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12 Linguistic prerequisites in the primate lineage

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12.1 Language evolution

Language is perhaps the single most important feature that distinguishes humans from the rest of the living world. Human language is an open-ended system of communication in which syntactic rules encode information of great complexity, and it is therefore of particular interest how this capacity has evolved. Theories of language origins are all faced with one particular problem: how to explain the evolution of a highly complex and sophisticated cognitive capacity in an extremely short period of time. Humans probably did not have the anatomical and neural prerequisites to produce the full range of modern speech until very recently (Lieberman 2000: 136). A recent comparative genetic analysis has provided additional empirical support, showing that non-human primates differ genetically from modern humans in a region on chromosome 7, which codes for the FOXP2 protein (Enard et al. 2002). Other work has shown that the FOXP2 gene is crucially involved in the development of normal speech abilities in humans (Fisher et al. 1998). The genetic differences in this region distinguishing us from our closest living relatives are the result of a few mutations, which have not become stabilized in the human population until very recently, about 200,000 years ago. Overall, this has led to the hypothesis that the human-specific form of the FOXP2 protein is essentially involved in brain development, affecting the ability to fine-control orofacial movements and thus the capacity to develop proficient speech (Enard et al. 2002). Yet a time period of 200,000 years, which equals about 7,000 generations, could be too short to evolve the entire necessary cognitive apparatus underlying the language capacity. In addition, neurobiological work suggests that the brain regions most heavily involved in language processes in humans did not arise de novo, but evolved from older structures already present in the primate lineage (e.g. Cantalupo and Hopkins 2001; Hopkins et al. 1998). During language evolution these regions became substrates for language processing because the previous functions made them especially suitable for the new problems posed by language (Deacon 1997).

The hypothesis is, therefore, that many of the cognitive capacities that are prerequisite for language are phylogenetically much older, and evolved in the primate lineage long before the advent of modern humans. A systematic investigation of the linguistic capacities of non-human primates, therefore, is likely to shed light on the evolutionary history of the cognitive capacities necessary for language. Of particular interest are abilities that resemble the semantic and syntactic abilities of modern humans, as these two are central to virtually all definitions of language.

12.2 Semanticity in primate vocal communication

12.2.1 *The function and meaning of primate alarm calls*

It has been known for some time that in some non-human primates, particular vocalizations provide nearby listeners with information about some object or event that is physically separate from the calling individual, such as the appearance of a predator, the discovery of particular food, or the occurrence of a unique social event. The best-known example of natural semantic communication comes from studies of the alarm call behaviour of East African vervet monkeys, *Cercopithecus aethiops.* These monkeys produce acoustically distinct alarm calls to leopards, eagles, and snakes (Struhsaker 1967). When exemplars of these calls are played in the absence of actual predators, individuals respond as if they have seen the corresponding predator themselves (Seyfarth et al. 1980). These and other studies (e.g. Gouzoules et al. 1984; Hauser 1998; Macedonia 1990; Eckardt and Zuberbühler 2004; Crockford and Boesch 2003; Slocombe and Zuberbühler ms) have shown that primates are in fact able to produce acoustically distinct vocalizations in response to discrete external events. The suggestion is that these are examples of true semantic communication, since recipients treat these vocalizations as indicators of the actual object or event (Seyfarth et al. 1980).

A potential problem with this conclusion has always been that some species with a considerably less complicated nervous system than primates also produce specific signals in response to objects that are physically separate from them. For example, honeybees (*Apis melifera*) are able to inform each other about the presence and location of distant food sources (von Frisch 1973). Here, signallers produce a visual signal (a specific dance motion) in response to an event (the location of a food source) which describes the event sufficiently accurately for recipients to find it using only the signal. From a functional perspective, therefore, there does not seem to be a difference between the vervet monkey alarm calls and the honeybees' dance language, although the underlying mental mechanisms could be profoundly different. In both cases an external object and a corresponding signal elicit the same behaviour, thus satisfying the functional criterion for semanticity (Macedonia and Evans 1993). Bee language and monkey alarm calls, in other words, could be examples of mere *perceptual processing* and thus be fundamentally different from the kind of semanticity observed in human language. Signallers might simply produce a signal in response to a physical stimulus, such as the solar angle, whereas recipients might simply attend to physical dimensions of the signal, rather than its associated meaning. Human semanticity, however, is of a different kind. Here, the physical properties of speech sounds are only relevant insofar as they refer to an associated cognitive structure, the mental representation or concept shared by both the signaller and the recipient (see, for instance, Yates and Tule 1979). According to this dichotomy, human language is based on a conceptual semanticity, while bee language is based on a mere perceptual, or functional, semanticity. Research on animal semantic communication has traditionally not distinguished between perceptual and conceptual semanticity. Instead, examples of animals producing discrete signals to discrete external events have been called *functionally* referential (e.g. Evans et al. 1993; Hauser 1996: 508), thereby evading further debate about the underlying cognitive structures.

