in activity evoked within the STG by the different stimulus classes ($P < 0.05$). Species-specific vocalizations elicited increased activity in the STG that was confined to cytoarchitectonic area Tpt in the posterior perisylvian cortex and to contiguous sections of posterior TPO. These vocalizations also elicited increased activation of other perisylvian areas, including the ventrolateral portions of the frontal cortex (PMv) as well as the posterior parietal cortex (PPC). The frontal area (PMv), located ventral to the arcuate sulcus and extending onto the cortical convexity, was centered in area F5. Activation of the posterior parietal cortex (PPC) was centered in the intraparietal sulcus and extended into areas 5 and 7. The significant clusters of activation are illustrated, in each subject, for areas PMv (**Fig. 3a**), Tpt (**Fig. 3b**) and PPC (**Fig. 3c**). These regions, in addition to those reported previously[8], constitute the only areas in which rCBF responses were significantly greater for species-specific calls than for nonbiological sounds in all three monkeys ($P < 0.05$). There were no significant differences ($P < 0.05$) between coos and screams in any of the regions included in this report.

We extracted normalized rCBF values from each monkey's scans ($n = 16$) using regions demarcated by significant clusters identified in the contrasts (coos versus nonbiological, screams versus nonbiological; nonbiological versus coos, nonbiological versus screams). We performed a repeated-measures ANOVA (Methods) and found a significant main effect for condition. *Post-hoc* comparisons demonstrated that coos and screams did not differ from each other, but both evoked greater activity than nonbiological sounds in Tpt ($P < 0.01$), ventral premotor cortex (PMv) ($P < 0.025$) and posterior parietal cortex (PPC) ($P < 0.025$) (**Fig. 4**), whereas nonbiological sounds evoked greater activity in areas R ($P < 0.001$) and A1 ($P < 0.005$) (**Fig. 5**). Inter-regional covariance patterns also indicated differences between monkeys' responses to the different stimulus classes (**Supplementary Note**).

DISCUSSION

Consistent with an earlier report[6], both species-specific calls and nonbiological sounds produced a characteristic pattern of activity in the STG: namely, increasing rCBF along the anterior-posterior axis with greater overall activity in the right hemisphere (**Supplementary Note** and **Supplementary Fig. 1**). Nevertheless, voxelwise contrasts revealed significant differences in the responses within the STG to the

