

TOOL BEHAVIOUR IN HIGHER PRIMATES

Cataloguing of individual spontaneous tool activities in gorillas, chimpanzees and orangutans has shown that there are many common features in using of tools among great apes both under laboratory conditions, or in captivity in general, and under wild living conditions. We have demonstrated how markedly, even basically, the quality and quantity of tool activities can be influenced by the equipment of a given ZOO and availability of the object suitable for manipulations and potential tool using or tool making. Plastic boxes become something like universal tools for gorilla from ZOO Praha. Perhaps it is a raising tool tradition also in Prague gorillas, however, this tradition has apparently no analogy in wild conditions. The plastic box using becomes ritualized in many cases, in agonistic behaviour for example, where the using of boxes is a transmitter of an aggression or as an drumming amplifier. We have found in our study that tool activities became a part of various types of behaviour. They usually occur during feeding, aggression, games or other play behaviour, and during social and comfort behaviour as well.

Keywords: monkeys, apes, tool, lateralization, tradition.

Introduction

Tool behaviour, tool using and tool making has been one of the most important, even central, topics of biological and evolutionary anthropology and primatology for many decades. The discussions has concerned more and more of primate tool behaviour since 70th of the last century when tool using in wild-living primates was generally recognised as common and biologically and ecologically important phenomenon [Guilmet, 1977; Kitahara-Frishi, 1977]. The understanding of primate tool using and tool making has gradually shifted from tool using as a commonly recognised feature of primates and namely great apes [McGrew, 1992; Sygyiyama, 1993, 1998; Breuer et al., 2005] to the complex understanding of primate tool using and tool making, or tool behaviour in general, as a part of a broader complex that includes traditions and social learning. An existence of a basic cultural features has been recognised at least in some great ape species [Laland, Hoopit, 2003; McGrew, 2001; 2003; van Schaik et al., 2003; Whiten et al., 1999].

Several important problems of primate tool behaviour have been discussed during last decades. Namely laterality and tool making in non-human primates belong to the most important ones.

Laterality of primates has been gradually shifted to the problems of great ape laterality of tool using

because of remarkable similarities of hominid, orang-utan, gorilla, chimpanzee and humans, brain and behaviour that is based on very close genetic relations of great apes and humans. Since those times some observations in wild living populations, however, have shown some degree of laterality also in wild living chimpanzees [cf. Lonsdorf, Hopkins, 2005].

Traditions in primate tool using and tool making including problem of existence of culture in primates is another very important problem [van Schaik et al., 2003; Whiten et al., 1999]. However, there is a question about origin of comparable tradition in captive apes [Hayashi et al., 2005] that seems to have a positive answer. Some studies have demonstrated [Hayashi et al., 2005] a possibility of origin of traditions in tool using also in captive apes.

Aims of the study

This study deals with the problems of tool activities, tool using and tool making, in non-human primates. The research has three basic approaches. First, obtaining of empirical data by the ad libitum method and the cataloguing of various types of tool activities both in monkeys and in apes. Second, various experiments with tool use and manipulation with captive or wild-living primates directed to the use of tools, or more

precisely various kind of sticks, to approach a distant bite. Third, observation of various species of primates by the focal animal sample method where the tool behaviour of observed primates has been recorded with subsequent statistical evaluation of the results of observation in individual studied groups.

Analysis of laterality in primates has been of a special importance in our study. We have studied use of hands during tool activities and manipulations in various primates species both the spontaneous activities and those during directed experiments.

Material and methods

We have studied the following species of higher primates: *Cebus apella*, *Papio hamadryas*, *Pan troglodytes*, *Gorilla gorilla* and *Pongo pygmaeus* (tab. 1).

We used classical ethological methods namely focal animal sampling and ad libitum sampling with using of defined categories of data directed to the using of tools and its behavioural and manipulative context.

