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Who, me? Can baboons infer the target of vocalizations?

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We describe a playback experiment designed to test whether free-ranging baboons, *Papio hamadryas ursinus*, recognize when a call is directed at themselves rather than at other individuals. Female subjects were played the threat-grunt of a more dominant female under one of two conditions: after they had been threatened by that female and after they had groomed with that female. Subjects showed a shorter latency both to look towards the speaker and to move away from the area after aggression than after grooming. In the 15 min following playback, subjects who had recently been threatened were less likely to approach their former opponents and less likely to tolerate those females' approaches than during matched control periods. In contrast, subjects were equally likely to tolerate approaches by the dominant signaller following postgroom trials and during matched control periods. Combined with results from previous experiments testing baboons' responses to 'reconciliatory' grunts, these results suggest that baboons make inferences about the directedness of vocalizations even in the absence of visual cues, and that the nature of prior interactions affects subsequent behaviour. When attending to vocal signals, baboons appear to take into account not only the signaller's identity and her probable subsequent behaviour, but also the target of her attention. The ability to integrate these cues may represent a first crucial step towards the recognition of other individuals' intentions and motives.

During conversation, humans regularly make inferences about the motives and beliefs of their intended recipients (Grice 1957). Depending on these inferences, we may view another's actions as deliberate, accidental, directed at ourselves or directed at someone else. In contrast, while animal vocalizations can be elicited by a wide variety of stimuli and often function to alter the behaviour of listeners (reviewed in Bradbury & Vehrencamp 1998), there is no evidence that signallers take into account their audience's mental state when producing vocalizations. Similarly, listeners' responses seem governed primarily by learned behavioural contingencies rather than any appreciation of signallers' knowledge or beliefs (reviewed in Cheney & Seyfarth 1996; Seyfarth & Cheney 2003).

Despite their apparent insensitivity to other individuals' mental states, monkeys are very attentive to other individuals' direction of gaze (Perrett & Emery 1994; Emery 2000; Ghazanfar & Santos 2004). They use gaze to target opponents and to recruit other individuals' support in aggressive alliances (Sato & Nakamura 2001; Tomasello et al. 2001). They may also be able to use another individual's direction of gaze to make inferences about her intentions, to infer, for example, that an individual is more likely to defend a food item when she is looking at it than when her gaze is averted (Flombaum & Santos 2005; Santos et al., in press; also see Hare et al. 2000, 2001). We still know very little, however, about nonhuman primates' ability to infer the target of other individuals' vocalizations. Given the importance of such inferences in human speech, this is surprising.

As in many other nonhuman primate species, social interactions among chacma baboons, *Papio hamadryas ursinus*, are mediated not only by different facial expressions, postures and gestures, but also by a variety of vocalizations. Their most common vocalization is a low-amplitude grunt, which is given during friendly interactions and functions to facilitate social interactions (Cheney et al. 1995; Silk et al. 1996). Baboon groups can include over 75 individuals, however, so the intended recipient of a grunt is not always immediately apparent (at least not to human observers). For example, in a typical social interaction a dominant female

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approaches two subordinate females, one of whom has an infant, and utters a grunt. The mother with the infant remains seated, while the other female moves away. How does a female decide whether to stay or leave? To a large degree, her response may depend upon both gaze direction and relatively simple contingencies. Vocalizing females are often looking at one particular individual, and recipients are doubtless sensitive to gaze direction. Similarly, both of the subordinate females have probably learned that grunts are correlated with infant handling and other friendly interactions, and that dominant females rarely grunt when supplanting more subordinate individuals (Cheney et al. 1995; Silk et al. 1996). As a result, both females infer that the grunt is directed at the female with an infant. The female with the infant therefore remains seated, and the other female moves away.

When accompanying visual signals are absent, however, the interpretation of vocal signals may be more difficult. Baboons often forage in woodland where other individuals can be heard but not seen, and they approach other individuals from a variety of directions and angles. Vocal signals like grunts are individually distinctive (Owren et al. 1997; Rendall et al. 1999), so listeners can readily identify an unseen caller. In the absence of visual cues, however, listeners may find it difficult to determine the signaller's intended recipient, and hence the appropriate behavioural response. Again, relatively simple contingencies, including the nature of recent interactions, may guide listeners' responses.

