Chapter 11
Language Origins

11.1 Introduction

Language in the human sense is a complex system with *phonemes* (bundles of speech sounds) assembled into *morphemes* (meaningful units) and morphemes connected by rules of *syntax*. Baboon analogies suggest that the behavior and cognition of early hominins contained separate elements that eventually came together to form the basis for human language. Some of these elements were favored by natural selection because they supported communication. Others originally had different functions, but were coopted into the communication system.

11.2 Components of Language

Baboons, especially in experimental settings, have provided evidence for numerous hypotheses about the origins of language. A group of scientists based in France has developed the idea that language evolved from a combination of cognitive, neurological, and anatomical components (Fagot et al. 2019). They argue that baboons and humans share a number of the features that are central to language. Some are domain-general cognitive functions. That is, they contribute to a variety of mental processes, some of which can support communicative behavior. Other features are more domain-specific, that is, evolved to function in a communication system. For example, baboons are comparable to humans in their capacities for vocal and gestural production (Chap. 10).

The French group considered baboons an “excellent” model for the study of language evolution because of the “multidimensionality” of knowledge about the genus. They seem to be virtually unanimous in the opinion that the relevant features shared by baboons and humans are homologies that originated in the common

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ancestor of apes and monkeys. The main alternative is the view emphasized in this book, that such similarities are more likely to be analogies arising from the common circumstances of baboon and hominin evolution. Of course, the component view of language origins opens the possibility that different components evolved at different times. In any case there is agreement that baboons can be a valuable source for understanding the evolution of language.

A survey by Prieur et al. (2020) demonstrated that many of the prelinguistic components found in baboons also occur in various other primate species. However, the combination of these components in baboons may be unique, at least among monkeys. As with other aspects of behavior discussed earlier, baboons provide the only model in which the patterns are manifested in environments like those that early hominins occupied.

11.3 Language and Concepts

Fitch (2019) made an important argument about the primate origin of language that complements the conventional emphasis on performance. Fitch's premise is that a defining feature of human language is the flexible representation and recombination of *concepts*. From this he infers that precursors for important components of language should be sought in animal cognition rather than animal communication.

Fitch's hypothesis counters a long-standing assumption that limits the comparative approach to the study of language. According to this view, the absence of some feature of human language from animal communication is evidence for an evolutionary discontinuity between the species. Analysis of animal concepts may provide a more complete understanding of an animal's communicative potential and its significance for comparison with human language.

The key point is that an animal communication system typically expresses only a small subset of the concepts that can be mentally represented and manipulated by that species. Thus, if a particular concept is not expressed in a species' communication system, this is not evidence that the species lacks that concept. Exclusive focus on overt signals will lead to underestimation of conceptual abilities and a flawed comparative analysis of language evolution. Therefore, animal cognition provides a crucial (and often neglected) source of evidence regarding the biology and evolution of human language.

Fitch's primate examples are chimpanzees and vervet monkeys (the latter is *Chlorocebus pygerythrus*, previously classified as *Cercopithecus aethiops*). Vervets have received a great deal of attention for a set of referential alarm calls that distinguish leopards, eagles, and snakes (Price et al. 2015). Fitch argues that concepts in vervet cognition go far beyond these calls. Mental representations of vervets include concepts that are undoubtedly shared with many other primates (e.g., *dominant other*) along with concepts that are probably more specific to the genus. For example, vervets have complex spatial representations of their environment and the ability to mentally track the locations of hidden group members. They can socially learn how to access food and rapidly absorb new social preferences about what to eat based on color. None of this cognitive sophistication is in any way detectable in their vocal communication system.

Fitch acknowledges that similar examples could be provided for many other well-studied primates. This could certainly include baboons. For example, vervet alarm calls can be compared to baboon calls that distinguish raptors, mammalian predators, and crocodiles (Chap. 6). Spatial representations of baboons probably go far beyond those of vervets, because baboon troops typically range more widely and encounter a greater variety of habitats. As to concepts not expressed in overt communication, there is evidence from experiments that address baboon cognition.

11.4 Domain-General Functions in Language Origins

According to Fagot et al. (2019) language is a multilevel phenomenon that requires integrative processes. Many of these are domain-general processes that can also fulfill nonlinguistic functions. This point of view seems to articulate well with the argument for concepts, discussed above. Fitch looks for the antecedents of language in adaptive mental processes; Fagot and colleagues seek the roots of language in domain-general mental functions. In both instances, the cognitive phenomena are not necessarily communicative in themselves, much less linguistic. However, they lend themselves to processes of evolutionary integration that produced language. Both approaches look to nonhuman animals for clues to these roots of language. The premise in each case is that early hominins may have had the same capability (perhaps for different reasons) and that the capability could have fed into the early evolution of language.

