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Cognitive Brain Research 25 (2005) 210 – 216
COGNITIVE BRAIN RESEARCH
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Research Report

Hand preferences for unimanual and coordinated bimanual tasks in baboons (*Papio anubis*)

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Accepted 18 May 2005
Available online 1 July 2005

Abstract

This study examined hand preference in baboons in a sample of 94 subjects for a unimanual task and in a sample of 104 subjects for a bimanual task. For the unimanual task, handedness was assessed by observing simple reaching for grains. For the bimanual task, tubes lined with peanut butter inside were presented to the baboons. The hand and the finger used to remove peanut butter were recorded. Population-level right-handedness was found for the bimanual but not the unimanual task. In addition, test–retest correlations showed consistency in hand use across time for the coordinated bimanual task but not the simple reaching task. No significant effects of age and sex on the direction and strength of hand preferences were found for either task. These are the first evidences of population-level handedness in baboons and the results are discussed in the context of evolutionary theories of cerebral dominance.

Theme: Neural basis of behavior
Topic: Learning and memory: systems and functions—animals

Keywords: Handedness; Laterality; Grasping; Moto skill; Bimanual coordination; Monkey

1. Introduction

Research on handedness in nonhuman primates continues to be a topic of significant interest in comparative psychology and neuroscience. Historically, right handedness was considered a hallmark of human evolution [38] but a number of recent studies in various primate species have reported evidence of population-level handedness (see Refs. [3,23,37]. Despite the evidence of population-level handedness in nonhuman primates, there remain many who are skeptical of the findings in terms of consistency between samples of primates and the generality of findings between species [31,32]. From a comparative perspective, one of the difficulties in comparing the distribution of handedness in different primates is the lack of similar or identical tasks between studies and species. If common measures are not used between species, then any differences observed could be attributed to the tasks rather than the species variable. Thus, comparative studies of handedness using identical measures are critical for evaluating and creating a reasonable evolutionary time frame for the emergence of population-level handedness in human and nonhuman primates. One purpose of this study was to compare the handedness of baboons with findings previously reported in apes and monkeys on a measure requiring coordinated bimanual actions, referred to as the TUBE task. The TUBE task was originally described by Hopkins [18] in chimpanzees and since the original publication, additional species have been tested including gorillas and orangutans [25], rhesus monkeys [39,40], and capuchin monkeys [34,39]. For the TUBE task in apes,

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doi:10.1016/j.cogbrainres.2005.05.012

Hopkins et al. [25] found population-level right handedness in chimpanzees and population-level left-handedness for the orangutans. Gorillas were borderline significant right-handed and therefore were more similar to the chimpanzees than orangutans. In Old World monkeys, Westergaard and Suomi [39] initially reported population-level right-handedness in rhesus monkeys but then reported left-handedness in nursery-reared infant rhesus monkeys [40]. More recently, Bennett, Suomi, and Hopkins [2] found no evidence of population-level handedness for the TUBE task in a sample of 120 rhesus monkeys. In New World monkeys, Westergaard and Suomi [39] found no evidence of population-level handedness in capuchin monkeys while Spinozzi et al. [34] found evidence of population-level right-handedness in the same species.

To date, baboons have not been tested on the TUBE task and we sought to evaluate whether any evidence of population-level handedness was evident in this species for this measure of hand use. The TUBE task was selected as the bimanual task for several reasons. First, as noted, the TUBE task has been measured in other species and therefore our results could be compared to other species. Second, at least in chimpanzees, the TUBE task has good test–retest reliability over time, across test sessions and between different samples of chimpanzees [21,24,26]. Lastly, hand preferences for the TUBE task, but not other measures of hand use, correlate with neuroanatomical asymmetries measured from magnetic resonance imaging [22]. Thus, the TUBE task has neurobiological correlates in the chimpanzee brain compared to other measures of handedness. Arguably, these findings collectively make the TUBE task an ideal measure of manual specialization in nonhuman primates.

