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Why is mutual grooming rare despite its function?: A hypothesis for cognitive constraints

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Abstract

Mutual grooming, where both participants groom each other simultaneously, is a type of allogrooming and probably also plays an important role as a social and hygienic function; however, it has attracted little attention, probably due to its rarity compared to prevailing unidirectional grooming in many social animals, such as primate species. While previous studies have shown that mutual grooming has functional significance, such as promoting social bonds and maximising short-term benefits, we do not know why mutual grooming is much rarer than unidirectional grooming, and its restrictive factors have been mostly uninvestigated. In this paper, we propose a hypothesis of cognitive constraints in which cognitive complexity is assumed as an underpinning mechanism for mutual grooming, thereby restricting its prevalence across animal species. To achieve joint action and its symmetric nature, mutual grooming is considered to require behavioural coordination between participants, which could be facilitated by active communication and further by joint commitment based on a mutual understanding of intention between the two. The fact that joint commitment has been proved only in a limited number of animals may support this cognitive demand hypothesis, although it definitely calls for further in-depth investigation and comparative studies across primate and non-primate species.

Keywords: mutual grooming, bidirectional allogrooming, joint action, behavioural coordination, joint commitment, cognitive demand hypothesis

Introduction

Allogrooming is one of the joint actions observed in many mammals, serving hygienic and social functions, such as establishing and maintaining affiliative relationships and facilitating reciprocal exchange. Allogrooming, particularly in non-human primates, is considered to function similarly to vocal conversation in humans. Although vocal conversation in humans is more efficient and less restricted temporally and spatially than allogrooming, which requires physical interaction, Nakamura [1] indicated that chimpanzees (*Pan troglodytes*) achieve a mostly equivalent amount of social interactions to human conversation, thanks to their wide variety of grooming styles, sometimes involving multiple individuals engaging in grooming simultaneously.

Allogrooming can be divided into two types: unidirectional grooming (A grooms B unilaterally) and mutual grooming (A and B groom each other simultaneously). These two have distinct cost and benefit structures. In unidirectional grooming, a groomee receives benefits, whereas a groomer incurs costs; a groomer may not receive immediate social benefits if the recipient does not reciprocate, although grooming may not be plainly costly as a groomer may also receive some benefits such as decreased stress levels [2]. Mutual grooming, on the other hand, involves partners engaging in grooming at the same time, enabling both partners to experience both costs and benefits simultaneously.

Among non-human primates, mutual grooming is much less popular than unidirectional grooming. While mutual grooming is common in chimpanzees and ring-tailed lemurs, it is rare or non-existent in other primates [3, 4, 5, 6, 7]. Even in chimpanzees, grooming sessions mostly consist of unidirectional grooming, and mutual grooming is just additional. No primate species perform mutual grooming exclusively. Until now, little research and discussion has focused on mutual grooming, and the evolution and mechanisms of this social interaction have not been well understood. This paper explores the functional significance of mutual grooming, examines why it is rare despite its functional advantages, and proposes a hypothesis of cognitive constraints based on the proximity mechanisms underlying mutual grooming.

Functional significance in mutual grooming

Three hypotheses have been proposed to explain the possible functional significance of mutual grooming: the immediate investment hypothesis, the social bonding hypothesis, and the switching hypothesis. The immediate investment hypothesis posits that mutual grooming

signals willingness to invest in grooming sessions and that longer and fairer grooming enables immediate payback and, therefore maximises short-term gains. Machanda *et al.* [5], using 16 years of data from wild chimpanzees, supported this hypothesis by finding that grooming sessions with mutual grooming 1) were longer and more equitable than those without and 2) had more unidirectional grooming switches than those without. Allanic *et al.* [6] also found similar supporting results with 6 bonobos and 7 chimpanzees in captivity. Schino and Alessandrini [7] examined this hypothesis in a zoo setting with ring-tailed lemurs. Their findings indicated that they were less likely to terminate grooming if it was mutual grooming than if it was not, and that the average duration of mutual grooming episodes was significantly longer than that of unidirectional grooming episodes.

