

Monkeys and Apes: Are Their Cognitive Skills Really So Different?

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ABSTRACT Differences in cognitive skills across taxa, and between monkeys and apes in particular, have been explained by different hypotheses, although these often are not supported by systematic interspecific comparisons. Here, we directly compared the cognitive performance of the four great apes and three monkey species (spider monkeys, capuchin monkeys, and long-tailed macaques), differing in their phylogenetic-relatedness and socioecology. We tested subjects on their ability to remember object locations (memory task), track object displacements (transposition task), and obtain out-of-reach rewards (support task). Our results showed no support for an overall clear-cut distinction in cognitive skills between monkeys and apes as species performance

varied substantially across tasks. Although we found differences in performance at tracking object displacements between monkeys and apes, interspecific differences in the other two tasks were better explained in terms of differential socioecology, especially differential levels of fission–fusion dynamics. A cluster analysis using mean scores of each condition of the three tasks for each species suggested that the only dichotomy might be between members of the genus *Pan* and the rest of the tested species. These findings evidence the importance of using multiple tasks across multiple species in a comparative perspective to test different explanations for the enhancement of specific cognitive skills. *Am J Phys Anthropol* 143:188–197, 2010. © 2010 Wiley-Liss, Inc.

The last two decades have witnessed an intense debate about the selective pressures that have shaped the evolution of intelligence in primates and other animals. Although some hypotheses have focused on ecological aspects (Clutton-Brock and Harvey, 1980; Milton, 1981; Harvey and Krebs, 1990; Reader and Laland, 2002; Zuberbuehler and Byrne, 2006) others have focused on social (Jolly, 1966; Humphrey, 1976; Byrne and Whiten, 1988; Dunbar, 1998) or socioecological aspects (Barrett et al., 2003; Dunbar and Shultz, 2007; Aureli et al., 2008). In addition, there has also been much discussion about how different cognitive skills vary across different taxa, and whether this variation should be attributed to the existence of differently enhanced domain-specific skills across taxa, rather than to different levels of domain-general cognitive abilities (or “g” for general intelligence) (e.g., Bitterman, 1965; Macphail, 1987; Banerjee et al., 2009). Focusing on primates, several authors have argued that ape cognition is substantially different from that of monkeys. Rumbaugh and Pate (1984) plotted performance on the transfer index (a measure of reversal learning that corrects for the effort devoted to learn the original discrimination) in various primate species and argued for a difference between great apes and other primates. However, although their effort was mainly aimed to compare primate species after eliminating the influence of species’ specific cognitive skills, the transfer index only tackled visual learning and could not be considered a real measure of “g.” Deaner et al. (2006) conducted a meta-analysis on a larger number of species

and multiple tasks on learning and problem solving and concluded that great apes outperformed other taxa in their overall performance. They interpreted the data as evidence for a significant difference in “some sort of ‘g’” between monkeys and apes. Byrne and Whiten (1988) also noted a disproportionate number of tactical deception episodes reported for great apes as compared to monkeys and prosimians. They interpreted the data in support of the idea that great apes possess more sophisticated mind-reading abilities than other primates. Mirror self-directed behavior, and its implications for self-awareness (Gallup, 1982), is another area where important differences have been uncovered between monkeys and apes (Anderson,

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1984; Inoue-Nakamura, 1997). More recently, some authors have suggested that great apes show enhanced cognition in complex manipulatory skills or future planning when compared to monkeys (e.g., Byrne, 1995; Barrett et al., 2003), but they have produced no systematic comparative data to support such arguments.

In contrast to the view of phylogenetic differences in cognitive skills, Tomasello and Call (1997) argued that the cognitive differences between monkeys and apes are not substantial and had often been overestimated. These authors noted that much of the data showing the most striking differences between apes and monkeys derived from comparing untrained monkeys to a few intensively studied and often highly human-trained chimpanzees and bonobos (Rumbaugh, 1977; Matsuzawa, 1985; Savage-Rumbaugh, 1986; Biro and Matsuzawa, 2001; Beran, 2004). Such comparison is problematic because highly trained apes often outperform untrained conspecifics (Call and Tomasello, 1996; Bania et al., 2009). Moreover, there is also much evidence based on systematic comparisons that counters the ape-monkey dichotomy. For example, a study measuring object manipulation in 74 different primate species grouped capuchin monkeys together with the two apes, while the other monkeys were divided in two groupings, regardless of phylogenetic relatedness (Torigoe, 1985). Other studies have showed that not only apes but also monkey species can engage in tactical deception, with subordinates being able to withhold information from dominant partners (e.g., Coussi-Korbel, 1994; Ducoing and Thierry, 2003; Amici et al., 2009). Methodological shortcomings might also explain some of the putative cognitive differences between monkeys and apes. For instance, although apes and monkeys have been suggested to have different mind-reading capabilities, this position is currently debatable in light of recent systematic studies on perspective taking in monkeys (e.g., Flombaum and Santos, 2005; Santos et al., 2006a; see Call and Santos, in press, for a review).