The second purpose of the current study was to evaluate the influence of unimanual and bimanual tasks on handedness in baboons. Recently, it has been argued that tasks requiring bimanual coordination are important for eliciting individual and species-level handed preference because the hands must be used in a coordinated fashion with different roles of each hand (e.g., Refs. [5,6,9,15,19]. Moreover, tasks requiring coordinated actions remove the potential influence of postural or situational factors on the expression of hand preference, unlike tasks requiring unimanual actions such as simple reaching, the most common measure of hand use employed in nonhuman primates (see Ref. [28] for review). It was hypothesized that if bimanual handedness tasks are more sensitive to individual and species-level handedness, then the baboons should be more lateralized for the bimanual than unimanual handedness task.

2. Methods

2.1. Subjects

A sample of 147 captive baboons (*Papio anubis*) participated in this study. The baboons ranged in age from 1 to 22 years ($M = 6.98$, SE = 0.42). The monkeys were born and raised by their conspecific mothers at the Primate Field Station of the Centre of Primatology (Rousset, France). The baboons were housed in different outdoor compounds (from 15 to 650 m^2) and each compound was connected to an indoor building. The baboons were living in large, relaxed, social groups with minimal interactions with humans. Each outdoor compound contained a wooden climbing structure with a sliding ramp and tires to swing on for the animals. The baboons could pass freely between the indoor building and outdoor compound, except during observation periods when they were locked in the outdoor compound. Water was available ad libitum and monkey chow, fresh fruits, and vegetables were given in the late afternoon after the day's last test. Three times a week, the monkeys were given bananas, white cabbage, oranges, and corn.

2.2. Procedure

Two different behavioral tasks were used to assess hand preferences in the baboons: a unimanual task and a coordinated bimanual task referred to as low-level and high-level manual activities according to Fagot and Vauclair [10,12]. Ninety-four animals (41 males and 53 females—19 juveniles, 28 adolescents, and 47 adults) were tested with a unimanual task and 104 monkeys (38 males and 66 females—11 juveniles, 20 adolescents, 68 adults, and 5 unknowns) were tested with a bimanual task.

2.2.1. The unimanual task

Hand preferences for the unimanual task were assessed by observing hand use when reaching for food. Previous studies have shown that posture can influence hand preferences for reaching (see Ref. [41]); thus, some constraints on hand use were followed to minimize postural influences on hand use and to allow a free choice between the two hands. Specifically, during each trial, the subject had to be seated and had to grasp food in front of it in sagittal median plan to count as a reaching response. A mixture of different small grains was abundantly dispersed in the baboons' park to favor seated posture and to limit competition between animals.

All baboons were tested in the social group. An individual animal was the "focal" animal until at least 100 responses were made by this animal. The hand used to grasp the grains was recorded for each response. A minimum of 100 responses was required for each subject. All data were collected during a single test session. If the number of responses of the "focal" animal was insufficient, grains were dispersed again until 100 responses or more were recorded. Twenty baboons were retested 4 months after the initial testing session to assess consistency in hand use for this task.

2.2.2. The coordinated bimanual task

Hand preferences for a coordinated bimanual task were assessed using an opaque poly-vinyl-chloride (PVC) tube (see Ref. [18] and Fig. 1). The tubes were 4 cm in diameter and 24 cm in length. Prior to each set of observations, peanut butter was smeared on the inside of the tube with a stick at approximately 4 cm from the edge. The tube was given to the baboons in social groups (in their home cage or in the park). Several subjects began to use their tongue to remove peanut butter before inserting one finger in the tube while holding it with the opposite hand. Often, dominant baboons were the first of their group who got the tube and this behavior limited the number of subjects that could be tested. Thus, we collected data from subordinate animals via different ways. Firstly, when dominant baboons decided to drop the tube, subordinate animals could try to remove food from it. Secondly, we isolated some of them to perform the bimanual task (those that would willingly leave their group). Thirdly, dominant baboons were also isolated in order to enable us to test other animals. Fourthly, we provided additional tubes to animals that remained in social groups so as to minimize competition between individuals. In these cases, we focused on a focal subject within a testing session. As a result, the distribution of dominant and subordinate animals in our sample is well balanced. The hand and the finger used to remove the peanut butter were recorded until the subject dropped the tube or stopped extracting the peanut butter. A trial was recorded each time a baboon inserted its finger in the tube and brought it to its mouth. Feeding attempts while using the feet to hold the tube were not recorded as a response. A minimum of 15 responses was obtained from each subject. Each tube was fastened to a chain in order to recover it after observations. Twenty-one baboons which were initially tested on the bimanual task were retested 8 months later in order to assess consistency in hand use for this task.

