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A syntactic rule in forest monkey communication

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Syntactic rules allow a speaker to combine signals with existing meanings to create an infinite number of new meanings. Even though combinatory rules have also been found in some animal communication systems, they have never been clearly linked to concurrent changes in meaning. The present field experiment indicates that wild Diana monkeys, *Cercopithecus diana*, may comprehend the semantic changes caused by a combinatory rule present in the natural communication of another primate, the Campbell's monkey, *C. campbelli*. Campbell's males give acoustically distinct alarm calls to leopards, *Panthera pardus*, and crowned-hawk eagles, *Stephanoaetus coronatus*, and Diana monkeys respond to these calls with their own corresponding alarm calls. However, in less dangerous situations, Campbell's males emit a pair of low, resounding 'boom' calls before their alarm calls. Playbacks of boom-introduced Campbell's alarm calls no longer elicited alarm calls in Diana monkeys, indicating that the booms have affected the semantic specificity of the subsequent alarm calls. When the booms preceded the alarm calls of Diana monkeys, however, they were no longer effective as semantic modifiers, indicating that they are meaningful only in conjunction with Campbell's alarm calls. I discuss the implications of these findings for the evolution of syntactic abilities.

A number of experimental studies have shown that there are interesting parallels between human linguistic behaviour and the way nonhuman primates use some of their vocalizations in the wild (Seyfarth & Cheney 1996). Several guenon species, for instance, are known to produce different alarm calls to refer to different classes of predators (e.g. Struhsaker 1967; Seyfarth et al. 1980; Zuberbühler et al. 1997; Zuberbühler 2001). West African Diana monkeys, *Cercopithecus diana*, produce acoustically distinct alarm calls to leopards, *Panthera pardus*, and crowned-hawk eagles, *Stephanoaetus coronatus*, two of their main predators (Zuberbühler 2000d). Playback experiments have shown that monkeys treat these vocalizations as semantic signals, in the sense that they compare signals according to their meanings and not just their acoustic properties (Zuberbühler et al. 1999). However, to date there has been no evidence that nonhuman primates go beyond this simple semanticity, in which single calls are the primary unit of analysis, to combine call units into more complex utterances with different meanings (Ghazanfar & Hauser 1999).

The ability to take preceding signals into account is probably widespread in the animal world. Structural rules have been observed in several natural communication systems, including those of some primate species (Robinson 1979, 1984; Cleveland & Snowdon 1982; Snowdon 1982; Hailman & Ficken 1987; Mitani & Marler 1989). A distinction has been made between 'phonological' and 'lexical' syntax (Marler 1977), with phonological syntax referring to the rules that specify the assembly of smaller vocal units into larger ones, and lexical syntax to the corresponding changes in meaning. Although phonological syntax is frequently observed in animal communication, the evidence for lexical syntax is scarce. Lexical syntax requires evidence for a rule that encodes new meanings independent of the meanings of the compounds and recipients that comprehend the semantic change invoked by the rule (Nowak et al. 2000).

A number of observations suggest that lexical syntax might be within the cognitive capacities of nonhuman primates, although no systematic studies have been carried out. Marler (1977) noted that the long-distance calls given by the males in a number of forest-dwelling primates often consisted of different vocal compounds, some of which have different functions, if uttered separately. Black-and-white colobus, *Colobus guereza*, for example, introduce their 'roars' with a brief 'snort' call. According to Marler (1972), the two-call compound functions in the maintenance of spacing between