Classification of the tools used by primates:

1 – paper; 2 – sticks, branches; 3 – box; 4 – substrate – bedding and other materials; 5 – cloth, jute bag etc.; 6 – ropes, cable etc.; 7 – food; 8 – animal – animals in the group who used as a tool („living ladder, stand“, etc.).

Tool use and manipulative activities were studied with connection with next type of behaviour:

1 – Locomotor, 2 – feeding, 3 – social, 4 – play, 5 – parental, 6 – agonistic, 7 – sexual, 8 – nest building, 9 – comfort behaviour.

We also recorded modification of a different type of materials as tools. This category was evaluated as YES or NO.

Spreadsheet program QuattroPro 9.0 has been used for management of the ethological data. A program package Statistica 6.0 was used for computing of our quantitative data. Details on used statistical methods can be found elsewhere, (StatSoft, 1999). Significance of the tests has been set to 5 % level, however, 10 % has been taken as sufficient in exceptional cases. This is due to the frequent missing data or empty cells in tables because of numerous categories and subcategories, like species, sex and age, in examined samples which is a general problem of some biological data [Havránek, 1993].

We used mainly Statistica 6.0 Crosstabulation subprogramme in Tables and Banners Basic statistic programme (including e. g. Pearson Chi-square, Maximum-likelihood Chi-square, Fisher exact test, McNemar Chi-square, Coefficient Phi, Spearman R, Kendall tau and Uncertainty coefficients) for the statistical evaluation of data on tool use in chimpanzee, orangutan and gorilla.

Results

Monkeys

Our results have shown that not only apes but also some monkey species, namely the brown

Table 1

Primate species include in the study

Species	Year	Zoo, Laboratory
<i>Cebus apella</i>	1978	Koltushi, Russia
<i>Papio hamadryas</i>	1977–1982 2000	Sukhumi Primate Center, Abchazia, Rezervation Gumista, Abchazia, Sankt-Petersburg Zoo, Russia
<i>Pan troglodytes</i>	1977–1985 1984–2002 1999, 2000, 2002 2000, 2006 1988–2006	Koltushi, Russia Zoo Dvur Kralove, Czech Republic. Chester Zoo, U. K. Arnhem Zoo, Holand Zoo Liberec, Czech Republic
<i>Gorilla gorilla</i>	1984–2000 2000, 2006 2001–2002, 2005–2008	Zoo Dvur Kralove, Czech Republic Apeldoorn Zoo, Holand Zoo Prague, Czech Republic
<i>Pongo pygmaeus</i>	1984–2002 1999, 2000, 2002 1994–2002 1994–2006	Zoo Dvur Kralove, Czech Republic Chester Zoo, U. K. Zoo Usti nad Labem, Czech Republic Zoo Liberec, Czech Republic

capuchins (*Cebus apella*), are able to use tools both spontaneously and in directed ethological experiment (fig. 1, 2). In this experiment the following conditioned reflex was worked out with the dominating individual: to pull nearer the titbit with the help of a T-shaped stick, so that the stick placed by the experimenter on the board be pulled right to the individual, without any additional manipulations. All individuals included in the experiment could follow the process of learning by the dominating individual. Then the dominating individual “the demonstrator” was transferred to the cage housing the other individuals and the whole group “received” the task” to get hold of the titbit placed out of reach. The positions of T-shaped sticks are shown in fig. 2. At the very beginning of the experiment two capuchine monkeys tried to reach the titbit with the stick. They took the stick, threw it to the titbit and pulled it nearer. The movements of the monkeys in

this phase of the experiment were very quick and the throwing of the stick was rather inaccurate. To get the titbit they had to make 15–20 attempts and only one of the was successful.

We must add that the monkey “demonstrator” used the stick only in position a (fig. 2) while the other individuals, the “imitating” monkeys used it in position a and b. If the monkeys took the stick out of the cage, it immediately lost its “tool” characteristic and never again was it used for an attempt to get the titbit.

