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Development of infant baboons' responses to graded bark variants

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We studied the development of infant baboons' (*Papio cynocephalus ursinus*) responses to conspecific 'barks' in a free-ranging population in the Okavango Delta, Botswana. These barks grade from tonal, harmonically rich calls into calls with a more noisy, harsh structure. Typically, tonal variants are given when the signaller is at risk of losing contact with the group or a particular individual ('contact barks'), whereas harsh variants are given in response to predators ('alarm barks'). We conducted focal observations and playback experiments in which we presented variants of barks recorded from resident adult females. By six months of age, infants reliably discriminated between typical alarm and contact barks and they responded more strongly to intermediate alarm calls than to typical contact barks. Infants of six months and older also recognized their mothers by voice. The ability to discriminate between different call variants developed with increasing age. At two and a half months of age, infants failed to respond at all, whereas at four months they responded irrespective of the call type that was presented. At six months, infants showed adult-like responses by responding strongly to alarm barks but ignoring contact barks. We concluded that infants gradually learn to attach the appropriate meaning to alarm and contact barks.

Keywords: baboon; infant; playback; communication; ontogeny

1. INTRODUCTION

Non-human primate vocalizations are commonly viewed as the substrate for the evolution of human language (Pinker 1994; Hauser 1996). However, in terms of vocal production, there are striking differences between humans and non-human primates. Whereas humans are eventually able to produce tens of thousands of words, non-human primates emit a rather limited set of calls that appear more or less fully formed at birth with only limited signs of modifiability. Humans and non-human primates are more alike in terms of comprehension. Like humans, non-human primates can learn to attach the appropriate meaning to a variety of auditory stimuli, including calls of their own and other species (reviewed in Seyfarth & Cheney 1997). As in humans, the appropriate responses in non-human primates seem to develop gradually with age.

For example, Seyfarth & Cheney (1986) investigated vervet (*Cercopithecus aethiops*) infants' responses to different alarm calls. The alarm calls of vervet monkeys are acoustically distinct and also elicit qualitatively different responses (Struhsaker 1967; Seyfarth *et al.* 1980). After playback of the different alarm calls, infants of three to four months of age typically ran to their mothers, no matter which call was broadcast. Between the age of four and six months, their behaviour became more adult-like. However, in several instances infants produced a 'wrong' behavioural strategy. Infants were more likely to respond correctly when they had first looked at an adult. After the age of approximately six months, most infants responded to alarm calls as adults did (Seyfarth & Cheney 1980), suggesting that experience plays a role in the formation of the appropriate response. This conclusion was supported by a study of vervet infants' responses to the alarm call of another species. Vervets attend to the alarm calls of the superb starling (*Spreo superbus*) (Cheney & Seyfarth 1985). These alarm calls occur at different rates in different habitats. Vervet infants in one area who were exposed to starling alarm calls at higher rates responded to these calls appropriately at an earlier age than did infants in another area who were exposed to these calls at lower rates (Hauser 1988).

To date, studies that have addressed the development of infants' responses to different calls have focused on calls that are acoustically distinct. However, the vocal repertoires of many primate species typically consist of a mixture of acoustically graded and discrete calls, with gradation occurring both within and between call types (see Hammerschmidt & Fischer 1998). In this study, we set out to investigate if and when infants learn to discriminate between calls that form a graded continuum. As a model, we chose the 'bark' of adult female baboons (*Papio cynocephalus ursinus*) (Hall & DeVore 1965; Byrne 1981). These barks grade from clear, harmonically rich calls into calls with a more noisy, harsh structure. The clear version is usually given when a caller finds herself in a situation where she is apparently separated from the group or her offspring ('contact barks') (see Cheney *et al.* 1996; Rendall *et al.* 2000), whereas the harsher variant is usually given when a female spots a potential predator ('alarm barks'). However, there are also intermediate forms between the two subtypes and these acoustically intermediate calls can occur in both contexts (Fischer *et al.* 2000).

