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Proximate Factors of Different Types of Grooming Hand-Clasp in Mahale Chimpanzees: Implications for Chimpanzee Social Customs¹

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Whether one would call it culture (e.g., Nishida 1987) or not (e.g., Tomasello, Kruger, and Ratner 1993), it has become clear from the accumulated data of long-term field studies of wild chimpanzees (Pan troglodytes) that they show quite a wide range of behavioral diversity that cannot simply be explained in terms of ecological differences (Whiten et al. 1999). Although de Waal (1999) has celebrated the maturity of “cultural primatology,” studies of culture in nonhuman primates still seem to have a long way to go.

Laboratory studies have supplied us useful information on, for example, whether particular kinds of social learning occur in nonhuman animals (see review by Tomasello and Call 1997). These studies are important because culture is usually regarded as being transmitted through some kind of social means and the details of such processes are often difficult to see in the wild. However, the settings of such studies are often too restricted, unnatural, or unusual for animals to show their potentials in the wild. Wrangham and others (1994) have pointed to the importance of recording and describing behavioral diversity in wild chimpanzees and likened it to ethnography (the term used earlier by McGrew [1992]). Many researchers have compiled and reviewed data on chimpanzee behavioral diversity (e.g., Nishida 1987, Sugiyama 1997, McGrew 1998, Boesch and Tomasello 1998, Whiten et al. 2001, Humle and Matsuzawa 2001). However, commenting on a paper on cetacean culture employing similar “ethnographic” methodology, Ingold (2001) has criticized such lists of behaviors as still being a million miles from the practice of ethnography by cultural anthropologists or sociologists. His critique is too demanding in its insistence that culture requires intentions, purposes, and values. Such concepts in anthropology are usually obtained by fully language-based interviews, and even so it is hard to know another's true intentions, purposes, and values because people sometimes do not or cannot say what they really think or intend. Nevertheless, his critique is partly justified in that such lists of traits tend to leave behind the stuff of everyday life (Fox and King 2002), and to understand their “culture” we still need more detailed descriptions of what chimpanzees do in the wild.

Among the so-called cultural behaviors of chimpanzees, various types of tool use have been relatively well described (e.g., McGrew 1992), but social behaviors or social customs have received less attention (see review by Nakamura 2002). The grooming hand-clasp is the first case of social behavior documented as custom in the chimpanzees

of K-group in the Mahale Mountains of western Tanzania (McGrew and Tutin 1978). It is also observed in Mahale M-group, Kibale (both Kanyawara and Ngogo), Kalinzu, Lopé, and Taï (performed only habitually) but never in Gombe, Budongo, or Bossou (see Nakamura 2002). It has also appeared in at least one captive chimpanzee colony (de Waal and Seres 1997). McGrew and others (2001) have reported that there are two different types of grooming hand-clasp: palm-to-palm and non-palm-to-palm. In the former type, the two chimpanzees truly clasp each other's hands with mutual palmar contact (fig. 1, A), while in the latter only one or neither hand clasps the other (fig. 1, B–D) and usually the hands are flexed with one limb resting on the other (as in fig. 1, C). In their retrospective analysis of photographs and videos, they argue that the palm-to-palm hand-clasp dominated in K-group and was not observed in M-group. Although these observations may seem minor, their implications are important because there are so many subtle behavioral variations in human gestural communication (see, e.g., Morris 1994). A detailed study of these minute differences would be important for understanding the origin of the behavioral variations among cultures.

Unfortunately, McGrew and colleagues' analysis is based on a rather small number of samples (9 photos from K-group and 6 from M-group), and the identities of the K-group individuals are not presented. Thus we cannot rule out the possibility that some individual(s) contributed a large proportion of the samples. The objective of this paper is to test McGrew and colleagues' idea that the palm-to-palm hand-clasp is a custom of K-group and not of M-group with a larger data set. In addition, we would like to investigate the proximate factors that likely produce the different types of grooming handclasp, considering whether consistent patterns are observed only at an individual level or also at the level of the group.