Fig. 1. Picture of an adult Olive baboon performing the TUBE task.

2.3. Data analysis

Following the handedness literature (see Ref. [20]), we have used two different methods to characterize individual handedness for each measure. First, a z score was calculated for each subject on the basis of the total left- and right-hand responses. This score was used to classify baboons as left-handed ($z \leq 1.96$), right-handed ($z \geq 1.96$), or ambiguously handed ($-1.96 < z < 1.96$). Secondly, a handedness index (HI) was calculated for each animal to quantify the degree of individual lateral biases following the formula HI = [(number right responses minus number left responses)/(Total responses)]. The HI varied on a continuum from -1.0 to 1.0. Positive values and negative values indicate a right-hand bias and a left-hand bias, respectively. The absolute values (ABS-HI) reflected the strength of hand preference.

3. Results

3.1. Direction of hand preference

3.1.1. Unimanual task

Ninety-four baboons were tested with this task. On the basis of individual z scores, 27 baboons were classified as right-handed, 25 left-handed, and 42 as ambiguously handed. This distribution did not differ significantly from chance based on a chi-square goodness-of-fit test, $\chi^2(2, N = 94) = 5.51$, $P > 0.05$. In addition, the difference between the number of right-handed and the number of left-handed subjects was not significant, $\chi^2(1, N = 52) = 0.08$, $P > 0.05$, indicating that there was no population-level handedness in this sample of baboons for this measure. Analysis of the HI data confirmed the chi-square results. A one-sample t test failed to reveal a significant population-level bias $t(93) = 0.06$, n.s. (mean HI = 0.00, SE = 0.05).

3.1.2. Coordinated bimanual tube task

One hundred and four baboons were tested on this task. The number of responses per subject varied from 17 to 311 observations ($M = 79.52$, SE = 5.65). On the basis of individual z scores, 52 subjects were classified as right-handed, 33 as left-handed and 19 as ambiguously handed. This distribution significantly differed from chance based on a chi-square goodness-of-fit test, $\chi^2(2, N = 104) = 15.83$, $P < 0.001$. Additionally, the number of right-handed baboons was significantly higher than the number of left-handed $\chi^2(1, N = 85) = 4.25$, $P < 0.05$ and ambiguously handed subjects, $\chi^2 (1, N = 71) = 15.34$, $P < 0.001$. Thus, for the TUBE task, there was a population-level right-handedness in this sample of baboons. The mean HI score was equal to 0.13 (SE = 0.06), and this result shows a clear right-hand bias in the population, as revealed by a one-sample t test

$t(104) = 2.16$, $P < 0.05$. It is interesting to note that the mean ABS-HI score per subject is very similar for right- (MHI = 0.66, SE = 0.04) and left-handed subjects (MHI = 0.65, SE = 0.04), indicating that strength of hand preference did not differ between these two cohorts.

It has been suggested by some authors (e.g., Ref. [32]) that the individual differences in the total number of responses can skew the distribution of handedness values. Because the total N varied between 17 and 311 responses, whether the variation in z scores was potentially skewed by sample size was assessed by creating a funnel plot. The sample sizes were plotted against the individual z scores and, as can be seen on Fig. 2, as sample sizes increased, fewer ambiguously handed individuals fell in the center of the funnel. This indicates that sampling bias and variation in the total number of responses do not explain the observed pattern of population-level handedness for the tube task.

3.2. Digit use on the TUBE task

As noted in the Methods section, we recorded the digit used by the baboons to extract the peanut butter from the tube. On average, 92.4% of the insertions into the tube were made with the index digit, 7.4% with simultaneously two or three digits (including 7.3% with the index and middle digits), and 0.2% with the thumb. A within-subjects design ANOVA (with data of simultaneous use of several digits and data of use of the thumb collapsed into one category because the thumb was rarely used) indicated that this difference was significant, $F(1,170) = 1034.04$, $P < 0.001$.