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neighbouring groups, while the snort, if given separately, serves as an alarm call. Another potentially interesting example comes from the chimpanzee, *Pan troglodytes*, ‘pant hoots’, the introductory notes of which seem to resemble a ‘whimper’ call, which is a mild alarm signal (Marler & Tenaza 1977). Compounding is structurally even more elaborate in the titi monkey, *Callicebus moloch*, where both males and females incorporate several call types into rapid sequences depending on the social circumstance (Robinson 1979). A playback experiment suggested that recipients discriminated between normal and abnormal call sequences because abnormal sequences elicited longer bouts of moaning, a call typically given by individuals that seem disturbed. Similarly, analyses of the singing behaviour of male gibbons, *Hylobates agilis*, have shown that males use a limited number of notes to construct their songs, following a framework of rules (Mitani & Marler 1989). Subsequent playback of songs with normally and abnormally rearranged notes revealed that only normal songs elicited ‘squeaks’, a vocalization given by males in territorial disputes, indicating that males distinguished between proper and improper sequences. Finally, wedge-capped capuchin monkeys, *Cebus olivaceus*, combine different call types to form compound sequences following certain rules, but again no evidence was found that these compounds changed the overall meaning of the utterances (Robinson 1984). In sum, although there is evidence for structural rules in animal communication, these rules have never been convincingly linked with concurrent changes in meaning.

A syntactic phenomenon in the vocal communication system of the Campbell’s monkey, *Cercopithecus campbelli*, suggests that nonhuman primates may be able to go beyond event labelling, as shown for some of their predator alarm calls, and may combine calls into a structurally more complex unit with a different meaning. In their natural rainforest habitat, male Campbell’s monkeys produce two acoustically distinct alarm call types, one to crowned-hawk eagles (the ‘eagle’ alarm call) and another one to leopards (the ‘leopard’ alarm call; Zuberbühler 2001). Sympatric Diana monkeys, which often form mixed-species associations with Campbell’s monkeys, understand the meaning of these alarm calls and use them to predict the presence of the corresponding predator (Zuberbühler 2000a). When hearing Campbell’s eagle alarm calls, for example, both the adult males and the females respond with their own acoustically different eagle alarm calls. In addition to the two alarm calls, male Campbell’s monkeys possess another type of loud call, a brief and low-pitched ‘boom’ vocalization (Fig. 1a). This call type is given in pairs separated by some seconds of silence and typically precedes an alarm call series by about 25 s. Boom-introduced alarm call series are given to a number of disturbances, 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 direct threat in each, unlike when callers are surprised by a close predator. Natural boom-introduced Campbell’s alarm calls strongly resemble Campbell’s leopard alarm calls, although no systematic acoustic analysis has been carried out yet. When hearing natural boom-introduced Campbell’s alarm calls, Diana monkeys show no changes in their vocal behaviour, which contrasts sharply to their vocal response to normal (that is boom-free) Campbell’s alarm calls (see Zuberbühler 2000a).

I tested wild groups of Diana monkeys in the Taï forest, Côte d’Ivoire, for their understanding of Campbell’s monkeys’ alarm calls. Diana monkeys were chosen as study subjects because their vocal behaviour and cognitive capacities have already been investigated in some detail. Diana monkeys understand the meaning of other species’ alarm calls even though these calls are acoustically completely different from their own, suggesting that their vocal response is based on a learned understanding of the calls’ meanings (e.g. Zuberbühler 2000b, c). I did not use Campbell’s monkeys as subjects because the vocal behaviour of the females has not yet been investigated systematically.

To investigate whether the booms caused semantic changes in subsequent alarm calls I conducted a playback experiment consisting of eight conditions (Fig. 2). In two baseline conditions, different Diana monkey groups heard a series of five male Campbell’s monkey alarm calls given to a leopard or a crowned-hawk eagle. Subjects were expected to respond strongly, that is, to give many leopard or eagle alarm calls, as they do to real predators or playbacks of their vocalizations, respectively (Zuberbühler 2000a). In the two test conditions, different Diana monkey groups heard playbacks of the same Campbell’s alarm call series, but this time two booms were artificially added 25 s before the alarm calls to match the natural emission pattern. If the booms affected the semantic specificity of subsequent alarm calls, then the monkeys should give significantly fewer predator-specific alarm calls in the test conditions than the baseline conditions. In the four control conditions, subjects heard series of five male Diana monkey leopard or eagle alarm calls, either with or without preceding booms. Diana monkeys themselves do not produce booms (Fig. 1b, c). These controls were conducted to rule out the hypothesis that the booms simply had a silencing effect to any subsequent series of alarm calls. If there were a long-term dependency between the booms and Campbell’s alarm calls, however, then subjects should respond strongly (i.e. give many leopard or eagle alarm calls) to Diana monkey alarm calls, regardless of whether booms preceded the calls. Figure 2 depicts the spectrographic representations of the vocalizations used as playback stimuli. The males of both species reliably alarm call to predators and other disturbances, suggesting that none of the playback conditions represented an anomalous event.

