Handedness found in a wild group of moor monkeys in the Karaenta Nature Reserve, South Sulawesi, Indonesia

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Abstract Hand preference of wild moor monkeys Macaca maurus was investigated in food reaching situations at the Karaenta Nature Reserve, South Sulawesi, Indonesia. The frequency picking up sweet-corn grains to take into the mouth by either hand of monkeys was counted directly at the feeding ground where sweet-corn grains were scattered for monkeys. Among the 20 monkeys examined, 8 were right-handed, 8 were left-handed, and 4 were ambilateral. The results indicated the prevailed hand preference on individual level but not either trends of left- or right-hand preference on population level. The trend toward a higher proportion of left-handed monkeys found in Japanese and rhesus monkeys was not found. Some other characteristics found in moor monkeys are discussed in comparison with those previous findings in Japanese and Tibetan macaques in order to evaluate variations within the genus Macaca [Current Zoology 56 (2): 209–212, 2010].

Key words Moor macaque, Macaca maurus, Handedness, Laterality, Sulawesi

Hemispheric specialization that may cause behavioral lateralization has been considered unique to human evolution and the assumptions of this view were predicated on the absence of population level behavioral asymmetries in non-human animals, including primates. It has become, however, apparent that lateralization of the nervous systems and side biases in behavior are much more common than once thought and it now seems that they are so widespread in vertebrates and even in invertebrates (Corballis, 2007; MacNeilage et al, 1987; Roger, 2007; Warren, 1980).

To date, the handedness of many primate species has been studied. Detailed examinations of 241 published data sets of 40 species of non-human primates indicated that there was no clear evidence showing preferences in hand use at the population level as there is with human beings (McGrew and Marchant, 1997). It can be, however, found that some population level or task-dependent preferences on either hand use are emerged in many species. Captive chimpanzees, for instance, prefer to use right-hand for eating (Hopkins, 1994; Hopkins et al., 2007). There is little doubt that modern prosimians tend to be left-handed and no study of prosimians has shown a significant right-hand preference (MacNeilage, 2007). Several former studies have suggested the relatively dominant left-hand preference in food reaching tasks in some macaque species (Fagot et al., 1991; Itani et al., 1963; Kubota, 1990; Tokuda, 1969; Watanabe and Kawai, 1993; Watanabe et al., 2007; Westergaad et al., 1998). However, such studies are still very limited in number and most current information on the handedness of macaques has come from only two species; Japanese macaques Macaca fuscata and rhesus monkeys Macaca mulatta. The question of whether population-level handedness exists in non-human primates remains a topic of considerable theoretical and empirical debates (Hopkins et al., 2007; McGrew and Marchant, 1997; Papandemetriou et al., 2005). It is, thus, debatable whether the trends are common to all species of macaques or in the other primate taxa. It should be confirmed by experimental data how many degrees of variation there are both within and between species. It was argued that simple reaching, as an indicator of hemisphere specialization, is not the best measure of handedness in non-human primates and the behavior can be strongly influenced by situation and postural factors (Hopkins, 2007). If the population level hand preference is detected, however, it may strongly suggest the hemisphere specialization of the species.

MacNeilage et al. (1987) suggested a hypothesis for the evolution of handedness in relation to brain asymmetry. The hypothesis, however, was not supported satisfactorily from experimental data (McGrew and Mar-
chant, 1997, but see MacNeilage, 2007). More information on the other species is essential for understanding general trends within genus *Macaca*, since it includes 20 species (Brandon-Jones et al., 2004) as well as on many other little-known species in the other primate taxa. Such detailed studies on the variations within a species and/or between closely related species could help increase understanding of the general evolutionary trends of hand preference. I have conducted a field survey of moor macaques *M. maurus*, and obtained information on hand preference in food reaching tasks. I report the results and discuss some characteristics found in moor monkeys comparing with our former findings on Japanese and Tibetan macaques *M. thibetana* (Watanabe and Kawai, 1993; Watanabe et al., 2007).