For example, after 13% of aggressive disputes, dominant females grunt to their former victims. These grunts appear to serve a reconciliatory function, both reducing the anxiety of subordinate females (Cheney et al. 1995) and influencing their subsequent interactions. In an earlier experiment that attempted to mimic vocal reconciliation (Cheney & Seyfarth 1997), subordinate females were played the grunt of their former opponent in the minutes immediately following a dispute. After hearing their opponent's grunt, subjects approached their opponent and tolerated their opponent's approaches at significantly higher rates than they did under baseline conditions, suggesting that they interpreted the grunt as a signal of friendly intent. In contrast, when subjects heard either another female's grunt or no grunt, they avoided their former opponent. Significantly, hearing another female's grunt in the absence of a recent interaction did not alter subjects' behaviour towards that female. Instead, they appeared to interpret such calls as directed at someone else.

These observations suggest that monkeys have a rudimentary understanding of other individuals' intentions towards themselves, an ability that constitutes a crucial precursor to the attribution of other individuals' mental states. Alternatively, a recent interaction with a particular individual might simply prime baboons to attend preferentially to that individual's vocalizations. This more parsimonious explanation does not require that baboons make inferences about the directedness of calls.

To test between these hypotheses, we used playback experiments to examine whether female baboons' responses to another female's vocalizations are influenced by the nature of prior interactions with that individual. The playback experiment followed a matched-pair design. In one condition, a subordinate female was played the threat-grunts of a dominant female shortly after that female had threatened her. Threat-grunts are tonal, multisyllable, staccato calls that are produced when baboons are threatening more subordinate individuals. Previous playback experiments (Bergman et al. 2003) indicate that threat-grunts, like other vocalizations given by baboons (Owren et al. 1997; Rendall et al. 1999; Fischer et al. 2001, 2004) and many other primates (e.g. Hammerschmidt & Todt 1995; reviews by Seyfarth & Cheney 2003; Fischer 2004; Ghazanfar & Santos 2004) are individually distinctive. Threat-grunts are acoustically different from grunts given in friendly interactions and easy to distinguish by ear. Females threaten their former victims again within 5 min following approximately 14% of fights (D. L. Cheney, unpublished data). Therefore, we hypothesized that subjects would interpret these threat-grunts as an indicator of renewed aggression directed at them. In the other condition, the same subordinate female was played the same dominant female's threat-grunts shortly after the two females had groomed. Because females almost never threaten a recent grooming partner (<1% of all grooming interactions; D. L. Cheney, unpublished data), we predicted that in this case subjects would interpret the call as directed at someone else.

If baboons take into account signaller identity, call type and the nature of recent interactions when inferring the target of a vocal signal, we predicted that they would respond more strongly to threat-grunts after aggression than after a grooming interaction. Moreover, we predicted that after aggression, subjects would be less likely to approach the dominant signaller and more likely to retreat from her approaches than during a matched control period conducted after the subject had been threatened by a different dominant female. In contrast, we predicted that subjects would be no less likely to approach and to tolerate the approach of the dominant signaller after they had recently groomed with that female than they were during a matched control period conducted after the subject had groomed with another dominant female. In other words, we expected that baboons would interpret the threat-grunts differently: directed at themselves after aggression, and directed at someone else after grooming. In contrast, if baboons' responses to threat-grunts were simply the result of priming through recent interactions, we expected that responses would be similar under both playback conditions.

METHODS

Study Area and Subjects

The study was conducted in the Moremi Game Reserve, situated in the Okavango Delta of Botswana. The habitat consists of a seasonal floodplain interspersed with slightly elevated wooded 'islands' (Bulger & Hamilton 1987; Cheney et al. 2004). At the time of these experiments (June 2003–July 2004), the study group contained approximately 70 individuals, including an average of nine adult males and 22 adult females. The group has been observed since

1978, and all animals are fully habituated to human observers on foot. Maternal relatedness for all natal animals is known.