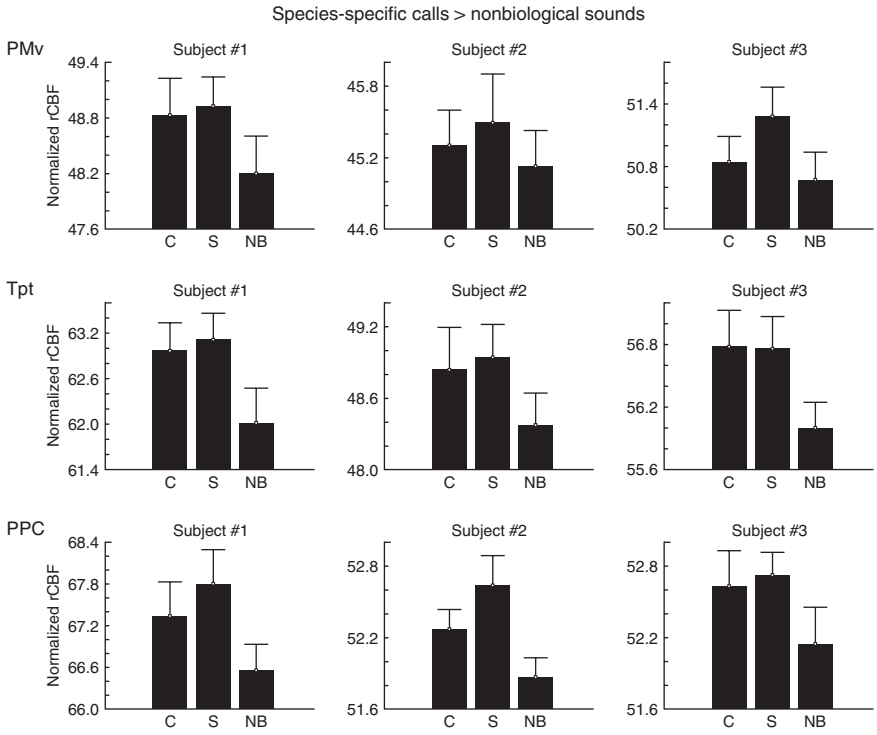

Figure 4 Histograms illustrating mean (± s.e.m.) normalized rCBF per monkey, derived from ventral premotor cortex (PMv), Tpt and posterior parietal cortex (PPC). ANOVA with planned comparisons, using the data from all three monkeys, revealed that coos and screams did not differ from each other but both evoked greater activity than nonbiological sounds: PMv ($F_{1,4} = 17.632$; $P < 0.025$ corrected); Tpt ($F_{1,4} = 50.914$; $P < 0.01$ corrected) and PPC ($F_{1,4} = 30.487$; $P < 0.025$ corrected). C, coos; S, screams; NB, nonbiological sounds.

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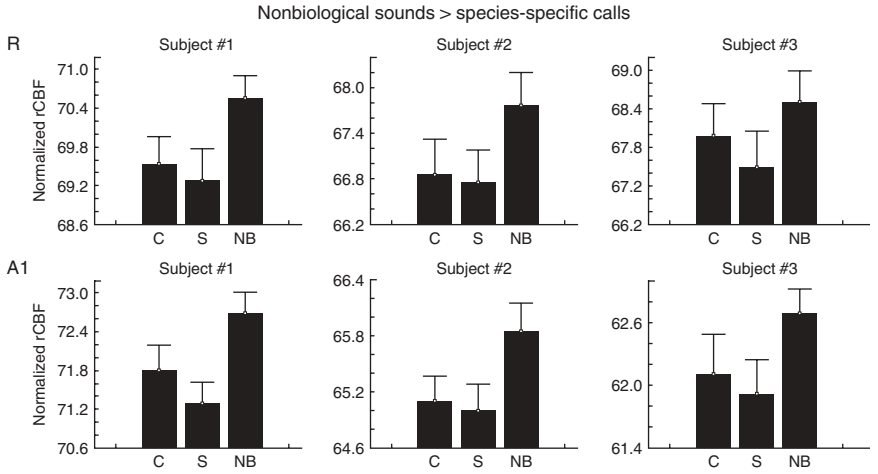

Figure 5 Histograms illustrating mean (± s.e.m.) normalized rCBF per monkey, derived from areas R and A1. ANOVA with planned comparisons, using the data from all three monkeys, revealed that nonbiological sounds evoked greater activity than both coos and screams: R ($F_{1,4} = 84.727$; $P < 0.001$ corrected); A1 ($F_{1,4} = 47.262$; $P < 0.005$ corrected). C, coos; S, screams; NB, nonbiological sounds.

two stimulus classes. Cortical surface localization of the results of these contrasts showed that nonbiological sounds (which, in general, were associated with greater activity throughout) evoked significantly larger responses in early auditory areas R and A1 ($P < 0.05$). The stronger activity elicited in these regions may have been driven, in part, by stimulus novelty, as the monkeys had not been previously exposed to the nonbiological sounds, which had a broader and more heterogeneous acoustic range than either coos or screams (in order to span the acoustic space defined by these stimuli). The primary auditory cortex is strongly activated by relatively new acoustic 'oddball' stimuli within a class of sounds[21] and therefore may be more likely to respond to a more heterogeneous set of stimuli (in this case, the nonbiological sounds) than to more homogeneous sets of sounds (the separate sets of coos and screams).

In marked contrast, species-specific calls were associated with a significantly larger response ($P < 0.05$) in a single location within the STG: area Tpt, a central element of the posterior perisylvian cortex. Moreover, calls were associated with substantially greater activation of additional perisylvian regions in the frontal and parietal lobes. Previous research has provided information about the functional characteristics of these regions, including features that may be shared by humans and nonhuman primates, which may aid in the interpretation of these findings.