Perhaps because McGrew and colleagues strictly define only palm-to-palm (i.e., mutual palmar contact), with non-palm-to-palm being treated as a complementary set of palm-to-palm, the non-palm-to-palm pattern includes several types that grade into each other. Some grooming hand-clasps (e.g., fig. 1, B) are regarded as non-palm-to-palm even though their arms are both stretched as in the typical palm-to-palm. However, in other types of non-palm-to-palm, the hands are much more flexed (fig. 1, D). Thus, we made additional analyses on the angles of the wrist and the elbow rather than using palm contact as a single measure.

METHODS

We analyzed photographs and videotapes of the grooming hand-clasp performed by the chimpanzees of K (Kajabala)-group and M (Mimikire)-group. These two groups have been habituated and studied for decades (Nishida 1990, Nishida, Uehara, and Kawanaka 2002). K-group was the initial focus of detailed studies after habituation in 1965 (Nishida 1968), but it had become almost extinct by 1983, and some females subsequently transferred to neighboring M-group (Nishida et al. 1985). K-group continued to exist for more than four years as a bisexual group, but by 1987 only a lone male was left, and he was observed sporadically until at least 1992 (Uehara et al. 1994). M-group has been continuously studied since 1968 (Nishida and Kawanaka 1972).

We analyzed 24 photographs of the grooming hand-clasp in K-group taken between 1973 and 1978 and 20 photographs and 56 still images from videotapes of the grooming hand-clasp in M-group taken between 1994 and 2000. We used only photographs in which both participants were identifiable. When we took a still image from a video, we chose the frame in which the clasped hands reached the highest point.

For individual analyses, we used only data on those who showed the grooming hand-clasp with at least three different partners to see whether they showed a consistent tendency regardless of the partner. Table 1 shows the profiles of individuals who met this condition. Of these individuals, GW and MA, who immigrated from K-group to M-group, are especially interesting. GW was observed to perform the grooming hand-clasp in both groups, but MA did not perform it when he was in K-group, perhaps because of his youth. For each individual, the two researchers independently judged the following three variables: angle of the wrist, angle of the elbow, and palm contact. The angles of the wrist and the elbow were roughly categorized as straight (180° – 150°), middle (150° – 120°), and flexed (120° –). Any finer estimation would have been unreliable because of the different conditions of the photographs and/or the different angles of the individuals shown in them. We also judged whether the individual's palm made contact with the other's hand, wrist, or arm. The results of these analyses by the two researchers were combined, and we used data for statistical analysis only when the judgments of the two agreed.

RESULTS

Palm-to-palm and non-palm-to-palm

Palm-to-palm hand-clasps were observed in M-group. The proportion of palm-to-palm hand-clasps was significantly higher in K-group (41.7%, 10/24) than in M-group (5.3%, 4/76) (Fisher's exact probability test, $p < .001$, two-tailed). However, in contrast to McGrew and colleagues' results, it was not dominant over non-palm-to-palm even in K-group. It is notable that all four cases of palm-to-palm in M-group included GW as one of the participants. In each case, GW performed palm-to-palm with different partners (namely, PR, WX, XT, and NK) and also performed the non-palm-to-palm pattern with these individuals. Angle of the wrist. Table 2 shows the results for angle of the wrist. Most cases were judged as either straight or flexed, and in most cases (91%) the judg-

ments of the two researchers agreed. KM and GW (when in M-group) were significantly biased straight, while SB, DE, DG, CT, PM, and PI were significantly biased flexed. Although others did not show significant bias (perhaps because of smaller sample sizes), they also seemed to have a tendency to be biased either straight or flexed.

At the group level, M-group members were significantly biased flexed (Wilcoxon signed rank test, $n = 11$, $T = 10.5$, $p < .05$), while no such tendencies were found in K-group members. Both groups included individuals representing straight and flexed types, but the only individual who consistently showed the straight type in M-group was GW. When GW was in K-group, she also showed the straight type. Although her samples in K-group were too few for a statistical test, she showed the straight type in three of the four cases and the remaining case was judged straight by one researcher and as middle by the other. In brief, GW almost always showed the straight type, whether in K-group in the 1970s or in M-group between 1994 and 2000. Among males, who usually experience only a single group (except for MA [see table 1]), KM and SB of K-group showed opposite tendencies, whereas all the males with enough samples in M-group were significantly biased flexed (those with fewer samples also seemed to show the same tendency) except for PR, who showed a mixture of the two types. Angle of the elbow. Table 3 shows the results for the angle of the elbow. These angles were more often judged middle than the angles of the wrist, and the agreement between the two evaluators was only 64%, much less than for the wrist angles. This does not mean, however, that the elbow angles are difficult to estimate (see discussion). At the individual level, two K-group males (KM and SB) and one M-group male (PR) were significantly biased straight. No individuals were judged significantly biased flexed.

