Inferences about food location in three cercopithecine species: an insight into the socioecological cognition of primates.

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Abstract

Many animal species use a variety of cognitive strategies to locate food resources. One strategy is to make inferences by exclusion, *i.e.* perceiving the absence of reward as a cue that another location should be investigated. The use of such advanced cognitive strategies may be more prominent in species that are known to frequently solve social challenges, and inferential reasoning has mainly been investigated in social species such as corvids, dogs, dolphins and non-human primates. In this paper we investigate how far social intricacy may explain the disparity of reasoning performances observed in three cercopithecine species that differ in the density of their social network and the diversity of their social partners.

We used standard reasoning tasks, testing the volume concept and inference by exclusion using visual and auditory modalities. We showed that Old World monkeys can infer the location of invisible food by exclusion. In addition, Tonkean macaques and olive baboons had greater performances in most tasks compared to rhesus macaques. These responses are consistent with the social complexity displayed by these three species. We suggest that the cognitive strategies required to navigate through a demanding social world are involved in the understanding of the physical domain.

Keywords: Inference by exclusion, causal reasoning, social complexity, *Macaca tonkeana, Papio hamadryas Anubis, M. mulatta*.

Introduction

Among the various strategies animals can use to locate food is their capacity to remember several food locations and sometimes use indirect information to infer the position of hidden food. These inferential abilities are most certainly vital for survival (Parker and Gibson 1977) and their comparison across several species has shed some light on our knowledge of the evolution of cognition (Tomasello & Call 1997). To date, two main hypotheses have been advanced to explain these abilities. First, animal cognition and its complexity may mirror the foraging needs of each species. In primates and in some species of other orders, the need to use tools to obtain food may well improve their general cognitive performances (Parker & Gibson 1977). Secondly, cognition may evolve to better solve social challenges, in accordance with the social intelligence hypothesis (Jolly, 1966; Humphrey, 1976 but see Kummer et al. 1990 and Menzel, 1997). Social challenges may vary in several ways. For example, species living in complex organizations and/or in fission-fusion societies face a greater need to remember absent group members, their links and their past interactions on a long-term basis (Cheney & Seyfarth 1990). Social complexity may also predict transitive reasoning in highly social ringtailed lemurs (*Lemur catta*) in comparison to the less social mongoose lemurs (*Eulemur mongoz*) (Maclean et al., 2008). The effect of sociality may also be seen in bird cognition. Social species such as pinyon jays (*Gymnorhinus cyanocephalus*) outperformed the more solitary western scrub jays (*Aphelocoma californica*), in a task testing transitive inference, a useful skill to efficiently assess dominance relationship between known and unknown individuals (Paz-y-Mino et al. 2004). Furthermore, the density of social networks and diversity of social partners may also have shaped the inferential reasoning performances of animals. In cercopithecines, which live in permanent multi-male-multi-female groups (Smuts et al. 1987), group composition varies in the number of possible partners an individual can interact with; the higher the diversity of partners, the more cognitive flexibility should be required when processing the social environment. In the context of socioecological cognition (Cunningham & Janson, 2007) the cercopithecine sub-family is a good model to investigate whether reasoning skills in the social domain can be detected within causal reasoning skills. Indeed, cercopithecines show flexibility in variation in relevant variables (e.g. group size, within-group agonism, social structure) (Dunbar, 1988; Hinde, 1983; Thierry et al, 2007)

In standard inference by exclusion tasks, animals must infer from the absence of a cue that another location should be investigated. In the visual modality, great and lesser apes, baboons and capuchin monkeys can use the absence of a visible reward in one container as an indication to choose an alternate container (Call, 2001, 2004; Sabbatini & Visalberghi, 2008; Paulkner et al. 2009; Schmidt & Fischer 2009; Hill et al. 2011). In the auditory modality, some apes can perceive the lack of noise as an indicator that a container is empty (Call, 2004), leading them to select the other container. Capuchins and baboons tested in a similar experimental setup generally fail (Paulkner et al. 2009; Sabbatini & Visalberghi 2008; Schmitt & Fischer 2009). The inferential abilities of great apes have been confirmed using other paradigms. Call (2007) found that bonobos, gorillas and orangutans use the information provided by the inclination of a wooden board to infer the presence of food. Given the contrasted results between species, we think it is necessary to use a variety of tasks to establish a complete picture of inferential abilities (see also Amici et al. 2010). Relatively little work has been done on Old World monkeys in this respect, and our knowledge in this field is quite fragmented.