METHODS

I conducted playback trials between December 1999 and March 2000 on a pool of at least 50 Diana monkey groups living in a ca. 50-km^2 study area of tropical rainforest surrounding the C.R.E. research station (Centre de Recherche en Ecologie, 5°50′N, 7°21′W) in the Taï forest. Both Diana and Campbell’s monkey groups are regularly found throughout the study area at densities of 1–2

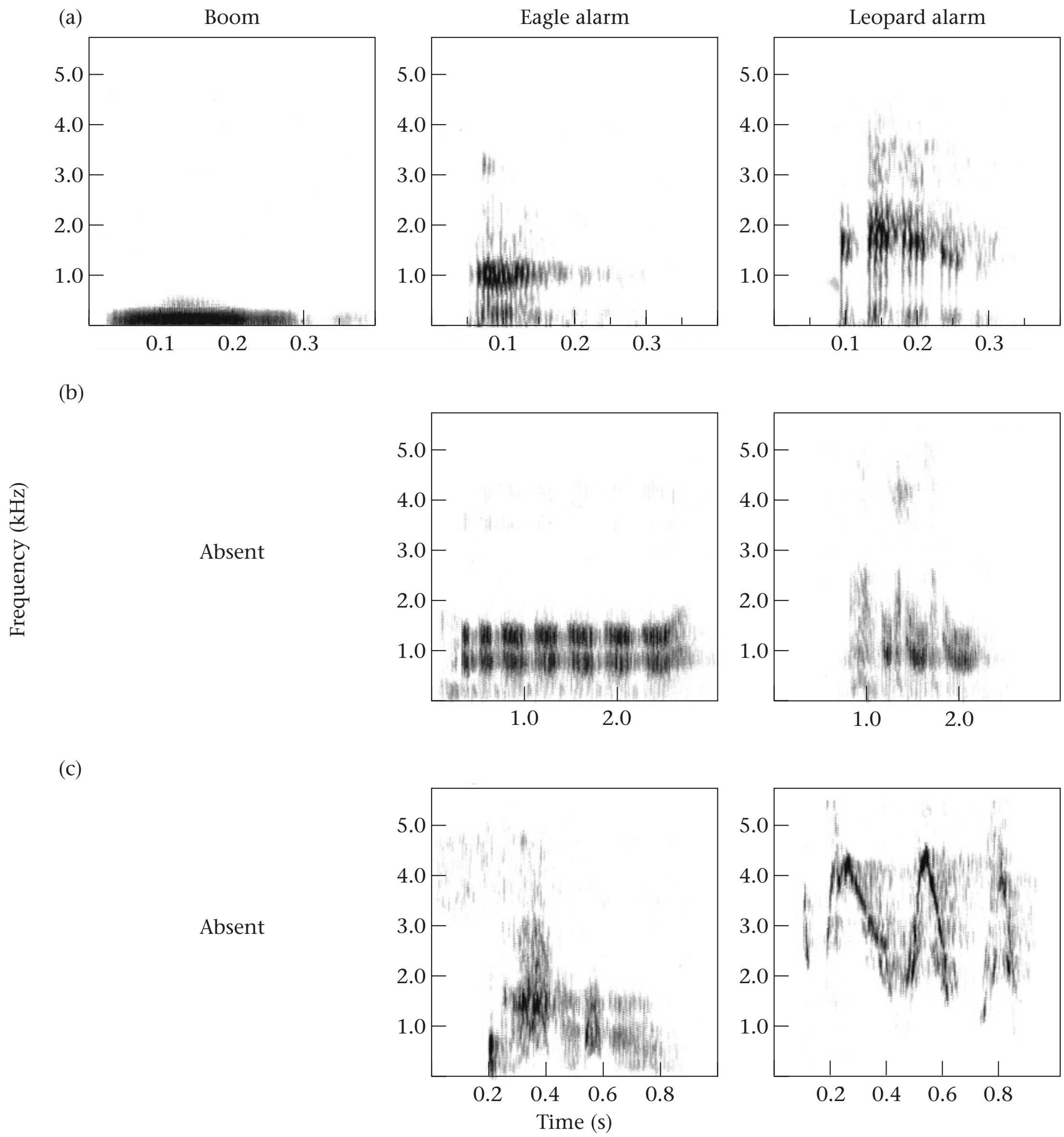

Figure 1. Spectrographic illustrations of the vocalizations used in this study. (a) Male Campbell's monkey, (b) male Diana monkey, (c) female Diana monkey. Male Campbell's and male Diana monkey alarm calls were used as playback stimuli (see text). Recordings were digitized at a sampling rate of 44 kHz (16 bits accuracy) and displayed using a 256-point Fourier transformation (Hamming window function) that resulted in wide-band spectrograms (analysis resolution: 700 Hz with 21.5 Hz/0.72 ms accuracy).

groups/km^2. Both species live in small groups, consisting of one adult male and several adult females with their offspring on a stable home range that is defended against neighbouring conspecific groups. None of the groups tested in this experiment was habituated to human presence.

To conduct a playback trial, I searched for monkey groups throughout the study area. Once I located a group I slowly and silently approached to within ca. 50 m of the group and set up the playback and recording equipment. I did not use a group for analysis if I was detected before or during a playback trial. This decision was straightforward because unhabituated monkeys respond with strong antipredator behaviour to the presence of humans, usually by giving a few alarm calls followed by flight. To avoid habituation to playback stimuli, I did not expose a particular group more than once to a particular playback stimulus. I did this by determining the location of the experimental groups with a Magellan Pioneer GPS and a map.

The calls used as playback stimuli were recorded in the study area from three different Campbell's monkey males (male 1: booms; male 2: eagle alarm calls; male 3: leopard alam calls). Playback stimuli were edited to series of five equally spaced alarm calls (about 5 s between individual calls), either presented alone or preceded by two booms. The two booms were separated from each other by ca. 7 s of silence and from the subsequent alarm calls by ca. 25 s