At the group level, we cannot conduct a statistical test on K-group because of the small number of samples ($n = 5$), but it is notable that straight judgments by both judges were most frequent for all of these five individuals and no one was ever judged flexed by both judges. There was no significant difference between straight and flexed in M-group members (Wilcoxon, $n = 11$, $T = 11.5$, n.s.), and many individuals performed the flexed type of handclasp as often as the straight type. Interestingly, GW, who also never showed the flexed type when she was in K-group, performed the flexed type in three instances in M-group.

Palm contact

Table 4 shows the results for palm contact. The agreement of the two judges was 81%. There were no clear individual tendencies, but KM and GW, who showed straight wrists, tended to show palm contact more often. However, PM and PI, who showed flexed wrists, also consistently contacted palms. There was no individual whose palm was consistently without contact.

DISCUSSION

Is palm-to-palm a custom of K-group?

In a strict sense, our results have disproved McGrew and others' (2001) claim that the palm-to-palm hand-clasp is a custom only of K-group because palm-to-palm was observed in M-group as well. This does not, however, mean that their hypothesis is invalid, because all of the observa-

tions of palm-to-palm in M-group included GW, who had transferred from K-group. It is therefore possible that palm-to-palm is a custom only of K-group, where GW had acquired it. The occurrences of the palm-to-palm handclasp in M-group do not mean that GW had successfully transmitted the pattern to M-group, because it was much less frequent than in K-group and no M-group individual performed it without her. It is also noted that a very flexed type of grooming hand-clasp (see fig. 1, D) was observed only in M-group. This is not likely a chronological difference because we have one photograph of M-group chimpanzees (perhaps two adult males) taken in 1973 showing a very flexed type of hand-clasp.

Proximate factors of the grooming hand-clasp.

In the palm-to-palm hand-clasp described by McGrew and others (2001), the wrists of the two performers stretch and palms are truly clasped. It occurs when both of the participants individually employ the straight type of hand-clasp in their wrists and elbows and the contact type in their palms. When one participant straightens its wrist, its palm will likely contact the other's hand or arm. Since non-palm-to-palm is defined as a complementary set of palm-to-palm, it includes various types of grooming hand-clasp. Non-palm-to-palm hand-clasps occur when one or both of the participants flex wrists and make no palm contact. Different types of non-palm-to-palm occur when one party straightens (fig. 1, B) or flexes (fig. 1, D) the wrist, and the degree of flexion also creates variations. Our data showed that individuals had consistent tendencies for wrist angles but not for elbow angles. In wrist angles, few cases were judged middle and the two evaluators' judgments mostly agreed. This means that individuals' wrist angles are usually either completely flexed or completely straight. For the elbow angles, however, a judgment of middle was more common, and disagreement between the two evaluators' judgments may have occurred in the case of angles on the boundary between two grades. For instance, when one's elbow is about 150°, it may be judged as straight or middle, while there may not be such fluctuations of judgment when the angle is closer to 180° or 90°.

Only two individuals, one in each group, consistently showed straight wrists. Again, the one in M-group was GW. If palm-to-palm is a custom of K-group, there should be more individuals showing the straight wrist type, but the other male in K-group (SB) consistently flexed his wrist. Therefore we assume that making the wrist straight may not have been a custom of K-group. The flexed wrist may, however, be a custom of M-group, especially for males. Straight elbows seem to be the norm in K-group but not in M-group.