Experiments with capuchins have also shown that it is a process of social learning that plays an important role in ability to use tool in brown capuchins. In this respect the brown capuchins are quite close to that of the great apes [Vancatova, 1984]. This confirm some previous opinions that some New World monkeys are able of sophisticated tool using including social learning of tool using [Jalles-Filho et al., 2001]. However, there are still



Fig. 1. Capuchin use a stick as a tool (Koltushi, Russia)

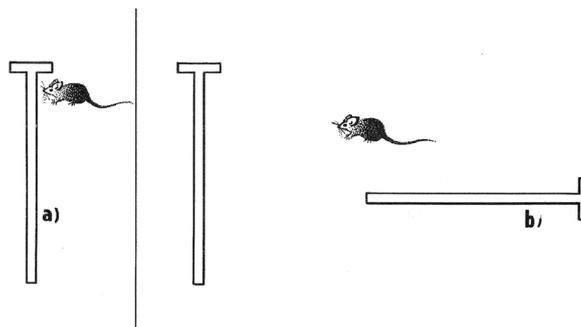


Fig. 2. The scheme of experiments with capuchins (Koltushi, Russia)

some important differences among capuchins and great apes [Chevalier-Skolnikoff, 1989].

Other experiments directed to the approaching of a distant bite by a tool have proved our previous hypothesis and common knowledge. Hamadryas baboons were not able to use spontaneously tools without preceding special process of learning (fig. 3–5). It is a remarkable difference of catarhine monkeys and great apes.

Apes

Case studies

Cataloguing of individual spontaneous tool activities in three great ape species has shown that

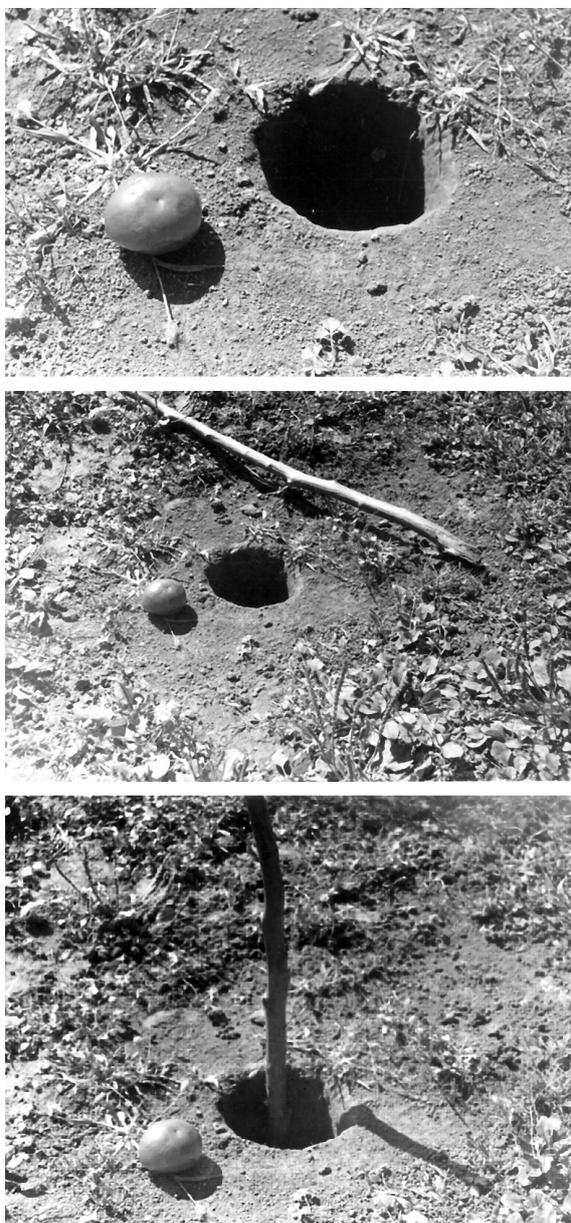


Fig. 3–5. The scheme of experiments with hamadryas baboons (Gumista natural reserve, Abchazia)