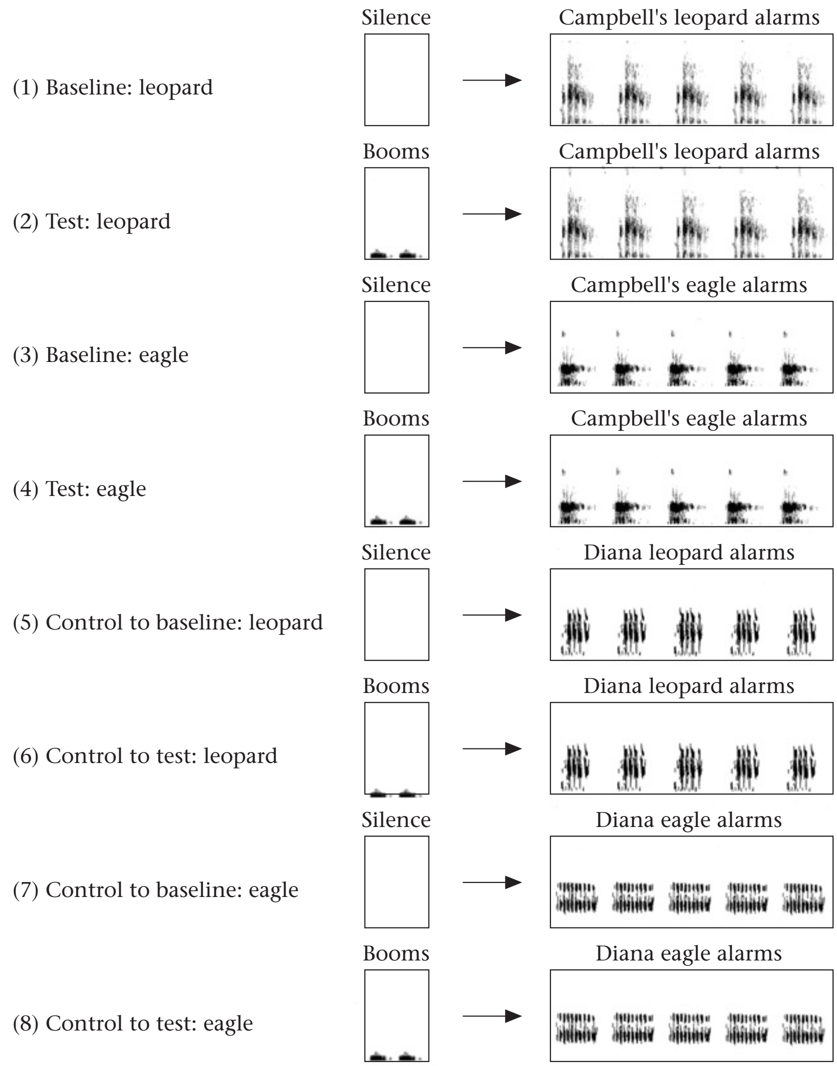

Figure 2. Experimental design of the playback study illustrating the eight conditions.

of silence to mimic the temporal emission pattern of naturally produced boom-introduced alarm calls of male Campbell's monkeys (Fig. 2). Vocalizations were played back in an amplitude range of 90–100 dB. Within this natural range, amplitude had no effect on the vocal response of Diana monkeys to Campbell's alarm calls (Zuberbühler 2000a). Monkey alarm calls in response to predators occur very frequently under natural conditions, such that these playback trials did not constitute an abnormal situation and caused hardly any extra stress for the monkeys.

Stimuli were played back on a Nagra DSM speaker-amplifier connected to a Sony WMD6C Professional Walkman. The monkeys' vocal responses were recorded on analogue tapes with a Sony TCM5000EV recorder and a Sennheiser ME67 directional microphone. All recordings were digitized with the sound-editing software Canary 1.2.4 (Charif et al. 1995) running on a Macintosh computer to calculate alarm call rates and spectrographic representations of the calls.

RESULTS

Diana monkeys gave different vocal responses to the different playback stimuli. Playbacks of Campbell's eagle alarm calls usually caused the Diana monkey males and females to give their own eagle alarm calls, but no leopard alarm calls (Figs 3a, 4a). Playback of Campbell's booms alone did not cause any noticeable change in the vocal behaviour of the Diana monkeys, but these calls had a significant effect on how Diana monkeys responded to subsequent Campbell's alarm calls. If the booms preceded playbacks of Campbell's eagle alarms, Diana monkeys no longer responded with eagle alarm calls (Table 1, Figs 3a, 4a). Analogously, playbacks of Campbell's leopard alarm calls usually caused the Diana monkeys to give leopard alarm calls, but no eagle alarm calls (Fig. 3c, 4c). Again, if the booms preceded playbacks of Campbell's leopard alarms, Diana monkeys no longer responded with leopard alarm calls (Table 1, Figs 3c, 4c).