Figure 2 summarizes our hypothesis for proximate factors of the grooming hand-clasp. In K-group, the wrist may be straight or flexed, depending on the individual, but everyone's elbow should be straight. In M-group, the wrist should be flexed, but the elbow can be anything from straight to flexed, even in the same individual. The grooming hand-clasp becomes palm-to-palm when two individuals in the shaded square in figure 2 perform it with each other and therefore probably occurs among some members of K-group. In M-group, because wrists are usually flexed, palm-to-palm is not expected to occur frequently. However, in accordance with GW's consistently straight wrist, some

M-group members seem to have given way so that some palm-to-palm contact occurred with her. However, GW also seems to have changed her K-group style somewhat in accordance with the norm of M-group members, often flexing her elbow.

Interestingly, one adolescent male, PR, showed a rather extraordinary style among M-group males: he often made his wrist straight and consistently made his elbow straight. (His mother, PI, showed the typical M-group style [flexed wrist and continuous elbow].) One possibility is that this was because of his small body size: he was in early adolescence in 2000 and smaller than adult conspecifics. If an individual with a shorter hand performed the grooming hand-clasp with an adult, he would have to straighten his arm to reach the same height. However, another explanation is possible: PR's mother was closely associated with GW during his childhood and very often groomed with her in 1996–97 (Nakamura, unpublished data). Because PR stayed close to PI, he often joined in grooming with GW. Thus, it is possible that, when he was sensitive to learning the grooming hand-clasp (at four to five years), he spent a long time with GW's nonstandard style and learned it socially. It will be interesting to see how his pattern develops as he becomes an adult.

Changes in the custom in relation to group transfer. Although our findings call for some corrections of the ideas of McGrew and others, we have confirmed that there was a subtle but concrete difference between the two neighboring groups. Because chimpanzee females usually transfer between groups (Nishida and Kawanaka 1972), they have to cope with such differences. McGrew and others predict that females will change their customs when they move to a different group, but our data do not support this idea: GW persisted in her old style 21 years after her immigration to M-group, despite its being different from the M-group norm. There are some reports of females' showing idiosyncratic feeding habits (Matsuzawa 1994, Sakamaki 1998), implying that they retained the customs of their former groups. However, our results are much more complicated than the cases of feeding in that GW not only retained parts of her old style but also modified some of them. Another M-group female, NK, had also immigrated from K-group, but we did not have enough data to judge whether she showed a similar pattern. There was no evidence that MA, a K-group-born M-group male, showed any K-group like styles, perhaps because he was very young when he transferred to M-group (Takahata and Takahata 1989).

It is impossible to know now what really happened when GW, with her heterogeneous pattern, immigrated into M-group. However, her current pattern implies that no sanction-like responses occurred. Given that she partly changed her ways and some members of M-group adopted some of her patterns, it can be said that they did not wholly reject or compromise with the unfamiliar pattern but somehow coped with it through repeated interactions in their daily life.

In detailed studies of chimpanzee tool use, stress is often placed on the way in which "transmissible particles of information" (Ingold 2001) are transferred from one individual to another or functionally shaped. However, as our study has shown, what chimpanzees are doing in social customs does not seem to be a simple transfer of such information and is questionable whether it is useful to look

for the functions of these patterns. If we regard “culture” as properties emerging through social interaction, without emphasizing its intellectual or functional aspects, studying the way in which chimpanzees shape their social customs may help us to understand the generation of culture.

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TABLE 1 Profiles of Individuals Used in the Analysis

Names	Abbreviations	Observation Group ^a	Natal Group	Year of Birth	Year of Immigration		Remarks
					To K	To M	
Males							
Kamemanfu	KM	K	K?	Unknown	–	–	–
Sobongo	SB	K	K?	1958?	–	–	–
Kalunde	DE	M	M?	1963?	–	–	–
Masudi	MA	M	K	1977	–	1982b	–
Fanana	FN	M	M?	1978?	–	–	–
Dogura	DG	M	M?	1981?	–	–	–
Carter	CT	M	M	1985	–	–	–
Pimu	PM	M	M	1988	–	–	Son of FT
Primus	PR	M	M	1991	–	–	Son of PI
Females							
Wantangwa	WT	K	Other?	Unknown	Unknown	–	–
Chausiku	CH	K	K	1958	–	1979	–
Wakusi	WX	M	Other?	1961?	–	Unknown	–
Gwekulo	GW	K, M	Other?	1962?	1972	1979	–
Fatuma	FT	M	Other?	1963?	–	Unknown	Mother of PM
Pinky	PI	M	Other	1972?	–	1983	Mother of PR
Christina	XT	M	Other	1975?	–	1987	–
Miya	MJ	M	Other	1980?	–	1991	–

NOTE: Question marks represent estimations.