In this paper, we studied rhesus macaques (*Macaca mulatta),* Tonkean macaques (*M. tonkeana*) and olive baboons (*Papio h. anubis*). Despite living in different types of habitat, these three species display a semi-terrestrial life and a similar feeding ecology. They all live in complex social networks of multi-male multi-female groups organized in several matrilines. Baboons and macaques are capable of dissimulation, triadic interactions, coalitions and complex social strategies (Chaffin et al. 1995; Ducoing & Thierry 2003; Noë 1994; Petit & Thierry 1994a; it et al. 1997; Smuts & Watanabe 1990; Strum 1982; Thierry et al. 2008). However, despite structural similarities in their social life, these three species display differences in terms of how many social partners an individual generally interacts with. Whilst interindividual interactions in rhesus macaques are mainly limited to kin and close-ranking partners (Sueur et al. 2011), they extend beyond these limits in Olive baboons (Silk et al. 2010) and Tonkean macaques (Sueur et al. 2011). Rhesus macaques could be argued to have lower degrees of social complexity, at least with regard to this particular measure. The social environment therefore may be less demanding in the first species than in the two others. Indeed, elaborated social strategies are common in Tonkean macaques, exist in olive baboons and are scarce in rhesus macaques. This combination of sharing the same basic social system with different degrees in the depth of their social networks is therefore particularly useful when testing a hypothesis on the relation between social intricacy and inferential abilities.

Here, we compared the responses of the three species in tasks that explored their capacity to reason about the physical properties of objects and their ability to display inferential reasoning by exclusion. Our procedure closely followed those used previously to test great apes in these same tasks (Call 2004, 2006). Given the characteristics of their social world, we predict that Tonkean macaques should globally outperform baboons, themselves performing better than rhesus macaques in the physical domain. To facilitate the reading, we keep this order (Tonkean macaques, Olive baboons, rhesus macaques) in every part of the paper.

Methods

Subjects

Eight Tonkean macaques, fourteen olive baboons and eight rhesus macaques living in social groups of various sizes took part in this study. There were 6 females and 24 males ranging from 3 to 28 years of age. When not specified, all individuals participated to the experiments. Subjects were all housed in similar conditions at several primate centres and zoological parks in Europe, with indoor and outdoor enclosures (ranging from 20 m^2 to one ha) enriched with wooden sitting perches and/or natural vegetation. Subjects were individually tested in their outdoor cages (other group members were kept in another compartment during testing and could not approach). Monkey chow and water were available *ad libitum*, and fruit and vegetables were provided once a week after testing. Table 1 presents the name, species, age, sex, location and experimental participation of each subject. All individuals were naive regarding our experimental procedure at the beginning of the study.

Data analysis

We fitted generalized linear mixed models on the binary variable (1 for "correct choice" / 0 for "incorrect choice") with a Binomial family and a Logit link function (Brown and Prescott 2006). Pseudoreplication due to repeated observations of the same individual across sessions was taken into consideration by adding the individual and the session as random effects. Best fitting models were selected on the basis of the lowest AIC, i.e. Akaike Information Criterion. Fisher tests were conducted on group responses. All statistical tests were two-tailed and α was set at 0.05. Average values are given as means ±SE (standard error).

Insert table 1 about here

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1. Experiment 1: Concept of Volume

The first experiment investigated whether monkeys inferred the presence of a food reward located under a board, based on this board's inclined orientation (cf. call 2007).

1.1. Method

1.1.1. Subjects

Seven Tonkean macaques, 14 olive baboons and seven rhesus macaques took part in this experiment (Table 1).