11.4.1 Memory

Memory is essential for the retention of language basics and for control of specific communications. Long-term memory is crucial for the storage of phonology, semantics, grammatical rules, pragmatics, and many other aspects of language (Fagot et al. 2019). Guinea baboons have displayed "impressive" long-term memory, retaining a large percentage of pictures from samples of thousands for at least a year. These results were comparable to those obtained with a human subject (Fagot and Cook 2006).

Short-term memory is important in language for keeping track of the words in a sentence and for the rapid verbal learning of the words in a lexicon (Fagot et al. 2019). Experiments show that baboons can store a large amount of information in short-term memory and that they can maintain this information in a small temporal range, measurable in seconds (Fagot and de Lillo 2011; Rodriguez et al. 2011). It seems that baboons have weaker working-memory capacities than humans, but that the two taxa have roughly identical long-term memory capacities. Early hominins could probably retain a substantial lexicon of signals, but actual communication exchanges might have been brief.

11.4.2 Categorization

Categorization is an essential process in the acquisition of language (Fagot et al. 2019). At the structural level, syntactic categories (e.g., noun or verb) are fundamental in grammatical structure. At the semantic level, nouns often refer to categories (e.g., *cat*, referring to all cats). Baboons, like many other animals, can form categories according to concrete criteria and some more abstract criteria. Guinea baboons, after training, can assign examples to correct categories; for instance, different alphanumeric characters (Vauclair and Fagot 1996). Olive baboons (*Papio anubis*) classified foods versus nonfoods (Bovet and Vauclair 1998).

Guinea baboons can also form categories based on relational properties (e.g., including openness versus closedness, Barbet and Fagot 2011) and spatial relations (e.g., far/near, Dépy et al. 1998; above/below. Dépy et al. 1999). For early hominins, the ability to make such distinctions might have facilitated communication about the proximity of predators or the height of foods or sleeping branches in trees.

11.4.3 Statistical Regularities

The ability to detect statistical regularities facilitates language acquisition and processing, including categorization (Fagot et al. 2019). Guinea baboons were trained with touch screens to discriminate real English four-letter words from four-letter strings that were not words (Grainger et al. 2012). Further examination of the baboons‘ strategies with a modeling approach showed that discrimination between the words and nonwords involved learning of particular bigrams or trigrams that were statistically more frequent in the words than in the nonwords (Hannagan et al. 2014). This performance can be accounted for by the baboon‘s ability to detect the statistical regularities between and among words, and to develop an open-ended representation of the word and nonword categories on that basis (Fagot 2017). In an experiment with spatial cueing, Guinea baboons demonstrated statistical learning mechanisms similar to those of humans (Goujon and Fagot 2013). A similar recognition capability might have been the basis for infusion of symbolic content in the cognitive processes and communication capability of early hominins.

11.4.4 Analogical Reasoning

Analogical reasoning can be considered a form of categorization that is based on abstract relationships (Fagot et al. 2019). Developmental studies in human children have shown a close relationship between analogical reasoning and the acquisition of linguistic labels (Christie and Gentner 2013). Analogical studies in Guinea baboons used a relational matching task based on Fagot and Thompson (2011). First, the subject sees one pair of objects that are either identical or different. Then, two comparison pairs are shown, and the baboon must indicate the stimulus pair with the same relationship to each other as the sample pair. Correct response to the test requires at least some understanding of the relation between relations.

With pairs of shapes as the stimuli, 6 of 29 baboons solved the matching test and 5 of these 6 then transferred this ability to novel sets of shapes. These results suggest that some Guinea baboons have the capacity to categorize stimuli with regard to both concrete and more abstract criteria, an ability that is critical for language (Fagot et al. 2019). In a simpler version of the test, Fagot et al. (2001) showed that two Guinea baboons could solve the problem when represented by same or different icons. Manipulation of such icons suggests the possibility of manipulating words. The limited capability shown here seems to suggest that early hominins might have had the potential for analogical reasoning in a few individuals, but that it was not common enough to be a factor in the communication system.