3.3. Consistency in hand use

Consistency and stability in hand use between the two test sessions were assessed by calculating a Pearson product–moment correlation on the HI scores of the 20 baboons tested on simple reaching and the 21 baboons tested on the TUBE task. For simple reaching, the correlation coefficient was positive but not significant: $r(18) = 0.34$, $P > 0.10$, indicating that hand preferences assessed via this unimanual task were not consistent and stable across time. In contrast, for the TUBE task, a significant positive correlation coefficient was found: $r(19) = 0.66$, $P < 0.01$. This indicates that hand preferences assessed with the tube task were consistent and stable across time in our sample of baboons.

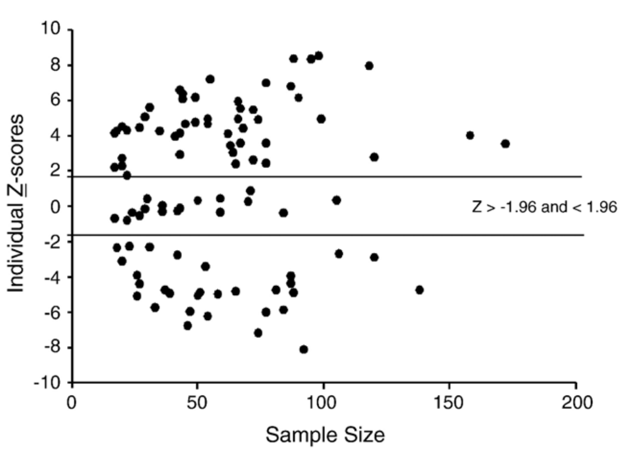

Fig. 2. Funnel plot of sample size (N) against the z scores for all individuals tested on the TUBE task. Lines indicated z-score values of −1.96 and 1.96, which represent the values at $P < 0.05$.

3.4. Potential effects of age and sex

3.4.1. Direction of hand preference

The effects of age and sex were assessed using an analysis of variance (ANOVA) with the HI score serving as the dependent measure. For the TUBE task, no significant differences in direction of hand preference were found between age classes, $F(2,99) = 0.31$, $P > 0.05$ (the mean HI score per subject was 0.22, SE = 0.22 for juveniles, 0.19, SE = 0.12 for adolescents, and 0.09, SE = 0.08 for adults), or between sexes, $F(1,104) = 0.08$, $P > 0.05$ (the mean HI score per subject was 0.14, SE = 0.10 for males and 0.10, SE = 0.08 for females). For the unimanual task, no significant differences in direction of hand preference were found between age classes, $F(2,94) = 0.21$, $P > 0.05$ (the mean HI score per subject was −0.02, SE = 0.12 for juveniles, −0.05, SE = 0.11 for adolescents, and 0.03, SE = 0.08 for adults), or between subject sexes, $F(1,94) = 0.68$, $P > 0.05$ (the mean HI score per subject was 0.05, SE = 0.08 for males and −0.04, SE = 0.08 for females).

3.4.2. Strength of hand preference

An analysis of variance (ANOVA) with the ABS-HI score serving as the dependent measure indicated no significant differences in strength of hand preference for the tube task between age classes, $F(2,99) = 1.65$, $P > 0.05$ (the mean ABS-HI score per subject was 0.68, SE = 0.08 for juveniles, 0.47, SE = 0.07 for adolescents, and 0.55, SE = 0.04 for adults) and between subject sexes, $F(1,104) = 0.22$, $P > 0.05$ (the mean ABS-HI score per subject was 0.56, SE = 0.05 for males and 0.53, SE = 0.04 for females).

For the unimanual task, no significant differences in strength of hand preference were found between age classes, $F(2,94) = 0.10$, $P > 0.05$ (mean ABS-HI score per subject was 0.36, SE = 0.08 for juveniles, 0.41, SE = 0.07 for adolescents, and 0.39, SE = 0.05 for adults) and between sexes, $F(1,94) = 1.92$, $P > 0.05$ (mean ABS-HI score per subject was 0.34, SE = 0.06 for males and 0.44, SE = 0.05 for females).

3.5. Comparison in handedness between unimanual and bimanual tasks

Lastly, forty-nine subjects were tested on both the unimanual and bimanual tasks. To test whether shifts in hand preference were evident in the same individuals depending on the nature of the handedness task, we compared the HI and ABS-HI scores for these individuals. The baboons were significantly more right-handed for the TUBE (mean = 0.15) compared to the reaching task (mean = −0.10), $t(48) = 2.96$, $P < 0.005$. In addition, the baboons were significantly more lateralized for their hand use in the TUBE (mean = 0.56) compared to the reaching task (mean = 0.41), $t(48) = 2.41$, $P < 0.006$.