1 Materials and Method

Moor macaques were observed from November 6 to December 27, 1991, in the Karaenta Nature Reserve, South Sulawesi, Indonesia. The subject group had been provisioned intermittently since 1981 (Watanabe and Matsumura, 1996) and included 20 individuals except for newborn babies in 1991. The provisioning site was settled in the forest, and once or twice a day only when researchers visited there for observation wardens provisioned about 1 litter of sweet-corn grains. The group of moor macaques foraged the area of about 30 ha near the provisioning site and could be attracted by whistle of the warden. It was therefore possible to observe monkeys every day. Most data was obtained within 20 minutes after the wardens gave the provisions and the monkeys took it from the provisioning site, approximately 20 square meters (Fig. 1). When each individual picked up sweet-corn grains and took it into the mouth, the frequencies of right- and left-hand uses were counted directly. Monkeys usually sat down calmly on the ground where sweet-corn grains were scattered and took it continuously for a while (feeding bout). The counting was carried out until it exceeded 100 times or more in total as far as the feeding bout was not interrupted by other activities or interfered by other individuals. Furthermore, the observations were repeated for each subject individual two to six times (M=3.8 times) on the different days. Handedness was judged by the relative frequencies of either hand used for picking up sweet-corn grains given to them on the ground; that is, right- or left-hand superiority for each individual is measured statistically from the total figure of hand uses by <0.05 significant level in non-parametric binomial tests (two-tailed). The other individuals (P>0.05) remained are classified as ambilateral. Mann-Whitney *U* test was used for comparison between age-sex classes as well as between species based on the handedness index by Hopkins et al. (2007). For the details of subject group see Watanabe and Matsumura (1996) and Matsumura (1998).

![Fig. 1 Observation site of the moor macaques](image)

The provisions, sweet-corn grains, were given to the monkeys on the ground and the monkeys could take it freely.

2 Results

The handedness of 20 individuals (7 males and 13 females) was examined during the study period (Table 1). Among them, 8 individuals were right-handed, 8 were left-handed, and 4 were ambilateral. Among group members, thus, most of them (80%) indicated hand preference on individual level but they did not show either trends of left- or right-hand preference on population level. No statistical differences in the distribution of individual handed indexes were found between males and females (Mann-Whitney *U* test, *z*=−0.912, *P*=0.362) or between adults and juveniles (*z*=−0.674, *P*=0.500). The distribution of absolute values of handedness index, however, was significantly different between males and females (*z*=−2.025, *P*=0.043); that is, females showed more lateralized hand uses to either sides than males. No statistical differences was found in the absolute values of handedness index between adults and juveniles (*z*=−0.754, *P*=0.451).

It was noteworthy that most monkeys continually showed partial or exclusive tendencies to prefer the hand with which they had been classified. Ambilateral monkeys, further, showed rather stable trends to use both hand evenly in most sessions (Table 1).
Table 1  Hand preference in moor monkeys for picking up sweet-corn grains

| Session 1 | Session 2 | Session 3 | Session 4 | Session 5 | Session 6 |
|-----------|-----------|-----------|-----------|-----------|-----------|
| Hand preference for picking up sweet-corn grains |
| TOTAL     | L         | R         | P          | L         | R         | P          | L         | R         | P          | L         | R         | P          |
| MALES     |           |           |            |           |           |            |           |           |            |           |           |            |
| A♂1       | 243       | 179       | 0.002 R    | 57        | 48        | 0.435      | 64        | 59        | 0.719      | 58        | 29        | 0.002      | 64        | 43        | 0.053      |
| A♂2       | 204       | 122       | 0.000 R    | 62        | 1         | 0.000      | 49        | 44        | 0.679      | 42        | 30        | 0.195      | 51        | 47        | 0.762      |
| A♂3       | 162       | 145       | 0.361 A    | 36        | 12        | 0.001      | 41        | 45        | 0.747      | 44        | 33        | 0.254      | 41        | 55        | 0.184      |
| J♂1 (5)   | 87        | 226       | 0.000 L    | 28        | 30        | 0.896      | 12        | 64        | 0.000      | 42        | 62        | 0.062      | 5         | 70        | 0.000      |
| J♂2 (5)   | 154       | 46        | 0.000 R    | 20        | 2         | 0.000      | 72        | 35        | 0.000      | 62        | 9         | 0.000      |           |           |            |
| J♂3 (2)   | 217       | 123       | 0.000 R    | 46        | 27        | 0.000      | 36        | 35        | 1.000      | 60        | 28        | 0.001      | 31        | 27        | 0.694      | 44        | 6         | 0.000      |
| J♂4 (2)   | 69        | 85        | 0.227 A    | 34        | 36        | 0.905      | 35        | 45        | 0.156      |           |           |            |           |           |            |
| FEMALES   |           |           |            |           |           |            |           |           |            |           |           |            |
| A♀1       | 0         | 111       | 0.000 L    | 0         | 58        | 0.000      | 0         | 53        | 0.000      |           |           |            |           |           |            |
| A♀2       | 0         | 167       | 0.000 L    | 0         | 50        | 0.000      | 0         | 40        | 0.000      | 0         | 39        | 0.000      | 0         | 38        | 0.000      |
| A♀3       | 252       | 0         | 0.000 R    | 58        | 0         | 0.000      | 36        | 0         | 0.000      | 101       | 0         | 0.000      | 57        | 0         | 0.000      |
| A♀4       | 166       | 151       | 0.432 A    | 62        | 65        | 0.859      | 48        | 39        | 0.391      | 29        | 21        | 0.322      | 27        | 26        | 1.000      |
| A♀5       | 42        | 257       | 0.000 L    | 10        | 122       | 0.000      | 16        | 76        | 0.000      | 16        | 59        | 0.000      |           |           |            |
| A♀6       | 157       | 141       | 0.385 A    | 36        | 33        | 0.810      | 61        | 68        | 0.597      | 60        | 40        | 0.057      |           |           |            |
| A♀7       | 299       | 45        | 0.000 R    | 67        | 0         | 0.000      | 62        | 2         | 0.000      | 58        | 5         | 0.000      | 50        | 0         | 0.000      | 17        | 24        | 0.349      | 45        | 14        | 0.000      |
| A♀8       | 6         | 161       | 0.000 L    | 3         | 63        | 0.000      | 3         | 46        | 0.000      | 0         | 52        | 0.000      |           |           |            |
| A♀9       | 192       | 10        | 0.000 R    | 79        | 10        | 0.000      | 60        | 0         | 0.000      | 53        | 0         | 0.000      |           |           |            |
| A♀10      | 189       | 11        | 0.000 R    | 94        | 10        | 0.000      | 52        | 1         | 0.000      | 43        | 0         | 0.000      |           |           |            |
| J♀1 (4)   | 103       | 187       | 0.000 L    | 20        | 39        | 0.018      | 5         | 50        | 0.000      | 78        | 98        | 0.152      |           |           |            |
| J♀2 (2)   | 124       | 200       | 0.000 L    | 28        | 23        | 0.576      | 25        | 25        | 1.000      | 11        | 19        | 0.200      | 32        | 39        | 0.477      | 11        | 51        | 0.000      | 17        | 43        | 0.001      |
| J♀3 (2)   | 41        | 91        | 0.000 L    | 27        | 45        | 0.044      | 14        | 46        | 0.000      |           |           |            |           |           |            |