there are many common features in using of tools among great apes both under laboratory conditions, or in captivity in general, and under wild living conditions. However, our study also demonstrated how markedly, even basically, the quality and quantity of tool activities can be influenced by the equipment of a given ZOO and availability of the object suitable for manipulations and potential tool using or tool making. For example, missing of free stones in secluded area causes a very low frequency of this type of tool behaviour. Similarly, protection of trees in a secluded area, if there are any, by electric or other barriers causes that apes do not build nests in trees which is common for all examined ape species under wild conditions. It should also be mentioned that some features of great ape tool activities could be *de facto* an imitation of simulation of similar human behaviour like cleaning of windows in captive orangutans. However, some features of tool behaviour in great ape cannot be a simple imitation of human behaviour and they are apparently a part of play behaviour or even a part of a local tradition in a given ape group.

Examples of tool use activity of gorillas in captivity:

1. Spontaneous using of plastic boxes as a step-stool or seat (Prague ZOO)

In December 2005 we observed spontaneously using of boxes from the vegetable which gorillas had for the play in the cage. All females from the group used this boxes as a step-stool in which they can step. One of them brought once more box and makes pyramid from this boxes. After that she set up on the pyramids and observed the situation through the window in the indoor area (fig. 6–11). All females in Prague group used the plastic box as a stool or stand very frequently for achievement of a higher level in the indoor area.

2. Use of a box as a table or tray

Adult male Richard used the box as a table or tray in which he takes cake. He walked in bipedal position, he has a box with cake in the hands and continuing bipedal walking.

3. Spontaneous use of plastic boxes or other objects as weapons

Other way of a spontaneous use of plastic boxes as weapons was observed during conflict situations. This was especially during introducing of female Kamba into the group where the conflicts had been relatively frequent. In this

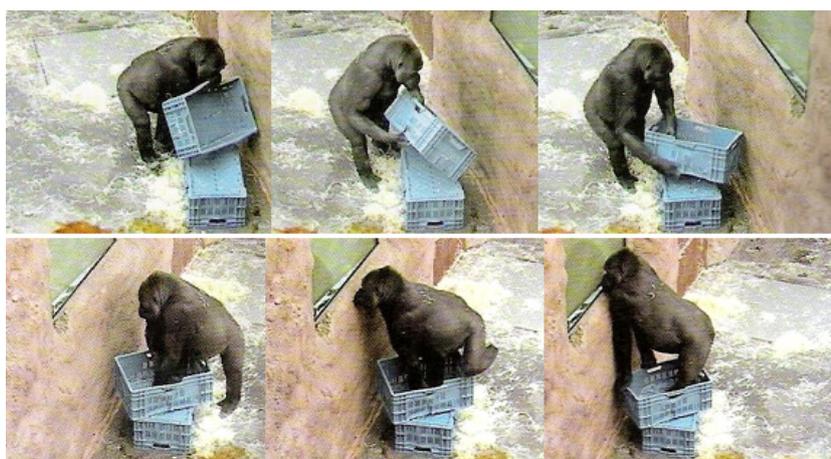


Fig. 6–11. Gorilla female makes of pyramid from the boxes

case gorilla thrown plastic box in direction of enemy as a weapon. Similar type of behaviour was observed also in 1988 in Zoo Praha. Male Assumbo picked away the bark from the stabs in the outdoor area and through them in direction of visitors. In Apeldoorn Zoo, The Netherlands, we have observed in 1999 that the subadults male use the branches in a similar way against individuals of similar age.

4. Making and use tool in an experimental situation

To make feeding behaviour in gorillas group more variable, keepers put food in a different places of the secluded area, in various holes, etc. Silverback male Richard was offered by wooden objects with hollows. The dried fruits (currant) were in those hollows. To get the fruit Richard made small sticks by a biting of branches situated in the secluded area.