The narrow focus of much comparative research has compromised the broad generalizations with regard to ape-monkey cognition. Such narrow scope derives from three main sources. First, primate cognition, just like much of comparative psychology (Beach, 1950), has greatly focused on few primate species, such as chimpanzees, macaques, and capuchin monkeys, so that ape-monkey comparison has been often reduced to chimpanzee-macaque or chimpanzee-capuchin monkey comparisons (Call and Mendes, Unpublished manuscript. Chimpanzism: a continuing problem in ape cognition research). Although the situation has improved in the last 50 years (Shettleworth, 2009), great disparities in the research attention devoted to various genera still remain. Even those studies including multiple species of monkeys and apes have indeed paid little attention to the "unexpected" but potentially revealing differences in performance between species. For instance, Deaner et al. (2006) attached little importance to the fact that spider monkeys outperformed gorillas (and other monkey species) in their meta-analysis, thus challenging a neat ape-monkey segregation. Amici et al. (2008) explicitly addressed the issue of spider monkeys' "peculiar" position in a study on inhibitory control in seven primate species. They found that spider monkeys outperformed gorillas and other monkey species in a series of cognitive tasks, thus confirming Deaner et al.'s (2006) findings. Following Aureli et al. (2008), they argued that socioecological factors, in particular high levels of fission-fusion dynam-

ics, were important in the enhancement of certain cognitive abilities such as inhibitory control.

Second, most comparative studies have a narrow focus, concentrating on few but frequently investigated abilities (e.g., learning) while disregarding other less investigated but equally important aspects of cognition. However, in their everyday lives, primates use several abilities to solve problems, like memory and reasoning. Remembering the location of hidden objects, tracking their movements in space and using objects to get access to out-of-reach rewards (i.e., tool functionality), for example, allow individuals to deal with several daily physical and social challenges and are therefore important skills that deserve further analysis (Barth and Call, 2006; Herrmann et al., 2008). Despite having so far received little consideration, the systematic investigation of these skills would clearly contribute to the comparative study of cognition.

Third, some of the tasks used to compare primate taxa are substantially biased in favor of great apes, not taking into account different predispositions across taxa (e.g., manipulatory skills and tool-use). Of course, this is not to say that specialized cognition should play no role in species comparisons, but it is important to focus on a wider range of cognitive abilities, including those for which no taxon-predisposition is known.

The aim of this study was to investigate possible differences between monkeys and apes in three tasks measuring different cognitive skills. We aimed to map the distribution of these skills across the tested species, without attempting to generalize from those skills to others or to identify a "g" factor common to all these skills. We administered three different tasks involving remembering object locations (memory task), tracking object displacements (transposition task), and obtaining rewards out of the subject's reach (support task). We selected these tasks because they are easy to administer to multiple species and individuals and require only a few trials to be diagnostic. Moreover, each of these tasks has already been successfully used to test different primate species, although methodological differences have not usually allowed direct interspecific comparisons. Finally, these tasks were selected because they allowed us to investigate the distribution of three important cognitive abilities that are used by primates to deal with several daily physical and social challenges. In particular, remembering object locations can be useful when foraging to know the locations already exploited and those in which food has been recently seen (Milton, 1988; Call, 2000). In addition, memory skills can be useful to locate conspecifics and to maintain social relationships, retain knowledge about them and refrain from continuously renegotiating long-term relationships (Call, 2003; Fiset and Doré, 2006; Aureli et al., 2008). Similarly, tracking object movements also seems essential to forage on moving items when mainly relying on visual cues, but also to keep track of moving conspecifics. Finally, using objects to access out-of-reach rewards allows individuals to obtain otherwise inaccessible food resources (Parker and Gibson, 1979). Next, we provide some background information on each of these three tasks.

Memory task. One classical way to assess whether subjects remember the location of objects consists of hiding a food reward under one of several opaque containers before letting the subject retrieve it. Numerous studies have shown that many species can remember the location of food rewards after different delays (e.g., Har-

low, 1932; Menzel, 1973; Balda and Kamil, 1992; MacDonald, 1994; Barth and Call, 2006). Although there has been a number of studies devoted to investigating this question in monkeys and apes (see Fobes and King, 1982; Tomasello and Call, 1997, for reviews), quite surprisingly there have been very few studies comparing monkeys and apes using the same methods. Even those studies that compared multiple species with the same method (e.g., Harlow, 1932) often involved very small samples for some of the species ($N < 3$).

Transposition task. Tracking the displacement of hidden objects has also been investigated extensively in nonhuman animals, mostly using the stage 6 object invisible displacement task (Piaget, 1952; see Tomasello and Call, 1997; Rooijakkers et al., 2009, for reviews). This task consists of moving an object placed inside an opaque container between multiple opaque containers and leaving the object inside one of the containers. Upon concluding the visit to the containers, the experimenter shows that the object is no longer located inside the original container and subjects have to find the object. Much less is known about the related transposition task (Sophian, 1984), in which the object is placed under one of the containers while the subject is watching and the containers are subsequently shuffled. Great apes, 3- to 4-year-old children and African gray parrots can solve transposition tasks, including the most demanding version that involves the containers crossing their paths and occupying their original respective positions when they come to rest (Sophian, 1984, 1986; Pepperberg et al., 1997; Beran and Minahan, 2000; Call, 2003; Beran et al., 2005; Barth and Call, 2006; Rooijakkers et al., 2009). In contrast, cats, dogs and 2-year-old children experience serious difficulties with this task (Doré et al., 1996; Barth and Call, 2006; Rooijakkers et al., 2009). In fact, Barth and Call (2006) showed that 2-year-old children find this task harder than the traditional stage-6 invisible displacement task. Currently, there is no information about the performance of monkeys on transposition tasks.