The social bonding hypothesis assumes that mutual grooming promotes dyadic social bonds. This hypothesis is based on the idea that mutual grooming, in contrast to unidirectional grooming, requires active cooperation among participants. Therefore, mutual grooming is a suitable indicator of strong social bonds between partners. Boesch and Boesch-Achermann [8] observed regional differences in chimpanzee mutual grooming, proposing that frequent mutual grooming in areas with high intergroup conflicts helps maintain male group cohesion. Fedurek and Dunbar [3] studied a group of 32 zoo-housed chimpanzees and, found that dominant individuals demonstrated more tolerance toward individuals who engaged in mutual grooming than those who had engaged only in unidirectional grooming. They also showed less frequent rejection of grooming with mutual grooming partners than with unidirectional grooming partners. In addition, they frequently engaged in mutual grooming with kin and socially close individuals. These results support the social bonding function of mutual grooming. Furthermore, Yamanashi *et al.* [9] examined social interactions among 37 captive chimpanzees, and found a negative correlation between the proportion of aggressive interactions and the proportion of mutual grooming, which also suggests a positive link between mutual grooming and affiliative relationships. Therefore, it is plausible that mutual grooming has some advantages for social bonding, although this should be investigated further as some previous studies have raised questions about this hypothesis by reporting non-significant relationships between mutual grooming and measures of social bonding in both wild and captive chimpanzees [5, 6].

The switching hypothesis (or null hypothesis) states that mutual grooming has no specific function and, merely results from the coincidental overlap of unidirectional grooming [4]. If this hypothesis is correct, it is predicted that 1) grooming sessions would rarely initiate from mutual grooming, 2) the role of groomer and groomee would switch before and after mutual grooming ($A \rightarrow B$, $A \rightleftharpoons B$, $A \leftarrow B$, but not $A \rightarrow B$, $A \rightleftharpoons B$, $A \rightarrow B$), and 3) the duration of mutual grooming would be relatively short. However, Machanda *et al.* [5], Schino and

Alessandrini [7], and Allanic *et al* [6] did not support this hypothesis in chimpanzees and captive bonobos and lemurs, although in bonobos, which demonstrate much less mutual grooming than chimpanzees [10], their infrequent mutual grooming might align with this switching hypothesis at least under wild environment.

The rarity of mutual grooming and its possible constraints: The Cognitive Demand Hypothesis

Despite the functional significance and efficiency of mutual grooming, why is it less common compared to unidirectional grooming in non-human primates and why does its frequency vary greatly among species? One explanation is that the fission-fusion social dynamics may facilitate mutual grooming [11]. Species characterised by fission-fusion society, like chimpanzees, may experience unpredictable separations between interacting individuals, where the imbalance of benefit and cost inherent in unidirectional grooming might not be reciprocated, leading to the risk of one individual bearing only the cost. Therefore, mutual grooming, which secures immediate reciprocity, might be more frequent in these species. However, this explanation does not fully correspond to the fact that some non-fission-fusion species, like ring-tailed lemurs, show mutual grooming, whereas some fission-fusion species, such as Geoffroy's spider monkey, do not [12]. More importantly, this can explain why fission-fusion species develop mutual grooming but cannot explain why other species do not demonstrate mutual grooming despite its functional benefits. This also does not explain the difference in the rate of mutual grooming between chimpanzees and bonobos that both have fission-fusion societies [6].

Then, what factors limit mutual grooming? Nakamura [1] briefly mentioned the possibility that mutual grooming, where the participant is both an actor and a recipient simultaneously, may require certain cognitive abilities, which could explain its rarity in non-human primates. To date, however, no further in-depth discussions or investigations regarding the cognitive abilities required for mutual grooming have been conducted. In this study, we propose the hypothesis that mutual grooming as a cooperative joint action requires highly sophisticated cognitive abilities that restrict the prevalence of mutual grooming across animal species. In humans, in particular, many joint actions can be achieved by participants' sharing intentions, coordinating actions, and experiencing mutual obligations to perform joint actions [13]. This sense of mutual obligation in joint actions is referred to as joint commitment and is considered a crucial cognitive process underlying human cooperation [14]. This cognitive process may also be essential for mutual grooming among non-human animals. Mutual grooming, by definition, requires both parties to participate actively; thus, it is naturally assumed that it is not achieved or is easily collapsed if there is an imbalance in the

motivation to participate between the two. In other words, mutual grooming should not be based on a unilateral desire to groom but requires mutual agreement or coordination. In this sense, mutual grooming seems distinctive from some other joint activities, such as coalitional aggression and joint mobbing of predators that could be achieved to some extent even without mutual agreement or coordination between individuals. This situation, where cognitively demanding mutual agreement or coordination, is required for mutual grooming is considered to occur particularly in social animals, such as group-living primates, that have a clear hierarchical dominance structure in which commonly the lowest ranking individual of the dyads grooms the higher-ranking individual more than the reverse. Due to this imbalance between two individuals, regarding mutual grooming, they need to align their motivation regardless of the rank difference and social distance between partners. Therefore, it is possible that more active behavioural coordination and careful agreement may be required for successful mutual grooming in pairs with greater rank differences or greater social distance.

