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Brief touch is different from a massage:
insights from nonhuman primates

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Abstract

Recent findings have shown that the neurophysiological mechanisms involved in human massage and caress are similar to those involved in grooming of nonhuman primates. In contrast, little is known about the neurophysiological mechanisms of brief touch in both human and other primates. Here we review evidence for brief touch in nonhuman primates and contrast its patterns and potential functions with those better known of grooming. We show that brief touch is not an affiliative behavior as it functions to assess the competitive tendencies of unfamiliar individuals and former opponents, to test the state of a social relationship and to signal benign intent. Thus, brief touch plays an important role, complementary to that of grooming, in the regulation of social relationships.

Introduction

Tactile communication is one of the various types of communication that humans as well as other animals use. Stroking, caressing, cuddling and embracing are among the tactile communication behaviors derived from the mother-infant repertoire that are universally present in humans [1]. Many of these behaviors are also exchanged between group members in a variety of nonhuman primate species (hereafter primates). The most studied of these behaviors is allogrooming (i.e. grooming another individual, in contrast to selfgrooming), which involves a stroking motion and has been viewed as equivalent to human massage [2*].

Allogrooming (hereafter grooming) is a common feature in many nonprimate mammals [e.g. 3] and birds [e.g. 4] but only in monkeys and apes the touching involved in grooming is mostly done with the hands [5]. Such touching is typically done in coordination between the two hands with one sweeping the hair and the other plucking for potential skin debris, ectoparasites and pieces of vegetation [6]. Apart from an obvious hygienic function [7], grooming must have other functions as many monkey and ape species spend considerable amount of time engaging in such a behavior [8]. Receiving grooming likely has a calming effect as it reduces heart rate [9] and behavioral indicators of anxiety [10]. It also provides a pleasant sensation associated with beta endorphin release [11]. Such effects can be viewed as mechanisms to prompt primates in engaging in such a type of touch for social purposes. The social function of grooming is supported by a correlation between the amount of grooming and group size and by the uneven way each group member distributes grooming across potential partners [5]. In this respect grooming is considered an important affiliative interaction for the regulation of social relationships between group members [12]. Grooming can be exchanged for grooming [13] and for other services and commodities such as tolerance around resources [14,15] and support in within-group conflicts [16]. As most of such exchanges occur on a long-term basis [17], grooming is considered a tool to establish and maintain valuable social relationships [5]. This perspective is supported by the findings of long-term studies in which individuals with strong relationships based on grooming exchanges have high survival and reproductive success [18-20].

Primates engage in other tactile communication apart from grooming. Several types of touching are typically included in species behavioral repertoires [e.g. 21-23], but they are rarely the focus of specific research. Thus, apart from some notable exceptions (e.g., greeting rituals; see below), little is known about brief touch in primates. The aim of our paper is to review evidence for the neglected form of brief touch and contrast its patterns and potential functions with those better known of grooming. We do so by focusing on research topics where brief touch has been explicitly investigated, such as first encounters between unfamiliar individuals, postconflict behavior, embraces and greeting rituals.

First encounters between unfamiliar individuals

Differences in patterns and potential functions between brief touch and grooming are clearly shown during the establishment of new social relationships. Little is known about the establishment of social relationships between unfamiliar adult primates in the wild; insight comes from captive studies in which pairs of unfamiliar individuals were introduced to one another. When two individuals meet for the first time, they do not have a history of past interactions that can inform each of them about the likely behavior of their partner. In Kummer's [24] pioneering work with geladas (*Theropithecus gelada*), the first type of interaction between unfamiliar individuals was typically aggressive, which was followed by presenting and mounting, and only later grooming took place. A similar sequence of interactions was found during first encounters in chimpanzees (*Pan troglodytes*) [25]. After aggressive interactions, the unfamiliar individuals engaged in brief touch, such as embrace, kiss, hand in mouth, genital inspection and mounting, which occurred more frequently between individuals more closely matched in competitive abilities than between those more obviously mismatched (inferred from the dominance rank distance they eventually obtained after group formation). Thus, brief touch seems to be used as a safer alternative to long-lasting contact, such as grooming, in situations that could potentially escalate. Grooming was the last interaction type to occur during first encounters between unfamiliar chimpanzees and played a role in promoting tolerance and reducing aggression [25]. There was a difference between the two studies. In geladas, the first aggressive step was often skipped in female-male pairs [24], whereas this was not the case in chimpanzees where aggression rates were actually higher in female-male pairs than in female-female pairs [25].