1.1.2. Materials

Two wooden boards (25 cm X 11 cm), two solid wooden wedges 3 cm high and a wooden platform were used. Subjects were rewarded with a 3 cm piece of banana.

1.1.3. Procedure and design

The experimenter placed the wooden platform in front of the subject. Subjects were accustomed to this procedure and quickly approached the apparatus. Then, the experimenter placed the two wooden boards about 30 cm apart behind an opaque screen and showed the reward to the subject. Hiding the manipulations from the subject, the experimenter then touched the two boards in succession to prevent the subject from using arm movements as a cue for the location of food, placing the reward either on or under one of the boards, according to the condition. After baiting, the experimenter removed the screen and pushed the platform against the mesh within reaching distance of the subject. The subject could then respond by lifting one of the two boards. The first board touched by the subject was scored as its choice. There were three experimental conditions:

Baseline: The reward was placed on top of one of the boards, so that both boards remained flat on the platform.

Inclined: The reward was hidden under one of the boards providing an inclined orientation to the board of approximately 30°. The other board remained flat on the platform.

Control: The reward was placed under one of the boards, and a 3 cm high wooden wedge was also placed underneath each board so that both boards acquired an inclined orientation.

Each subject took part in six 12-trial sessions (four trials per condition per session) for a total of 24 trials per condition. All conditions were randomly presented during a session with the restriction that they should be uniformly distributed across a session. The position of the reward (left vs. right) was semi-randomly assigned, as the reward was placed the same number of times on each side, and no more than twice in a row on the same side.

1.2. Results

Figure 1 presents the percentage of correct trials across conditions for each species.

The interaction between condition and species affected the overall rate of correct trials (N = 28; best fitting model: AIC=1918). All species performed better in the baseline condition than in the inclined condition (Multiple Tukey-Kraemer comparisons, z=11.89, P=0.0001) and in the control one (Multiple Tukey-Kraemer comparisons, z=13.98, P=0.0001) and better in the inclined condition than in the control one (Multiple Tukey-Kraemer comparisons, z=4.83, P=0.001). Whatever the condition, multiple Tukey-Kraemer comparisons revealed that Tonkean macaques performed significantly better than both baboons (z=5.17, P=0.0001) and rhesus macaques (z=4.22, P=0.0001) whereas the two latter did not differ (z=0.39, P=0.92).

Insert figure 1 about here

To investigate in details the interaction condition x species, we ran fisher tests. All species selected the correct alternative above chance level in the baseline condition (t>42.0, p<0.001, Fisher tests) and none did so in the control condition (t<0.71 in all cases, P>0.50). Tonkean macaques performed clearly above chance in the inclined condition (only 13.1% of incorrect choices, t_6=9.72, p<0.001). Baboons also performed above chance in the inclined condition but less so than Tonkean macaques (notwithstanding 43.32% of incorrect choices, t_{13}=3.91, p=0.002). Rhesus macaques did not select the correct alternative in the inclined condition (t_6=1.64, p=0.15).

1.3. Discussion

Tonkean macaques located the food according to the orientation of the board in the inclined condition and thus outperformed the two other species. Rhesus macaques showed no understanding that the inclination of the board could be used as a cue to locate food. In all other experimental conditions, the three species did not differ from each other and produced the expected response, choosing the board with a visible reward in the baseline condition and making a random choice in the control one.

2. Experiments 2 to 4: Use of visual and auditory cues to locate food

In these experiments, we assessed whether monkeys inferred the location of a reward with the specific use of the presence (or absence) of visual or auditory cues (cf. Call 2004). In a first step (experiment 2), we assessed whether monkeys are capable of using full visual and/or auditory information to find a piece of food hidden in one of two boxes. In order to further investigate their inferential abilities, we run experiments 3 & 4. In experiment 3, we investigated whether monkeys could infer from partial visual information (i.e. no visible food in box A) that the alternative location (i.e. box B) should be chosen. In experiment 4, we assessed whether monkeys could infer from partial auditory information (i.e. no sound coming from the shaken box A), that only the alternative box (i.e. box B) may contain a reward.