Like many other species of Old World monkeys, female baboons in this population form linear dominance hierarchies that remain stable over long periods (Silk et al. 1999; Bergman et al. 2003; Cheney et al. 2004). Daughters acquire ranks similar to those of their mothers, and members of the same matriline are typically adjacently ranked. Females remain in their natal groups throughout their lives; males usually emigrate to neighbouring groups at sexual maturity. Dominance ranks were determined by the outcome of approach–retreat interactions (supplants). Only six of 665 female supplants during this study (0.9%) were counter to the established hierarchy.

Experimental Protocol

To determine whether prior interactions affect females' responses to threat-grunts, we played a tape recording of a dominant female's threat-grunts to an unrelated subordinate subject under one of two conditions. In one condition, the subject heard the dominant female's threat-grunts within 5 min after the female had threatened (chased, bit, or lunged at) her. In the other condition, the subject was played the dominant female's threat-grunts within 5 min after the two females had terminated a grooming interaction. After each playback, the subject was observed for 15 min to determine whether she subsequently approached or interacted with the dominant female.

All threat-grunts used as stimuli had been recorded within the previous year using Sennheiser ME88 microphones and Sony Walkman Pro cassette recorders. Calls were digitized and analysed using Cool Edit (Syntrillium, Phoenix, Arizona, U.S.A.) software to ensure that all were of similar duration ($\overline{X} \pm \mathrm{SE} = 2.4 \pm 0.1$ s) and had similar call bout characteristics, including call rate and intercall intervals. Playback sequences were similar in amplitude and matched the amplitude of naturally occurring calls. To avoid the possibility that some threat-grunts might be more salient or of greater intensity than others, the same threat-grunt sequence was played to a given subject in each of the two conditions, creating a matched-pair experimental design. If the same dominant female appeared in another trial involving a different subordinate female, we used a different threat-grunt whenever possible. No threat-grunt sequence was played to more than four subjects. Playbacks were conducted within 5 min of the termination of fighting or grooming, after the participants had separated and moved out of sight and earshot of each other ($\overline{X} \pm \mathrm{SE}$ latency to playback: postaggression $= 4.0 \pm 0.9$ min; postgroom $= 3.9 \pm 1.2$ min). To the best of our knowledge, subjects were at least 30 m from the signaller at the time of playback.

Threat-grunts were played from a Bose Roommate II speaker concealed in vegetation approximately 5 m from the subject. Trials were initiated as soon as the subject became stationary and either sat or fed with her face oriented at a 90–135° angle from the speaker. We used a Sony DCR-TRV25 digital video camera to record subjects' orientation responses relative to the speaker immediately before and after the playback. Video films were analysed using Ulead 5.0 (Ulead Systems, Torrance, California, U.S.A.) software. Videotapes were analysed by A. L. Engh; a subset was also analysed by D. L. Cheney to confirm scoring consistency.

Playbacks were conducted opportunistically, after we observed fights or grooming sessions between particular females. No individual, however, was the subject in more than one experiment in a single day, and trials involving different subjects were always separated by at least 2 h. Females produce threat-grunts at a mean rate of 1 per hour, so our schedule ensured that trials occurred at a far lower rate than did naturally occurring calls.

Two dependent variables were scored in the video analysis: look towards the speaker and move more than 2 m away from the speaker. Latency to look towards the speaker or move more than 2 m away from their location at the time of the playback was scored from call onset time. We considered subjects to be looking towards the speaker as soon as they moved their heads in the direction of the speaker (±30°). In the analysis of subjects' behaviour in the 15 min following playbacks, we noted whether the subordinate subject subsequently came within 2 m of the dominant signaller and interacted with her, and, if so, what the nature of their first interaction was. By focusing only on the initial contact between the two females, the effects of the threat-grunt on the subject's behaviour could be examined in the absence of confounding effects of subsequent interactions.

We compared each subject's behaviour in the 15 min following each playback with a matched control period chosen at random from another postplayback sample when the same subject had been either threatened or groomed by a different dominant female. Thus, for example, a trial in which subject D heard female A's threat-grunt after being threatened by A was matched with another trial in which D heard female B's threat-grunt after being threatened by B. Each postaggression playback was matched with another postaggression playback, and each postgroom playback was matched with another postgroom playback. Control samples for any given subject were chosen at random and used only once. There was no significant difference in rank disparity between the caller and the subject in experimental and control trials for either postaggression (paired t test: $t_{85} = 1.104$, $P = 0.276$) or postgroom playbacks ($t_{85} = 0.169$, $P = 0.867$).