Support task. Using a stick to get an out-of-reach reward is perhaps the best known example of using an object to get another object. This behavior, however, requires a fair amount of fine motor control which may compromise large-scale multispecies comparisons. One alternative to the stick task is the cloth task, which consists of pulling a cloth to bring within the subject's reach an object that has been placed on it. Support tasks have often been used to investigate species' perception of the physical relation between the cloth and the reward. In the simplest arrangement, subjects have to choose to pull one of two cloths, one with a reward on it and one with a reward off it. Several primate species have been tested with this paradigm with mixed results. Although most monkeys tested could solve the support task only after some training (Natale, 1989; Spinozzi and Potì, 1989; Hauser, 1997; Hauser et al., 1999; Fujita et al., 2003; Santos et al., 2005a,b, 2006b; but see Spaulding and Hauser, 2005), great apes spontaneously discriminated between the functional and the nonfunctional cloth (Povinelli, 2000; Herrmann et al., 2008). This might indicate that apes perceive certain object-object relations that monkeys do not. Moreover, comparative research showed no relation between performance at this task and the use of tools in the wild, since bonobos' and gorillas' performance was equivalent to that of chimpanzees and orangutans (Herrmann et al., 2008).

We administered the three tasks to three monkey species (spider monkeys, *Ateles geoffroyi*; capuchin monkeys, *Cebus apella*; and long-tailed macaques, *Macaca fascicularis*) and the four great apes (chimpanzees, *Pan troglodytes*; bonobos, *Pan paniscus*; orangutans, *Pongo pygmaeus*; and gorillas, *Gorilla gorilla*). Administering multiple tasks to multiple individuals of multiple species offered several important advantages. First, it reduced the possibility that methodological differences were the reason for possible interspecific differences observed. Second, it allowed us a multidimensional assessment of cognitive abilities, so that species might differ in some abilities but not in others. Third, the inclusion of species that varied in their phylogenetic relatedness and socioecology (McGrew et al., 1996; Fragaszy et al., 2004; Thierry, 2007; Campbell, 2008) allowed us to evaluate the role played by several factors in the enhancement of the tested cognitive skills. In particular, we examined the effect of i) phylogenetic relatedness (comparing monkeys with great apes), ii) diet categorization (the overall folivorous gorillas compared with the other more frugivorous species), and iii) levels of fission-fusion dynamics (species experiencing higher levels of fission-fusion dynamics, such as chimpanzees, bonobos, orangutans, and spider monkeys, with species living in more cohesive groups, such as gorillas, capuchin monkeys, and long-tailed macaques).

METHODS

Subjects

We tested 15 spider monkeys at the Centenario Zoo in Merida, Mexico, 12 capuchin monkeys at the ISTC-CNR Primate Center in Rome, Italy, and 12 long-tailed macaques at the Research Group Behavioral Biology, University of Utrecht, Netherlands. Some of the ape data had been previously collected and published as part of other studies (Barth and Call, 2006; Herrmann et al., 2008). In such cases, we refrained from testing ape subjects again and we used the already published data for interspecific comparisons because they represented the first time that subjects had been confronted with the tasks used here. In this study, we therefore refrained from reporting any comparisons between the apes, as they had been the focus of the previous studies. In the memory task, we also tested seven chimpanzees, five bonobos, eight orangutans, and four gorillas housed at the Wolfgang Koehler Primate Research Center in the Leipzig Zoo, Germany.

Subjects were of both sexes and various ages, and they were all born in captivity, except for spider monkeys. Not all subjects participated in all experiments (see electronic Supp. Info., Table S1, for each subject's experimental participation, species, sex, and age). Subjects were all housed in social groups with their conspecifics, in enclosures with outdoor and indoor areas. All of the subjects were previously used to being temporally isolated in testing rooms and were tested by the same familiar experimenter only after they were comfortable with the set-up and the testing room. In those very few cases in which the subject was reluctant to be alone, another individual was present and the trial was only started when there were no interactions between the two individuals. All subjects had previously participated in experimental tasks, but none of them had been previously tested on the present tasks. Subjects were not

