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Language Evolution: The Origin of Meaning in Primates

Research on alarm calls has yielded rare glimpses into the minds of our closest relatives. A new study suggests that primates monitor the effect alarm calls have on others.

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Most primates vocalise when threatened by a predator. These alarm signals, after the Old Italian all' arme ('to arms'), have proved particularly valuable tools for examining cognitive processes in non-human animals. While call comprehension is relatively well researched in primates, very little is known about the social factors that influence call production [1]. A new study [2] by Dutch researchers has provided unexpected findings of almost Orwellian dimensions: When threatened by a predator, male Thomas langurs (*Presbytis thomasi*) do not stop producing alarm calls until every single other group member has responded with at least one alarm call. Males thus seem to monitor the calling behaviour of each group member and keep track of who has and who has not responded with alarm calls.

Alarm calls have attracted the attention of comparative psychologists, particularly those interested in the origins of language and semantic signalling [3]. The classic example is the vervet monkey alarm call system, in which individuals produce acoustically distinct vocalisations to several predators such as eagles, leopards or pythons. When monkeys hear another's alarm calls to a python, for instance, they respond by scanning the surrounding area for the snake they assume is present [4]. Another example is the West African Diana monkey, which produces one type of alarm call when encountering a leopard, and another one when faced with an eagle [5]. Most importantly, these calls indicate the biological class of the predator and are not simple responses to situational circumstances or perceived threat [6].

In primates, the ontogenetic process leading to the production of acoustically different call types is probably under strong genetic control. Infant vervet monkeys give eagle-like alarm calls to numerous flying objects, including storks and falling leaves. Only with experience do they learn to restrict call use to genuinely dangerous raptors [7]. It appears that primates innately conceptualise the world along particular criteria, and respond with species-specific vocal signals to them. Some researchers have thus questioned the relevance of primate alarm calls for understanding language evolution and human cognition [8]. How could genetically determined vocal behaviour be relevant for understanding the origins of language, a system based on arbitrary and socially learned vocal utterances?

The meaning of a term, it has been argued, is nothing more than its use [9]. In rainforests, the primary habitat of many primate species, primate biomass can reach several hundred individuals per square kilometre and, with visual contact strictly limited, vocalisations are the main mode of communication. As a result, primates mature in a rich world of sound with countless contingencies between vocalisations and events. But to what degree are primates capable of taking advantage of the surrounding semantic landscape? There is good evidence that primates not only behave adaptively to other individuals' alarm calls, but that they understand something about the causal structure of the events responsible for the various vocal signals produced by conspecifics and other animals [10–14].

The most striking difference between humans and other primates lies in the production abilities. Although non-human primates can engage in vocal tract filtering and produce acoustically complex structures, not unlike human vowels, they do not normally proceed to assemble them into larger, more complex strings [15]. Like other primates, humans produce a finite number of innately determined sound units, or 'phones', but they can

freely assemble them into rapid and complex sequences to form syllables, words, and sentences. This concatenation ability is at the core of all languages, raw material for vocal imitation and responsible for the generation of an infinite number of novel sequences.

Some interesting exceptions need to be mentioned nonetheless. Like other primates, free-ranging male Campbell's monkeys (*C. campbelli*) produce acoustically distinct alarm calls to leopards and eagles. However, if males encounter unspecific or less threatening events, such as sounds of a falling tree or fleeing antelope, they produce a pair of low sounding 'booms' before a series of alarm calls. Nearby recipients hardly respond to these boom-introduced alarm calls, as if the booms have altered the semantic meaning of the subsequent alarm calls from a predator-specific label to more general sign of disturbance [16]. Work on free-ranging putty-nosed monkeys (*C. nictitans*) in Nigeria has revealed related results. Here, the males produce two basic alarm call types, 'hacks' and 'pyows'. Surprisingly, however, these calls are not predator-specific because males produce them to both eagles and leopards. Instead males concatenate the two calls into longer sequences, and some of them are highly predator-specific. In this species, it is the call sequence, and not the individual call, that carries meaning [17].

A largely neglected area of research concerns the question of whether primates take the composition of their audience into account and, related to that, whether callers intentionally inform each other about events they have just witnessed (rather than responding to the events directly). Although primates are clearly sensitive to the composition of their audience [18], they do not seem to take into account each other's mental states. For example, mothers do not adjust their alarm call production depending on whether their offspring is aware or still ignorant of impending danger [19]. There is a distinct possibility that non-human primates referential signalling thus takes place in a remarkable state of mind-blindness.

With their recent study, Wich and de Vries [2] have opened a new and unexpected way of investigating audience effects. In their field experiment, alarm calls were elicited from free-ranging Sumatran Thomas langurs with a model tiger. The vocal responses of twelve different groups were analysed, all consisting of one adult male and one to several females with their offspring. The authors noted that the males differed in the number of calls they produced to the predator model. Males only stopped alarm calling after each independent individual in the group had given at least one alarm call. The authors also reported that, after having heard the last individual's calls, the male sometimes oriented towards that particular group member in order to produce a few more alarm calls, as if he wished to acknowledge to that animal that he had heard the calls.

These findings were interpreted as evidence of the males' ability to keep track and remember which group members had and had not given alarm calls. These sorts of data have not been reported from the wild before, and the implications concerning the mental representations potentially involved are simply spectacular. Exceptional claims require exceptional evidence, and Wich and de Vries [2] were careful in addressing a number of alternative explanations. First, readers were assured that it was possible to determine, with confidence, which group members had already produced alarm calls at any given time. Second, the authors ruled out the most obvious alternative explanation: that the data were a mere artefact of males simply responding to other group members' alarm calls. If all individuals eventually gave alarm calls, the outcome would have been the same. This was not the case, the authors argued, because males sometimes stopped calling before other group members produced their last call.

Although the new paper [2] is convincing as it stands, experimental evidence will eventually be required to further establish the idea that males actively monitor and manoeuvre the calling behaviour of others. The most straightforward way of testing this would be to assess the effects of experimentally introduced alarm calls on the males' own calling behaviour. If they authors are right, then experimental calls of previously silent individuals should have the power to terminate the male's calling behaviour within a few minutes, while calls of individuals that had already called before should have no effect, regardless of numbers and quality. The patterns of alarm calling behaviour in all-male groups are of some interest, as is the calling behaviour of the group's male in cases when an individual is temporarily removed from the group. Will males simply call on forever?

Wich and de Vries [2] offer some explanations for the function of this extraordinary behaviour. Males play a crucial role as sentinels, immediately producing alarm calls to any disturbance, to which other group members respond with climbing into the trees. The best response to tigers is to remain off the ground because they are unable to pursue monkeys through the canopy. Hence, the males' primary objective may be to keep others from descending to the ground. Producing alarm calls until every other group member has done the same ensures the male that everyone is aware of the danger. Whether or not this is based on an abstract understanding of other's knowledge cannot be answered with the data, but the system certainly has the potential to address this crucial question.

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