11.4.5 Pragmatics and Semantics

Campbell and Tyler (2018) asserted that pragmatics and semantics can be considered domain-general features of language because they are involved in many other cognitive functions. In humans, neural regions involved in semantics during language processing overlap with those that underlie object processing and other functions. Cheney and Seyfarth (2014, 2016) described the operation of pragmatics and semantics in the communication of chacma baboons. A baboon, hearing a call from another, builds a mental representation of the call by associating it with the caller's identity (including rank and kinship connections) as well as recent events involving that individual. In this sense, the process is combinatorial and provides a foundation for semantics (Cheney and Seyfarth 2018). The system is adaptive because it contributes to reproductive success in a long-lived species in which individuals depend on strong social bonds with other individuals and on recognition of social relationships between other troop members. This would obviously apply to early hominins.

11.5 Domain-Specific Components: Vocalization and Speech

Baboons and humans share some physical and mental functions that are specific to the evolution of language rather than being domain-general (Fagot et al. 2019). These include vocal capabilities that evolved in connection with nonlinguistic communication (Chap. 10). Given this view of their origins, it seems more appropriate to label them *communication-specific* rather than *language-specific*. There are two major schools of thought as to the primary mover at the beginning of language evolution. One emphasizes vocalizations and the other emphasizes gestures. Baboons provide evidence for both.

11.5.1 Protophones and the Vocalization-First Theory

Protophones are speech-like sounds produced by human infants during roughly the first year of life. These include vowel-like sounds and also syllables and syllable sequences such as *da* and *dada.* Oller et al. (2021) studied such sounds in human infants, as an approach to determining the prime mover in language origins. Protophone production seemed to be endogenous in that (1) the infants produced them at a high rate even when alone and (2) they did not direct the majority of these sounds to a listener when one was present. Additional evidence for an innate basis is that infants born deaf produce protophones at rates comparable to those of hearing babies.

In another study, protophones were at least 35 times more frequent than gestures at the age of 3 months. The ratio declined, but was still greater than 2.5 at the age of 11 months (Burkhardt-Reed et al. 2021). In cases of directed signals (indicated by gaze), protophones were about twice as likely to be directed to a receiver as were gestures (36% vs. 16%).

Oller et al. (2021) took the early prominence of protophones to be evidence for the vocalization-first theory of language origin. They suggested that the adaptive value of these sounds was to project infant wellness to hominin caregivers who were occupied with other activities. One reason for this supposition is that a long period of infant helplessness must have placed more pressure on hominin caregivers. Second, Oller and colleagues assumed that hominins lived in increasingly larger groups than apes and that the alloparenting became a key factor in hominin life. This situation required the infant to broadcast its fitness status to a broader audience, which fits with the *Homo erectus* scenario of Swedell and Plummer (2019), based on hamadryas baboons (Chap. 9).

Other baboons provide an alternative view. Many baboons live in larger groups than most or all apes. In both troops and multilevel societies, the circle of acquaintances may number 200 or more. There is little or no alloparenting in this genus. The key issue, then, is infant helplessness. Two points can be made. First, it is not clear when in hominin evolution this became a crucial issue. Second, insofar as mothers needed help, the fact that male baboons provide a certain amount of care for infants and juveniles suggests that increased male attention to the young might have eased the hominin mother's burden. Protophones might have evolved to signal infant wellness to a concerned male that might otherwise be attending to other business.

11.5.2 Vowel-Like Sounds

Some protophones proved to be the basis for vowels, a vital aspect of language evolution (Boë et al. 2019). Vowels are the core of speech production and are essential to the acoustic value of consonants. This relationship makes possible the formation of morphemes (units of meaning) that can then be arranged into larger utterances. The basic sounds (phonemes) of a particular human language are a distinctive set and are culturally transmitted, but the phonemes in every language are drawn from a universal set of speech sounds that is based on the vocal anatomy and physiology of humans (Boë et al. 2017).

An influential theory (Lieberman et al. 1969) held that early hominins could not have made vowel sounds because the high position of the larynx in the vocal tract limited modification of the vocal tract shape by tongue, lip, or jaw maneuvers. This hypothesis was countered by the demonstration that human babies produce the same range of sounds as adults despite having a high larynx (De Boysson-Bardies et al. 1989). It can now be added that Guinea baboons make vowel-like sounds with a high larynx (Boë et al. 2017).