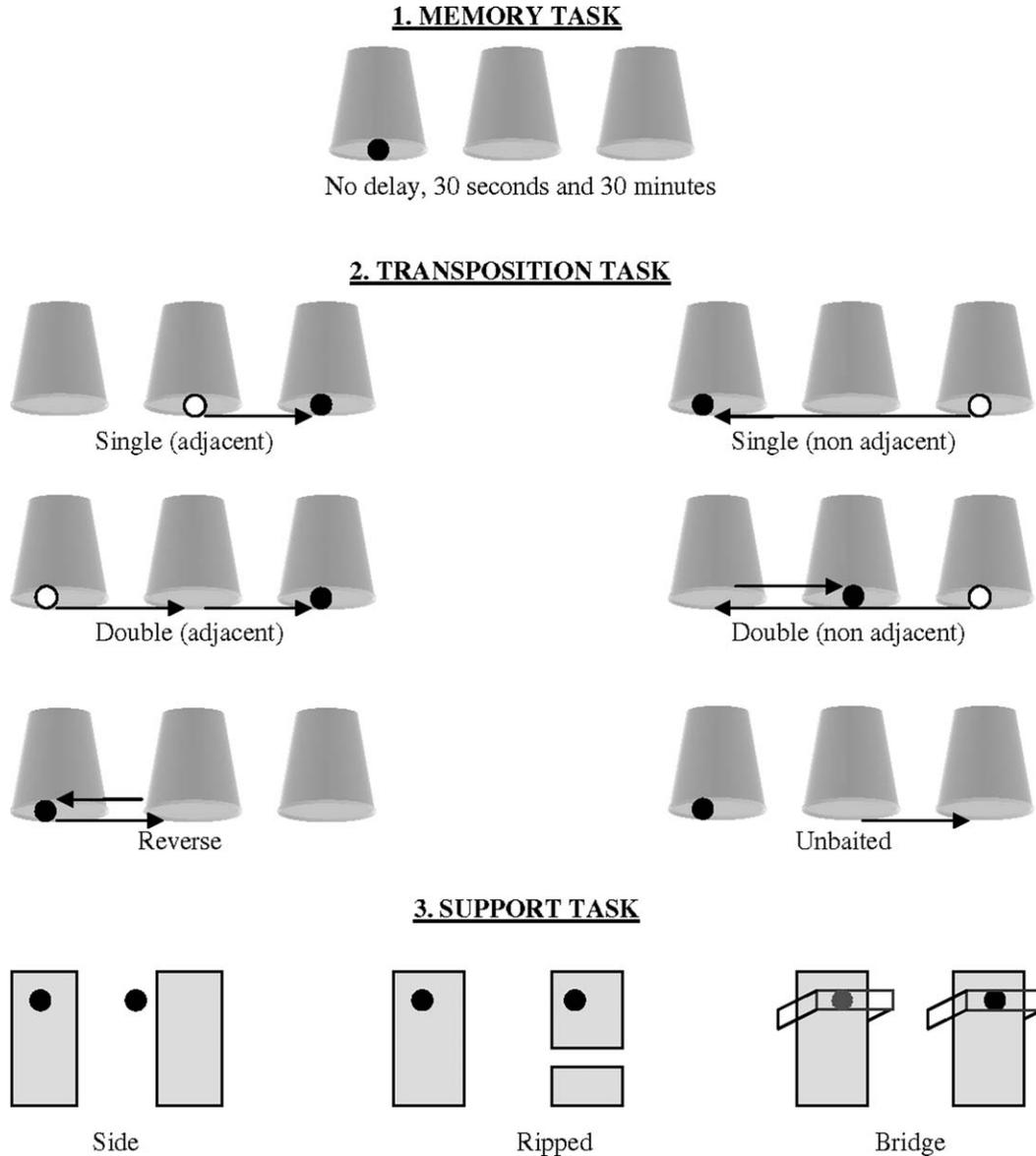


Fig. 1. Illustration of the experimental set-up for the three tasks. White dots represent the initial position of the food reward and black dots the final one. Black arrows represent the movement of food rewards. In the support task, the left alternative for each condition represents the correct choice.

deprived of food or water at any time before or during the experiment.

Materials and procedure

We used a plastic table placed between the experimenter and the subject, where the experimenter presented the test materials to the subject. When necessary, the subject was denied visual access to the baiting procedure by interposing an opaque screen between the subject and the table. The rewards consisted of seeds, raisins, or pieces of banana depending on the subjects' preferences. Other test materials varied as a function of the task (Fig. 1). In the transposition and memory tasks, materials consisted of three identical opaque plastic cups (approximately 6 cm × 6 cm × 15 cm). In the support task, materials consisted of two large cloth pieces (15 cm

× 20 cm), two small cloth pieces (15 cm × 12 cm and 15 cm × 8 cm, respectively) and two plastic "bridges" (approximately 21 cm × 3 cm × 6 cm).

The basic general procedure was the same for each task. The experimenter sat in front of the subject, prepared the test materials on the table, presented them to the subject and allowed her to select one of the alternatives presented. The specific manipulations depended on the administered task.

Memory task. We followed the basic procedure used by Barth and Call (2006). The experimenter aligned three identical cups upside down, approximately 20 cm from each other, so that each cup occupied the left, center, and right positions on the table. At the beginning of each trial, the experimenter showed the subject that all cups were empty by letting them rest on one side with

the cup top side directed to the subject. Then, in full view of the subject, the experimenter baited one of the three cups, placed them on an upside down orientation hiding the food reward (starting from the baited cup and following with the unbaited ones), and waited a certain time before letting the subject make her choice. In the no-delay condition, subjects were allowed to select a cup right after the baiting was completed, while in the 30-s and 30-min delay conditions subjects were not allowed to choose one of the cups until the corresponding time had elapsed. Subjects received three no-delay trials and three 30-s delay trials in the first session. Subjects received three 30-min delay trials in three different sessions because of their longer duration. For all conditions, the location of food was randomly assigned to the left, middle, and right cup.

Transposition task. We followed the procedure used by Barth and Call (2006). The procedure was the same as in the memory task, except that there was no time delay between the baiting procedure and the subject's choice. After baiting one of the three cups and placing them on an upside down orientation, the experimenter proceeded to switch the locations of the cups without revealing their content. There were four different conditions depending on the swapping manipulation that was implemented. 1) Single: the baited cup and another either adjacent or nonadjacent empty cup switched locations, while the third cup remained stationary during the trial. 2) Double: the baited cup switched location twice, either with an adjacent cup in the first or in the second displacement, so that all cups changed their original locations. 3) Reverse: the single condition was performed, but the two cups returned to their original locations after a second swapping manipulation. 4) Unbaited: the two empty cups switched locations while the baited cup remained stationary. After one of the manipulations was concluded, the experimenter pushed the table towards the subject to allow her to choose one cup. Subjects received a single session composed of six trials in a randomized order (two for the single, two for the double, one for the reverse, and one for the unbaited conditions). The position of the reward was counterbalanced across trials, appearing an equal number of times under each cup.