2.1. Experiment 2: Full information

In this experiment, subjects were given full visual or auditory information to choose between two locations and select the box containing a reward.

2.1.1. Method

2.1.1.1. Subjects

Eight Tonkean macaques, eight rhesus macaques and fourteen olive baboons took part in this experiment (Table 1).

2.1.1.2. Materials

Two opaque boxes with their respective lids were placed on a platform about 30 cm apart. The rewards were a piece of banana, three Mini-Smarties® or a piece of banana with a Mini-Smartie®, depending on the condition (see below).

2.1.1.3. Procedure and design

The experimenter sat facing the subject behind the platform. All the subjects were habituated to this procedure and quickly approached the experimenter and sat facing the experimenter as soon as she sat behind the platform. The experimenter placed the open boxes on the platform behind an opaque screen, then showed the reward to the subject, before inserting her hand successively into both boxes, leaving the reward in one of the boxes. In half of the trials the experimenter left the reward in the left-hand box, whereas in the other half the experimenter left the reward in the right-hand box. The experimenter placed the lids on the boxes, removed the screen and gave the cue depending on the modality condition. The two sensory modalities were assessed in the three following conditions:

Visual: The experimenter removed the top of both boxes in succession (left then right), showing its contents to the subject by tilting each open box toward the subject, making sure that the subject had seen the location of the reward, before replacing the top on the box. *Auditory*: The experimenter lifted the left-hand box and shook it, without opening it, using a sideways motion for approximately 2-3 s and replaced the box on the table. Next, the experimenter repeated the same manipulation with the right-hand box. Shaking the baited box produced an audible rattling noise, whereas shaking the empty box did not.

Control: The experimenter lifted both boxes in succession (left then right) without opening or shaking them. This last condition assessed the possibility that subjects used inadvertent cues given by the experimenter, the food itself, or the baiting procedure to find the food, or presented a side preference bias.

After administering each cue, the experimenter pushed the boxes against the fence so that the subjects could choose one of them. The first box touched by the subject was scored as its choice. As previously, each subject took part in six 12-trial sessions (four trials per condition per session) for a total of 24 trials per condition. All conditions were presented in random order during a session with the restriction that they should be uniformly distributed across a session. The position of the reward (left *vs.* right) was randomly determined with the restriction that it could not appear more than twice in a row on the same side. The rewards were a piece of banana in the visual condition, three Mini-Smarties® in the auditory condition and a piece of banana with a Mini-Smartie® on it in the control condition.

2.1.2. Results

Figure 2 shows the percentage of correct trials across conditions for each species.

The interaction between condition and species affected the overall rate of correct trials (N = 30; best fitting model: AIC=2248). All species performed differently in each condition. They were better in the visual condition than in the auditory condition (Multiple Tukey-Kraemer comparisons, z=11.14, P=0.001) and better in the auditory condition than in the control one ((Multiple Tukey-Kraemer comparisons, z=6.54, P=0.0001). Whatever the condition, multiple Tukey-Kraemer comparisons revealed that both Tonkean macaques (z=4.23, P=0.001) and baboons (z=3.44, P=0.002) performed significantly better than rhesus macaques.

Insert figure 2 about here

To investigate in details the interaction condition x species, we ran fisher tests. All species performed above chance level in the visual condition (Tonkean macaques: t_7=22.68, p<0.001; baboons: t_{13}=21.84, p<0.001; rhesus: t_7=11.09, p<0.001), but at chance levels in the control condition (Tonkean macaques: t_7=0.55, p=0.60; baboons: t_{13}=0.38, p=0.71; rhesus macaques:

t_7=1.00, p=0.35). Additionally, Tonkean macaques and baboons but not rhesus macaques performed above chance in the auditory condition (Tonkean macaques: t_7=5.45, p=0.001; baboons: t_{13}=5.66, p<0.001; rhesus macaques: t_7=0.63, p=0.55).

2.1.3 Discussion

All species successfully relied on the visual information to locate the food. Visual cues were more informative than auditory ones for all species. Still, most Tonkean macaques and baboons successfully used the auditory information to locate the food. Note that in the case of the rhesus macaques, we observed a retreat reaction when hearing the baited box being shaken. This could explain their lack of understanding.