Our matched control samples served two functions. First, they allowed us to examine whether a subject who heard a dominant female's threat-grunt after being threatened (or groomed) by that female was less likely to approach or tolerate that female's approach than she was during a control period when she had recently been threatened (or groomed) by a different dominant female. Second, they permitted us to determine whether simply hearing any dominant female's threat-grunt influenced subjects' interactions with all dominant females generally. Thus, for example, if female D avoided female A only after being threatened specifically by A, D should not also avoid A in the sample conducted after she had been threatened by female B.

Earlier experiments examining reconciliatory grunts (Cheney & Seyfarth 1997) found that subjects responded specifically to the grunt of their former opponent; playbacks of a different female's grunt did not affect subjects' subsequent interactions. In the current experiments, therefore, we predicted that playback of a given dominant female's threat-grunts after prior aggression would influence subjects' subsequent interactions with that female only, and not with all dominant females generally.

All subjects and signallers were adult females (>6 years of age) who were unrelated to each other (i.e. from different matrilines). Subject sample size was constrained by several factors. First, although the group included an average of 22 adult females, we were unable to use the five highest-ranking females as subjects because they were members of the same matriline and therefore related to any female who could have threatened them. Second, seven females died of predation during the study. Third, some dyads were never observed to engage in aggressive or grooming interactions.

We were able to complete matched-pair trials for 21 dyads, involving 12 different dominant female signallers and 10 different subordinate subjects ($\overline{X} \pm \mathrm{SE} = 2.0 \pm 0.4$ trials per subject). One of these dyads could not be matched to a postgroom control. There were also 23 other dyads involving 17 dominant signallers and 12 different subjects for which we were able to complete only one postgroom or postaggression trial ($\overline{X} \pm \mathrm{SE} = 1.8 \pm 0.2$ trials per subject postaggression; 1.9 ± 0.6 trials per subject postgroom). These dyads were included in the pooled analyses ($\overline{X} \pm \mathrm{SE} = 3.6 \pm 0.4$ trials per subject postaggression; 3.6 ± 0.9 trials per subject postgroom), but are listed separately in Table 1. Because we anticipated that females' responses might vary depending upon signaller identity, we also conducted another set of statistical analyses using mean values for each subject.

Wilcoxon signed-ranks tests were calculated using SYSTAT 8.0 (SPSS, Chicago, Illinois, U.S.A.) software; sign tests were calculated using the formula in Siegel & Castellan (1988). Our hypotheses generated clear, directional predictions, so we used one-tailed statistical tests when comparing groups ($\alpha = 0.05$). When multiple tests of the same hypothesis were undertaken, we conducted a sequential Bonferroni adjustment. P values that remained significant after this adjustment are marked with asterisks.

RESULTS

Responses to Playbacks

Subjects responded more strongly to the playback of a dominant female's threat-grunt when that female had recently threatened them than when the same female had recently groomed them. Subjects' latency to look towards the speaker in the 10 s following playback was significantly shorter in postaggression trials than in postgroom trials (one-tailed Wilcoxon signed-ranks test, corrected for ties: $T = 2.12$, $N = 21$, 5 ties, $P = 0.017$*; Fig. 1). Similarly, subjects showed a shorter latency to move away from the areas after aggression than after grooming ($T = 2.373$, $N = 21$, 3 ties, $P = 0.009$*; Fig. 2). In the more conservative analysis comparing each subject's mean response latencies, we still found females to have shorter latencies to look towards the speaker ($T = 1.84$, $N = 10$, $P = 0.033$) and to move away ($T = 1.78$, $N = 10$, $P = 0.037$) in postaggression trials than in postgroom trials.