Support task. We followed the basic procedure used by Herrmann et al. (2008). While the opaque screen prevented the subject from seeing the experimenter's actions, the experimenter placed a pair of cloth pieces and two food rewards on the table. Neither of the two rewards was directly accessible, but one of them could be obtained by pulling one of the two cloth pieces. We administered three different conditions. First, Side: two large cloth pieces were placed on the two sides of the table; one food reward was placed at the far end of one cloth piece and the other one on the table, directly next to the far end of the other cloth piece; the subject could only obtain the food by pulling the cloth with the food reward on top of it. Second, Ripped: one large cloth piece was placed on one side, and the two small cloth pieces on the other side; between the two small pieces there was a 3-cm gap, so that they were visibly disconnected; the food rewards were placed at the same distance from the subject on each side, at the far ends of the 20 and 12 cm cloth pieces respectively; the subject could only obtain the food by pulling the 20 cm cloth piece. Third, Bridge: two large cloth pieces were placed on the two

sides of the table as in the side condition; each of two bridges was placed at the far ends of the two cloth pieces so that the cloth piece ran under the bridge; one food reward was placed on the top of one bridge, and the other one on the cloth under the other bridge; the subject could only obtain the food by pulling the cloth with the food under the bridge because when the food was on the bridge pulling the cloth had no effect on it. After the baiting was completed, the experimenter revealed the table and pushed it towards the subject to choose one cloth piece. Each subject participated in 18 trials (six for each condition) administered in a single session. The order of conditions was randomized between trials, but each condition was never presented more than three times in a row. The position of the accessible food reward was also counterbalanced, appearing an equal number of times on both sides and not on the same side for more than three trials in a row.

Scoring and data analyses

We videotaped all the trials and scored them on a check-sheet that was later checked against the videotapes for accuracy. A second observer coded 25% of all the trials to assess the interobserver reliability of the subjects' behaviors. Interobserver reliability was very good (Cohen's $k = 0.87$). We scored the first alternative (cup or cloth) touched by the subject as her choice. We minimized the influence of learning by administering a reduced number of trials per task. Our dependent variable was the percentage of correct trials. Because the homogeneity of variance assumption was violated, we used nonparametric statistics to analyze the effect of species (Kruskal–Wallis and Mann–Whitney tests), condition, and deviation from chance (Wilcoxon test) on the percentage of correct trials. When the result of the Kruskal–Wallis test was significant, Mann–Whitney tests were used for pair-wise comparisons (Cohen and Cohen, 1983). All tests were two-tailed with the α level set at 0.05, but in case of multiple pair-wise comparisons it was decreased to 0.01. To visualize overall interspecific differences and similarities, we conducted a cluster analysis using the mean scores of each of the 10 conditions of the three tasks for each species. We calculated the sum of the squared Euclidean distance across the scores for each pair of species, and we used the resulting matrix to perform a cluster analysis, using the average linkage between groups as the agglomeration method.

RESULTS

Memory task

Monkeys. All monkey species performed above chance level in the no-delay condition ($T \geq 77$, $P \leq 0.001$ in all cases) and the 30-s condition ($T \geq 35$, $P \leq 0.016$ in all cases; Fig. 2). In contrast, only spider monkeys performed above chance in the 30-min condition ($T = 65$, $P = 0.002$). Compared to the no-delay condition, both capuchin monkeys and macaques significantly decreased their performance in the 30-s and the 30-min conditions ($T = 17.5$, $P \leq 0.008$ in all cases). Spider monkeys only performed significantly worse in the 30-min condition as compared to the no-delay condition ($T = 55$, $P = 0.002$).

Species comparisons. There were no significant differences among species in the no-delay condition ($\chi^2(6) = 7.946$, $P = 0.242$; Fig. 2). In contrast, there were significant differences among species in the 30-sec condition

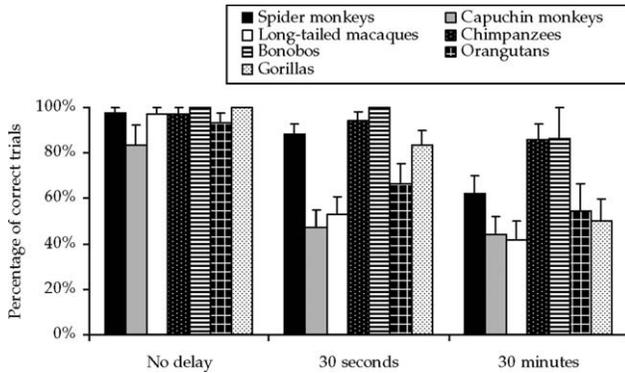


Fig. 2. For each species, mean percentage (+SE) of correct trials in each condition of the memory task.

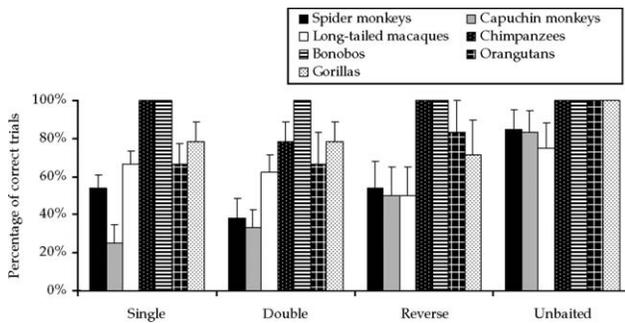


Fig. 3. For each species, mean percentage (+SE) of correct trials in each condition of the transposition task. Data on the great apes come from Barth and Call (2006).