5. Spontaneous use of branch to reach food

Richard, who had observed a plate with fruits left there by chance by the keeper, took a branch in secluded area and he tried to reach the plate and to snap it to the bars of the cage.

6. Spontaneous use of part of tree as a ladder

Spontaneous use of part of tree as a ladder was observed in one adult female in summer 1999 in Zoo Apeldoorn, The Netherlands. The large trees are situated in the secluded area constructed in way preventing reaching trees. One adult female took a large piece of wood putting it on a concrete wall and used it as a ladder to reach the proximate tree to climb on it. Then she eat the leafs and barks.

7. Spontaneous use of plastic boxes as drums of drummers

Gorilla females in Prague Zoo group frequently drums on plastic boxes. Such drumming differs from the chest beating during agonistic behaviour and it is in fact a way of play behavior of gorillas.

8. Spontaneous use of plastic boxes as a drum during agonistic behaviours

Drumming in such cases is not a part of play behaviour but it was clearly agonistic. In such a case gorillas put the box at chest in way like chest beating in conflict situation. Such situation has been followed by an attack and throwing box against the enemy. This behaviour has been observed in adults individuals in Prague ZOO only.

10. Spontaneous use of bedding as cushion during sitting

Adult females frequently collected cushion (excelsior), making from it accumulation resembling bedding and put it bellow it during sitting on hard surface.

11. Spontaneous nest making

Many object are used for nest making on the ground. Besides cushion (excelsior, wooden shaving) they are part of cloth, paper, paper boxes disassembled in parts, branches, etc. Gorillas put the objects around themselves in a sitting position. They frequently slept in them.

12. Spontaneous making of primitive shoes

In a winter period we observed that female Kijiwu used excelsior as a primitive shoes – “mufflers” – for the walking on the snow. Kijiwu kept the excelsior pillows (from the wooden shaving) by the foot fingers. Similar behaviour was observed a year later when the ground in

the cage was wet after cleaning. Kijiwu used the excelsior pillars again as a primitive shoes to walk across the wet part of the ground.

Tool behaviour of apes in captivity

We have found in our study that tool activities became a part of various types of behaviour. They usually occur during feeding, aggression, games or other play behaviour, and during social and comfort behaviour as well. Investigatory probe, play-start, drag-branch, leaf-sponge, comb, insect-pound, leaf-wipe, ground-night-nest, food-pound onto wood, food-pound onto other, club, fluid-dip, lever open, aimed-throw, leaf-napkin, power, toothpick, springle, loopback, jamping with pole, cover, are the most frequent type of tool in all examined groups of chimpanzees. Adult chimpanzee females have statistically significant occurrence of combination stick – termite nest. Branches or clubs are relatively frequently used as a weapon in chimpanzees. Stick is used for many purposes and in a broad behavioural context. Substrate and cloth are other tools usual during tool activities in great apes namely in orangutans.

Tool manufacturing or modification has been studied in adult great apes only. Any kind of tool modification is very rare in great ape males and if there is any the tool modification is exclusively made by the right hand. Females modify the tool more frequently but again with right hand

preference but they frequently use also both hand during the modification process.

There is extremely interesting situation in tool using in chimpanzee females. Since juvenile age chimpanzee females prefer left hand to manipulate with wooden sticks at the artificial termite nests in Chester ZOO. They use the same hand for putting stick into the nest and taking it out of the nest (fig. 12, 13).

However, while juvenile females are almost exclusively left handed (possible imitation of mother behaviour) subadult females use relatively frequently both hands. The situation changes in adult females where right hand is preferred in approximately one third of the observed cases.

Adult males use for manipulation with wooden sticks at artificial termite nests either right or left hand respectively. Using of both hands has never been observed. Adult females use left hand in approximately two third of observed cases, right hand in almost one third of the cases and both hands use makes about 5 % of this tool behaviour.