Two recent experiments with Diana monkeys and Campbell's monkeys living in the Taï forest of Western Ivory Coast have addressed this issue, and results suggest that primates process their calls on a conceptual level and therefore exceed the definition of functional referentiality. The following findings derived from long-term observations concerning the natural history of these two species are relevant. Both species live in small groups with one adult male and several adult females with their offspring. The females remain in their natal group in both species, and young males leave their native group and sometimes associate with other monkey species before trying to take over a group of females themselves (Uster and Zuberbühler 2001; Wolters and Zuberbühler 2003). In the Taï forest, both Diana monkeys and Campbell's monkeys are hunted by leopards, *Panthera pardus*, crowned eagles, *Stephanoaetus coronatus*, and chimpanzees, *Pan troglodytes* (Zuberbühler and Jenny 2002; Shultz 2001; Boesch and Boesch 1989). Because of the high predation pressure, both species frequently form mixed-species associations, and some groups spend up to 90 per cent of their time in association with each other (Wolters and Zuberbühler 2003). In both species, individuals produce acoustically distinct alarm calls in response to crowned eagles and leopards, and there is a sexual dimorphism in the call structure of the adult males and females (Zuberbühler et al. 1997; Zuberbühler 2001). Figure 12.1 depicts spectrographic illustrations of the male alarm calls of the

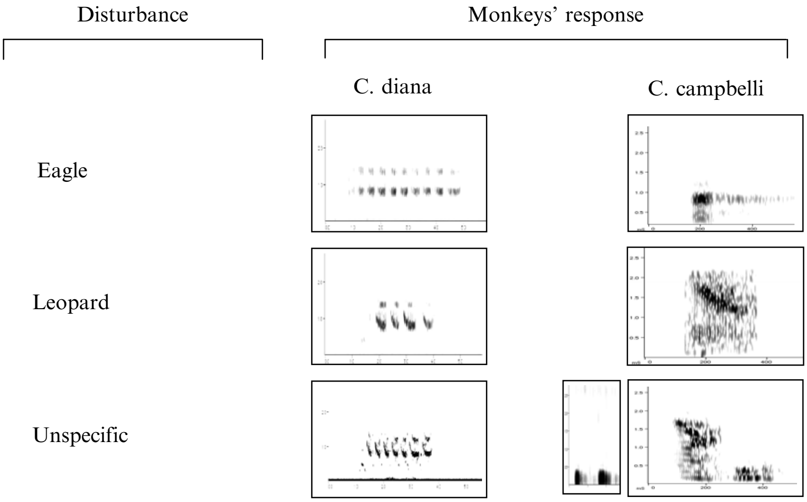

Fig. 12.1 Typical alarm calls produced by male Diana monkeys and Campbell's monkeys in response to leopards, crowned eagles, and unspecific disturbances, such as falling trees. Campbell's monkeys usually utter pairs of booms before an alarm-call series in response to unspecific disturbances. In both species, the female alarm calls are acoustically different from those of the males; spectrograms are published elsewhere (Zuberbühler et al. 1997).

Campbell’s and Diana monkeys, exemplars of which served in the playback experiments discussed below.

To investigate whether the acoustically different alarm calls of these monkeys in fact denoted different predator types, a series of playback experiments was conducted. Wild groups of Campbell’s or Diana monkeys were sought throughout a roughly 100-km^2 large study area surrounding the CRE research station in the western part of the Taï National Park, about 25 km east of the Liberian border (5° 50′N, 7° 20’W). The Taï Forest is classified as a tropical moist forest, with a protected area of about 4000 km^2, the largest remaining block of primary forest in West Africa (Martin 1991). Once a monkey group was located, typically by hearing their contact calls from a distance, the experimenter slowly and silently approached to about 50m from the group and set up the playback and recording equipment without being detected by the monkeys. Then a short recording was played back to simulate the presence of either a leopard or a crowned eagle. Playback stimuli were chosen from among the following types: (a) a fifteen-second recording of leopard growls; (b) five male Diana monkey leopard alarm calls; (c) five male Campbell’s monkey leopard alarm calls; (d) a fifteen-second recording of crowned eagle shrieks; (e) five male Diana monkey eagle alarm calls; or (f) five male Campbell’s monkey eagle alarm calls.

Female Diana monkeys responded to predator vocalizations and to male Diana monkey or Campbell’s monkey alarm calls by giving their own acoustically distinct alarm calls. These vocal responses were highly selective in the sense that playbacks of eagle shrieks, male Diana monkey eagle alarm calls, or male Campbell’s monkey eagle alarm calls all elicited only one type of predator-specific alarm call from females— the females’ eagle alarm call. In contrast, playback of leopard growls, Diana males’ leopard alarm calls, or Campbell’s males’ leopard alarm calls all elicited an acoustically different alarm call—the females’ leopard alarm call. Figure 12.2 summarizes the vocal responses of female Diana monkeys to these playbacks as stacked columns, comprising of the number of predator-specific eagle or leopard alarm calls given in the first minute, in addition to a number of other unspecific call types.

Results suggest that the main organizing principle in the responses of the female Diana monkeys to the six different playback stimuli were the meaning, or predator type, indicated by the playback stimuli, rather than

