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Odor signals in wild western lowland gorillas: an involuntary and extra-group communication hypothesis



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ABSTRACT

Odors constitute one of the most ancient ways of communication among animals. Whereas the key role of olfactory communication is well established in insects or rodents, its contribution to primate behavior remains very speculative. In a recent report, Klailova and Lee [1] studied the variations of intensity of the typical steroid musk odor produced by wild adult male gorilla silverbacks during encounters with opponents from other social units (lone males or other groups). The odor intensity increased in situations of potential conflicts, when the silverback encountered another male gorilla, which constitutes a potential threat for his infants and mate competitor for his females. Importantly, the odor intensity was greater when the silverback reacted with a demonstrative threat display, and milder when he decided to react quietly and avoid the conflict by sneaking away. According to the authors, this indicates that silverback gorillas can flexibly adjust the odor signal to the social context, and the mild signal associated with the quiet response is used within the silverback's group to promote cohesion. Rather, based on both physiological and behavioral data, we propose that (1) the odor intensity varies monotonically with arousal, across all situations, and (2) that the function of the odor signal is most relevant for the interactions between males of different groups. In such framework, the odor stimulus might also constitute a non-visual signal indicator of the emitter's identity, and therefore play a role in the regulation of the interactions with other gorillas. Establishing the balance among those potential functions is critical to understand the role of odors in the regulation of social and ecological interactions in primates.

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1. Commentary

Olfactory communication is widespread in the animal kingdom [2]. Olfaction is one of the oldest senses and in most mammals, it is critical for fundamental biological functions such as social interactions and reproduction (e.g. marking territories in carnivores, urine dropping, etc.). This is also true in primates, even if they are sometimes defined as microsmatic, with poor olfaction and a large predominance of vision [2–4]. However, we can all remember a set of vivid memories based on olfactory experience, with these memories often related to a key biological function, such as feeding in the classical example of Proust's madeleine. Thus, even in primates, odors have a strong impact on behavior.

A recent interesting report published in *Plos One* [1] pointed out an innovative hypothesis on the potential function of the typical strong musk-steroid odor emitted by silverback males in gorillas. Traditionally

such pungent male scent has been identified as emitted in a "stressful" or "fearful" situation [5]. Klailova and Lee [1] claimed that the "silverbacks appear to use odor as a modifiable form of communication, where odor acts as a context dependent signaling mechanism to group members and extra group units". Using detailed observations, Klailova and Lee [1] scored the odor intensity of the silverback of one habituated group of western gorillas in the Dzanga-Ndoki National Park, Central African Republic, showing that the intensity of the male scent varied in relation to the intensity of the interactions with adult males from other social units (either solitary or other group holders). The strongest intensity of male odor was detected during heavy interunit encounters when, the group silverback displayed or vocalized loudly towards the intruder male of the other social unit but also when his within-group cohesion was low, particularly when the females with dependent infant, were far from him [1].

The authors speculated that the silverbacks "use odor as a modifiable form of communication", a "context dependent signaling mechanism" to alert the other group members through the emission of higher intensity of his scent [1]. Harem-holder silverbacks are usually very protective by actively defending the group, particularly females with

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dependent infants, who are the target of potential infanticide by outside males trying to acquire females from other groups [6,7, Bai Hokou long term data]. In that framework, a silverback can probably be considered as an "aggressive machine": he promptly demonstrates his strength and power with spectacular displays to discourage any potential matecompetitor to approach their harem [5]. Thus, during intergroup encounters, one of the typical reactions of a harem-holder silverback is to perform impressive threat displays. However, the silverback could also show an alternative much quieter reaction. Typically, this quiet reaction consists in fleeing silently from the area with the whole group, trying to leave the intruder male behind (Masi, personal observation) or to hide with his group [1]. This quiet behavioral reaction was associated with a milder odor signal, compared to the strong odor associated with the intense interaction [1]. The authors proposed that this mild odor signal enabled "the protector silverback to communicate with and re-assure group members, and may make it difficult for extra-unit silverback to eavesdrop", and thereby promote within-group cohesion. Thus, based on the difference in odor intensity between these two extreme types of behavioral situations (aggressive display vs. quiet escape), the authors concluded "our results suggest (a) that silverback odor strength can be 'turned up' or 'turned down' as well as 'turned on' or 'turned off' as a function of the context and relationship between the emitter and perceiver(s), and (b) that varying odor intensities may communicate different context specific types of information". We could say then that Klailova and Lee [1] favor a within-group voluntary communication hypothesis for the function of the pungent smell in male gorillas. We believe though that results a) and b) coincide: the odor intensity varies with the social context, but because of a very simple underlying physiological mechanism, not under voluntary control. In this commentary we would like to provide other possible functions of smell emission in gorillas in relation to extra-group social context, formulating a potential second hypothesis, the involuntary and extra-group communication hypothesis and discussing the potential physiological basis of the odor signaling in gorillas.