Our experiments with young chimpanzees with approaching of a distant object (bite most usually) have shown that there is an evident relation among manipulation abilities and brain development in chimpanzee youngsters. Chimpanzees are able of active tool using and manipulation as late as in two years of age and they were able to make a more complicated tool in age of 40 months only. The process of learning by the method of trial and

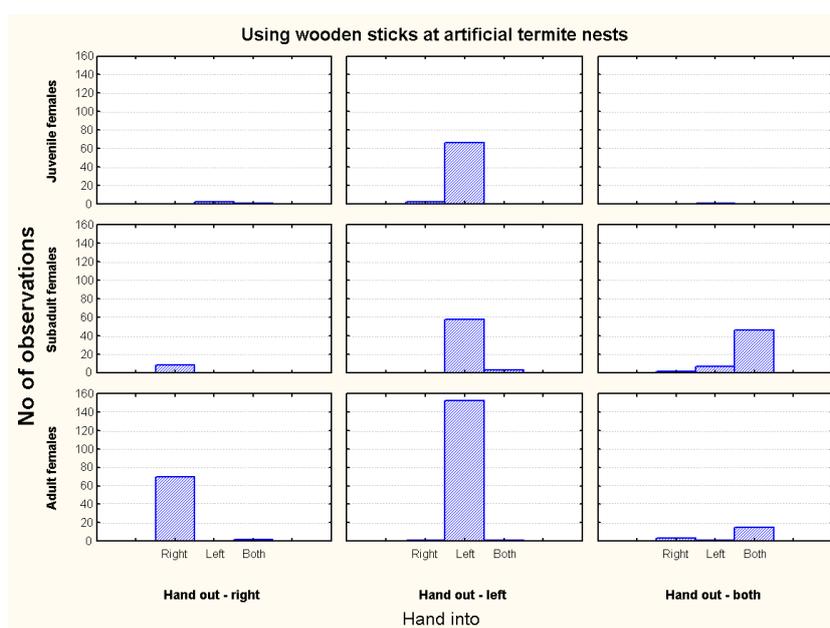


Fig. 12. Using sticks by chimpanzees at artificial termite nest (Chester Zoo, U.K.) – Hand into the hole

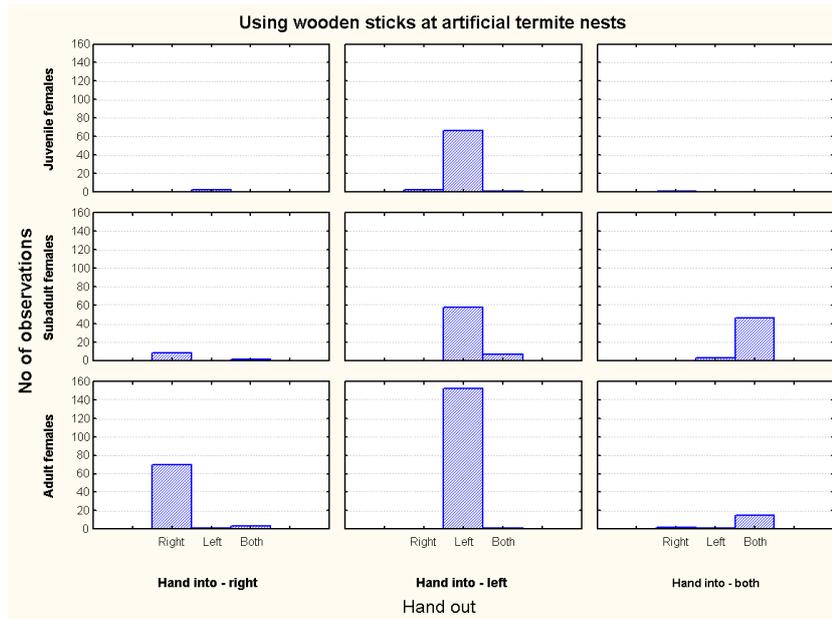


Fig. 13. Using sticks by chimpanzees at artificial termite nest (Chester Zoo, U.K.) – Hand out from the hole

error and an imitation of adult individuals plays an important role in ontogeny of tool behaviour in chimpanzees.