In this paper, we describe the results of three playback experiments investigating infants' responses to alarm and contact barks. In the first set of experiments, we examined whether infants over the age of six months respond appropriately to four different call variants, i.e. 'typical'

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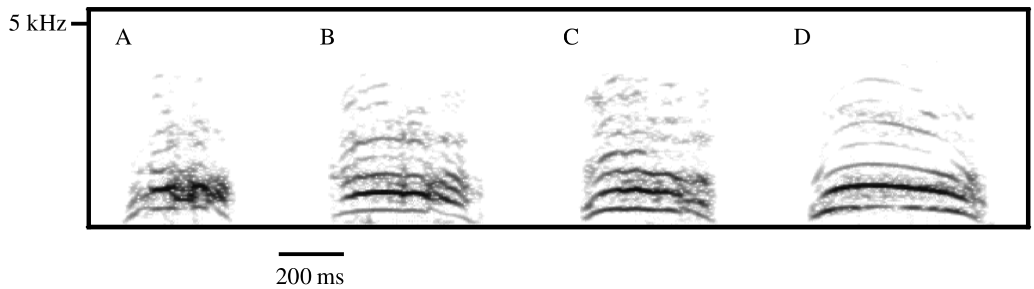

Figure 1. Spectrograms of the calls used in the playback experiments. (*a*) Typical alarm bark, (*b*) intermediate alarm bark, (*c*) intermediate contact bark and (*d*) typical contact bark. These calls were recorded from the same female.

contact and alarm barks and 'intermediate' contact and alarm barks. In the second set of experiments, we compared infants' responses to maternal contact barks versus the barks of unrelated females. Finally, we examined the developmental trajectory of young infants' responses to typical variants of alarm and contact barks. Previous playback experiments have revealed that adult baboons respond relatively strongly to harsh alarm barks but only weakly or not at all to intermediate alarm barks or contact barks (Fischer *et al.* 2001). We therefore wished to determine whether young infants also failed to respond to these call types or whether adults' apparent inability to discriminate between these calls could be related to some other factor such as motivation.

2. METHODS

(a) *Study site and subjects*

The study was carried out over an 18-month period (January 1998 to July 1999) on a group of free-ranging baboons in the Moremi Wildlife Reserve, Botswana. For a more detailed description of the study group and habitat, see Hamilton *et al.* (1976). During the course of the study, group size ranged from 79 to 84 animals. The study subjects were infants born between September 1997 and December 1998. Out of the 21 infants born during that period, two died within one month of birth and two at four months of age. Surviving infants were grouped into two cohorts. All infants born between September 1997 and February 1998 made up the first cohort. It included 11 infants, with seven females and four males. One of these female infants died before all tests could be completed. The second cohort included those infants that were born after July 1998. It consisted of six infants, with four females and two males.

(b) *Call selection*

All calls used for playback experiments were recorded from adult females living in the group at the time of the study. Calls classified as contact barks were recorded when the signaller was separated from the group, either alone or with a small party of other animals or when she had apparently lost contact with her infant. Calls classified as alarm barks were recorded when the signaller had either spotted lions (*Panthera leo*) or crocodiles (*Crocodilus niloticus*). We selected calls for playback depending on the results of an acoustic analysis presented in detail elsewhere (Fischer *et al.* 2000). According to the outcome of this analysis, we established four categories of calls, i.e. typical (harsh) alarm barks, intermediate alarm barks, intermediate contact barks and typical (tonal) contact barks. Figure 1 presents spectrograms of calls that were used in the playback experiments.

Table 1. *Infant age ($x \pm s.d.$), number of call exemplars and number of callers represented separately in the playback experiments for the older and younger cohorts*

treatment/age class	age (weeks)	number of call pairs	number of callers
older cohort			
typical exemplars	34 ± 9.0	8	8
intermediate exemplars	44 ± 7.0	7	5
maternal contact	37 ± 5.0	10	15
younger cohort			
two and a half months	10 ± 1.3	6	6
four months	18 ± 1.0	6	6
six months	29 ± 1.4	6	6

(c) *Experimental protocol*

Trials were conducted opportunistically in contexts that we assessed as relaxed and when neither contact nor alarm barks had been heard within the previous 30 min. When these conditions had been met, we searched for a target infant and followed it until the situation appeared to be suitable for experimentation, i.e. the infant was not playing, climbing a tree or sleeping. Infants in the first two sets of experiments were required to be out of sight of the mother and, to the best of our knowledge, at least 50 m away from her. Younger infants were tested in the presence of their mothers but out of arm's reach.