($\chi^2(6) = 35.109$, $P < 0.001$). Pair-wise comparisons revealed that chimpanzees, bonobos, and spider monkeys outperformed capuchin monkeys and macaques ($U \geq 0$, $P \leq 0.001$ in all cases), while gorillas outperformed capuchin monkeys ($U = 14$, $P = 0.004$). Similarly, there were significant differences among species in the 30-min condition ($\chi^2(6) = 16.554$, $P = 0.011$). Pair-wise comparisons revealed that chimpanzees outperformed capuchin monkeys and macaques ($U = 9.5$, $P \leq 0.005$ in both cases).

Transposition task

Monkeys. All monkey species performed above chance level in the unbaited condition ($T \geq 72$, $P \leq 0.004$ in all cases; Fig. 3). In addition, macaques performed above chance level in the single ($T = 78$, $P < 0.001$) and double ($T = 70$, $P = 0.015$) conditions. Spider monkeys also performed above chance in the single condition ($T = 80$, $P = 0.014$). Compared to the unbaited condition, both capuchin monkeys and spider monkeys significantly decreased their performance in the single and double conditions ($T \geq 49.5$, $P \leq 0.021$ in all cases).

Species comparisons. There were significant differences among species in the single condition ($\chi^2(6) = 29.855$, $P < 0.001$; Fig. 3). Pair-wise comparisons revealed that chimpanzees and bonobos outperformed spider monkeys and capuchin monkeys ($U \geq 2$, $P \leq 0.006$ in all cases), while chimpanzees also outperformed macaques ($U = 14$, $P = 0.013$). Moreover, gorillas, spider monkeys and macaques outperformed capuchin monkeys ($U \geq 11$, $P \leq 0.014$ in all cases). Similarly, there were significant differences among species in the double condi-

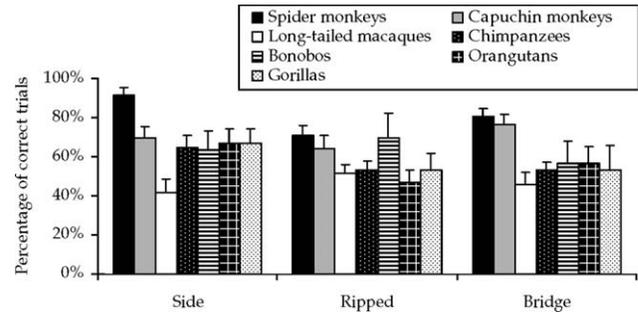


Fig. 4. For each species, mean percentage (+SE) of correct trials in each condition of the support task. Data on the great apes come from Herrmann et al. (2008).

tion ($\chi^2(6) = 19.372$, $P = 0.004$). Pair-wise comparisons revealed that bonobos outperformed spider monkeys and capuchin monkeys ($U \geq 2$, $P \leq 0.008$ in both cases). In contrast, there were no significant differences among species in the reverse ($\chi^2(6) = 9.925$, $P = 0.128$) or unbaited condition ($\chi^2(6) = 5.691$, $P = 0.459$).

Support task

Monkeys. Spider monkeys performed above chance level in all conditions ($T \geq 55.5$, $P < 0.051$ in all cases; Fig. 4). In contrast, neither capuchin monkeys nor macaques performed above chance in any of the conditions ($T \leq 38.5$, $P > 0.059$ in all cases).

Species comparisons. There were significant differences among species in the side condition ($\chi^2(6) = 14.945$, $P = 0.021$; Fig. 4). Pair-wise comparisons revealed that spider monkeys outperformed capuchin monkeys and macaques ($U \geq 21$, $P \leq 0.006$ in both cases). There were also significant differences among species in the ripped condition ($\chi^2(6) = 13.763$, $P = 0.032$). However, pair-wise comparisons did not reveal any significant differences between species ($U \leq 82$, $P > 0.020$ in all cases). Finally, there were also significant differences among species in the bridge condition ($\chi^2(6) = 17.163$, $P = 0.009$). Pair-wise comparisons revealed that spider monkeys outperformed gorillas and macaques ($U \geq 21$, $P = 0.002$ in both cases).

Grouping species

A cluster analysis based on the mean scores of the 10 conditions of the three tasks for each species segregated members of the genus *Pan* from the rest of the species (Fig. 5). A second distinguishable grouping was composed of gorillas, orangutans and macaques, whereas spider monkeys and capuchin monkeys remained on their own.