In nonhuman primates, Tpt, due to its anatomical connectivity and cytoarchitectonic organization, has been considered a possible homolog of the planum temporale (PT) in humans[12–14]. PT-Tpt has been associated with important nonlinguistic functions such as sequence processing and extraction of temporal order from auditory information in both monkeys[22] and humans[23,24]. Notably, however, the PT is a constituent of the posterior perisylvian language area first described by Wernicke[11] and highlighted in later anatomical studies[25]. Human neuroimaging and neuropsychological studies have demonstrated that PT-Tpt has an important role in speech-voice perception[26] and in auditory language comprehension[27].

Similarly, the posterior parietal region showed significantly enhanced responses to species-specific calls ($P < 0.05$), extending inferolaterally into area 7, which may represent a homolog of the human inferior parietal lobule (IPL)[28]. The IPL is considered a discrete but integral portion of the posterior perisylvian language cortex in humans[29] and is connected to other elements of this system by what has been described as the indirect perisylvian pathway[30].

In monkeys, chimpanzees and humans, both PT-Tpt and posterior parietal cortex are polysensory areas, transitional regions located between specialized unimodal cortices and higher order temporal and parietal association areas. These regions integrate sensory information from multiple modalities[12], making connections between sensory domains that in and of themselves may have provided a necessary foundation for the development of language[29,31]. In both nonhuman primates and humans, PT-Tpt and portions of the parietal cortex project to the anterior perisylvian cortex[19,20,32], another area in which activity was greater for conspecific calls than for nonbiological sounds. (This region seems to be distinct from a nearby area in the ventrolateral prefrontal cortex that is responsive to the acoustic features of conspecific calls[33].) Notably, as with the Tpt, connectivity patterns and cytoarchitectonic organization indicate that the activated portion of the frontal cortex represents a presumptive homolog of human perisylvian language cortex, in this case Broca's area (BA 44/45) in the dorsal frontal operculum[15–20]. In human imaging and neuropsychological investigations, the involvement of this region in language processing is unambiguous. The human BA 44/45 is one of the crucial nodes in the perisylvian language network, shown to be active for both speech production and comprehension[27,34,35].

Although a clear role for the frontal cortex in the production of species-specific calls in nonhuman primate species remains to be demonstrated[36], the activated portion of frontal cortex, as a key component of the lateral premotor system, is involved in the organization of orofacial and laryngeal movements[19,20,37–39]. However, a wealth of additional evidence indicates that this region, by virtue of its connections with postcentral sensory areas, supports a variety of diverse processes that extend beyond simple motor control, mediating complex interactions between cognitive, sensory and motor systems[32]. The ventral premotor cortex has a role at the interface between kinematics and dynamics, encoding movements not simply in terms of force and direction, but—based upon information processed in posterior polysensory regions—on the basis of more abstract relationships between an agent and its object[40]. In performing such operations, the perisylvian regions seem to function as an integrated system, in which activity in anterior areas is gated by the pragmatic implications, or meaning, of stimuli processed in posterior regions. Indeed, in humans, the ventrolateral frontal regions have a prominent role in retrieving and selecting relevant information stored in posterior cortices[41] in order to regulate behavior. Similarly, in nonhuman primates, anterior perisylvian areas seem to make use of integrated sensory information in the course of decision making that precedes action execution[15,32], selecting behavioral responses by connecting a perceived stimulus with an anticipated outcome. According to this model, the perisylvian areas would, in our monkeys, be processing the pragmatic implications of meaningful auditory stimuli—using information derived from the conspecific vocal signal to organize goal-directed responses[15,42] that are dependent on the nature of the calls.

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How might such a role have placed the perisylvian system in a position to be recruited for use during the evolution of language? Although these regions are clearly not performing linguistic computations in the macaque, they might be serving a relevant and roughly parallel 'prelinguistic' function, playing a role in associating the sound and meaning of species-specific vocalizations. If the perisylvian system had such a role in a common ancestor, these elementary antecedent operations may have been exapted during the emergence of more complex neural mechanisms that couple sound and meaning in human language.

Anatomical and functional asymmetries of the perisylvian language areas have been extensively demonstrated in humans, and earlier studies have reported anatomical asymmetry of the PT homolog in apes[43]. Previous studies, however, have not documented similar anatomical or functional asymmetries of these areas in the macaque brain. Consistent with this, our results, while revealing a network of areas related to species-specific calls that seem to be homologous to the human perisylvian language areas, do not show clearcut lateralization effects.