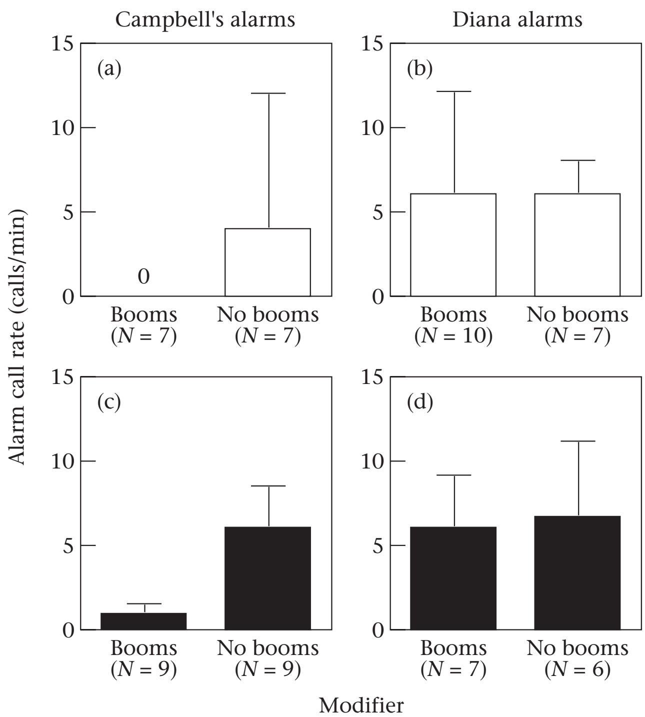

Figure 3. Alarm call responses of female Diana monkeys from different groups to different playback conditions. Each condition consisted of five Campbell's (a, c) or Diana monkey (b, d) alarm calls with or without preceding booms. (a,b) Eagle alarm calls; (c,d) leopard alarm calls. Bars indicate the median call rates and the third quartile during the first minute after beginning of a playback. □: Eagle alarm call given in response; ■: leopard alarm call given in response.

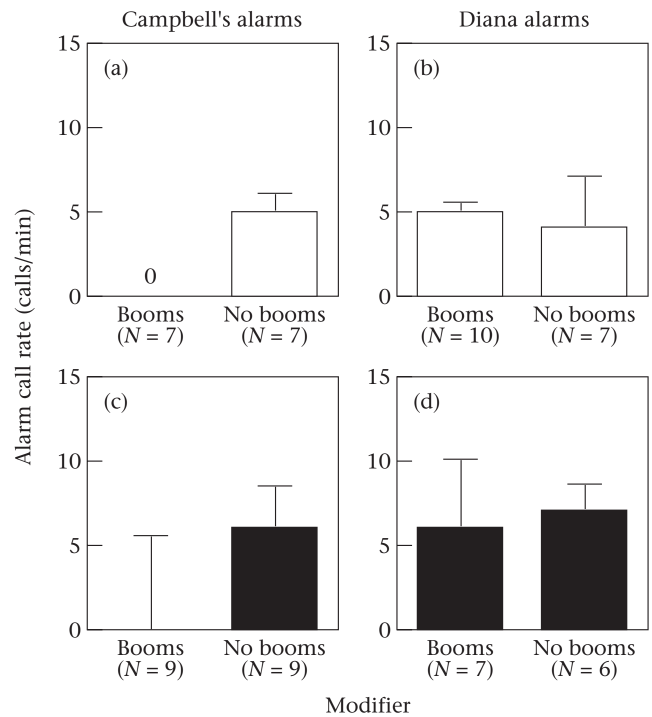

Figure 4. Alarm call responses of male Diana monkeys from different groups to different playback conditions. Each condition consisted of five Campbell's (a, c) or Diana monkey (b, d) alarm calls with or without preceding booms. (a,b) Eagle alarm calls; (c,d) leopard alarm calls. Bars indicate the median call rates and the third quartile during the first minute after beginning of a playback. □: Eagle alarm call given in response; ■: leopard alarm call given in response.

When recordings of conspecific Diana monkeys were used as playback stimuli instead of the Campbell's alarm calls (control trials), the booms of the Campbell's monkeys no longer had an effect on how the monkeys responded to subsequent alarm calls. When hearing recordings of conspecific Diana monkey eagle alarm calls both adult males and females responded with their own eagle alarm calls, regardless of whether the recordings were preceded by Campbell's booms (Figs 3b, 4b). Analogously, when hearing recordings of conspecific Diana monkey leopard alarm calls both adult males and females responded with their own leopard alarm calls, regardless of whether the recordings were preceded by Campbell's booms (Figs 3d, 4d).

DISCUSSION

These results suggest that Campbell's monkeys' booms affected the Diana monkeys' interpretation of subsequent Campbell's alarm calls by indicating that whatever message followed the booms did not require the normal immediate antipredator response. Experimentally adding booms before an alarm call series created structurally more complex utterances with different meanings from the alarm calls alone. Judging from the Diana monkeys' responses to these playback stimuli the booms have actively modified the meaning of the subsequent alarm call series and transformed them from highly specific predator labels, requiring immediate antipredator responses, into more general signals of disturbance that do not require any direct responses.