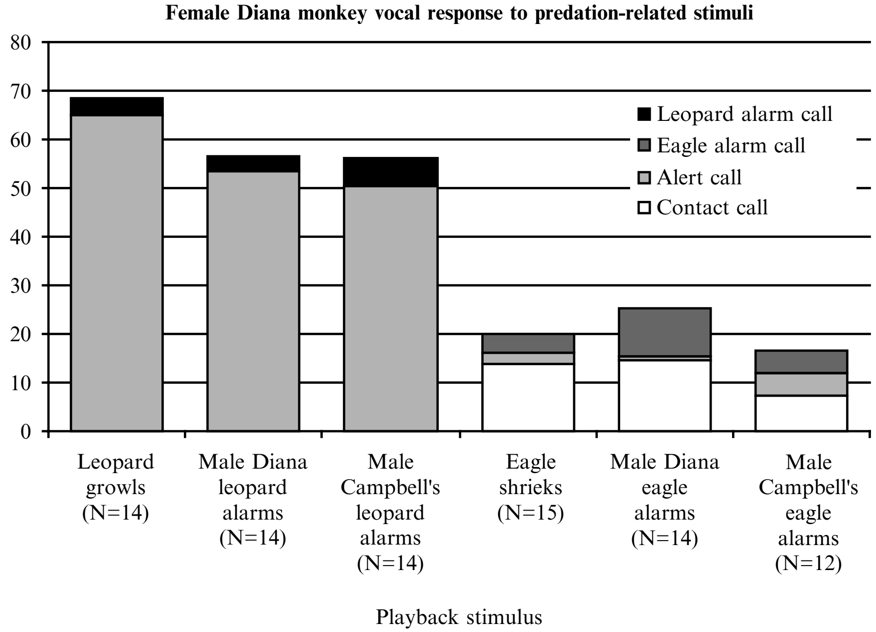

Fig. 12.2 Vocal responses of female Diana monkeys to playbacks of predator vocalizations or alarm call series of male Diana or Campbell's monkeys (data from Zuberbühler et al. 1997; Zuberbühler 2000a). Stacked bars depict median alarm call responses of female Diana monkeys from different groups in response to the different playback conditions during the first minute after beginning of a playback. Sample sizes refer to the number of different Diana monkey groups tested with a particular playback stimulus type.

the more proximate stimulus properties, such as the acoustic features of the signal or the biological species of the signaller.

These results raised a number of questions. In particular, why did male and female Diana monkeys evolve acoustically different alarm calls for the same predators? Note that the alarm calls of the female Campbell's monkeys are also acoustically different from the males', but no systematic investigation has yet been conducted. Clearly, the male calls described in Figure 12.1 function as alarm calls: they advertise to predators that they have been recognized and so further hunting will be futile (Zuberbühler, Jenny, and Bshary 1999), a function also described for some bird alarm calls (e.g. Perrins 1968). At the same time, they warn recipients about the presence of specific predators (Zuberbühler et al. 1997), suggesting that they have evolved through ordinary natural selection (Maynard Smith 1965). However, a recent analysis suggested that sexual selection had exerted additional selection pressure on the evolution of these calls (Zuberbühler 2002a). The polygynous mating system of these forest monkeys leads to intense competition of males for access over a group of females, and this mating system is a notorious target of sexual selection, typically resulting in the evolution of conspicuous male traits (Anderson 1994). Sexual selection, in other words, appears to have acted on male alarm calls and transformed them into structurally distinct loud calls, by selectively affecting the calls' transmission features and by favouring call usage to indicate male quality.

12.2.2 *Cognitive processes underlying call production*

What mental processes underlie call production in these monkeys? Studies of a number of non-primate species, such as California ground squirrels, *Spermophilus beecheyi*, and domestic chickens, *Gallus domesticus*, indicate that callers may simply respond to degrees of threat, rather than predator class (e.g. Owings and Hennessy 1984; Gyger et al. 1987). For example, ground squirrels appear to respond to a predator's distance, rather than its biological class. To investigate which aspects the monkeys responded to when giving alarm calls, the presence of a predator was simulated in various ways. The playback speaker was positioned in the vicinity of Diana monkey groups, such that (a) the distance to the group was either 'close' or 'far' (about 25 m or 75 m), (b) the elevation of the speaker was either 'below' or 'above' the group (about 2 m or 30 m off the ground), and (c) the predator was either a 'leopard' or an 'eagle' (fifteen-second playback of leopard growls or eagle shrieks).

Results of both male and female alarm call behaviour in response to these variations clearly showed that Diana monkeys consistently responded to predator type, regardless of distance or direction of predator attack (Figure 12.3). The same experiment was also conducted with Campbell's monkeys, confirming that predator type was the main determinant of alarm calling behaviour in this species as well (Zuberbühler 2001). Primate alarm calls, in sum, appear to label the predator type and not the degree of perceived threat.

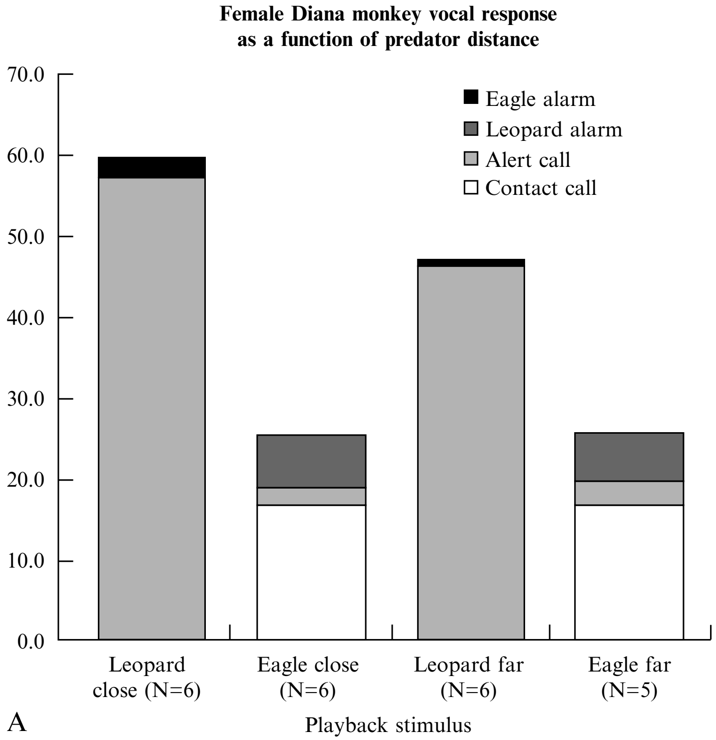

FIG. 12.3a Vocal responses of female Diana monkeys to playbacks of predator vocalizations presented with varying degrees of threat caused by different predator distances (data from Zuberbühler 2000c). Sample sizes refer to the number of different Diana monkey groups tested with a particular playback condition. Stacked bars depict median vocal responses from different groups during the first minute after beginning of a playback.