DISCUSSION

We found no compelling support for an overall clear-cut distinction in cognitive skills between monkeys and apes. We found instead that species performance varied substantially across tasks. Whereas the transposition task segregated monkeys and apes, the other two tasks did not. Consequently, a phylogeny-based explanation is insufficient to account for the observed inter-specific variation across all the three tasks (Fig. 5). Similarly, an explanation merely based on broad diet categorization of the tested species cannot explain our results. If the infor-

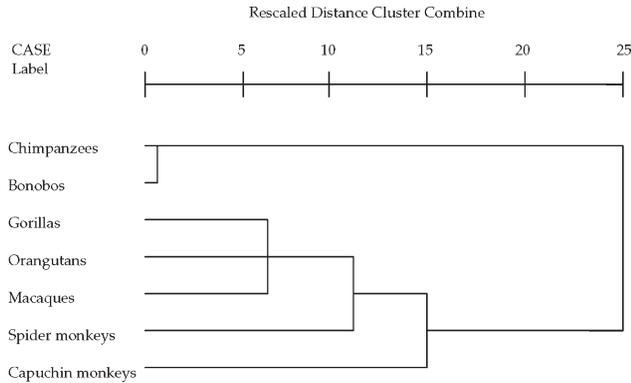


Fig. 5. Dendrograms based on a hierarchical cluster analysis of the scores of all the conditions of the three tasks combined.

mation processing demands of finding food were the major selective pressure for enhanced cognitive skills (Clutton-Brock and Harvey, 1980; Milton, 1981), more frugivorous species should have outperformed more folivorous gorillas, but this was not the case in any of the three tasks.

In this study, the transposition task revealed clear differences between monkeys and apes (Fig. 3). In particular, all monkey species were significantly outperformed by chimpanzees, and partially by bonobos and gorillas. Object displacements and learning tasks have long constituted the main type of data used to support a cognitive dichotomy between monkeys and apes (Deaner et al., 2006). This study, by directly comparing several monkey and ape species in a series of invisible object displacements, confirms such a dichotomy in transposition tasks.

In the other two tasks, however, this cognitive dichotomy between monkeys and apes could not be confirmed. In the support task, for example, spider monkeys performed significantly better than gorillas, providing no support for the existence of a clear-cut distinction between monkeys and apes (Fig. 4). These results also confirm previous findings showing that both monkeys and apes can solve certain basic tool-using tasks even without prior training (Povinelli, 2000; Spalding and Hauser, 2005; Herrmann et al., 2008). Moreover, the outstanding performance of spider monkeys confirms the results of a classical comparative study in which spider monkeys outperformed macaques (*Macaca mulatta*, *M. nemestrina*, *M. fascicularis*), sooty mangabeys (*Cercocebus atys*), baboons (*Papio hamadryas*), mandrills (*Papio sphinx*), capuchin monkeys and a mona monkey (*Cercopithecus mona*) in a support task (Harlow and Settlege, 1934).

A greater predisposition to use tools did not account for our results in the support task. Indeed spider monkeys (for which no special tool use propensity is known) were the best performers, significantly outperforming capuchin monkeys. This is extremely interesting considering that capuchin monkeys regularly use tools in the wild and in the laboratory (Fragaszy et al., 2004), even though they may not have a deep knowledge of the causal relationships underlying certain tool using tasks (Visalberghi and Limongelli, 1994). Differential training procedures or past experience with similar materials and objects cannot explain the different performance of species (Herrmann et al., 2008), since in this study no sub-

ject received training prior to the test. Moreover, spider monkeys were the best performers despite their complete naivety to the materials used.

An explanation based on levels of fission–fusion dynamics could potentially explain this pattern of results in the support task, with species experiencing higher levels of fission–fusion dynamics outperforming species living in more cohesive groups. High levels of fission–fusion dynamics are experienced when individuals living in a large community fission and fuse in subgroups of variable size and composition (Aureli et al., 2008). High levels of fission–fusion dynamics have been linked to enhanced cognitive skills for both ecological and social reasons. First of all, this flexible association pattern is thought to be an optimal compromise between the conflicting pressures of avoiding predators and minimizing feeding competition over extremely patchy and unpredictable food resources (Kummer, 1971; Boesch and Boesch-Achermann, 2000). This kind of sparsely and patchily distributed food resources would call for an extra processing capacity to remember the location of food and better predict when and where to forage (Clutton-Brock and Harvey, 1980; Milton, 1981). Second, high levels of fission–fusion dynamics might be cognitively demanding from a social point of view. When individuals are separated in subgroups for a variable amount of time, the enhancement of certain cognitive skills could allow individuals to better track changes in their own relationships and in the relationships between other group members (Milton, 2000; Barrett et al., 2003; Dunbar, 2003; Aureli et al., 2008). Given that social adaptations are often responses to ecological demands, which might be better dealt with socially than through individual effort (Dunbar and Schultz, 2007), ecological and social explanations might concur in predicting higher levels of fission–fusion dynamics being associated with the enhancement of specific cognitive skills, such as inhibitory control, memory and analogical reasoning (Barrett et al., 2003; Aureli et al., 2008).

The results of the support task are consistent with Amici et al.'s (2008) results showing that spider monkeys possessed enhanced inhibitory control as compared to species living in more cohesive groups, including gorillas. The enhanced and more flexible inhibitory control of spider monkeys was also supported by their better performance in withholding of information tasks relative to the other two monkey species (Amici et al., 2009). It is currently unclear whether spider monkeys' high performance in the support task is due to their enhanced inhibitory skills, allowing them to better assess a situation before acting, or to other abilities, such as a broader apprehension of relations between entities. Aureli et al. (2008) hypothesized that species with higher levels of fission–fusion dynamics might show an enhanced ability to understand relations between relations (analogical reasoning). These species have to retain much “off-line” information because they constantly deal with fragmented and varying social information and cannot witness most of the interactions happening between other group members (Barrett et al., 2003; Aureli et al., 2008). To reduce the cognitive load of retaining much off-line information, species with higher levels of fission–fusion dynamics might thus show enhanced analogical reasoning. In a support task, this could result in species with higher levels of fission–fusion dynamics better understanding the physical relationship between a functional tool and the food in one condition, and extending this knowledge to

other conditions. Finally, different performance across conditions, at least in some species, is consistent with Herrmann et al. (2008) who found that support tasks involving connectivity (ripped condition) are harder to master than those involving contact (side and bridge conditions).