Once the conditions were met, one observer hid the playback equipment (a Sony DAT TCD-D100 recorder (Sony, Tokyo, Japan) and BOSE Roommate II powered loudspeaker (BOSE, Framingham, MA, USA)) behind bushes or tall grass. We placed the speaker at an approximate right angle to the subject at a mean distance of 17.9 m (range 15–21 m) from the subject. The playback was initiated when the subject had been looking away from the loudspeaker for at least 10 s so that no baseline looking time had to be taken into account. We filmed the behaviour of the subject using a Sony Hi8 camcorder CCD-TR750 for *ca.* 20 s prior to the playback and 20 s thereafter. We also noted the subject's behaviour as well as the date, time, location of the playback and number and identity of individuals in the vicinity. Playbacks mimicked an animal calling at a distance of 20–30 m (for details on call amplitude and more details on the experimental settings, see Fischer *et al.* (2001)).

Older infants first heard one call type (e.g. an alarm bark) and then, at least three days later, the other call type (a contact bark). Pairs of calls were recorded from the same female in order to control for caller identity. We selected typical contact and alarm barks for the first series of trials. In a second series, we presented intermediate contact and alarm bark variants.

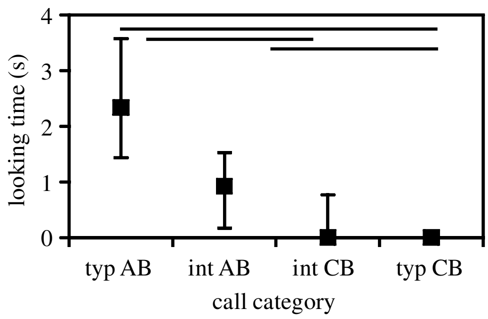

Figure 2. Response durations (medians ± interquartile ranges) after presentation of single exemplars of baboon barks (typ, typical; int, intermediate; AB, alarm barks; CB, contact barks). Bars indicate significant differences between treatments.

Infants were unrelated to the female whose calls were played and the order of presentation was balanced across subjects. In the second set of experiments, we presented infants with maternal contact barks. Table 1 gives a breakdown of infant ages, the number of call exemplars used and the number of callers represented. Although there was considerable variation in age between infants, we opted for doing as many tests as possible as soon as we had completed acoustic analysis because we were afraid of losing study subjects to infanticide or predation (Palombit *et al.* 2000). Finally, in order to examine the development of infants' responses, we tested infants of the younger cohort in three different age classes (table 1). Each infant was presented with typical exemplars of alarm and contact barks for each age class. The order of presentation was balanced across subjects.

(d) *Data analysis*

We analysed subjects' responses on a frame-by-frame basis using Adobe Premiere Software 'lite' v. 1.4 (Adobe, San José, CA, USA). We first digitized the respective video clips (25 frames s^{-1}), assigned a random code to the clips and flagged the onset of the calls. We later analysed the recordings blind to the experimental condition with the audio channel turned off. We measured the latency to respond (time between onset of call and onset of response) and scored only responses that occurred within 2 s of the onset of any given call. We determined the duration of responses that involved a head turn of at least *ca.* 45° for responses that involved a visual orientation to the loudspeaker. In those cases when infants startled or jumped into a tree, we measured the time from the beginning of the startle response to the end of the visual orientation towards the speaker. When infants began to approach the speaker, we determined only the time spent looking prior to the approach because looking time could not be determined reliably once the infant was moving. In order to test for differences in response duration in relation to call type and age, we used the repeated samples with missing values test on ranked data (Mundry 1999), a permutation test that delivers a variant of a Friedman one-way analysis of variance which accepts missing values. We used the same test for conducting follow-up pairwise comparisons between treatments.

3. RESULTS

(a) *Responses to naturally occurring calls*

We registered the responses of infants to contact and alarm barks during focal observations when infants were not in ventro-ventral contact with their mothers. We considered only responses to the first call in any given bout (14 alarm barks and 51 contact barks). We broke down responses separately for infants aged two to three months, four to five months and six months and older. At two to three months, infants responded to neither call type (none out of four alarm barks and none out of ten contact barks). Four- to five-month-old infants responded to two out of two alarm barks and none out of 12 contact barks. Older infants responded to alarm barks more often by looking, running to their mother or climbing up a tree (four out of eight alarm barks), but the propensity to respond to contact barks was low (one out of 29 barks).