Postconflict behavior

In the aftermath of aggression, primates engage in a variety of interactions with different partners. Whereas friendly reunions between former opponents serve mainly a reconciliatory function by showing benign intent and restoring their relationship [26-28], friendly contacts between a bystander and the recipient of aggression appear to have multiple functions [29]. De Waal and colleagues conducted pioneering work on chimpanzees and bonobos. In chimpanzees, they emphasized the use of brief touch, such as kiss for friendly reunions between former opponents and embrace for friendly contacts between a bystander and the recipient of aggression [30]. In bonobos, they observed a variety of brief sexual contacts often used in socially tense situations [31]. Fraser and colleagues later confirmed that chimpanzees kiss and embrace each other much more often in postconflict contexts than in other contexts (by comparing their occurrence in post-conflict observations with their occurrence in matched-control observations), whereas grooming is more likely in other contexts than in postconflict contexts [32]. In various species of macaques, brief touch, such as clasping, hold-bottom and standing grasp, is more often used during friendly reunions between former opponents than in other contexts [33-35]. The use of such brief touch is particularly common in macaque species characterized by high conciliatory tendencies, supporting the view that it functions as appeasement promoting reconciliation between previous opponents [36]. In stumptail macaques (*Macaca arctoides*) two clusters of behaviors were identified for postconflict friendly contacts between former opponents [37]. Short-lasting behaviors, such as brief touch, were exchanged soon after the end of the conflict by opponents that remained in relatively close proximity, with most of them occurring in the first postconflict minute. Long-lasting contacts, such as grooming, occurred later and were more likely to be exchanged between close associates. Thus, whereas grooming may be used to restore valuable relationships, brief touch may be used more indiscriminately by any pair of opponents as an appeasement to prevent the immediate reoccurrence of aggression [37]. Bystanders of the same species directed more frequently brief touch, but not grooming, toward recipients of aggression than at baseline, suggesting the use of brief touch to appease the recipient of aggression and reduce the likelihood of the bystander becoming a target of redirected aggression [38; cf. 39].

Embraces

Differences between brief touch and grooming are well illustrated in spider monkeys (*Ateles* spp.). Female primates are highly attracted to other females' infants [40] and typically groom mothers to have access to the infant [41,42*]. This is, however, not the case in spider monkeys, in which females embrace, rather than groom, mothers to access their young infants [43] (an embrace is a face-to-face hug with one or both arms wrapped around the neck or back of the partner, which lasts 2-3 seconds). Whereas males reciprocate grooming with other males regardless of their age, males who differed in age do not reciprocate embraces, and most embraces are given by younger males to older males [44]. Thus, embraces may serve to reduce the likelihood of aggression from older to younger males, which is rare but can be injurious or even lethal [45,46].

This view is supported by post-fusion patterns of grooming and embraces. Spider monkeys fission and fuse in subgroups of variable composition throughout the day [47]. Aggression between members of different subgroups after fusion is typically much higher than at baseline [48]. Individuals from joining subgroups exchange less grooming and more embraces when approaching one another in the aftermath of a fusion [48,49], and post-fusion aggression is dramatically reduced when embraces take places [48]. Grooming is expected to be associated with components of social relationships such as value and compatibility [50]. In a Principal Component Analysis of spider monkeys' social interactions, grooming indeed loaded high in a component along with proximity measures [51,52]. In contrast, embraces loaded high on a separate component along with aggression [51]. Overall, embraces appear to serve a different function than grooming, which is considered the prevalent affiliative interaction in primates [5]. Embraces seem to be an assessment tool, signaling benign intent, facilitating friendly interactions by reducing uncertainty and risk [12], and thus resemble greeting rituals in other species [53,54].

Greeting rituals

A variety of primate species engage in greeting rituals (hereafter greetings), which typically include the exchange of vocalizations, facial expressions and brief touch such as clasping, fondling of the genitals, embraces and mounts. Unlike grooming, greetings are exchanged mostly between males [55,56].

In those species in which males have more antagonistic relationships, greetings are rare, whereas in species in which males have more cooperative, though often tense or ambivalent, relationships, greetings are more common [57,58*]. Greetings seem to be used to test and confirm the state of the relationship between two males [59,60] and involve considerable risks, as males touch and fondle each other's genitals. Risky interactions are hypothesized to be best suited to test the strength of a social relationship [61; see 62 for other forms of risky contacts hypothesized to function as testing mechanisms]. In contrast, primates seem to avoid taking risks while grooming as subordinates prefer to groom dominants on their back, so as to avoid both direct eye contact and the possibility of an immediate attack [63*]. Indeed, primate grooming is often directed at the partner’s back, something that may be based on a neurobiological mechanism, given that the back appears to be more densely innervated by fibres associated with pleasant sensation when the skin is gently stroked [64,65; see next section].

Greetings are also common in some primate species after a temporary separation. For example, both captive and wild tufted capuchin monkey males (genus *Sapajus*) greet each other excitedly when meeting again after being separated. These greetings include loud screaming, running into each other and embracing [55,66]. As in the case of first encounters between unfamiliar individuals, greetings involving clasping and mounting occur during the excited phase that immediately follows reunions, whereas grooming occurs only later, when the monkeys have calmed down [67].

Neurophysiological mechanisms

In the last two decades there have been several reviews on the neurophysiology of touch in primates [2,5,68]. Although the broad term “touch” appeared in their titles, the reviews focused on grooming. This bias was likely due to the evidence being available. Whereas the effects of receiving grooming on heart rate [9] and endorphins [11] have been known for a while, recent discoveries have emphasized further similarities between grooming and human massage and caress [2].