12.2.3 *Cognitive processes underlying call perception*

Complex cognitive processes reveal themselves through evidence of 'flexible behavioural adaptations in which individual organisms make informed choices based on mental representations', according to Tomasello and Call (1997: 12). The bee-language example has raised questions about the underlying cognitive processes of alarm call perception in non-human primates. Two basic models of call perception can be distinguished. First, monkeys might respond to alarm calls in a rather inflexible manner by simply attending to the calls' physical features rather than an

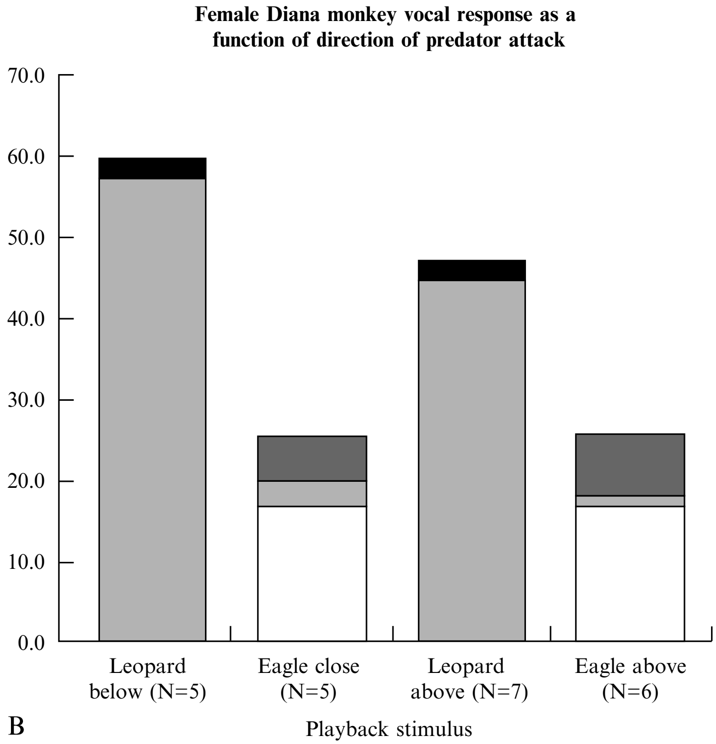

Fig. 12.3b Vocal responses of female Diana monkeys to playbacks of predator vocalizations presented with varying degrees of threat caused by different directions of probable predator attack (data from Zuberbühler 2000c). Sample sizes refer to the number of different Diana monkey groups tested with a particular playback condition. Stacked bars depict median vocal responses from different groups during the first minute after beginning of a playback.

associated mental representation of the predator class. This model is sufficient to explain communication about food sources in honeybees. Alternatively, the monkeys' processing of their own alarm calls could be of the kind that presumably underlies language perception. Here, the acoustic properties of a vocal stimulus are only relevant insofar as they refer to an associated mental structure (e.g. Yates and Tule 1979). A playback experiment was designed to distinguish between these two hypotheses.

Under field conditions, the choice of experimental techniques useful for investigating cognitive processes is limited and typically restricted to some variant of the habituation–dishabituation technique originally developed for prelinguistic children (Eimas et al. 1971). In a typical experimental design, the subject is exposed to a first set of stimuli, which are presented repeatedly until the subject loses interest (i.e. until it habituates). In the second test phase, the experimenter presents a second set of stimuli, which differ in some important feature from the first one. If the subject is able to perceive the difference between the two sets of stimuli, then it is expected to show renewed interest (i.e. it dishabituates). Zuberbühler, Cheney, and Seyfarth (1999) and Zuberbühler (2000a) have applied one form of this technique, the prime–probe procedure, to primates living in undisturbed natural conditions, in order to investigate the cognitive processes underlying their alarm-call behaviour. The prime–probe technique differs from a standard habituation–dishabituation protocol because it does not have a long habituation phase, in which stimuli are presented over and over again until the subject ceases to respond. Instead, it simply provides the animal with a one-off exposure to some critical information and then tests the effect of this manipulation on the animal's subsequent response to an experimental probe stimulus. Figure 12.4 illustrates the experimental design of a prime–probe experiment.

In each trial, the playback speaker was positioned in the vicinity of one of several wild Diana monkey groups to play two stimuli, a prime and a probe, which were separated by five minutes of silence. Monkeys were primed with either predator vocalizations (baseline condition) or monkey alarm calls given in response to the predators (test and control conditions). After a short (five minute) period of silence, the probe stimulus was presented, again from the same hidden speaker position. Baseline, test, and control condition differed in the acoustic and the semantic similarity between the prime and probe stimuli. In the baseline condition, both the acoustic and semantic features were alike: for example, subjects heard a fifteen-second recording of eagle shrieks (indicating the presence of a crowned eagle) followed by a second recording of eagle shrieks five minutes later. The prediction was that monkeys would produce many eagle alarm calls to the first set of eagle shrieks (the prime stimulus), but only few eagle alarm calls to the second set of eagle shrieks (the probe stimulus). This was expected because the information of the probe stimulus was redundant, both acoustically and semantically. In the test condition, subjects heard a Diana monkey's alarm calls (e.g. to an eagle) followed by vocalizations of the corresponding predator (e.g. eagle