In order to determine whether young infants' failure to respond to contact and alarm barks might be due to a general lack of motor or perceptual skills, we noted 103 instances when adult males grunted to infants younger than two months of age. These observations suggested that young infants were in fact capable of responding to at least some vocalizations. In 37 cases infants looked towards the male, in three cases they looked and geckered, in eight cases they looked at and approached him (three times with an open-mouth 'playface') and in eight cases they avoided the male's approach (three times by running away and screaming). They showed no apparent response in the remaining 47 cases. On average, at this age, infants spent 22% of the observation time off the mothers' body but within 1 m and 19% of the time further than 1 m away.

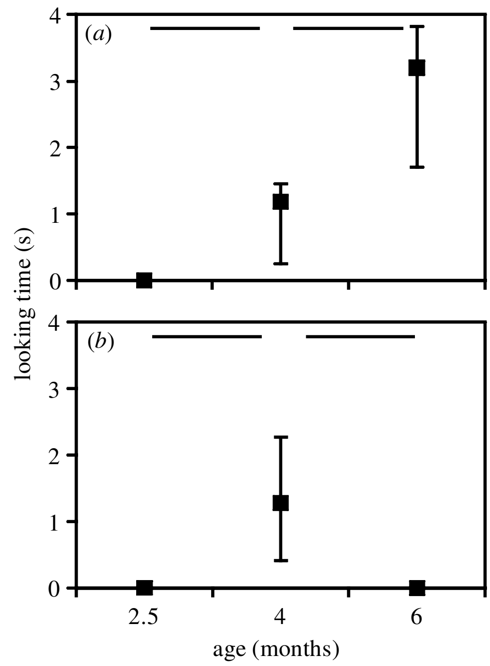

Figure 3. Response durations (medians ± interquartile ranges) in the different age classes after playback of (*a*) typical alarm barks and (*b*) typical contact barks. Bars indicate significant ($p < 0.1$) differences between treatments.

(b) *Playback experiments*

The playback experiments corroborated observational data in suggesting that infants respond to alarm barks but not to contact barks. Infants of an average age of nine months responded strongly and reliably to the playback of an alarm call. All 11 infants looked towards the loudspeaker, while one also startled and two jumped up a tree. In contrast, after playback of a typical contact bark, only two out of 11 infants looked towards the loudspeaker and the remaining nine infants failed to show any response. After playback of an intermediate alarm bark, two out of the ten infants startled, five looked towards the loudspeaker and three showed no apparent response. After playback of an intermediate contact bark, four out of ten infants looked towards the speaker.

Figure 2 presents the data on response duration after playback of the four different call types. Infants looked longest after playback of typical alarm barks, less long after playback of an acoustically intermediate alarm call, only briefly after playback of an intermediate contact bark and hardly at all after playback of a typical contact bark. A comparison of the time spent looking towards the speaker revealed significant differences between responses to the different call categories ($p < 0.01$). A post hoc comparison yielded significant differences between responses to typical alarm barks and typical contact barks ($p < 0.01$), between typical alarm barks and intermediate contact barks ($p < 0.01$) and between intermediate alarm barks and typical contact barks ($p < 0.05$).

Eight out of the ten infants looked towards the speaker after playback of their mother's contact bark. More significantly, in four cases they approached the speaker as if they were looking for their mother. In one case the infant emitted a contact call herself. In contrast, infants showed no apparent response after playback of the contact bark of an unrelated female. Infants looked towards the speaker significantly longer after playback of their mother's bark than after playback of another female's contact bark (mean s.e.m. looking time, maternal contact bark 1.4 ± 1.3 s and unrelated female 0.5 ± 0.2 s) ($p < 0.01$).

Experiments on infants of the younger cohort showed that, at two and a half months of age, infants failed to show any response to playbacks of either alarm or contact barks. At four months of age, four of the six infants looked towards the speaker after playback of an alarm call, while five of them did so after playback of a contact bark. At six months of age, five of the infants responded strongly to alarm barks, but none of them responded to contact barks. Figure 3 shows the looking time of the younger infants at different ages for the two call types. There were significant differences in response duration in relation to call type and age ($p < 0.01$). Follow-up tests showed that, at two and a half and four months of age, there were no significant differences in relation to call type. However, at six months of age, infants tended to respond more strongly to alarm than to contact barks ($p < 0.1$). Comparing responses within call types, six-month-old infants tended to respond more strongly to alarm barks than infants of two and a half months of age ($p < 0.1$). In contrast, four-month-old infants responded more strongly to contact barks than either infants of two and a half months of age ($p < 0.1$) or six months of age ($p < 0.1$).