^aThe group for which photographs of the grooming hand-clasp were available.

^bImmigrated with his mother (see Takahata and Takahata 1989).

TABLE 2 Angle of the Wrist in the Grooming Hand-Clasp

Individual ^a	S/S	S/M	M/M	M/F	F/F	?	Total	<i>p</i> (S/S vs. F/F) ^c
K-group								
KM	8	2	–	–	–	2	12	< .01
SB	–	–	2	–	13	–	15	< .001
WT	–	–	–	–	5	–	5	–
CH	1	–	–	–	1	2	4	–
GW ^b	3	1	–	–	–	–	4	–
Total	12	3	2	0	19	4	40	
M-group								
DE	1	–	–	–	15	–	16	< .001
MA	–	–	2	–	4	–	6	–
FN	–	–	–	–	5	–	5	–
DG	–	–	1	–	10	–	11	< .01
CT	–	–	–	–	9	–	9	< .01
PM	–	–	–	–	8	–	8	< .01
PR	5	–	–	1	5	3	14	n.s.
WX	2	2	–	–	2	–	6	–
GW ^b	15	–	2	–	–	1	18	< .01
FT	1	–	2	–	5	–	8	n.s.
PI	1	–	–	–	16	–	17	< .001
XT	1	–	–	–	6	1	8	n.s.
MJ	1	–	–	–	6	1	8	n.s.
Total	27	2	7	1	91	6	134	

NOTE: S, straight; M, middle; F, flexed; ?, not visible or uncertain. S/S means that the judgments of the two researchers were both straight, S/M means that one researcher judged the angle straight and the other middle, and so forth.

^aSee table 1.

^bData on GW are available in both groups.

^cBinomial test.

TABLE 3 Angle of the Elbow in the Grooming Hand-Clasp

Individual ^a	S/S	S/M	M/M	M/F	F/F	?	Total	<i>p</i> (S/S vs. F/F) ^c
K-group								
KM	8	3	–	–	–	1	12	< .01
SB	9	5	1	–	–	–	15	< .01
WT	4	–	1	–	–	–	5	–
CH	1	1	–	–	–	2	4	–
GW ^b	3	–	–	1	–	–	4	–
Total	25	9	2	1	0	3	40	
M-group								
DE	2	4	3	3	4	–	16	n.s.
MA	3	1	1	–	1	–	6	–
FN	1	2	1	1	–	–	5	–
DG	1	4	2	1	3	–	11	–
CT	1	2	2	2	2	–	9	–
PM	1	3	2	1	1	–	8	–
PR	8	1	5	–	–	–	14	< .01
WX	3	3	–	–	–	–	6	–
GW ^b	9	4	2	–	3	–	18	n.s.
FT	2	3	1	2	–	–	8	–
PI	4	2	3	4	4	–	17	n.s.
XT	5	1	1	–	1	–	8	n.s.
MJ	3	1	1	2	1	–	8	–
Total	43	31	24	16	20	0	134	

NOTE: S, straight; M, middle; F, flexed; ?, not visible or uncertain. S/S means that the judgments of the two researchers were both straight, S/M means that one researcher judged the angle straight and the other middle, and so forth.

^aSee table 1.

^bData on GW are available in both groups.

^cBinomial test.

TABLE 4 Palm Contact in Grooming Hand-Clasp

Individual ^a	+/+	+/-	-/-	?	Total	<i>p</i> (+/+ vs. -/-) ^c
K-group						
KM	12	–	–	–	12	< .001
SB	5	8	2	–	15	n.s.
WT	4	1	–	–	5	–
CH	2	–	–	2	4	–
GW ^b	4	–	–	–	4	–
Total	27	9	2	2	40	
M-group						
DE	4	4	4	4	16	n.s.
MA	4	2	–	–	6	–
FN	1	1	3	–	5	–
DG	5	2	4	–	11	n.s.
CT	4	–	4	1	9	n.s.
PM	6	1	–	1	8	< .05
PR	7	1	4	2	14	n.s.
WX	1	–	5	–	6	n.s.
GW ^b	18	–	–	–	18	< .001
FT	6	–	2	–	8	n.s.
PI	13	2	–	2	17	< .001
XT	3	2	3	–	8	n.s.
MJ	4	1	2	1	8	n.s.
Total	76	16	31	11	134	

NOTE: +, contact; -, no contact; ?, not visible or uncertain. +/+ means that the judgments by both researchers were contact, +/- means that one researcher judged contact and the other no contact, and so forth.