A♂ or ♀ indicates adults and J♂ or ♀ juveniles. The age estimated is shown in the parenthesis. Several trial sessions were repeated for each individual. Judgment for each individual is indicated on the basis of accumulated frequencies of left- and right-hand uses: L (left-handed), R (right-handed) and A (ambilateral). The bold numeral indicates significant difference of left- or right-hand uses. “l” indicates a frequency of left hand use and “r” a frequency of right hand use in each session.

3 Discussion

Population level laterality was not found in the group of moor monkeys, and this result is in accordance with studies of other species in genus *Macaca* (McGrew and Marchant, 1997; MacNeilage, 2007). Lateralized hand use was observed in individuals and preferences for both the right and left hands were evenly distributed. Some others were ambilateral. The dominance of left-hand preferred individuals for food reaching tasks could not be seen in the subject group of moor monkeys.

The dominance of left hand preference for food reaching tasks was demonstrated in Japanese and rhesus macaques (Fagot et al., 1991; Itani et al., 1963; Kubota, 1990; Tokuda, 1969; Watanabe and Kawai, 1993; Westergaad et al., 1998). Left hand preferred individuals, for instance, were 2.4 times more common than right-hand preferred individuals in Koshima monkeys (out of 79 individuals 17 were right-handed, 38 left-handed preferred and 24 ambilateral individuals; Watanabe and Kawai, 1993). The methods for evaluating the handedness of each individual were almost identical with this study. Our statistical examination, however, revealed that no significant difference found on the degree of lateralization between these two species (Mann Whitney U test, z = −1.565, P = 0.118 two-tailed). The trends indicated in moor macaques are somewhat similar with that in Tibetan macaques living in the Huangshan Mountains, Central China; out of 33 individuals 9 were right-hand, 11 left-hand preferred and 13 ambilateral individuals (Watanabe et al., 2007). The question is whether the almost equivalent number of left- and right-handed individuals in moor monkeys and Tibetan macaques indicates a species-specific difference or just a local variation, as was found in Japanese macaques. It is difficult to elucidate this without more data on other local populations of both species. It is noteworthy that Japanese and rhesus macaques belong to the same species group and may live widely adapting well to the secondary habitats while moor monkeys and Tibetan macaques belong to the other different groups within the genus *Macaca* and are confined.
to the original evergreen broadleaf forests (Fooden, 1982). If the results of our study are representative of moor monkeys as well as those of Tibetan macaques, however, they may imply a wide variation of hand preference within genus *Macaca* that does not always tend toward an abundance of left-hand preferred individuals within a population.

It is interesting that female moor monkeys showed more pronounced lateralization of hand uses than males. The male moor monkeys often showed the trend of ambilateral hand uses in many feeding bouts while the trends were more consistent in females. The reason is unknown, but males may be more aware of the presence of other group members and so, it is possible that they often change their positions during the feeding bouts.

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