Boë et al. (2017) recorded spontaneous vocalizations of 15 adult Guinea baboons living in a captive social group. The study focused on five types of vocalizations that contained *formants*, that is, resonance bands that determine the phonetic quality of a vowel. The vocalizations included grunts and wahoos (produced mainly by males), barks and yaks (mainly by females), and copulation calls (only by females). After splitting the wahoos into two syllables, they identified about 1400 "vowel-like segments" (VLSs). A VLS was defined as any continuous part of a vocalization that contained "a consistent and detectable formant structure."

Acoustical analysis of the VLSs revealed at least five distinct classes, distinguished by different tongue positions. Tongue movements were both vertical and horizontal, as is the case in human languages. Two features of the communicative use of these segments also resembled human vowel functions. First, each of two VLSs occurred in two different calls (bark calls and wahoos; male grunts and female copulation calls). Second (in the case of the wahoo) the baboons consistently produced two different VLSs in succession within a single utterance. All of these features together suggest the kind of system that language evolved from, and that the beginning of that evolutionary process might have taken place in early hominins (Boë et al. 2017). The five vowel-like segments covered a large portion of the baboon's vocal space, in a proportion almost equivalent to that found (for instance) in 12-year-old native speakers of American English. Though recorded in captivity, the vocalizations in this study were highly similar to those already described in the wild (e.g., Maciej et al. 2013), which suggests that the analysis is pertinent to the natural behavior of Guinea baboons.

11.5.3 Vowels Versus Consonants

Gannon et al. (2023) compared the social effectiveness of proto-vowels and proto-consonants in an "open plains" environment, using playbacks of orangutan calls that were broadcast on a South African savanna. Their measurements indicated that only the consonant-like calls were effectively perceptible beyond 100 m under these conditions. Given the occupation of such habitats by human ancestors, the researchers inferred that consonants played an early role in the evolution of language.

A study of early hominin auditory capabilities suggests a somewhat different inference. Quam et al. (2015) studied the anatomy of the outer and middle ear in *Australopithecus africanus*. They interpreted the proportions of the bones to indicate "an increased emphasis on short-range vocal communication in open habitats." Vowel-like vocalizations such as baboon grunts may have been of the greatest importance for ongoing communication in these hominins. From this viewpoint, consonants probably became important later in hominin evolution as a basis for more complex communications. Selection for short-range communication might have been related to the formation of more compact groups for predator defense on the savannas.

11.6 The Gesture-first Theory

The gesture-first theory is a hypothesis of language origin that is often placed in opposition to the vocal-first theory. According to this school of thought, gestural communication was the foundation of language and the basic capabilities were later expanded to encompass vocalization. The term "gesture" is sometimes used almost synonymously with communication signals of any kind. However, gesture in other accounts is limited to arm and hand movements.

11.6.1 Human and Primate Evidence

Fay et al. (2022) summarized evidence for the importance of gesture in human life, with the implication that language originated in communication with manual motions. People gesture while speaking in every culture, blind people gesture, and hearing people can (in experiments) communicate successfully with gestures alone. Gestural languages, with the same expressive range as spoken language, emerge rapidly in populations of deaf children and in communities with a high incidence of deafness. Observations like this stimulated the origin of the gesture-first theory in the eighteenth century. A modern revival has been stimulated by scientific research.

Two experiments by Fay et al. (2022) tested the gesture-first theory against the vocal-first theory. In each experiment, one group of human participants recorded gestures or vocalizations that they invented in order to convey meanings specified by the researchers (conventional language was prohibited). A second group viewed the recordings and tried to guess the meanings. The viewers in both experiments were Australian undergraduates. One set of communicators were from the Pacific island of Vanuatu. The second set consisted of ten vision-impaired and ten sighted Australians. Communication success was twice as high for gestured signals than for the vocal signals within cultures, across cultures, and for participants who were severely vision-impaired. The researchers inferred support for the gesture-first theory.

Fay et al. (2022) noted that another reason for revitalization of the gesture-first theory is new evidence from primates. Comparative studies have demonstrated greater flexibility in primate gestures than in vocal signals; experiments have had greater success in teaching primates sign language than vocal language; and similarities have been observed between the naturalistic gestures produced by human children and other primates. Chimpanzees are prominent in all of this work (and famous for it), but baboons have a role to play that is explored in the following sections.

11.6.2 Flexibility and Intent in Gestural Communication

The previous chapter described research by Molesti et al. (2016). They studied spontaneous gestural communication (with a broad definition) in social groups of captive olive baboons for 1 year and recorded almost 9000 gestures that they classified into 67 gesture types. The majority of these types (39) were visual (58% of the repertoire) and only 4 types were audible. The prominence of visual signals here is consistent with the gesture-first theory. The researchers explained this imbalance in terms of baboon evolution in environments like those that were prominent in hominin evolution.