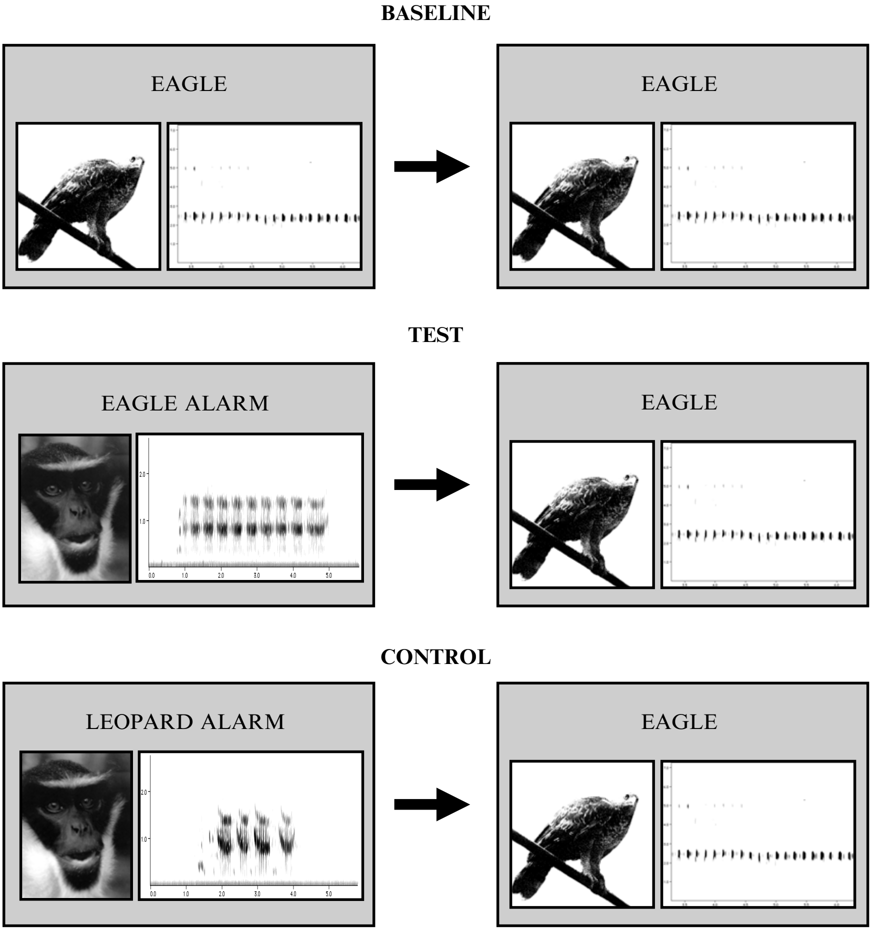

Fig. 12.4 Experimental design of a prime–probe experiment: Different Diana monkey groups were tested on two stimuli, the prime and the probe, separated by five minutes of silence. The prime–probe pairs test differed in similarity of the acoustic and semantic features across conditions as follows: (a) baseline condition—both the acoustic and the semantic features remain the same; (b) test condition—the acoustic features change but the semantic features remain the same; (c) control condition—both the acoustic and the semantic features change. If subjects are able to take the semantic features into account, they should transfer habituation between prime and probe stimuli in the baseline and test condition, but not in the control condition.

shrieks). In this condition, the semantic features remained the same across prime and probe stimuli, whereas the acoustic features changed. The prediction was that if the monkeys were able to attend to the semantic features of the alarm calls, then they were expected to produce only few (eagle) alarm calls in response to the probe. Alternatively, if they were unable to process the semantic features of the prime stimulus, then they were expected to produce many eagle alarm calls to the probe, because the acoustic features of the probe stimulus were novel to them. In the control condition, finally, both the acoustic and the semantic features changed between prime and probe, and therefore subjects were expected to produce many predator-specific alarm calls to both stimuli.

Data showed that the semantic content of the prime stimuli, not their acoustic features alone, explained the response patterns of the monkeys. That is, both eagle shrieks and leopard growls, two very powerful stimuli, lost their effectiveness in eliciting alarm calls as probe stimuli, if subjects were primed first with the corresponding male alarm calls. Figure 12.5 illustrates the response.

Results further showed that it did not matter whether the alarm calls used as prime stimuli were given by a conspecific Diana monkey male or by a heterospecific Campbell's monkey male. Although the alarm calls differed strongly in their acoustic structure, the priming effects remained the same: the monkeys ceased to respond to a predator if they were previously warned of its presence by a semantically corresponding alarm call, regardless of its species origin. These data showed that, although both the acoustic and the semantic properties of the stimuli varied between prime and probe stimuli, only variation in the semantic properties explained the monkeys' vocal response pattern. Data are consistent with the interpretation that recipients formed a mental representation of the predator type when hearing conspecific alarm calls and then were not surprised to detect the corresponding predator a few minutes later.

In sum, (1) the experiments reviewed so far show that primates are able to produce acoustically distinct vocalizations in response to discrete external events, in this case the presence of a particular predator type (Zuberbühler et al. 1997; Zuberbühler 2001). (2) Primate alarm calls do not appear to be the product of differences in the caller's perceived threat, but they label the biological class of a predator (Zuberbühler 2000a). (3) Primate alarm calls are meaningful to recipients because they elicit the same overall behaviour as do the corresponding predators (Zuberbühler