In summary, we have shown that two common types of species-specific vocalizations in nonhuman primates seem to be processed by homologs of the same core regions that process spoken language in humans. Even though their acoustic features differ markedly, both types of vocalizations elicited responses in these regions whereas acoustically matched stimuli that carry no behavioral salience for the monkeys did not. These responses thus do not seem to reflect the acoustic properties of the stimuli, but are instead probably related to their semantic features—that is, to the meaning encoded in them.

It is possible that the activations observed here may reflect neural systems that are discriminating in a general way between meaningful and nonmeaningful stimuli. These findings provide a basis for further research evaluating responses to conspecific calls as well as to meaningful stimuli *per se*, in order to determine whether activity in the network we have identified is differentially modulated by classes of stimuli with finer distinctions of meaning. Future studies should evaluate responses to both a wider range of species-specific vocalizations and to other categories of meaningful stimuli, such as heterospecific vocalizations and meaningful nonbiological sounds.

It was previously reported that conspecific vocalizations activate higher order visual-object processing areas (TEO, STS and TE) and areas associated with detecting and encoding salient affective material (the amygdala, hippocampus and ventromedial prefrontal cortex)[8]. The neural circuitry reported suggests that humans and monkeys have a common neural substrate for representing socially relevant object concepts[8,44]. Taken together, our results suggest that the perisylvian regions may be operating as part of a larger network that organizes conceptual representations of behaviorally relevant stimuli. These observations are consistent with the notion that language may have emerged from a broad neurocognitive network that enables the extraction of social information from conspecific vocalizations[2–4]. We suggest that coactivation of all the elements of this network—that is, perisylvian areas operating in concert with conceptual and sensory-motor systems—underlies communication in nonhuman primates and, as such, constitutes a plausible substrate upon which language may have evolved.

METHODS

Monkeys and stimuli. We used three adult rhesus macaques (*Macaca mulatta*, one male and two females), as previously reported[8]. All procedures and animal care were conducted in accordance with the US National Institutes of Health Guide for the Care and Use of Laboratory Animals. The monkey chair was custom-designed by Crist Instrument in collaboration with the authors. For each scanning session, the monkey was placed in the chair (tilted 70° backwards) and rolled into the scanner gantry for scanning. The PET suite environment (including the speaker) was occluded by a canopy of white sheets. Three auditory stimulus conditions (coos, screams and nonbiological sounds; 36 different exemplars of each) were used. In each session, three or four blocks of each condition were presented. Each session occurred on a separate day. Each monkey participated in five or six PET scan sessions over approximately a 2-week period, in order to obtain 16 scans per condition. The order of the exemplars in each block, as well as the order of the conditions, was pseudo-randomized to ensure novelty and avoid habituation.

Two classes of auditory stimuli were used in this study, namely, rhesus macaque species-specific calls and nonbiological sounds. The 'rhesus macaque species-specific vocalizations' included two types of vocalizations from the rhesus macaque vocal repertoire (coos and screams). A coo is a rhesus macaque affiliative vocalization produced in a wide variety of social contexts[3] (mean duration: 0.457 s; range: 0.233–0.888 s); a scream is a submissive rhesus macaque vocalization produced by subordinates following a threat or attack by a dominant[45]. Only tonal or arched screams were used (mean duration: 0.547 s; range: 0.122–1.320 s). The calls selected for this study were produced by several different individuals, all unfamiliar to our monkeys. The other type of auditory stimulus was the class of 'nonbiological sounds', a substantially diverse set of sounds that were novel to the monkeys. Sounds were produced by nonbiological sources and included sounds generated by musical instruments, environmental sounds and computer-synthesized noises. This sound set was tailored to match the mean frequency, rate, scale and duration of the set of rhesus species-specific vocalizations (mean duration: 0.498 s; range: 0.123–1.320 s).