2.2. Experiment 3: Partial Visual Information

The procedure was the same as in the visual condition of experiment 2 (full information), with the difference that a cue was given for only one of the boxes (either the baited or the empty one), therefore providing only partial information about the location of the reward.

2.2.1. Method

2.2.1.1. Subjects

All subjects that were above chance in the visual condition of experiment 2 took part in this experiment, except for one female Tonkean macaque that was not available during this testing period. Seven Tonkean macaques, fourteen olive baboons and eight rhesus macaques took part in this experiment (see Table 1).

2.2.1.2. Materials

The materials were the same as in Experiment 2. A banana piece was used as reward.

2.2.1.3. Procedure and design

The general procedure was the same as the one used in the visual condition of experiment 2. The experimenter baited one of the boxes and offered some information about the contents of the boxes, and subjects indicated their choice by touching one of the boxes. In the current experiment, the experimenter not only offered visual information or no information at all regarding the location of the reward, but also manipulated the amount of information provided to the subject. There were three conditions:

Partial Visual Baited: The experimenter showed the content of the baited box by tilting it forward so that the subject had seen the location of the reward and lifted the empty box.

Partial Visual Empty: The experimenter showed the contents of the empty box by tilting it and lifted the baited box. In this case, the subject had not seen the location of the reward but could infer it.

Control: The experimenter lifted both boxes in succession without opening any of them. The subject had no information to find the reward.

In each trial, the experimenter always gave the cue about the left-hand box first, then about the right-hand one regardless of which one was baited. The baited box was then touched first in half of the trials only, so that subjects could not use the order of contact of the boxes as relevant information. As previously, each subject took part in six 12-trial sessions (four trials per condition per session) for a total of 24 trials per condition. All conditions were presented in random order during a session with the restriction that they should be uniformly distributed across a session. The position of the reward (left *vs.* right) was randomly determined with the restriction that it could not appear more than twice in a row on the same side.

2.2.2. Results

Figure 3 presents the percentage of correct trials across conditions for each species.

The condition and species affected the overall rate of correct trials ($N = 29$; best fitting model: $AIC=2014$). All species performed similarly in both baited and empty conditions (Multiple Tukey-Kraemer comparisons, $z=1.39$, $P=0.344$) and were better in these two conditions than in the control one (Multiple Tukey-Kraemer comparisons baited vs. control: $z=11.47$, $P=0.001$ & empty vs. control: $z=12.55$, $P=0.0001$). Paired comparison tests show no further indication of species differences.

Insert figure 3 about here

Investigating in more details, all species performed above chance in the baited (Tonkean macaques: $t_5=42.60$, $p<0.001$; baboons: $t_{13}=4.04$, $p=0.001$; rhesus macaques: $t_5=6.14$, $p=0.002$) and empty conditions (Tonkean macaques: $t_5=3.56$, $p=0.016$; baboons: $t_{13}=9.21$, $p<0.001$; rhesus macaques: $t_5=2.83$, $p=0.037$) but not in the control condition (Tonkean macaques: $t_5=1.75$, $p=0.14$; baboons: $t_{13}=-2.88$, $p=0.13$; rhesus macaques: $t_5=0.67$, $p=0.53$).

2.2.3. Discussion

All species successfully relied on partial visual information to find the location of the food. This included inferring the correct location when no reward was visible in the demonstrated container. Baboons were particularly good at it.

2.3. Experiment 4: Partial Auditory Information

This experiment was conducted in a similar manner as the auditory condition of experiment 2 (full information), with the difference that information was given about one box only (either the baited or the empty one) therefore providing only a partial auditory cue.

2.3.1. Method

2.3.1.1. Subjects

Since rhesus macaques failed to fully understand the auditory condition in experiment 2, they were not tested in this experiment. For Tonkean macaques and olive baboons, all subjects who were above chance in the auditory condition of experiment 2 took part in this experiment, except for one female macaque that was not available during this testing period. Seven Tonkean macaques and seven olive baboons participated in this experiment (Table 1).