Mutual grooming also has some other distinctive characteristics, such as demanding close proximity and direct face-to-face contact between the two, which increases the cost of grooming compared to unidirectional grooming [3]. It has also been suggested that, in general, eye contact and face-to-face contact in close proximity could function as threats or act as signals of dominance in many non-human primates, and that direct physical aggression could easily occur [15]. This tendency is particularly pronounced in primate species with a clear dominance structure [15]. Due to this costly nature, participants must coordinate their willingness to participate with their partners, especially when their motivation or physical demands differ between them, although this issue could be solved to some extent without cognitively demanding coordination in socially tolerant or egalitarian species or animals that can avoid the face-to-face or eye-contact situation during mutual grooming.

Thus, in general, the cognitive requirement for joint commitment may restrict mutual grooming among non-human animals. It has previously been suggested that a sense of joint commitment is a human unique trait [16], and only a limited number of non-human species, if any, such as chimpanzees, may experience it or something similar [17, 18]. Heesen *et al* [17] examined the structure of social play and grooming in chimpanzees and bonobos, identifying "entry" and "ending" phases, marked by mutual gaze and signals before and after joint actions, similar to human interactions. They found that rank differences had no effect on these actions. However, a slight negative correlation was observed between social bond strength and interactions with signals in bonobos. In a related study [18], the authors explored joint commitment by analysing continuity in grooming or play after interruptions. Results indicated that grooming was often resumed from the same body part or activity, showing persistence in joint actions. Social bonds did not influence this resumption, suggesting that

relationship quality does not determine the likelihood of resuming joint actions but may influence communication during interruptions. The findings of these two studies indicate that the sense of joint commitment is not unique to humans and that this may serve as a basis for joint action like mutual grooming in these animals; however, we can still assume that this cognitive requirement cannot be achieved in many non-human animals, which may explain the rarity of mutual grooming.

We propose the cognitive demand hypothesis as one of plausible explanations for the rarity of mutual grooming but, not as either a necessary or sufficient condition. We must keep in mind that this hypothesis alone cannot explain all the factors that contribute to the rarity of mutual grooming. Among primates, mutual grooming is relatively common in bonobos, chimpanzees and ring-tailed lemurs. Many previous studies have shown that bonobos and chimpanzees are closely related to humans and have advanced cognitive abilities similar to humans, such as joint commitment. Therefore, the prevalence of mutual grooming in the two species could be explained by the cognitive demand hypothesis. On the other hand, ring-tailed lemurs are phylogenetically very distant from great apes, have a very small brain, and their cognitive abilities are unlikely to be comparable to those of apes. It is possible that ring-tailed lemurs engage in mutual grooming in a more automatic or obligatory way without social coordination, although we have not yet developed a way to distinguish between mutual grooming with and without advanced cognition. One of the differences in mutual grooming between apes (chimpanzees and bonobos) and ring-tailed lemurs is the physical form involved in it. While chimpanzees and bonobos predominantly use their hands with support of occasional use of mouth for grooming, ring-tailed lemurs frequently use their mouths in addition to their hands when grooming. The front teeth of the ring-tailed lemur are slightly skewed forward, which is suitable for grooming. Mouth-using grooming may have the potential to avoid the costly situation of face-to-face and direct eye contact in close distance, which might be key for lemurs to achieve mutual grooming even without highly sophisticated social cognition.

At this stage, it may be reasonable to consider that several factors, such as social system, along with the cognitive one, could interact and cause significant variation in the frequency of mutual grooming. As noted above, both chimpanzees and bonobos engage in mutual grooming, although chimpanzees engage in it more frequently [6]. This species difference shows a similar trend to the species difference in polyadic grooming, which requires participants to be both actor and receiver simultaneously as in mutual grooming. It has been suggested that differences in polyadic grooming frequency may result from differences in the need for cooperation between these species. Chimpanzees are more likely to engage in cooperative behaviours in groups, such as hunting and territorial defence, than

bonobos [19], and polyadic grooming may help strengthen existing social relationships for these cooperative behaviours to be successful [20]. This may also differentiate mutual grooming between these two species. Furthermore, even within a species, the frequency of mutual grooming may vary across environments. In bonobos, the frequency of mutual grooming is much higher in captive compared to wild [6]. Thus, the rarity of mutual grooming and interspecies differences in the frequency of mutual grooming are likely to be influenced by various factors, not just the need for cognitive skills,