4. DISCUSSION

Infant baboons gradually developed the ability to discriminate between calls that fell along a graded acoustic continuum. By the age of six months, they discriminated reliably between typical variants of alarm and contact barks. However, unlike adults, who respond only to typical alarm barks, older infants exhibited a graded series of responses to the four call variants. Older infants responded most strongly to typical alarm barks, less strongly to intermediate alarm calls, less strongly still to intermediate contact barks and hardly at all to typical contact barks. These results may indicate that infants respond in a continuous fashion to continuous variation in perceived urgency in the calls. Alternatively, because no infants responded to intermediate contact barks with a startle response but some infants did show a startle response to intermediate alarm barks, it might also be the case that infants place intermediate contact and alarm barks into two different categories. Small sample size unfortunately precludes an answer to this question. The infants' relatively strong responses to intermediate alarm barks suggests that the failure of adults to respond to this call variant is not due to an inability to discriminate between call types. Instead, it seems possible that adults' assessments of context and the level or urgency may override the information conveyed by the call (Rendall *et al.* 1999; Fischer *et al.* 2001).

It seems unlikely that the infants' responses were influenced by the frequency with which they heard each call type. Had the responses been mainly frequency dependent, then intermediate alarm calls, which accounted for only one-quarter of all alarm barks in the sample, should have elicited the strongest responses. This was not the case. Furthermore, infants responded strongly to the contact barks of their mothers, supporting the notion that infants learn to ignore contact barks from unrelated females rather than becoming simply habituated to their frequent occurrence.

Infants can not only discriminate between graded variants within a call type, but they are also able to dissect such a continuum along a different dimension, namely individuality. At the very least, they can discriminate maternal contact barks from other females' barks. These findings complement those of Rendall *et al.* (2000), whose observations and experiments demonstrated that females respond more strongly to their own infant's contact barks than to other infants' barks (for a comprehensive discussion of the mechanisms underlying both the production of and responses to contact calls, see Cheney *et al.* (1996) and Rendall *et al.* (2000)).

The fact that infants but not adults respond to intermediate alarm and contact barks indicates that infants do not simply copy adults' behaviour. Instead, the experiments on the younger infants suggested that they first learn to attend to barks in general and later learn to discriminate between different bark types. Infants' failure to respond to barks at two and a half months of age cannot be attributed to either a lack of general perceptual or motor skills; their responses to adult grunts demonstrated that, at the same age, they are able to produce a variety of behavioural responses to calls by other group members. Instead, one may hypothesize that infants learn to attend to events in their vicinity, such as the approach of a familiar male baboon, earlier than to events that, like the appearance of a lion, typically occur at larger distances and are thus more difficult to discern.

One might argue that the infants' gradual development is due to maturation rather than experience. However, evidence from other primate species suggests that experience plays a major role. First, when infant vervet monkeys first begin to give alarm calls, they overgeneralize and give, for example, eagle alarm calls to a variety of both non-threatening and threatening aerial species. Over time, they come to restrict their eagle alarm calls to the one or two raptor species that prey on vervets (Seyfarth & Cheney 1980). Second, both vervets and baboons respond to the alarm calls of conspecific birds and ungulates (Cheney & Seyfarth 1985, 1990; Hauser 1988; D. L. Cheney and R. M. Seyfarth, unpublished data.) It seems unlikely that these responses have a genetic basis. Finally, in a cross-fostering experiment in which Japanese (*Macaca fuscata*) and rhesus (*Macaca mulatta*) macaque infants were raised by members of the other species, adoptive mothers apparently learned to attend to the calls of their foster offspring even though the infant was a member of another species (Owren *et al.* 1993).

In fact, a basic association mechanism provides a simpler explanation for infants' development than does the unfolding of an intricate maturational process (Shettleworth 1998). Sounds in the environment provide a great deal of information once an animal has learned to associate a specific acoustic pattern with its source. It therefore seems quite plausible that they can also make use of this mechanism in order to associate conspecifics' calls with, for instance, the contexts in which they are given or the individual identity of the caller. In summary, the development of appropriate responses requires two prerequisites: first, infants must associate a particular call type with the external stimulus that evoked it and, second, infants must dissect the acoustic continuum of calls into different categories. Further research should be directed towards uncovering the detailed mechanisms underlying these processes.