The sounds were amplitude-normalized, and the stimulus-block sequences were created and presented using SIGNAL software (Engineering Design). Sounds were broadcast using a DAQCard-6062E (National Instruments) and an Advent speaker (Powered Partners AV570). The frequency response of the speaker was 40–30,000 Hz, and at a distance of 1.5 m, the mean and range of the broadcast amplitude were as follows: 67.33 dB SPL and 54.66–83.5 dB SPL for coos; 65.0 dB SPL and 50.0–86.66 dB SPL for screams; and 68.0 dB SPL and 50.66–83.0 dB SPL for nonbiological sounds.

The data set consisted of 108 samples of sounds (36 coo calls, 36 scream calls and 36 nonbiological control sounds). The mean duration of the species-specific calls (coos and screams) was 0.502 s (range, 0.122–1.32 s); that of the nonbiological sounds was 0.498 s (range, 0.123–1.32 s). Each of the two classes of sound (species-specific and nonbiological) was analyzed along three parameters—frequency, rate and scale—and a probability density function was computed for each parameter. The frequency-rate-scale representation of the sound was obtained using a well-established cortical model of the auditory pathway[46]. A probability density function (with integral = 1) was computed for each parameter, showing the distribution of frequency, rate and scale across each sound class. Sound frequency was evaluated at 128 points (logarithmically distributed in the range from 300 Hz to 12 kHz), amplitude envelope 'temporal' modulation rate at 5 points (log range 2–32 Hz), and scale (or sound density) at 5 points (log spectral density range 0.5–8 cycles per octave).

We used permutation methods to test the null hypothesis—namely, that conspecific calls (coos and screams) and nonbiological sounds did not differ significantly on any of these measures. The absolute differences summed (ADS) between each of the corresponding data points of the mean curves (derived from the 72 conspecific and 36 nonbiological vectors, respectively) were used as the test statistic. Once the ADS was computed from the original frequency (F), rate (R) or scale (S) data sets (these values were designated ADS*), the datasets were permuted 10,000 times. To do so, 72 vectors (analogous to the conspecific data) and 36 vectors (analogous to the nonbiological data) were randomly reassigned to these categories and the ADS recomputed, producing a distribution of randomly generated ADS statistics for each measure. The statistical significance of the original ADS* values was computed by finding the number of simulated ADS scores in the permuted distributions that exceeded these values, and dividing it by the total number of iterations (plus one). This value represents the probability that the ADS* value represents a statistically significant outlier in the related (F, R or S) distributions.

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Magnetic resonance imaging (MRI) images. MRI was performed in a 1.5-T Signa scanner (GE Medical Systems), using a 5-inch GP surface coil. T1-weighted MR images were obtained using a three-dimensional (3D) volume SPGR pulse sequence (TE 6, TR 25, flip angle 30); field of view (FOV) was 11 cm and slice thickness was 1 mm.

Positron emission tomography (PET) images. During the scanning sessions, the lights were dimmed. The speaker and all other objects in the room were hidden from view by a canopy constructed of white sheets. PET images were acquired in two-dimensional (2D) mode with a GE Advance scanner (GE Medical Systems). For each scan, stimulus presentation was initiated simultaneously with the beginning of intravenous injection of 50 mCi of [^{15}O]water diluted in 13 ml of saline. Each injection was performed over 20 s with 5 min between injections. A 60-s scan was acquired beginning automatically after a step increase in the scanner count rate, which reflects the arrival of the radioactivity in the brain. We acquired 35 slices; voxel size was 2 mm × 2 mm × 2 mm, and the full-width at half-maximum (FWHM) resolution was 6.5 mm in *x*-, *y*- and *z*-axes. The transverse and axial fields of view were 55 cm and 15 cm, respectively. Images were reconstructed using a transmission scan for attenuation correction. The PET images of regional cerebral blood flow reflect local neuronal activity during stimulus presentation.

Data analysis. We analyzed the PET brain images using software incorporated in MEDx (Sensor Systems). Structural realignment of the multiple PET images was accomplished using the FLIRT (FMRIB's Linear Image Registration Tool, v3.1) function intramodality routine (Model/DOF: Rigid Body (6-parameter model)).