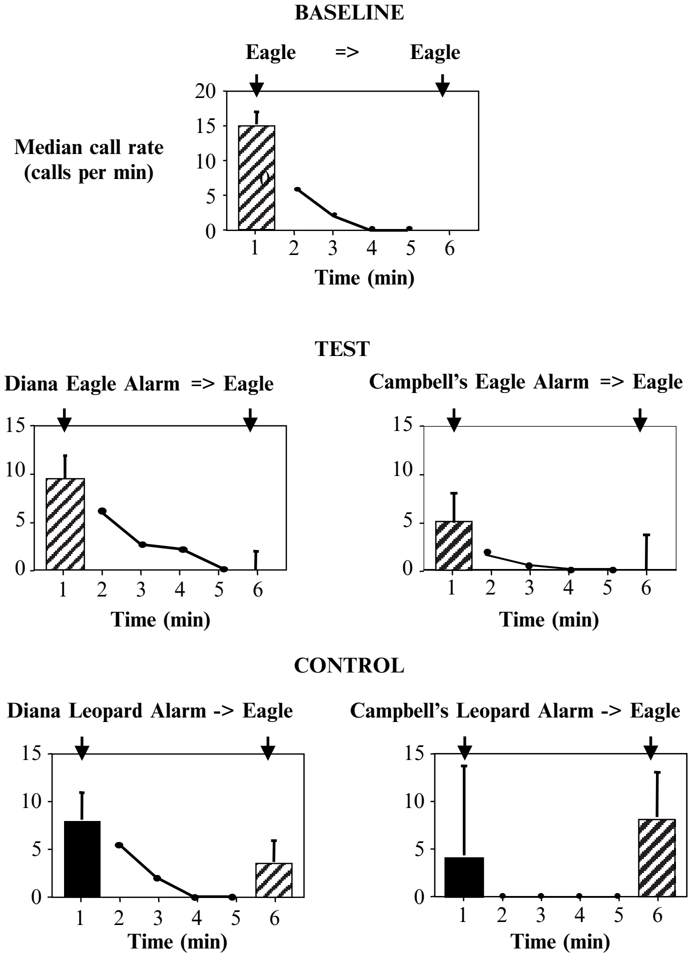

Fig. 12.5 Main results of the prime–probe experiments using the eagle shrieks as probe stimuli (data from Zuberbühler, Cheney, and Seyfarth 1999; Zuberbühler 2000a). Solid bars represent the median number of female leopard alarm calls; hatched bars represent the median number of female eagle alarm calls; error bars represent the third quartile. The connecting sloping lines represent the median alarm-call rates two, three, and four minutes after beginning of the experiment. As predicted by the semanticity hypothesis, the monkeys responded weakly to probe stimuli if they previously heard the same predator vocalization or the corresponding monkey alarm calls, suggesting that the semantic content of the stimuli drove the Diana monkeys' vocal response.

2000b). (4) Call processing appears to take place on a conceptual level involving mental representations of the predator class, since monkeys do not simply respond to the acoustic features of these calls, but behave as if the calls invoke mental representations of the associated external events (Zuberbühler, Cheney, and Seyfarth 1999).

12.3 Syntactic abilities

12.3.1 *Generative systems*

Pinker (1994: 83) identifies two 'tricks', or principles, that underlie human language. The first one concerns the arbitrariness of the sound–meaning combinations. There is nothing about the word *dog* that tells a non-native speaker what this sound pattern could mean. Instead, the meaning of each word has to be learned individually, a defining aspect of human development. The previously discussed experiments outlined the remarkable similarities between monkey alarm-call behaviour and Pinker's first trick of language. There is nothing about a Campbell's monkey eagle alarm calls that indicates to a Diana monkey that the caller has spotted a crowned eagle, and there is empirical evidence that monkeys have to learn the exact meaning of alarm calls individually (Zuberbühler 2000c). More recent work suggests that comparable abilities are also present in some bird species (Rainey et al. 2004; Rainey et al. ms; Pepperberg, Chapter 11).

Pinker's second trick refers to what von Humboldt (1836) has termed the ability of languages to 'make infinite use of finite means'. All languages possess a set of syntactic rules, which generate combined structures from a discrete set of elements, the lexicon; compare also the discussion of the parallel phenomenon in the sound system, in Chapter 3 (Studdert-Kennedy). According to Pinker, 'generative' (or 'discrete') combinatorial systems are rare in the natural world, one noteworthy exception being language, and another the genetic code, where four nucleotides combine to generate a vast number of genes. A crucial feature of generative combinatorial systems is that the property of the combination is distinct from the properties of its components. Generative combinatorial systems thus contrast with the more common *blending* combinatorial systems where the property of the combination lies between the properties of the components. Generative combinatorial systems exhibit two distinct behaviours. First, they possess enormous creative power and generate vast amounts of output. Second, although in the case of language this output is usually meaningful, this does not have to be the case. Generative combinatorial systems can just as easily produce rule-governed nonsense, if abandoned by the semantic system, for instance because of particular brain lesions (e.g. Wernicke 1874; see Pepperberg, Chapter 11).

12.3.2 *The evolution of syntactic abilities*

The evolution of the human syntactic capacity is widely seen as the central challenge for theories of language evolution (e.g. Hurford 1998). Although linguists typically stress the great structural complexity of language, the underlying cognitive skills do not necessarily have to be very complex. Moreover, there is considerable disagreement about the nature and evolution of the underlying cognitive mechanism responsible for generative combinatorial behaviour. Lightfoot (2000), for example, reviews Chomsky's claim that the grammar of a particular language is the derivate of a species-specific mental capacity, the universal grammar, which can take numerous forms, depending on the linguistic experience of the individual. According to this idea, universal grammar determines and constrains the range of possible hypotheses an individual can generate about linguistic structure, which ultimately enables young children to acquire their native language with relative ease. However, the evolutionary history of this mental capacity is controversial (Newmeyer 1998b). Some have argued that universal grammar has evolved in response to an ever-increasing repertoire (Nowak et al. 2000). Others have remained sceptical about the idea of universal grammar as a direct product of natural selection, mentioning alternative evolutionary accounts based on biological constraints or by-products of other adaptive processes (Lightfoot 2000). Unfortunately, this debate is plagued by an almost complete lack of empirical data.