Fay et al. (2022), in arguing for the gesture-first theory, emphasized that primate studies demonstrated greater flexibility in gestures than in vocal signals (see above). In order to explore flexibility in the baboon communication system, Molesti et al. (2016) identified eight contexts in the social life of their subjects: affiliative, playful, agonistic, submissive, sexual, parental, grooming, and "other". They found that several different gesture types were used in each context. For example, the baboons used about one-third of all types in the sexual and submissive contexts. Flexibility was also represented by the fact that most gesture types appeared in more than one context. On the average a single gesture type occurred in four different contexts.

With regard to another goal of the Molesti study, the baboons fulfilled “the main criteria of intentional communication” in that they performed goal-directed gestures to influence specific target individuals or audiences. This was manifested in four patterns of behavior: orientation toward the recipient, waiting for a response, sensitivity to the recipient’s attention, and adjustment of a signal based on the recipient’s attention. On average, the baboons performed about 90% of their gestures while looking at recipients; waited for a response in 87% of the interactions; and used 81% of their gestures when the target was paying attention. The baboons adjusted the modality of their gestures in response to lack of attention (for example, shifting from a visual signal to touching).

This systematic study shows at least one baboon species to be consistent with features of gestural communication in the great apes and some other monkeys. Sensitivity to the attention of signal recipients may be the most significant resemblance to findings from experiments with apes, other baboons, and some other monkeys. This growing body of evidence for primate intentionality suggests that intentionality was present in the interactions of early hominins, including but not limited to communicative behavior that may have laid the foundation for language.

11.6.3 Baboons in Gesture Experiments

Molesti et al. (2016) referred to the consistency of their findings with experimental research on baboons and a few other monkeys. This is exemplified by experiments in which olive baboons were taught to point to food rewards (raisins and banana slices), work that produced some conclusions not apparent in the Molesti study. Meunier et al. (2013b) taught the baboons to point to one baited container among others to get a reward from a human. Pointing and gazing varied according to the attentional status of the human (facing toward or away) and her ability to reach the reward. As in the baboons that were spontaneously communicating with each other (Molesti et al. 2016), the baboons in the experiment showed intentionality by their responsiveness to the attentional status of the target individual. The subjects were also able to respond to the added factor of the human’s ability to reach the baited container. Since the baboons in this experiment indicated an object to the communication partner, the behavior was interpreted as referential (adding to the discussion in Chap. 10).

Bourjade et al. (2014, 2015, 2019) continued experiments with the olive baboons that had been trained to perform food requesting gestures. In these experiments the human target either faced the baboons or stood in profile to them (rather than with her back toward them). The subjects were (a) tested immediately after training, and (b) tested again 1 year later. Test conditions varied the human cues to attention.

In immediate testing, the profile group baboons gestured toward untrained cues regardless of their relevance for visual communication. They were also less discriminating toward trained versus untrained cues than baboons trained by a human facing them. In delayed testing of the profile group, the number of gestures toward meaningful untrained cues increased. They were able to discriminate the positions of an experimenter's body and adjusted their gestural communication accordingly. The experimenters inferred that intentional gestures tuned to the audience's attention may first develop through associative learning processes. Hard-wired predispositions for recognizing eye gaze as a necessary component of visual attention are apparently not present in olive baboons, at least in the context of interspecific communication.

Bourjade and colleagues suggested that the baboons first learned their gestures as tools in the sense of means to an end, and then turned them into *semiotic* tools (i.e., communicatively meaningful). To express the thesis in more detail, they suggested that the "typical" training or experience equipped the baboons with a set of tools (gestures and coordination with human cues to attention) and conditions (fluency, contingency, congruency of explicit training with implicit learning) that might then scaffold their ability for "understanding," that is, forming and reasoning about expectations and categories.

In sum, we have baboons that were able to learn communication skills that developed into meaningful entities in association with intentionality, audience awareness, joint attention, persistence, and elaboration—ultimately leading to a kind of understanding (Bourjade 2019; Lamaury et al. 2019). This seems to describe the sort of combination of domain-general and domain-specific functions that Fagot et al. (2018) saw as the underpinnings of language. The presence of such potential in baboons suggests that language might have developed very early in hominin evolution and also provides some support for the gesture-first theory.