Future directions

We propose the cognitive demand hypothesis for the evolution of mutual grooming across species. This hypothesis posits that the complexity of cognitive mechanisms involved in mutual grooming affects its overall rarity across animal species. To test this hypothesis, we need to resolve the following unsolved problems. First, we must develop research or reanalysis that especially focus on mutual grooming by distinguishing it from unidirectional grooming. These two concepts can be diverged in terms of their mechanisms and functions because mutual grooming may require joint commitment among participants, whereas unidirectional grooming may require cognition for reciprocity to secure benefits. However, most previous studies on grooming have not explicitly distinguished between the two types of grooming, with much less emphasis on mutual grooming, thus lacking important basic data on the existence or frequency of mutual grooming in many animals. This has hampered our specific discussion of how non-human animals achieve this potentially important joint action.

Second, we need to make further in-depth investigation on communication and interaction between participants before, during and after mutual grooming. If this hypothesis is correct, animals that engage in mutual grooming should have an ability to experience joint commitment similar to that seen in human joint action [16, 17]. Specifically, the following outcomes are expected: 1) Before, during, and after mutual grooming, communication signals are observed to facilitate the exchange of intentions and the behaviour coordination in species that demonstrate frequent mutual grooming, and the frequency and duration of these signals are contingent upon the social dimension of the pairs. 2) When joint action is interrupted for some reason, partners are expected to re-engage in this activity as a continuation of joint commitment; thus, this re-engagement should be more frequent in mutual grooming than in unidirectional grooming. Further empirical studies are expected.

Third, further comparative studies are required to understand the evolution of mutual grooming. As discussed above, comparisons among primate species with quantitative data on mutual grooming will surely enhance our understanding of factors soliciting or constraining mutual grooming. For example, understanding if some species are obligatory

mutual groomers may suggest an alternative and simple cognitive mechanism that being groomed requires grooming in return. We would also emphasise the importance of broader comparative viewpoints involving other non-primate species. To date, systematic interspecies comparisons have been lacking, with only sporadic studies on primates and almost none involving non-primate species. Here, we propose the possibility of interspecies comparisons with equines as an example. We think equines are one of the desirable targets for this investigation in that while their mutual grooming appears obligatory due to their grooming form and grooming frequency, they have highly sophisticated social cognitive abilities. Equines perform the majority of allogrooming through mutual grooming (e.g., horses (*Equus caballus*) [21]) (Figure1). Many equine species are highly social animals, with some species building complex social structures such as multiple societies [22, 23]. Additionally, highly sophisticated social cognitive abilities, which are sometimes comparable to those of apes, have been recognised in horses [24, 25], and even joint commitment may be present during behavioural coordination in plain zebras [26]. Consequently, it is possible that mutual grooming among equines is facilitated by their high social cognitive abilities, suggesting the establishment of advanced cooperative relationships through joint commitment. In addition, interspecies comparisons with horses may help identify factors that distinguish true cognitive mutual grooming from obligatory grooming. Comparative studies across mammals, either with or without mutual grooming, may provide insights into the evolutionary origins of mutual grooming and joint commitment, as well as the origins of co-operative societies, by linking differences in cognitive traits and social structure across species with differences in variation in mutual grooming.

< insert Figure 1 here >

In conclusion, mutual grooming is an interesting and important social behaviour with respect to its function and proximate mechanisms, yet it remains mostly underexplored. While there has been not so much quantitative data that specifically focus on mutual grooming, mutual grooming itself is relatively rare among primate species. We posit the cognitive demand hypothesis as potential explanation of this phenomenon, or more precisely, to explain how animals are able to achieve mutual grooming, a grooming style which is efficient but costly. This could be a good first step for cultivating this novel research area and attracting researchers' attention to this interesting but underexplored mutual grooming. Testing this hypothesis could not only promote our understanding of the limiting factors influencing the rarity of mutual grooming, but also provide new perspectives on the evolution of cooperation that has been considered unique to humans. We hope this attempt will enhance future

research to clarify the detailed characteristics of grooming in each species, thereby promoting investigation from the perspectives of cognitive mechanisms, in-depth behavioural analyses, and interspecies comparisons.

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383 Figure caption

384 Figure 1. Horses' mutual grooming: they almost always groom each other simultaneously.

385 How they achieve this joint coordination should be investigated.



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