Dunbar [5] suggested that receiving the gentle sweeping movements common during grooming may activate a class of slow unmyelinated C-tactile afferent fibres (CTs) that are known to provide humans with pleasant sensation when their skin is gently stroked [69]. In recent experiments, receiving sweeping movements of grooming stimulated CTs in rhesus macaques (*Macaca mulatta*) [70], and the human sweeping of a rhesus macaque's back increased the monkey's nose skin temperature, which is an index of positive emotional state [71]. This evidence indicates that CTs in hairy skin could play an important role in affective touch in humans and other primates, which could be a starting point to explore the evolution of the neurophysiological mechanisms underlying the pleasantness induced by receiving such type of touch [2,68].

In humans, how receiving affective touch is perceived depends on the interaction partner and context [72,73*]. For example, whereas desirable touch is perceived as pleasant, the same touch stimulus may be perceived as unpleasant and promote avoidance if it comes from an undesirable person or if the contextual cues indicate that it may be associated with danger [74]. Similarly, oxytocin is released by received grooming in a relationship-specific manner in chimpanzees: oxytocin levels are higher after receiving grooming if the relationship with the partner is strong than if the relationship with the partner is weak [75]. Furthermore, urinary oxytocin levels vary across cotton-top tamarin (*Saguinus oedipus*) pairs depending on the amount of grooming exchanged within each pair [76].

As the various types of brief touch reviewed in the previous sections seem to play functions different from that of grooming in several primates, it is likely that the underlying neurophysiological mechanisms for brief touch are different from those of grooming. Still, brief touch may share similarities with grooming regarding the affective component and the factors modulating it, such as partner identity and context. This is because CT contributions may still be critical in types of human touch, such as holding hands, that do not involve CTs, possibly via conditioning [77*]. The specific effects of such touch are then modulated by factors like partner identity, such as when the emotional response to a threat is more strongly reduced by holding hands with one's spouse than by holding hands with a stranger, with the magnitude of the response depending on marital quality [78].

Conclusions

We reviewed the patterns of a variety of types of brief touch of primates and contrast them with those better known of grooming. We showed evidence that, unlike grooming, brief touch in primates is not an affiliative behavior as it functions to assess the competitive tendencies of unfamiliar individuals and former opponents, to test the state of a social relationship and to signal benign intent when approaching a group member to reduce uncertainty and aggression risk. Thus, brief touch plays an important, complementary role to that of grooming in the regulation of social relationships [12] (Figure 1).

In primates brief touch occurs especially when individuals meet either for the first time (e.g. first encounters between unfamiliar individuals) or after a period of separation (e.g. post-conflict reunions, after subgroup fusion, post-separation greetings), and when they approach each other to interact (e.g. spider monkey females' infant handling, baboon males' greeting rituals). This is indeed similar to the exchange of brief touch, such as handshakes, embraces, nose rubbing and kisses, occurring when humans are reunited with familiar individuals or meet unfamiliar individuals for the first time [1]. Interestingly, such brief touch has been interpreted as a 'disclaimer of aggression' [79]. Research on the potential function of such brief touch may therefore contribute to the understanding of human conflict management and have implication for the origin of human greeting rituals.

Our review illustrates that brief touch is a research topic at least as interesting as grooming is. Thus, it deserves noninvasive neurophysiological studies both in human and nonhuman primates. Relationship quality can be a modulator of brief touch, which is expected to occur especially in social relationships characterized by higher uncertainty and risk. Within a relationship there are likely asymmetries in the perception of uncertainty and risk [50], thus brief touch may be disproportionally used by one of the two relationship partners [e.g. 44]. Similarly, there are likely differences between giving and receiving brief touch. As in the case of human massage and primate grooming, the challenge is open for exciting discoveries on the neurophysiological mechanisms underlying brief touch in terms of relationship quality, partner asymmetries and the relative role of giving and receiving.

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* The authors evaluated a potential conflict between the grooming partners about the body areas where grooming is directed. Groomers tended to initiate grooming from "safe" areas, such the back and rump, whereas groomees solicited the switch to unsafe areas. Unlike dominants, subordinates prefer to direct grooming to safe areas, whereas they did not solicit preferentially grooming to safe areas.

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* The authors use knowledge of primates employing grooming to manage their social networks to explore how social touch contributes to the maintenance and reinforcement of human social networks. In both one Western and one East Asia country, the strength of the emotional relationship between the two persons involved in social touching was positively associated with permissible touch area. However, Western participants experienced social touching as more pleasurable than Asian participants.

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* The authors start by highlighting the importance of interoception in emotional experience for the Somatovisceral Afference Model of Emotion and the more recent theory of constructed emotion. They emphasize that CTs are considered as interoceptive despite their typically external origin, mostly derived by social stimuli, and thus might contribute to the emotion-related effects of social touch more generally. They propose that all social touch, with or without CTs stimulation, can directly influence the regulation of energy resources.

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Figure caption

Figure 1. Differences in key characteristics between grooming and brief touch and their complementary role.