Table 1. A summary of the first interaction between subordinate subjects and dominant signallers in each condition

			% Responding			
			Postaggression		Postgroom	
	Number of conditions*	N†	Playback	Control	Playback	Control
Subordinate approaches dominant	4	20	5	20	20	25
	2	23	13	30	17	17
	Total	43	9	26	19	21
Subordinate tolerates dominant's approach	4	20	15	35	35	25
	2	23	9	13	17	39
	Total	43	12	23	26	33
Subordinate is supplanted	4	20	20	0	0	0
	2	23	17	0	0	0
	Total	43	19	0	0	0

*Condition 4 = dyads that appeared in all four conditions (postaggression playback matched with postaggression control, and postgroom playback matched with postgroom control); condition 2 = dyads that appeared in two of the four conditions (either postaggression condition matched with postaggression control or postgroom condition matched with postgroom control); Total = total number of dyads. See text for details.
†*N* indicates the number of dyads in each condition.

First Interaction

In the postplayback samples we noted whether the dominant signaller and the subordinate subject subsequently came to within 2 m of each other and, if they did, which female was responsible for initiating contact and what form this contact took. Matched-pair comparisons

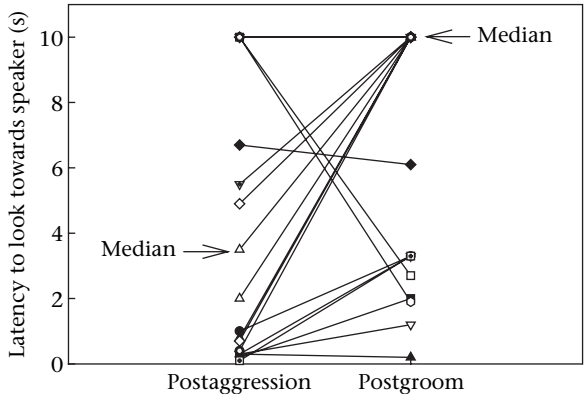

Figure 1. Subjects' latency to look towards the speaker in the 10 s after hearing the threat-grunt of a dominant female who had recently threatened or groomed them. $N = 21$ dyads in each paired trial. Each subject has a unique symbol.

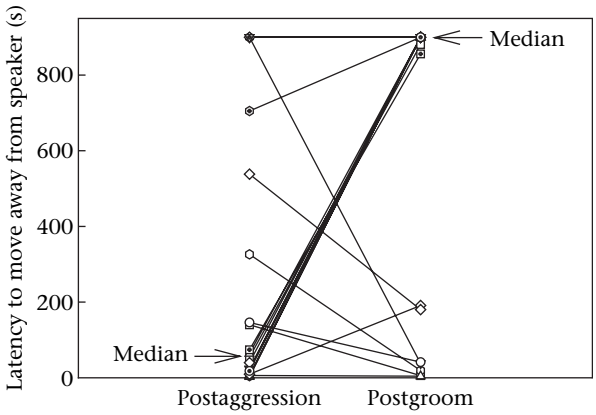

Figure 2. Subjects' latency to move more than 2 m away from the speaker after hearing the threat-grunt of a dominant female who had recently threatened or groomed them. $N = 21$ dyads in each paired trial. Each subject has a unique symbol.

were possible only for the 20 dyads from which we obtained postconflict samples in all four conditions. To increase the sample size, we pooled data from these dyads with data obtained from dyads observed in one playback condition (23 postaggression, 23 postgroom) and the respective matched control. Below and in Table 1, we present results from the pooled data. Table 1 also shows results from the 20 dyads that appeared in all four conditions. Dyads that appeared in all four conditions did not differ significantly in approach rates from dyads that appeared in only two conditions (subordinate approaches dominant: postaggression versus control: two-tailed Mann–Whitney U test: $U = 0.104$, $N_1 = 20$, $N_2 = 23$, $P = 0.999$; postgroom versus control: $U = 0.124$, $N_1 = 20$, $N_2 = 23$, $P = 0.993$; dominant approaches subordinate: postaggression versus control: $U = 0.113$, $N_1 = 20$, $N_2 = 23$, $P = 0.998$; postgroom versus control: $U = 0.207$, $N_1 = 20$, $N_2 = 23$, $P = 0.715$).

Because these experiments were conducted on free-ranging animals who had already separated before the playback trial began, there were many postplayback periods when the dominant signaller and the subordinate subject never came near each other again. In those cases when the females did approach each other, however, subjects' behaviour was consistent with the hypothesis that they interpreted threat-grunts after a fight as renewed aggression directed at themselves and threat-grunts after grooming as directed at someone else.