11.7 Language and Laterality

Laterality of behavior and the brain are characteristic of humans. The great majority of humans have a strong hand preference, which is associated with a difference between the cerebral hemispheres. This includes certain brain structures with a functional connection to language. Baboon evidence suggests that this system might have evolved early in hominin evolution and that it might have been involved in communication from the beginning (Vauclair & Meguerditchian 2018).

11.7.1 Communicative Laterality Versus Manipulative Laterality

Humans are mainly right-handed for many actions, including gestures, and these tendencies are strongly linked to dominance of the left cerebral hemisphere for language functions. In a series of experiments, olive baboons displayed strong tendencies toward laterality in gestural communication. The first experiment reported population-level right-handedness in 60 captive baboons for a species-specific communicative manual gesture called *hand slap*, a threat that consists of quick and repetitive slapping or rubbing of the hand on the substrate. This study added baboons to captive chimpanzees and human children as subjects with a right-hand bias for communicative gesturing (Meguerditchian and Vauclair 2006).

Further research addressed the question of whether or not handedness was a function of the gesture‘s communicative nature (Meguerditchian and Vauclair 2009). This study focused on two behaviors that had not been previously investigated: a communicative gesture (*food beg*) and a noncommunicative self-touching behavior (*muzzle wipe*) that served as a control. *Food beg* displayed a trend toward right-handedness that significantly correlated with the preferences of the same individuals for *hand slap*. Hand preferences for *muzzle wipe* did not reveal any trend toward bias at the group level or correlation with hand preferences for *food beg* or *hand slap*. These findings were viewed as support for a hypothesized gestural communication system, based on left-hemisphere dominance in the brain, that differs from the system involved in purely motor functions.

Handedness for the *slap* gesture was robust and consistent across time and two study populations (Meguerditchian et al. 2011). Thirty baboons from the earlier experiment were retested for hand preference in the gesture 4 years later, by an observer unaware of the previous data. Twenty-six of them displayed significant continuity in handedness across the time period in question. Replication of the study in 96 novel individuals revealed a degree of population-level right-handedness similar to the one expressed in the first group of 66 subjects.

A closer link to humans was established by comparing baboons with human infants (Meunier et al. 2012). Researchers studied hand preferences for grasping objects or pointing to objects placed at several different spatial positions. In both species, right-hand preference was significantly stronger for the communicative task than for grasping objects. Noting that spatial location could have been a confounding factor in the preceding experiment, Bourjade et al. (2013) compared the consistency of individuals' hand preference with regard to spatial variation of a communicative partner and a food item to grasp. They found more consistent hand preference for communicative gestures than for grasping actions.

Meunier et al. (2013a) reviewed four studies investigating hand preferences for grasping versus pointing to objects at several spatial positions in human infants and three species of primates. There was a strong convergence in the distribution of hand biases for the two kinds of tasks among human infants, baboons, and macaques. Capuchins, a manipulative species of the Americas, diverged. The researchers inferred that left-lateralized language may be derived from a gestural communication system in the common ancestor of macaques, baboons, and humans. However, the close phylogenetic relationship between baboons and macaques weakens this argument. The pattern in question could be an analogy between the hominin and baboon/macaque lineages.

11.7.2 Language and Brain Laterality

The neurological inferences from experiments such as those cited above have been supported by direct investigation of baboon brain structures that correspond to language-related structures in humans (Meguerditchian et al. 2016). Among primates other than the great apes, the baboon is a good model for such research (Fagot et al. 2019) because the baboon brain is on average twice as large as those of other monkeys, including the closely related macaques. It also has greater *gyrification*, that is, the formation of folds in the cerebral cortex. These features are associated with structures that are homologs for those found in humans.

11.7.3 Wernicke's Area

Wernicke's area is a part of the human brain in the temporal lobe that is frequently associated with language. It is part of the auditory association cortex. In the left hemisphere it performs various functions in language processing (Becker and Meguerditchian 2022). A "bank of tissues" called the planum temporale (PT) is the most reliable "landmark" for quantification of this area (Hopkins 2022). Both the surface area of the PT and the volume of the underlying gray matter consistently display significant leftward asymmetry. The asymmetry is present in newborn infants and increases in association with language development.