2.3.1.2. Materials

The materials were the same as in experiment 2.

2.3.1.3. Procedure and design

The general procedure was the same as that of the auditory condition of experiment 2. The experimenter baited one of the boxes and offered some information about the contents of the boxes, and subjects indicated their choice by touching one of the boxes. In the current experiment, the experimenter not only offered auditory information or no information at all regarding the location of the reward, but also manipulated the amount of information provided to the subject. There were three conditions:

Partial Auditory Baited: The experimenter shook the baited box and lifted the empty one without shaking it, so that at the end of these manipulations the subject had heard the noise created by the reward.

Partial Auditory Empty: The experimenter shook the empty box and lifted the baited one without shaking it, so that the subject did not hear the noise of a reward in the baited box, and could hence infer its position in the other box.

Control: The experimenter lifted both boxes in succession without shaking them, giving no auditory cues to the subject.

In each trial, the experimenter always gave the cue by manipulating the left-hand box first and then the right-hand one, regardless of which one was baited. The reward was three Mini-Smarties® in all conditions. As in previous experiments, each subject received six 12-trial sessions (four trials per condition per session) for a total of 24 trials per condition. All conditions were presented in random order during a session with the restriction that they should be uniformly distributed across a session. The position of the reward (left *vs.* right) was randomly determined with the restriction that it could not appear more than twice in a row on the same side.

2.3.2. Results

Figure 4 presents the percentage of correct trials across conditions for each species.

The interaction between condition and species affected the overall rate of correct trials (N = 14; best fitting model: AIC=1224). Both species performed differently in each condition. They were better in the baited condition than in empty and control conditions (Multiple Tukey-Kraemer comparisons, baited vs. empty: z=8.3, P=0.001 & baited vs. control: z=7.68, P=0.001). Whatever the condition, multiple Tukey-Kraemer comparisons revealed that Tonkean macaques performed significantly better than baboons (z=3.4, P=0.001).

Insert figure 4 about here

To investigate in details the interaction condition x species, we ran fisher tests. Tonkean macaques performed above chance in the baited condition (t_6=25.20, P<0.001) but not in the empty (t_6=0.66, P=0.53) or control conditions (t_6=0.93, P=0.39). Baboons performed above chance in the baited condition (t_6=2.83, P=0.03) but not in the empty (t_6=0.41, P=0.70) or control conditions (t_6=2.43, P=0.051)

2.3.3. Discussion

Tonkean macaques and olive baboons successfully located the food when shaking the box produced a sound. Neither species successfully inferred the location of the food when they had to rely on a shaken box that made no noise.

General discussion

To sum the results, we found that inferring the location of hidden food from the inclination of a board appeared to be systematic in Tonkean macaques, common in olive baboons and incomplete in rhesus macaques, as shown in the first experiment. Subsequent experiments showed that although all species displayed good inference skills in the visual modality, none of them understood that the absence of noise meant an absence of food. Moreover, rhesus macaques were unable to use auditory information even when both boxes were shaken, whilst the two other species succeeded in doing so.

Experimental factors and/or temperament may explain the differences found between species in our study. For example in experiment 2, rhesus macaques appeared more unsettled by the noise than the two other species. The set up (proximity with experimenter, isolation from the group, distractive stimuli in the room) may not be responsible for species differences since in some conditions (like the baited conditions), all specie performed similarly. However, we cannot discard an influence (even partial) of temperament on performances. Indeed, recent studies in macaques suggest that different social styles can lead to structural differences in personality dimensions (such as anxiety, confidence, reactivity levels) (Capitanio 1999; Konečná et al. 2012; Neumann 2013; Weiss et al. 2011).