Hearing the threat-grunts of a recent opponent affected subjects' interactions only with that opponent, and not all dominant females generally. Subjects tended to be less likely to approach the dominant signaller after postaggression playbacks than during matched control periods (one-tailed sign test corrected for ties: $X = 4$, $N = 43$, 28 ties, $P = 0.059$; correcting for subjects: $X = 3$, $N = 12$, 1 tie, $P = 0.113$; Fig. 3, Table 1). In contrast, subjects were no less likely to approach the dominant signaller after postgroom trials than they were during matched control periods (one-tailed sign test: $X = 5$, $N = 43$, 32 ties, $P = 0.500$; correcting for subjects: $X = 2$, $N = 9$, 5 ties, $P = 0.500$; Fig. 3, Table 1). Not surprisingly, playbacks did not affect the propensity of dominant signallers to approach subordinate subjects. They were as likely to approach these subjects following postaggression trials (two-tailed sign test: $X = 6$, $N = 43$, 28 ties, $P = 0.607$; correcting for subjects: $X = 5$, $N = 12$, 4 ties, $P = 0.727$) and postgroom trials (two-tailed sign test: $X = 6$, $N = 43$, 28 ties, $P = 0.607$; correcting for subjects: $X = 2$, $N = 9$, 4 ties, $P = 1.000$) as during the respective matched control periods.

When a dominant signaller approached a subject, the subject could either tolerate the approach and remain within 2 m of the signaller, or be supplanted and move more than 2 m away. Subordinate subjects were supplanted on 62% of the 13 occasions when they were approached by the dominant signaller following postaggression trials. In contrast, they were never supplanted when approached ($N = 9$) by the same female during matched control periods (one-tailed chi-square test: $\chi^2_1 = 8.8$, $P < 0.005$; correcting for subjects: $\chi^2_1 = 6.64$,

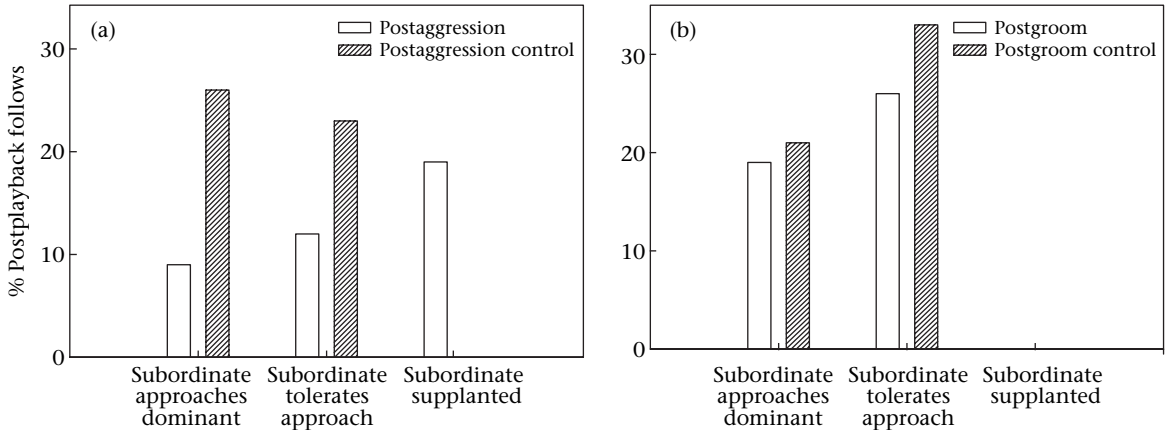

Figure 3. The proportion of postplayback follows in which subordinate subjects approached to within 2 m of the dominant signaller, tolerated the signaller's approach, or were supplanted by the signaller in the 15 min following threat-grunt playbacks. (a) Playbacks conducted after the subject received aggression from the signaller compared to control samples. (b) Playbacks conducted after the subject groomed with the signaller compared to control samples. See text for details about control samples. $N = 43$ dyads.

$P < 0.010$). Similarly, subjects were never supplanted when approached by the signaller following postgroom trials (one-tailed chi-square test: $\chi^2_1 = 10.11$, $P < 0.005$; correcting for subjects: $\chi^2_1 = 6.52$, $P < 0.010$).