4. Discussion

Several significant findings were revealed in this study. Firstly, baboons exhibited population-level right-handedness for a coordinated bimanual handedness task but not for simple reaching. Secondly, the monkeys most frequently used their index finger to extract the peanut butter from the tube when compared with other fingers. Thirdly, age and sex did not have a significant effect on either the direction or strength of hand preference. Finally, hand preferences for the TUBE task were stable and consistent over time whereas hand preferences for simple reaching were not. These results strengthen the interest of using the coordinated bimanual tube task instead of a unimanual task to assess handedness in populations of nonhuman primates. The use of coordinated bimanual and/or complex manual tasks has already been stressed (Refs. [10–12,19]) in order to obtain reliable indices of hand preferences.

Concerning the results of the unimanual task, the symmetrical distribution of hand biases for the population and the instability of individual hand preferences across time are consistent with previous findings in baboons [35]. The cumulative results lead us to conclude that the manual preferences obtained with this measure are a poor indicator of hemispheric specialization. Thus, hand preferences assessed using this kind of task seem to be under the influence of situational, postural and environmental factors. Simple reaching is considered a low-level manual activity with little motor or cognitive demands and this might explain the lack of pronounced preference for this measure [12].

Concerning the results of the TUBE task, the significant population-level right-handedness and the stability of individual manual asymmetries across time can be explained within the context of a specialization of the contralateral hemisphere. The TUBE task is considered as a high-level manual activity which required the coordinated use of the two hands and this constraint tends to minimize postural and situational influences on hand use [18]. Moreover, the complexity of the TUBE task from a motor and cognitive viewpoint might explain the emergence of hemispheric asymmetry for motor skills. It has been argued that bimanual coordination in the use of tools or feeding [6,7] could have a significant role in the appearance of human handedness and our results support this view. We would also stress that the TUBE task is a reliable and simple means to assess handedness from an experimental perspective. The TUBE task does not require training; it is effective, fast, and easy to set up and to repeat as many times as necessary. In addition, this task is sufficiently complex to induce hemispheric lateralization in a significant proportion of the subjects.

The significant preference for the index digit to extract the peanut butter from the tube by the baboons is consistent with the digit preference observed in other nonhuman primates that have performed the TUBE task (for example: chimpanzees, Ref. [18], macaques and capuchins, Ref. [39]). According to Hopkins [18], this finding suggest that the bimanual tube task required distal movements of the fingers and hand which are characteristic of a greater use of the contralateral hemisphere unlike gross or ballistic movements [4]. This may explain the evident lateral bias toward the use of right hand in the baboons.

One criticism that has been raised concerning the TUBE task is the use of events data to assess hand preferences compared to bouts of hand use for this task (see Refs. [5,29,31,32]). Specifically, it has been argued that each sequence of food extraction is not independent from the other and this may bias the data. We do not believe this argument can explain our results for two reasons. First, previous studies in chimpanzees have shown that the use of bouts compared to frequencies in hand use for the TUBE task has no effect on the handedness expression [24,27]. Second, it is argued that the recording of frequency in hand use for the TUBE tasks biases the data by increasing sample size (or N) and this enhances the probability of subjects being characterized as left- or right-handed. Certainly, recording frequency rather than bouts of hand use results in a larger sample size but there is no a priori to assume that recording frequency would result in more subjects being classified as right-handed. Presumably, recording frequency of hand use would be randomly distributed among left- and right-handed subjects (see Ref. [20]).