When considering the results all together, Tonkean macaques did well in most tasks. This is in accordance with their performances during previous food location experiments. They are known to spontaneously use a branch to reach unattainable food (Ducoing & Thierry 2005), to use mirrors to guide their search for hidden food (Anderson 1986) and visual traces of food on a congener's face to locate a distant food item (Drapier et al. 2002). Similarly to Schmitt and Fischer's findings (2009), olive baboons performed better when shown the empty box (partial visual empty condition) than when the food was visible (partial visual baited condition) which is counter-intuitive. We suppose that partial information led them to adopt a fixed and conservative strategy: avoiding touching the container that they saw was empty. In the auditory condition with full information, baboons performed well, a result that was not observed by Schmitt & Fischer (2009) despite the fact that their baboons received more than 200 trials in the auditory modality. Concerning rhesus macaques, our findings fit with the results of de Blois and Novak (1994), who found that their subjects failed in another inference task.

Concerning the different performances between modalities, understanding that food occupies space and/or may still exist despite being invisible is essential for efficient foraging, and thus survival. Not understanding or reasoning about auditory cues may be less crucial. Primates have been reported to match vocalizations with the corresponding emitter and to recognize the status of an animal through its calls (Cheney & Seyfarth 1990, 1999; Gouzoules et al. 1984). However, this ability may not strictly apply to non-social problem solving.

We may hypothesize that interspecific differences in performances could be a consequence of broadly different ecological pressures. Contrary to the other species, rhesus macaques face a great diversity of habitats (Fooden 1982) and we could expect this species to outperform others in reasoning skills, which was not observed. Given their omnivorous diets, the three species still have to adjust their foraging strategies to seasonal changes in food distribution (availability and location) and may face similar ecological constraints. Thus, we may turn to other explanations to account for these interspecific differences in the physical domain.

When relating to the social world of each species, the observed responses are generally consistent with the social complexity displayed by each species. However, contrary to our assumption that Tonkean macaques should globally outperform baboons and rhesus macaques, Tonkean macaques did not strictly outperform Olive baboons while both species displayed better performances than rhesus macaques in most tasks. As their high level of tolerance facilitates interactions with all group members, Tonkean macaques can develop positive relationships with many partners, regardless of their kinship and rank. For example, individuals nearly always reconcile after a fight to restore their relationships, and uninvolved third-party individuals favour peaceful interventions in fights between others and hence avoid jeopardizing their relationships with both opponents (Petit & Thierry 1994a; Demaria & Thierry 2001). This may require weighing up the implications of each intervention and reasoning about its consequences in terms of maintaining a complex network of allies. Savannah baboons live in large troops with more than hundreds of individuals (Smuts et al. 1987) and display strategic coalitions (Noë 1994) even if they show lower tendencies to reconcile than Tonkean macaques (Aureli et al. 2002; Petit & Thierry 1994b). Peaceful interventions also exist but are scarcer than in Sulawesi macaques (Petit et al. 1997). By comparison, the network of rhesus macaques is limited to the matriline and close-ranking congeners (Sueur et al. 2011). Reconciliation is rare and third-party interventions during conflicts take the form of aggressive coalitions (Demaria & Thierry 2001). Rhesus poorer reasoning performances are probably not linked to their learning or discrimination abilities that are known to be generally good (Harlow & Mears 1979; Rumbaugh et al. 1996). Further testing in this species is needed to confirm their lack of success in causal reasoning tasks, testing that may require increasing sample size.

Assuming that we can estimate social complexity from the above facts, we can hypothesize that it may have helped both Tonkean macaques and baboons to solve cognitive tasks better than rhesus macaques.

The potential impact of sociality on the evolution of cognition has also been documented in other cognitive abilities. Amici and colleagues (2008) found that inhibitory skills were correlated with the degree of fission fusion in nonhuman primates. In particular, species with higher levels of fission-fusion also showed better inhibitory skills regardless of the phylogenetic relationship between species. Thus, gorillas clustered with long-tailed macaques and capuchins, whereas spider monkeys clustered with chimpanzees, orangutans and bonobos (Amici et al. 2008). However such assumption needs further demonstration of the proximate mechanisms at stake.

Even if Reader and Laland (2002) argue that ‘physical’ intelligence and social intelligence co-vary since social and ecological factors are inseparable in the daily lives of social species (cf. Cunningham & Janson, 2007), the challenges of social life may be more demanding than those posed by the physical world (Humphrey, 1976; Tomasello & Call 1997 but see also Menzel, 1997). To complete our investigation and definitely determine how social demands may have shaped the evolution of cognition, it would be necessary to run similar comparisons between solitary and social species, as already done in birds (Paz-y-Miño et al. 2004).