12.3.3 *Primate precursors to syntactic abilities*

A recent study suggests that, as recipients, non-human primates possess some of the cognitive prerequisites required to deduce meaning from combinatorial rules (Zuberbühler 2002b). The study, again conducted with Diana and Campbell's monkeys, is based on a combinatorial rule present in the alarm-calling behaviour of the male Campbell's monkey: in some circumstances males produce a specific call, a brief and low-pitched 'boom' vocalization, in addition to the alarm calls described before (Figure 12.1). The boom calls are given in pairs separated by some seconds of silence, and typically precede an alarm call series by about thirty seconds. These call combinations are given in response to a number of discrete external events, such as a falling tree or large breaking branch, the far-away alarm calls of a neighbouring group, or a distant predator. Common to these contexts is the lack of an immediate danger, unlike situations in which callers are surprised by a close predator. When hearing 'boom'-introduced alarm-call combinations, Diana monkeys do not respond with their own alarm calls, which contrasts sharply to their vocal response to normal—that is, 'boom'-free—Campbell's monkey alarm calls (Figure 12.2). These observations have led to the hypothesis that the booms act as a modifier, selectively affecting the meaning of subsequent alarm calls.

To investigate whether this was the case and whether monkeys were in fact capable of understanding the semantic changes caused by the presence of 'boom' calls, the following playback experiment was conducted. In two baseline conditions, different Diana monkey groups heard a series of five male Campbell's monkey alarm calls given in response to a crowned eagle or a leopard. Subjects were expected to respond strongly, i.e. to produce many eagle or leopard alarm calls, as in the previous experiments (Figure 12.2). In the two test conditions, different Diana monkey groups heard playbacks of exactly the same Campbell's alarm call series, but this time two 'booms' were artificially added twenty-five seconds before the alarm calls to match the natural alarm-call pattern. If Diana monkeys understood that the 'booms' acted as modifiers (similar to hedges in language; see Lakoff 1972) to affect the semantic specificity of subsequent alarm calls, then they should give significantly fewer predator-specific alarm calls in the test conditions compared to the baseline conditions. Figure 12.6 illustrates the experimental design.

Results of this experiment replicated the natural observations. Playbacks of Campbell's eagle alarm calls caused the Diana monkeys to produce their own eagle alarm calls, while playbacks of Campbell's leopard alarm calls caused them to give leopard alarm calls (Figure 12.7). Playback of booms alone did not cause any noticeable change in Diana monkey vocal behaviour, but had a significant effect on how the monkeys responded to subsequent Campbell's alarm calls. Boom-introduced Campbell's leopard alarms elicited significantly fewer leopard alarm calls

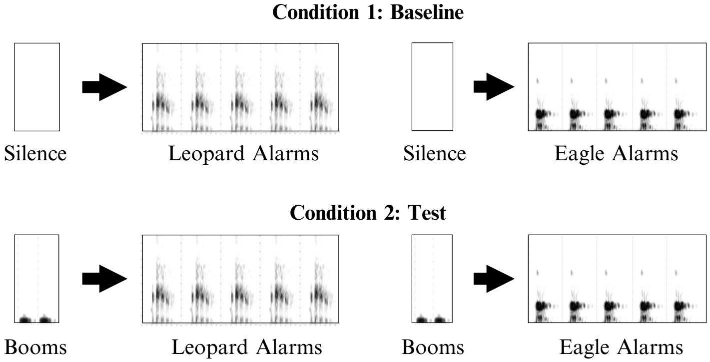

FIG. 12.6 Experimental design of the playback study representing the four different playback conditions (Zuberbühler 2002a)

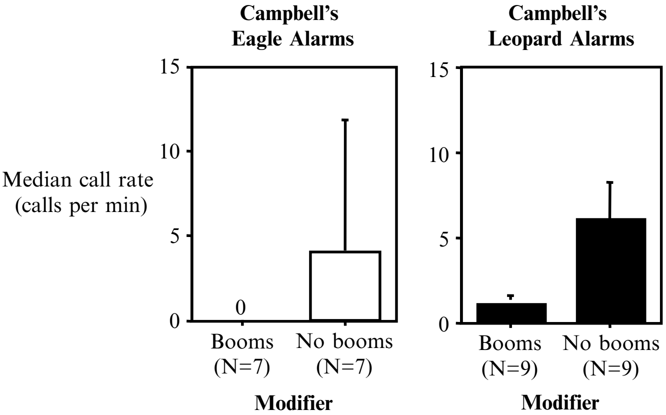

FIG. 12.7 Median alarm-call responses of female Diana monkeys from different groups to the different playback conditions. Black bars represent the median number of female Diana monkey leopard alarm calls; hatched bars represent the median number of female eagle alarm calls during the first minute after beginning of a playback (data from Zuberbühler 2002a). Vertical lines represent the third quartile. Playback of Campbell's monkey booms had a significant effect on how Diana monkeys responded to subsequent Campbell's eagle or leopard alarm calls, suggesting that the booms modified the meaning of the alarm calls.

in Diana monkeys, while boom-introduced Campbell's eagle alarms elicited significantly fewer eagle alarm calls than Campbell's alarm calls alone (Figure 12.7).

The booms, in other words, affected the way the Diana monkeys interpreted the meaning of subsequent Campbell's alarm calls. In particular, they seemed to indicate to nearby listeners that whatever message followed about half a minute later did not require any anti-predator response. Judging from the Diana monkeys' response to these playback stimuli, therefore, the booms modified the meaning of the subsequent alarm-call series and transformed them from highly specific predator labels, requiring immediate anti-predator responses, into more general signals of disturbance that did not require any direct responses.

12.3.4 *Is primate communication syntactic?*

The previous experiments showed that adding 'booms' before the alarm-call series of a Campbell's monkey created a structurally more complex utterance with a different meaning than that of alarm calls alone. But does this now qualify as an example of a syntactic rule? Recipients are clearly able to adjust to the meaning assigned to a particular call type and this adjustment is guided by an underlying rule imposed by the booms, which act as a modifier. Nevertheless, the behaviour of the signaller casts doubt on the statement that this is truly analogous to a syntactic rule in a human language: call production appears to be the product of a rather rigid calling behaviour with little flexibility. Alternatively, it appears that males make accurate judgements of the predatory threat of a situation and it is this assessment that appears to guide their decision as to whether or not to initiate an alarm-call sequence with a pair of booms. Further research will be necessary to determine the cognitive processes underlying the production of call combinations in these monkeys. As recipients, however, the monkeys have demonstrated significant cognitive flexibility. Rather than responding to individual calls they appear to take into account their functional role and importance as modifiers of semantic content.