The memory task also did not reveal a clear-cut distinction between monkeys and apes. In the memory task, species with higher levels of fission–fusion dynamics seemed to perform the best, with chimpanzees, bonobos, and spider monkeys outperforming long-tailed macaques and capuchin monkeys (Fig. 2). These results are consistent with Aureli et al.'s (2008) hypothesis that enhanced memory is required in species with higher levels of fission–fusion dynamics, possibly because individuals have to remember social information about other group members that are in different subgroups over long periods. It is unknown whether these species might also show an enhancement of particular kinds of memory, such as episodic-like memory. Because of the frequent changes in party composition, indeed, species with higher levels of fission–fusion dynamics might particularly benefit from not simply remembering temporarily absent group members, but also to better keep track of events and actions involving other group members over a long time-scale, to avoid continuous renegotiations of potentially important long-term relationships (Aureli et al., 2008). From an ecological perspective, the patchier spatial and temporal distribution of food resources could also be a major selective force in the development of advanced memory skills in species with higher levels of fission–fusion dynamics, since these species cannot rely on the “collective memory” of more cohesive groups as a source of transmission of information about food location (Milton, 1981). These socioecological explanations need, however, to be further investigated in memory tasks. In this study, for example, orangutans' performance did not significantly differ from gorillas' performance, which should not be the case if levels of fission–fusion dynamics were the only factor affecting species' performance.

This study highlighted that different species may perform differently when tested on different cognitive skills. A distinction in cognitive abilities between monkeys and apes was not supported, except for the results of the transposition task. Cognitive differences between monkeys and apes certainly exist, but their existence seems to be limited to certain cognitive skills such as reversal learning, mirror self-directed behavior or transpositions. Readers interested in dichotomous distinctions between taxa should not despair. The results of our overall cluster analysis suggested that such a dichotomy might exist between members of the genus *Pan* and the rest of the tested primate species (Fig. 5). However, just like any other averaged result, this outcome is a simplification of the actual data represented by the three different tasks and should be taken with caution.

The heterogeneity of our results across tasks confirms the difficulty to generalize results from one cognitive skill to another. Likewise, it is problematic to generalize from the results on the skills that we tested to the results existing in literature on self-recognition, inhibition, object manipulation or learning skills. Instead, our results emphasize that each cognitive skill represents a facet of intelligence that cannot be easily reduced to other ones. Monkeys and apes cannot be neatly classified into two homogeneous groups for every task. One could argue that although each task has its own idiosyncrasy,

all of them have some loading on a common “g” factor. However, Herrmann et al. (in press) administered a battery of 15 tasks testing various physical and social cognitive skills on more than 100 chimpanzees and failed to find a “g” factor. Instead, their analysis showed that tasks clustered in two different groups, one including spatial cognition tasks and the other the rest of the tasks. Interestingly, when the same battery of tasks was administered to 2-year-old children, no “g” factor could be evidenced, but tasks clustered in three different groups (spatial cognition tasks, social cognition tasks and the rest of the tasks). These results might at first seem surprising, mainly because several other studies have instead found evidence for a “g” factor in humans and other animals (e.g., rodents: Crinella and Yu, 1995; Locurto and Scanlon, 1998; cotton-top tamarins: Banerjee et al., 2009). However, some of those studies included quite homogeneous tasks as compared to those used in this study or by Herrmann et al. (in press). In particular, the tasks used with rodents have been criticized because they are heavily loaded on a spatial component and certain motivational conditions (Locurto et al., 2003), whereas the tasks used with other species did not include social cognition tasks. For example, Banerjee et al. (2009) included a social task, but the authors recognized that it was not a clear case of a cognitive task. Note that if Herrmann et al. (in press) had only concentrated on spatial tasks, they would have found a “g” factor also for chimpanzees. However, this would have excessively narrowed the focus to few tasks and “g” would have consequently lost much of its appeal as an indicator of general intelligence. The putative lack of a “g” factor, however, should not be taken as evidence for a primacy of domain specificity over general purpose intelligence, because the skills investigated here and in other studies are employed to solve a variety of social and nonsocial problems, not just a specific problem in a specific domain.

Differential levels of fission–fusion dynamics seemed to adequately explain the results obtained for both the memory and support tasks. These findings evidence the importance of using multiple tasks across multiple species in a comparative perspective to contrast different explanations for the enhancement of specific cognitive skills. Of course, testing a larger number of species differing in their phylogenetic-relatedness and aspects of their socioecology will allow a finer-grained analysis as to why specific cognitive skills might vary across taxa. This approach seems necessary to confirm the results of this study, especially when considering how large variation can be even within the same genus (e.g., Fujita, 1987). The conclusion that inter-specific differences in cognition might be better explained by different selective pressures, however, is not surprising if one considers cognition as a bundle of skills whose relative contribution varies across different taxa (e.g., Gallistel, 2000; Shettleworth, 2009). All species have inhibitory skills, for example, but species with higher fission–fusion dynamics might possess enhanced inhibition as compared to other species (Amici et al., 2008).

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