^aSee table 1.

^bData on GW are available in both groups.

^cBinomial test.



A



B



C



D

Fig. 1. Examples of various types of grooming handclasp observed in Mahale M-group. A, typical palm-to-palm, in which elbows and wrists of both parties are straight; B, both elbows straight but not palm-to-palm; C, elbow of one party straight and the other's flexed; D, a very flexed type not observed in K-group. (Drawn from video footage by Nakamura.)

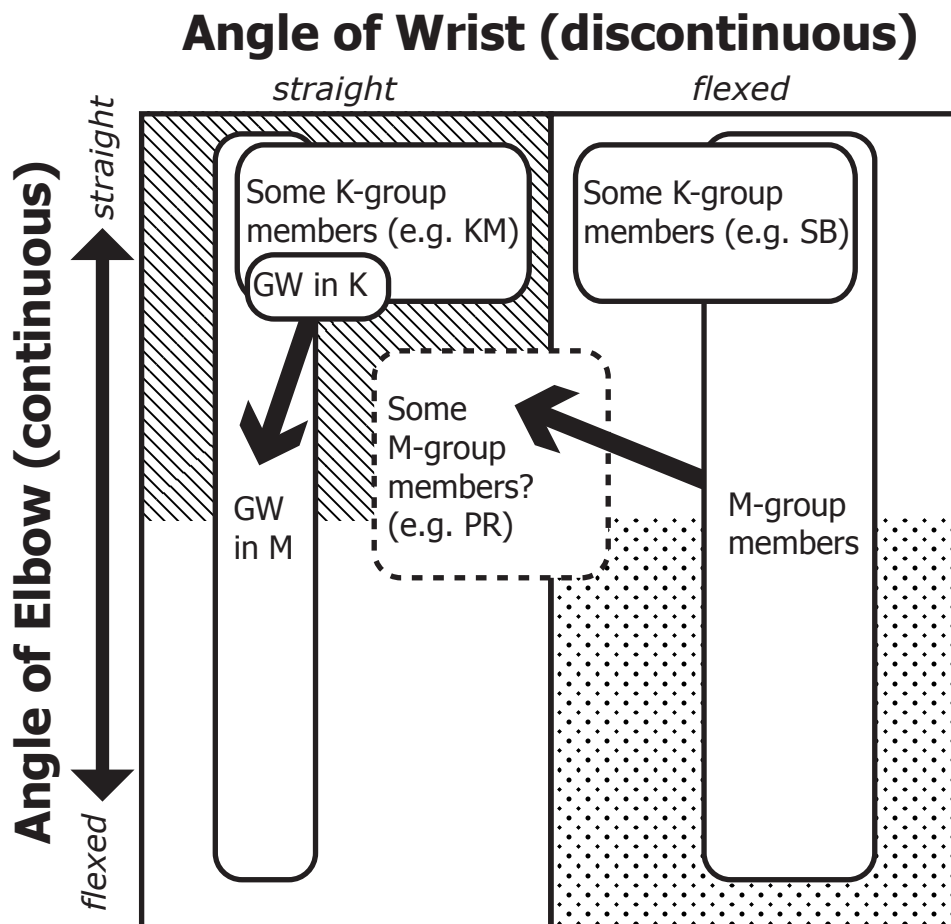


Fig. 2. Hypothetical schema of proximate factors of different grooming hand-clasps. When two individuals in the shaded part perform the grooming hand-clasp with each other, it becomes palm-to-palm, and when two individuals in the dotted part do so it becomes very flexed, as in figure 1, D. Arrows indicate possible effects of GW's immigration to M-group.