DISCUSSION

When played the threat-grunts of a more dominant female, subordinate subjects responded more strongly if they had recently been threatened by that female than if they had recently groomed with her. In the former condition, they showed a shorter latency both to look towards the speaker and to move away from the area. In the 15 min following playbacks, subjects who had recently been threatened tended to be less likely to approach their former opponent and less likely to tolerate her approaches than during matched control periods conducted after they had been threatened by a different dominant female. In contrast, subordinates were no less likely to tolerate approaches by the dominant signaller after postgroom trials than in matched control periods. Finally, compared with postaggression trials, approaches by the dominant signaller after postgroom trials were significantly more likely to be tolerated, and significantly less likely to result in a supplant.

As in previous experiments on reconciliatory grunts (Cheney & Seyfarth 1997), subjects' responses were specific to their former opponent. Hearing an opponent's threat-grunt did not affect the likelihood that subordinate subjects would approach another, uninvolved dominant female or the likelihood that they would be supplanted when approached. Taken together, the results of these experiments suggest that female baboons are able to make inferences about the directedness of vocalizations even in the absence of visual cues, and that the nature of prior interactions affects their subsequent behaviour.

The ability to distinguish signals that are directed at oneself from those that are directed at others appears to be widespread among animals. For example, studies of 'eavesdropping' in birds indicate that listeners readily distinguish between vocal signals that are directed at a third party as opposed to signals that are directed at themselves (Naguib et al. 1999; Peake et al. 2001, 2002). To date, however, most of the evidence for this ability has come from studies in which individuals are interacting with only one or a few other conspecifics, and when factors such as the location of the signaller and the nature and pattern of his song provide information about the intended recipient. The challenge of inferring both the intended target of a signal and the signaller's probable behaviour may be considerably more difficult in large social groups.

It is unlikely that baboons use simple distance or sight-based rules-of-thumb to determine the intended target of a call. Females often sit in close proximity to others, so a female cannot simply assume that all calls given by nearby signallers are directed at her, and that those given by more distant signallers are not. Indeed, baboons often respond vocally to signallers who are out of sight and widely separated from them (Rendall et al. 1999). Moreover, baboons can approach other individuals from a variety of directions and angles, and it is not at all unusual for signallers to utter grunts or threat-grunts as they approach a target from behind.

When making predictions about the behavioural consequences of a vocalization, baboons must take into account the identity of the signaller, call type (is it associated with aggression?), the nature of their prior interactions with the signaller (were they aggressive, friendly or neutral?), and the correlation between past interactions and future ones (does a recent grooming interaction lower or increase the likelihood of aggression?). It seems probable that learned contingencies guide baboons in these assessments. Because listeners' responses depend on simultaneous consideration of all of these factors, however, this learning is likely to be both complex and subtle.

Moreover, explanations based solely on behavioural contingencies seem unable to explain some aspects of listeners' behaviour, in particular their ability to infer the intended target of a vocalization. For example, in the earlier reconciliation experiments (Cheney & Seyfarth 1997), subjects who heard their opponent's reconciliatory grunt following a fight were even more likely to approach their opponent than they were under baseline conditions. If listeners' responses were guided only by learned contingencies, they should have associated the call only with a low probability of aggression. Hearing the call should have returned their behaviour to baseline tolerance levels, but it should not have induced them to increase their interactions with the signaller. Instead, females acted as if they interpreted the grunt as targeted specifically at themselves, as a directed signal of benign intent.

When attending to vocal signals, female baboons appear to take into account not only the signaller's identity and her probable subsequent behaviour, but also the target of her attention. The ability to integrate these social cues simultaneously may represent a first critical step towards the recognition of other individuals' intentions and motives. In children, inferences about other individuals' attention constitute an early precursor to language learning and full mental state attribution (e.g. references in Malle et al. 2001; Tomasello 2003). We may speculate that monkeys have a rudimentary understanding about other individuals' intentions towards themselves. If true, this would represent a crucial first step towards a communication system like language, in which speakers and listeners routinely assess each other's motives, beliefs and knowledge.

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