How relevant are these findings for understanding the evolutionary history of human syntactic abilities? On the one hand, there are interesting parallels between this communication system and some linguistic phenomena. For instance, linguistic hedges (Lakoff 1972), such as 'maybe' or 'kind of', have comparable semantic effects on subsequent sentence structures as the booms have on the subsequent alarm calls. Of course, this analogy is far from perfect, mainly because there is no evidence that the booms have comparable effects on the meaning of any other call, apart from the two alarm call types investigated. One the other hand, did the monkeys respond to the booms as a simple command that anything following no longer needs a response? To use behaviouristic terminology, did the booms simply act as an inhibitory stimulus for a subsequent stimulus, a behavioural phenomenon that can be demonstrated in a relatively simple conditioning preparation (e.g. Pearce & Wilson 1991)? The results of the control conditions suggested that the monkeys' response was more complex than that. If the booms preceded Diana rather than Campbell's monkeys' alarm calls, then the monkeys did not treat the booms as a semantic modifier, indicating that the inhibition hypothesis is inadequate to explain the

Table 1. Statistical comparison of Diana monkeys' responses to recordings of Campbell's monkey or conspecific Diana monkey alarm calls, played back either with or without preceding 'booms'

	Eagle alarms				Leopard alarms			
Dependent variables	U	N_1	N_2	P	U	N_1	N_2	P
Campbell's monkey								
No. of male eagle alarms	0.0	7	7	<0.001	40.5	9	9	1.0
No. of female eagle alarms	3.5	7	7	<0.003	36.0	9	9	>0.3
No. of male leopard alarms	24.5	7	7	1.0	19.0	9	9	<0.05
No. of female leopard alarms	24.5	7	7	1.0	7.5	9	9	<0.004
Diana monkey								
No. of male eagle alarms	30.0	10	7	>0.6	20.0	7	6	>0.8
No. of female eagle alarms	33.0	10	7	>0.8	21.0	7	6	1.0
No. of male leopard alarms	35.0	10	7	1.0	21.0	7	6	1.0
No. of female leopard alarms	31.0	10	7	>0.4	20.0	7	6	>0.8

Mann–Whitney U tests; two-tailed; N_1=Number of different Diana monkey groups tested with preceding booms; N_2=Number of different Diana monkey groups tested without preceding booms.

behaviour. In the control trials, a combination of meaning was logically not possible because the booms and the alarm calls were given by different individuals, who might have perceived different events. The monkeys seem to have taken this into account by responding to the constituent parts rather than the combined configuration of the playback stimuli.

A number of studies with captive animals that have been trained with human-designed artificial communication systems have reported similar syntactic abilities (Kako 1999). Although impressive, the evolutionary significance of the syntactic capacity demonstrated by these language-trained animals is difficult to evaluate, mainly because so little is known about their natural communicative abilities when unaffected by human influence (but see Janik 2000). It might be that their abilities are simply the result of an enormous training effort in which subjects finally managed to conform to the principles of an artificial syntactic task, perhaps even without really understanding it (but see Premack 1984). Alternatively, researchers might have tapped into a species' naturally existing syntactic abilities that have evolved in the context of their natural communicative behaviour (Savage-Rumbaugh et al. 1986; Pepperberg 1993). This study supports the latter interpretation.

In human languages, numerous syntactic rules, such as word order, case markers, or thematic roles, simultaneously determine the exact meaning of a sentence. In addition, syntactic rules are innovative and serve to create novel sentences with distinct meanings. This study does not provide evidence that primate communication is organized in such a way. It provides evidence, however, that some calls can be combined according to structural rules to form more complex utterances, and that these combinations are linked with underlying changes in meaning. The Campbell's booms do not elicit any specific behaviour in Diana monkeys, but they strongly affect the way monkeys interpret subsequent Campbell's alarm calls. Because syntactically organized communication is one of the distinctive features of our own species, it is crucial to provide a detailed account of the emergence of this behaviour. Thus, although the analogies to human language remain suggestive at best, these results show that nonhuman primates are able to generate and comprehend simple syntactic rules that affect the meaning of some of their calls. The corresponding cognitive abilities, therefore, are likely to have evolved long before the advent of human language.

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