Marie et al. (2018) used MRI images to quantify the PT area in 96 adult baboons and found population-level leftward asymmetry in size. The same asymmetry occurs in newborn olive baboons and, as in humans, differentiation increases during development (Becker et al. 2020). Baboons also display leftward bias in gray matter volume (Becker et al. 2022b). Such population-level asymmetries have not been found in rhesus macaques, bonnet macaques, or vervets (Hopkins 2022).

Compared to other primates, chimpanzees and (albeit with less evidence) baboons display "the most robust and consistent population-level asymmetry" of leftward bias in the planum temporale (Hopkins 2022). Studies of both species have used multiple research methods and different levels of analysis, applied to both surface area and gray matter volume. These findings suggest that asymmetry of the PT originated in the common ancestor of *Pan* and *Homo*, and was favored by the conditions in which baboons and early hominins evolved.

11.7.4 Other Brain Structures

Broca's area in humans was once considered the center of speech production. It is now known to have extensive connections in the language network of the brain (Becker and Meguerditchian 2022). Broca's area is involved with speech, gesture, syntax, and sign language. Comparison with other species is hampered by the fact that a homolog in other primates is difficult to discern. However, the inferior arcuate sulcus (IAS), which is part of Broca's area in humans, can be located in other primates. The "ventral portion and its depth" delimit the equivalent of the surface of Broca's area in the monkey brain (Meguerditchian et al. 2013).

Becker et al. (2022a) studied 50 olive baboons with in vivo anatomical MRI and found that communicative gesturing is related to the ventral portion of the inferior arcuate sulcus. Both direction and degree of gestural communication's handedness are associated with each other and correlated with contralateral depth asymmetry at this exact position. Baboons that prefer to communicate with their right hand have a deeper left-than-right IAS than those preferring to communicate with their left hand and vice versa. In contrast to handedness for object manipulation, gestural communication's lateralization is not associated with asymmetry in the depth of the central sulcus. This is consistent with previous work that found handedness for manipulative actions to be related to asymmetry in the central sulcus (Margiotoudi et al. 2019).

A variety of other language-related structures have homologs in baboons and perhaps in other primate species, especially chimpanzees. Becker and Meguerditchian (2022) name the planum parietale and the superior temporal sulcus among others. For example, significant depth asymmetry in favor of the right hemisphere was found in a specific portion of the superior temporal sulcus. The same asymmetry in the human brain is considered a landmark of communication and social cognition.

Becker and Meguerditchian (2022) hypothesized that asymmetries for language areas may not have initially evolved for language (cf. Fagot et al. 2019). Rather, each asymmetry could have evolved independently for different cognitive functions, to adapt to "unknown environmental pressures." This could explain the unclear relationship between structural and functional asymmetries related to language areas. As far as "unknown environmental pressures" are concerned, the study of wild baboon ecology may provide clarification in the future.

11.8 Language Learning

Some baboon experiments have been designed to investigate learning capabilities that might have underpinned the beginnings of language. Language combines abstract representations in a process called *compositionality*. This is a mental operation based on implicit recognition that the meaning of an expression is determined by its components and the rules that define their connection. Dautriche et al. (2022) tested Guinea baboons for a sense of compositionality. They chose negation as the key to the work because it is so fundamental to language and because forms of negation had previously been taught to some animals.

In the first experiment, the baboons learned to associate a cue with iconically related referents (e.g., a blue patch referring to all blue objects), and also to the complementary set associated with it (e.g., a blue patch referring to all *non*-blue objects). This was interpreted as showing the ability to comprehend negative compositional representations. In the second experiment the subjects learned to associate complex cues with the complementary object set. A complex cue in the second experiment was composed of the same cue as in the first experiment plus an additional visual element.

In related research, Chemla et al. (2019) administered a pattern extraction task to Guinea baboons. The results showed that the baboons are like humans in having a learning bias that helps them to discover connected patterns more easily than disconnected. For example, an implicit bias of this kind favors learning rules like "contains between 40% and 80% red" over rules like "contains about 30% red" or "100% red." The experimental task was made as similar as possible to a one that had previously been presented to humans, which was argued to reveal a bias responsible for shaping the lexicons of human languages. The baboon experiment involved subjects in a complex computer task that required learning of three rules of connectedness among icons. Of 23 voluntary participants, 9 failed the first condition and 9 eventually learned all three rules. The performance of some baboons in this task suggests that cognitive roots for regularities in the content and logic of human lexicons could have been present among early hominins.