The present study is the first report of population level right-handedness in a baboon species. For comparison of

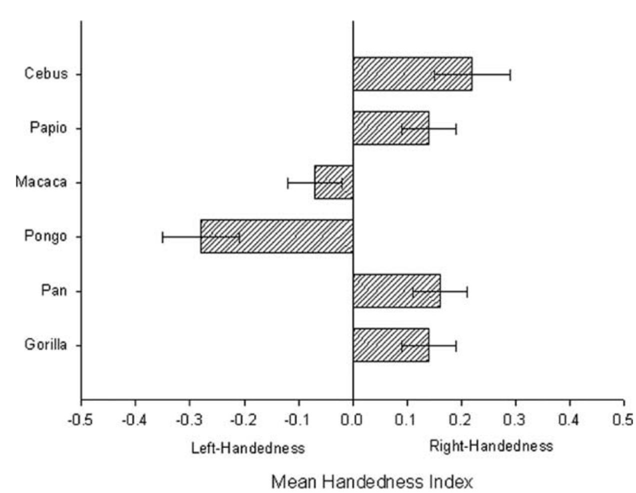

Fig. 3. Mean handedness indices (HI) (and SE) for different primate species that have been tested on the TUBE task. Papers contributing to the means included Refs. [2,23,24,34,39,40] and this study.

our results to previous findings on handedness in nonhuman primates using the TUBE task, we have plotted the mean handedness index for each species in Fig. 3. Unlike other Old World monkeys, such as the rhesus monkey, the baboons appear right-handed and more so resemble findings in gorillas and chimpanzees. The explanation for the handedness results in various primate species is not immediately clear. One interpretation might be that these results are consistent with the predictions of the postural origins theory of handedness (see Ref. [30]). The postural origins theory states that arboreal species (such as orang-utans) preferentially use their left hand for manual actions like grasping food, while the opposite hand is used to support the body in the trees whereas more terrestrial primates rather display a right-hand preference for manual tasks (e.g., chimpanzees, gorillas). Because baboons are highly terrestrial primates, the evidence of a right-hand bias is consistent with the postural origins theory but the lack of significant findings in rhesus monkeys, another terrestrial primate, is not. Rhesus monkeys and baboons also differ with respect to their handedness for simple reaching (see Ref. [28]). Several studies in semi-free ranging rhesus monkeys have reported population-level left-handedness [2,13,16], whereas semi-free ranging baboons show no significant population bias for simple reaching (Ref. [35]; this study). Thus, at least for these two species of primates, the overall results only partially support the postural origins theory. We can add that data from human studies indicating that both children and adults show consistent right-hand preferences for simple reaching (e.g., reaching for a small ball placed on a table); however, these biases are weaker (~60%) than those exhibited in bimanual or more complex manual tasks (see for a review: Ref. [14]).

The proportion of right-handedness observed for the TUBE task in the baboons was comparable to those reported in chimpanzees (see Ref. [21]), but it is significant to note that both species show significantly less right-handedness than what is often reported for humans (see Ref. [1]). The factor (or factors) that explain the difference in proportion of right- to left-handedness in human and nonhuman primates remains unclear. Some have suggested genetic factors (e.g., Ref. [8]) while others have postulated socio-cultural factors (e.g., Refs. [23,36]). Additional research is needed to resolve these potential explanations.

In conclusion, the results of this study showed significant population-level right-handedness in baboons for a task measuring coordinated bimanual actions but not simple reaching. It is argued here that the coordinated bimanual tube task is a reliable procedure to assess handedness in nonhuman primates and that the observed bias for this task more likely reflects a specialization of the hemisphere contralateral to the preferred hand (see Ref. [22]). Certainly, there is some evidence that unimanual tasks can elicit population-level handedness in nonhuman primates, particularly when the postural demands of the tasks increase (e.g., Refs. [17,33,37]), but our findings suggest that, when most situational factors are controlled, bimanual tasks elicit more consistent and robust degrees of hand use. Future research on primate handedness could benefit substantially by focusing on tasks or naturally occurring behaviors requiring bimanual coordination rather than simple, low-level tasks that have dominated previous studies. By focusing on measures of handedness that remove the potential influence of situational or postural factors as well as requiring complementary motor actions in different primate species, our understanding of the evolution of handedness will based on better methodological and theoretical grounds.

Acknowledgments

We are grateful to Dr. Guy Dubreuil for permission to conduct the study at the CNRS Field Station of Rousset. We also thank the caretakers and technical staff for their assistance and also Haurore Chautay and Julien Donnot for collecting some of the data. This research was supported by a grant from the European Science Foundation EUROCORES-OMLL program "The Origin of Man, Language and Languages" and by the French program OHLL (CNRS) "L'Origine de l'Homme, du Langage et des Langues".

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