Functional statistics (*t*-maps) were calculated using Statistical Parametric Mapping (SPM99, Wellcome Institute, Department of Cognitive Neurology, London, UK). Separate analyses were performed on the data acquired in each monkey. We identified regions that showed a significantly enhanced response to the species-specific calls versus the non-biological sounds (that is, to both coos versus nonbiological sounds and to screams versus nonbiological sounds) and vice versa. Significant clusters of activation were defined by a conjunction analysis for voxels more active for both coos versus nonbiological sounds and screams versus nonbiological sounds ($P < 0.05$). The functional activation *t*-maps were transformed and realigned with FLIRT intermodality routine and shadow transform functions, using each monkey's MRI image as a reference. Functional render statistics were used to fuse the functional activation maps with the respective high-resolution structural MRI so that the anatomical location of active areas could be identified. The general neuroanatomy was defined using ref. 47. The anatomical identification of specific cortical areas was reviewed and confirmed by experts in rhesus macaque neuroanatomy.

We developed an MRI-based anatomically segmented atlas to more precisely determine the anatomical locations of condition-dependent focal activity within the STG. Anatomically guided segmentation of the STG was performed using landmarks identifiable in the MRI scans of each monkey, based on the relationship between sulcal and gyral morphology and architectonic areas, as identified by previous anatomical and histological studies (M. Munoz & R.C. Saunders, *Soc. Neurosci. Abstr.* 535.10, 2003) and by published cytoarchitectonic maps[48,49] (**Supplementary Table 1**). The STG was subdivided into nine segments: temporal pole (TP), rostral supratemporal plane (rSTP), STG gyral surface (Ts1, Ts2 and Ts3), TPO, auditory core (R and A1) and temporoparietal (Tpt) (**Fig. 1**).

Data for the group analyses were obtained by extracting the rCBF values from the PET scans; regions were defined by the atlas described above, and clusters of significant activation were identified in the SPM contrasts. This process yielded 16 independent measurements for each stimulus condition per monkey (using a customized MEDx script). These data were submitted to a repeated-measures ANOVA with condition (coos, screams, nonbiological sounds) and scans (16 levels) as main factors. For all the analyses reported here, there was a significant main effect ($P < 0.05$) for condition, but not for scans, nor for the condition × scans interaction.

Note: Supplementary information is available on the Nature Neuroscience website.

ACKNOWLEDGMENTS
We wish to thank S. Suomi (US National Institutes of Health, Bethesda, Maryland, USA) for providing the monkeys; S.P. Wise, P. Gannon, T. Hackett, A. Poremba, R. Saunders and L. Ungerleider for help with the neuroanatomy; M.D. Hauser for providing his recordings of rhesus macaque conspecific calls; J. O'Malley, L. Prevost, S. Antonio, B. Forrest and J. Fellows for assistance with animal care and training; D. Robinson for help with preparation of the animal protocol; R. Carson, P. Herscovitch, J. Jacobs, T. Howe, J. Bacon, J. Chincuanco, T. San Juan and S. Conant for help in the design and execution of the PET experiments; and J. Solomon, J. Quinlivan, J. Officewala, N. Mesgarani, B. Swett, N. Jeffries and S. Milleville for assistance with data analysis. We also wish to thank M. Mishkin, S.P. Wise, L. Ungerleider, W.T. Fitch and M.D. Hauser, who reviewed the manuscript and provided valuable comments. This work was supported by the National Institute on Deafness and Other Communication Disorders Division of Intramural Research Programs (DIRP), by the National Institute of Mental Health DIRP and by a grant from Fundação para a Ciência e Tecnologia.

AUTHOR CONTRIBUTIONS
R.G.C. designed the studies, designed the equipment, created the stimuli blocks, trained the animals, ran the experiments, performed the image processing, organized and performed the data analysis, reviewed the results and wrote the paper; A.M. designed the studies, organized the data analysis, reviewed the results and wrote the paper; M.A.L. assisted in study design, designed the equipment, created the stimuli blocks, trained the animals, ran the experiments and performed the image processing and part of the data analysis; M.M. assisted with the neuroanatomy and created the MRI atlas; J.B.F. assisted in study design and performed the acoustic analysis; A.R.B. designed the studies, organized the data analysis, reviewed the results and wrote the paper.

COMPETING INTERESTS STATEMENT
The authors declare that they have no competing financial interests.

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