11.9 Summary and Discussion

A theory about the evolutionary origin of language envisions multiple roots consisting of diverse components that ultimately came together to form a unique system of communication in humans. Some of these components of language were domain-general cognitive abilities that performed a variety of functions. These included memory, categorization, analogical reasoning, and detection of statistical regularities. Other functions and capabilities were domain-specific, that is, originally evolved to facilitate communication.

In humans and other primates, vocal and gestural skills are paramount. Primates, including baboons, are considered by many to provide clues to early hominin developments along these lines. Consistent with the domain-general view of language is the idea that animal cognition should be considered because it includes more concepts than animals are able to convey in their communication systems.

Domain-general and domain-specific functions are intertwined in the controversy about the primary platform for language evolution. Some scientists argue that vocalizations were the basis for language while others maintain that gestures provided the foundation. Baboons provide evidence relevant to both sides.

Research on the vocalization side is exemplified by the work on protophones in infants. These speech-like sounds are much more frequent than gestures during the first year of life and are twice as likely to be directed toward a recipient. Among the protophones of infants are vowel-like sounds, antecedents of the vowels that are crucial to the structure of spoken language. Baboons can pronounce vowel-like sounds despite throat anatomy that supposedly prevented it. Thus, sound articulation necessary for speech could have existed in very early hominins. This is a case where baboons seem to be more relevant than chimpanzees. Despite a low larynx like humans, chimpanzees are not known to produce vowel-like sounds. Baboons have a high larynx and yet have been shown to produce a variety of vowel-like sounds in their natural communication.

With respect to the adaptive significance of protophones, it was hypothesized that they signaled infant well-being (or lack of it) to caretakers among early hominins who were busy with other tasks. It was further speculated that protophones became increasingly important as group size increased because of the involvement of multiple caretakers in a cooperative system. Baboons provide valuable models for the postulated social situation in that troops tend to be large, and multilevel societies of even greater size and complexity occur in two species. Baboon societies illustrate various possible distractions from childcare that would have made vocal signals of well-being adaptive for caretakers and their young. The idea that larger hominin societies entailed "cooperative breeding" can be linked to the evolutionary scenario of Swedell and Plummer (2019), based on hamadryas baboons (Chap. 9).

Gesture-first theorists point to the ubiquity of gestures in human communication and the fact that gestures can convey meaning effectively without speech. In experiments that pitted gestures against vocalizations, communication success was twice as high for gestures between people from different cultures, and for vision-impaired recipients.

Baboons display a substantial repertoire of spontaneous communicative gestures that are flexible and variable. In both spontaneous behavior and experimental situations, baboon gestural communication displays the kind of domain-general functions that are vital to language: intentionality, persistence, and elaboration. They also manifest capabilities more specific to communication, such as awareness of a partner's attentional status. Experimenters postulated a sequence in which the baboons learned gestures as simple "tools" and transformed them into semiotic tools as a basis for reasoning. This could be analogous to the development of language in hominins, and the existence of such capabilities in baboons suggests that language, expressed through gestures, might have emerged at a very early stage in hominin evolution.

Some proponents of the gesture-first theory have done extensive work on handedness in gesturing and associated laterality of brain structures. They have found that baboons display a hand preference in gestural communication that does not appear in the manipulations of objects. The distinction also occurs in human infants with regard to pointing and grasping. In a comparative study, baboons and closely related macaques converged with human infants while capuchin monkeys diverged.

There is some evidence that connects baboon handedness with parts of the brain that are homologs with brain structures that belong to the language network in humans. This is particularly true of the planum temporale, which borders Wernicke's area. Chimpanzees and baboons are alone (so far) in displaying a robust leftward bias in the planum temporale, according to diverse analyses of surface area and volume.

Experiments have probed further into baboon cognitive capabilities that can be related to language. One such area is compositionality, the ability to combine abstract representations (e.g., not + blue). In two complex experiments, baboons demonstrated this ability with regard to the abstract concept of negation. Another study indicated that the baboons had a learning bias that facilitated the discovery of connected patterns, favoring cognitive rules that link two variables (e.g., *between x and y* rather than *approximately x* or *all x*). Taken together, this research suggests capabilities for abstraction in early hominins that would have provided the basis for syntax and lexical generation.

In some experiments, large numbers of baboons performed well. This suggests that the language components under consideration might have been common in early hominins. In other experiments, only a few baboons responded correctly to tests. This seems to suggest that the language components in question might have existed in a few early hominin individuals. These components would not have contributed to the communication system at that time, although they might have spread later and contributed to the evolution of language.

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