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REFERENCES

Byrne, R. W. 1981 Distance vocalisations of Guinea baboons (*Papio papio*) in Senegal: an analysis of function. *Behaviour* **78**, 283–313.

Cheney, D. L. & Seyfarth, R. M. 1985 Social and nonsocial knowledge in vervet monkeys. *Phil. Trans. R. Soc. Lond.* B **308**, 187–201.

Cheney, D. L. & Seyfarth, R. M. 1990 *How monkeys see the world.* University of Chicago Press.

Cheney, D. L., Seyfarth, R. M. & Palombit, R. 1996 The function and mechanisms underlying baboon 'contact' barks. *Anim. Behav.* **52**, 507–518.

Fischer, J., Hammerschmidt, K., Cheney, D. L. & Seyfarth, R. M. 2000 Acoustic features of female chacma baboon barks. *Ethology.* (In the press.)

Fischer, J., Metz, M., Cheney, D. L. & Seyfarth, R. M. 2001 Baboon responses to graded bark variants? *Anim. Behav.* (Submitted.)

Hall, K. R. L. & DeVore, I. 1965 Baboon social behavior. In *Primate behavior: field studies of monkeys and apes* (ed. I. DeVore), pp. 53–110. New York: Holt, Rinehart and Winston.

Hamilton, W. J., Buskirk, R. E. & Buskirk, W. H. 1976 Defense of space and resources by chacma (*Papio ursinus*) baboon troops in an African desert and swamp. *Ecology* **57**, 1264–1272.

Hammerschmidt, K. & Fischer, J. 1998 The vocal repertoire of Barbary macaques: a quantitative analysis of a graded signal system. *Ethology* **104**, 203–216.

Hauser, M. D. 1988 How infant vervet monkeys learn to recognize starling alarm calls: the role of experience. *Behaviour* **105**, 187–201.

Hauser, M. D. 1996 *The evolution of communication.* Cambridge, MA: MIT Press.

Mundry, R. 1999 Testing related samples with missing values: a permutation approach. *Anim. Behav.* **58**, 1143–1153.

Owren, M. J., Dieter, J. A., Seyfarth, R. M. & Cheney, D. L. 1993 Vocalizations of rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques cross-fostered between species show evidence of only limited modification. *Dev. Psychobiol.* **26**, 389–406.

Palombit, R., Cheney, D. L., Fischer, J., Johnson, S., Rendall, D., Seyfarth, R. M. & Silk, J. B. 2000 Male infanticide and defense of infants in chacma baboons. In *Male infanticide and its implications* (ed. C. P. van Schaik & C. H. Janson), pp. 123–153. Cambridge University Press.

Pinker, S. 1994 *The language instinct.* New York: Morrow.

Rendall, D., Seyfarth, R. M., Cheney, D. L. & Owren, M. J. 1999 The meaning and function of grunt variants in baboons. *Anim. Behav.* **57**, 583–592.

Rendall, D., Cheney, D. L. & Seyfarth, R. M. 2000 Proximate factors mediating 'contact' calls in adult female baboons and their infants. *J. Comp. Psychol.* **114**, 36–46.

Seyfarth, R. M. & Cheney, D. L. 1980 The ontogeny of vervet monkey alarm calling behavior: a preliminary report. *Z. Tierpsychol.* **54**, 37–56.

Seyfarth, R. M. & Cheney, D. L. 1986 Vocal development in vervet monkeys. *Anim. Behav.* **34**, 1640–1658.

Seyfarth, R. M. & Cheney, D. L. 1997 Some features of vocal development in nonhuman primates. In *Social influences on vocal development* (ed. C. T. Snowdon & M. Hausberger), pp. 249–273. Cambridge University Press.

Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980 Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science* **210**, 801–803.

Shettleworth, S. J. 1998 *Cognition, evolution, and behavior.* New York: Oxford University Press.

Struhsaker, T. T. 1967 Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In *Social communication among primates* (ed. S. A. Altmann), pp. 281–384. University of Chicago Press.