We have found some specific differences in our study in analysis of using of a tool with a same purpose. The way of using of a tool and the material of the tool differ in three ZOO where the chimpanzees were studied. In this case the existence of local traditions or even local cultures in individual ZOO's can be discussed in connection with the a different way of transmission of abilities and specific differences in tool behaviour in a three studies groups of chimpanzees.

Two activities, nest building and covering, clearly prevailed in all examined orangutans, both male and females. The nests are usually build from paper, substrate or cloth and paper and cloth are the most frequent objects for covering. Tool activities are somewhat more variable in adult orangutans where using of a stick for approaching of an object occurs occasionally.

Our results have shown very specific tool behaviour in orangutans. Plain tools strongly prevails for various purposes while the stick is used rarely mostly in adults. The character of tools in orangutan induces also the way of hand use. Both hands are the most usual combination followed by right hand use in most remaining cases.

Our results of hand preference in orangutans correspond to those from observation of wild living populations. Strong preference of a right hand in using of non-plain tools is in well confidence

with our study of laterality during picture-making activities, where the orangutans are highly right handed.

Plastic boxes become something like universal tools for gorilla from ZOO Praha, similarly to the stick tools in chimpanzees. Perhaps it is a raising tool tradition also in Prague gorillas, however, this tradition has apparently no analogy in wild conditions. Nevertheless, the plastic box using becomes ritualized in many cases in agonistic behaviour for example where the using of boxes is a transmitter of an aggression of as an drumming amplifier.

Conclusions

The comparative analysis of tool behaviour in captive great apes is not easy at all. Despite the fact that each of the examined species have certain features that correspond more or less to those of wild living conditions, there are many specific factors that are able substantially influence character of tool behaviour of captive primates and namely great apes. In our study for example, it has been a regular environmental enrichment that could initiate a monopolization of tool behaviour around the artificial termite nest in Chester chimpanzees, presence of paper and cloth could increase specific tool activities in orangutans and presence of plastic boxes in cage could originate in a specific and very variable tool behaviour in Prague gorillas. We can even

speculate that such factors could have caused the origin of a local tradition, like left hand use at the termite nest in chimpanzees and plastic box tradition in examined gorillas.

The differences in hand preference in chimpanzee females on the one hand and females of gorillas and orangutans are of a high importance. However, it is difficult to judge how important is a genetic predisposition for left hand preference and how important is a role of social learning in the chimpanzee Chester group. Nevertheless, recently published study of wild living chimpanzees [Lonsdorf, Hopkins, 2005] present almost identical results to those of our study.

Accordingly, we can conclude that chimpanzees have some degree of laterality, where the use of hand depends on the tool that is used. Both captive and wild living chimpanzees prefer left hand during tool activities at termite nests.

An analysis of current hypotheses on the origin of tool behaviour in primates has demonstrated that, in our opinion, more basic factors had played role in the origin and evolution of tool behaviour, tool using and tool making. It is not possible to select just one of them, like play, aggression, presence of specific object in the living environment. We suppose that this process had a more complex nature and there were at least several important factors, or group of the factors. Some of them were important for changes in behaviour and social learning others for improving of manipulation and brain abilities.

Acknowledgements

The author especially want to thank Vaclav Vancata, Faculty of Education, Charles University in Prague for the help with the statistical analysis of the data, and the ape keepers for their kind co-operation with this study. Our thanks go also to Miroslav Bobek and his co-workers from the Radio station Leonardo Prague, Czech Republic) for the video and photo documentation of gorillas behaviour.

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Материал поступил в редколлегию 03.09.2008