Before discussing the possible role of these changes in odor concentration with social context, we would like to address the possible mechanisms underlying these odor responses in silverbacks. One of the key issues is that according to the authors [1], the change in odor concentration across social situations (conflict vs. quiet avoidance) could not be accounted for difference in arousal. They implied that the quiet response involved a high level of arousal but a quiet behavior (voluntarily, if the silverback wants to remain undetected). In other words, the animal would be just as excited (both subjectively and physiologically), but would not express it behaviorally. In addition, this active control of behavior would be associated with an active suppression of the odor concentration, to remain undetected. A more parsimonious hypothesis would be that the conflicting situation is simply more arousing than the quiet avoidance, and the odor concentration simply follows the level of arousal. In addition to being more parsimonious, this second hypothesis is supported by physiological data: in primates, socially relevant body odors are produced by the apocrine glands [4,8,9]. The activity of these glands is controlled by the autonomic nervous system, and the excretion of odors is under direct adrenergic control [10]. Thus, given the physiological properties of the system controlling the production of 'social odors', the activation of the sympathetic system enhances noradrenaline levels and stimulates odor production in a very automatic fashion. In other words, there is an inherent positive influence of autonomic arousal on the production of body odors, at least in humans [4]. In that framework, a simple account of the difference in odor intensity between the direct conflict and the quiet avoidance is that the former is associated with a higher level of arousal, a greater activation of the sympathetic system, a greater release of adrenaline and noradrenaline, a greater stimulation of the aprocrine glands and therefore, a higher production of body odors. To demonstrate the less parsimonious hypothesis proposed by the authors, which implies dissociation between arousal and odor production, they would have to show that the two behavioral situations evoke a similar level of arousal and/or that the silverback can specifically and voluntarily control its autonomic system (or its aprocrine glands).

After examining the physiological mechanisms underlying odor production, we can try to assess its function by considering its behavioral and ecological context. First, there are several reasons to think that silverbacks get more physiologically aroused during direct conflicts than during the quiet escape strategy. Even if such aggressive reactions seldom end up in a real physical contact contest between the two silverbacks (too costly and risky; [5,11,12], Bai Hokou, long term data), threat displays can be very powerful and long lasting. Thus these behaviors (charges, slaps on ground or trees, destruction of vegetation, cracking trunks or crashing vegetation, chest beating, loud vocalizations, etc.) are likely to induce substantial costs demanding great physical investment from the silverbacks who often are exhausted at the end of the contest (Masi, personal observation; Fig. 1). Furthermore, it is potentially stressful for the participants [13]. Given the mechanical relationship between the production of 'social odors' and arousal, it is not surprising that Klailova and Lee [1] found higher intensity of the odor during such interactions.

Beyond the direct conflict, other types of social context can also be interpreted in terms of arousal/stress. For instance, the silverback odor is more intense when the other group members and adult females with dependent infants were far away from him [1]. Due to the risk of infanticide and the potential of a female transfer, the cohesiveness of gorilla sociality, the level of stress of silverback harem-holders is likely to be higher when the group members are absent or are not in close proximity to (in sight) his protective supervision. Furthermore, during such inter-unit encounters, the opposing male can be a solitary male, thus a male who has not (yet) acquired females, and sometimes the scent of such lone male can be detected by the research team before, or even in the absence of, the direct contest with the protector silverback (Masi, personal observation). If such intruder male ranges solitarily, if the smell is modulated voluntarily and if it has an intra-group signaling function, what would be the reason for the lone silverback to emit his own scent? To whom is he communicating the cohesion or alert signal if he is solitary? In the hypothesis of a voluntary control, the emission of "zero olfactory response" would be certainly the most profitable strategy for him to remain undetected while closely approaching the females of the group. Note that the strong odor also emitted by silverbacks from different groups interacting in open clearings, questions again the need of a within-group olfactory communication, since in such a habitat the silverback has clear and wide visibility of all group members (Breuer, personal communication). In addition, this strong odor is also emitted by the silverback during aggressive displays/charges directed to human observers (Masi, personal



Fig. 1. Makumba, the silverback of Klailova and Lee's study, after a fight during an interaction with another silverback. The small wounds on his nose and the evident venas on his chest show the demanding great physical investment, the tiredness and the stress associated with such interactions.

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