Recently, Hauser and colleagues have argued that amongst the various syntactic rules, the capacity to implement recursion is the most crucial one, a defining feature of human language (Hauser et al. 2002; Fitch and Hauser 2004). According to this proposal, it is no longer the ability to deal with generative combinatorial systems in general, as suggested by Pinker (1994), but to master one particular one, recursion, that make us truly human. Although the Campbell's monkey example suggests that non-human primates can deal with combinatorial information, this is clearly not an example of a recursive rule. However, it is not entirely clear how indispensable recursion is in everyday spoken language (for instance, see Tomasello 2003). For example, textbooks often portray relative clauses as prototypical linguistic constructions to specify the reference of the subject. However, in spontaneous spoken speech people rarely employ relative clauses for this purpose (Fox and Thompson 1990). In general, relative clauses appear fairly late during language acquisition (Diessel and Tomasello 2000), suggesting that fully functional linguistic communication is possible without them. However, other authors have stressed that syntactic abilities are more likely to have evolved in the social domain, for example by aiding non-human primates to deal with hierarchical information inherent in their groups' social structure (Bergman et al. 2003).

How might the Campbell's monkey combinatorial communication system have evolved? As mentioned before, boom-introduced alarm calls are uttered when no direct danger is present and no anti-predator responses are required. Possibly, boom-introduced alarm calls serve as acoustic long-distance signals addressed to nearby rivals in search for a group of females, advertising the presence and vigour of the resident male. The ability of the recipients to deal with combinatorial information allows the male to produce acoustically conspicuous alarm calls in his dealings with competitors without causing semantic confusions in other group members. The male, in other words, is free to use an acoustically conspicuous signal, his alarm calls, to advertise his presence and vigour to other males without causing unnecessary anti-predator responses in other group members, such as costly escape responses or alarm-call behaviour.

12.4 Primate prerequisites to human linguistic abilities

As recipients, non-human primates have revealed highly sophisticated understanding of the semantic content associated with various of their calls, apparently involving mental representations of the referential situation (Tomasello and Zuberbühler 2002). These representations may include information on the possible causes of a call, rather than just a working knowledge on how best to respond to a particular call. This is further illustrated by the fact that the monkeys can respond differently to ground predator alarm calls of a familiar bird, the crested guinea fowls, *Guttera pucherani*, depending on whether the birds' alarm calls were caused by a leopard or by human poachers (Zuberbühler 2000d). This study suggested that primates attended to the likely cause of a call, rather than the call itself.

Despite a remarkable cognitive flexibility in call comprehension, in which vocal signals are responded to as outcomes of specific external events, non-human primates seem far less flexible as signallers than as recipients of calls. To date there is no evidence that they are able to invent and incorporate new call types into their repertoires or to combine calls creatively to produce novel meanings (see Franks and Rigby, Chapter 10), apart from the example discussed above. One possible explanation for this difference between human and non-human vocal communication has been linked to a lack of social intelligence in the latter case: non-human primates seem to have great difficulties understanding each other as mental agents and taking each other's mental states into account (Tomasello and Call 1997: 384; Cheney and Seyfarth 1998). It is perhaps this cognitive limitation that prevents non-human primates from using vocalizations intentionally in order to affect each other's knowledge in the way humans do. Alternatively, non-human primates might be hindered in their vocal expressive abilities, comparable to linguistically impaired humans suffering from a defective FOXP2 gene. Genetic defects in that region cause a severe form of speech and language impairment: individuals not only suffer from a striking articulatory impairment, but also from impaired syntactic abilities (Vargha-Khadem et al. 1995). Non-human primates similarly lack the ability to fine-control the larynx and mouth the way normal humans can (but see Riede and Zuberbühler 2003a, 2003b). Numerous attempts to teach non-human primates spoken language or to get them to imitate vocal signals have failed, suggesting that non-human primates do not possess the neural capacities required for speech production (but see Marshall et al. 1999; Taglialatela et al. 2003 for some evidence of vocal plasticity). Enard et al. (2002) suggest that the human version of the FOXP2 gene lead to increased fine control of the larynx and mouth, ultimately enabling more sophisticated vocalization. If this scenario is correct, then early humans entered this new round of evolution well prepared, because they already possessed a large number of communicative prelinguistic skills, which had evolved in the primate lineage long before to deal with a range of evolutionarily important events.

12.5 Conclusion

The studies reviewed in this chapter provide empirical evidence that two of the most basic linguistic capacities, i.e. the ability to assign meaning to acoustic units and the ability to adjust meaning as a function of a combinatorial rule, are present in non-human primates, at least as precursors. These cognitive abilities could be homologous to the ones utilized by humans to deal with semantic and syntactic problems in language processing. In monkeys, they are most vividly expressed in the behaviour of call recipients, but they might also drive some aspects of call production. If future work is able to confirm that these abilities are phylogenetically related (for example, because they are dealt with by homologous brain structures), then these abilities must be phylogenetically old, having emerged in the primate lineage before the Old World monkey clade split off from the great ape/human clade some thirty million years ago.

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FURTHER READING

On primate cognition, see Cheney and Seyfarth (1990) and Tomasello and Call (1997). See also Hauser (1996) on the evolution of communication, and the chapters in the volume edited by Tomasello (2003).