Acknowledgments

The authors are grateful to B. Thierry for fruitful comments and to J. Lignot (Munro Language Services) for language editing. While preparing the manuscript, Odile Petit was supported by the University of Strasbourg Institute for Advanced Studies (USIAS).

Ethical standards

The experiment complied with the "Principles of Animal Care" publication No. 86-23 (revised 1985) of the National Institutes of Health and with current legislation (L87-848) for animal experimentation. Permission was obtained from the Biomedical Primate Research

Centre animal experimentation committee (Dier Experimenten Commissie, DEC) to conduct the experiments with the rhesus macaques housed there (DEC-#532).

Conflict of Interest

The authors declare that they have no conflict of interest

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Tables

Table 1

Name, species, age, sex, location and the experiments in which each subject participated

Name	Species	Age (years)	Sex	Location	Experiments
Janek	*M. tonkeana*	11	M	Strasbourg	1 - 4
Milos	*M. tonkeana*	11	M	Strasbourg	1 - 4
Gaetan	*M. tonkeana*	10	M	Strasbourg	1 - 4
Paola	*M. tonkeana*	3	F	Strasbourg	1, 2
Tina	*M. tonkeana*	28	F	Mulhouse	2 - 4
Natchez	*M. tonkeana*	6	M	Rieti	1 - 4
Nabou	*M. tonkeana*	6	M	Rieti	1 - 4
Nina	*M. tonkeana*	7	F	Rieti	1 - 4
Klaas	*M. mulatta*	6	M	Rijswijk	1 – 3
Threelegs	*M. mulatta*	18	M	Rijswijk	1 – 3
Cocos	*M. mulatta*	4	M	Rijswijk	1 – 3
Ogun	*M. mulatta*	4	M	Rijswijk	1 – 3
Chat	*M. mulatta*	4	M	Rijswijk	1 – 3
River	*M. mulatta*	6	F	Rijswijk	2, 3
Mees	*M. mulatta*	8	F	Rijswijk	1 – 3
Castore	*M. mulatta*	6	M	Rieti	1 – 3
Prise	*P. anubis*	7	F	Rousset/Arc	1 – 4
Marius	*P. anubis*	9	M	Rousset/Arc	1 – 3
Raimu	*P. anubis*	6	M	Rousset/Arc	1 – 3
Momo	*P. anubis*	8	M	Rousset/Arc	1 – 4
Olav	*P. anubis*	8	M	Rousset/Arc	1 – 3
Rodolphe	*P. anubis*	6	M	Rousset/Arc	1 – 3
Balthazar	*P. anubis*	15	M	Rousset/Arc	1 – 3
Riri	*P. anubis*	6	M	Rousset/Arc	1 – 3
Paul	*P. anubis*	7	M	Rousset/Arc	1 – 4
Otto	*P. anubis*	8	M	Rousset/Arc	1 – 3
Rambo	*P. anubis*	5	M	Rousset/Arc	1 – 4
Alex	*P. anubis*	11	M	Rousset/Arc	1 – 4
Kiki	*P. anubis*	11	M	Rousset/Arc	1 – 4
Kiwi	*P. anubis*	10	M	Rousset/Arc	1 – 4

Locations: Centre de Primatologie, Strasbourg, France; Parc Zoologique, Mulhouse, France; Giardino Faunistico di Piano dell'Abatino, Rieti, Italy; Biomedical Primate Research Centre, Rijswijk, Netherlands; Station de Primatologie, Rousset-sur-Arc, France.

Figures captions

Fig.1 Mean percentage of correct trials across conditions for each species in experiment 1

Fig.2 Mean percentage of correct trials across conditions for each species in experiment 2

Fig.3 Mean percentage of correct trials across conditions for each species in experiment 3

Fig.4 Mean percentage of correct trials across conditions for each species in experiment 4

Figures

Figure 1

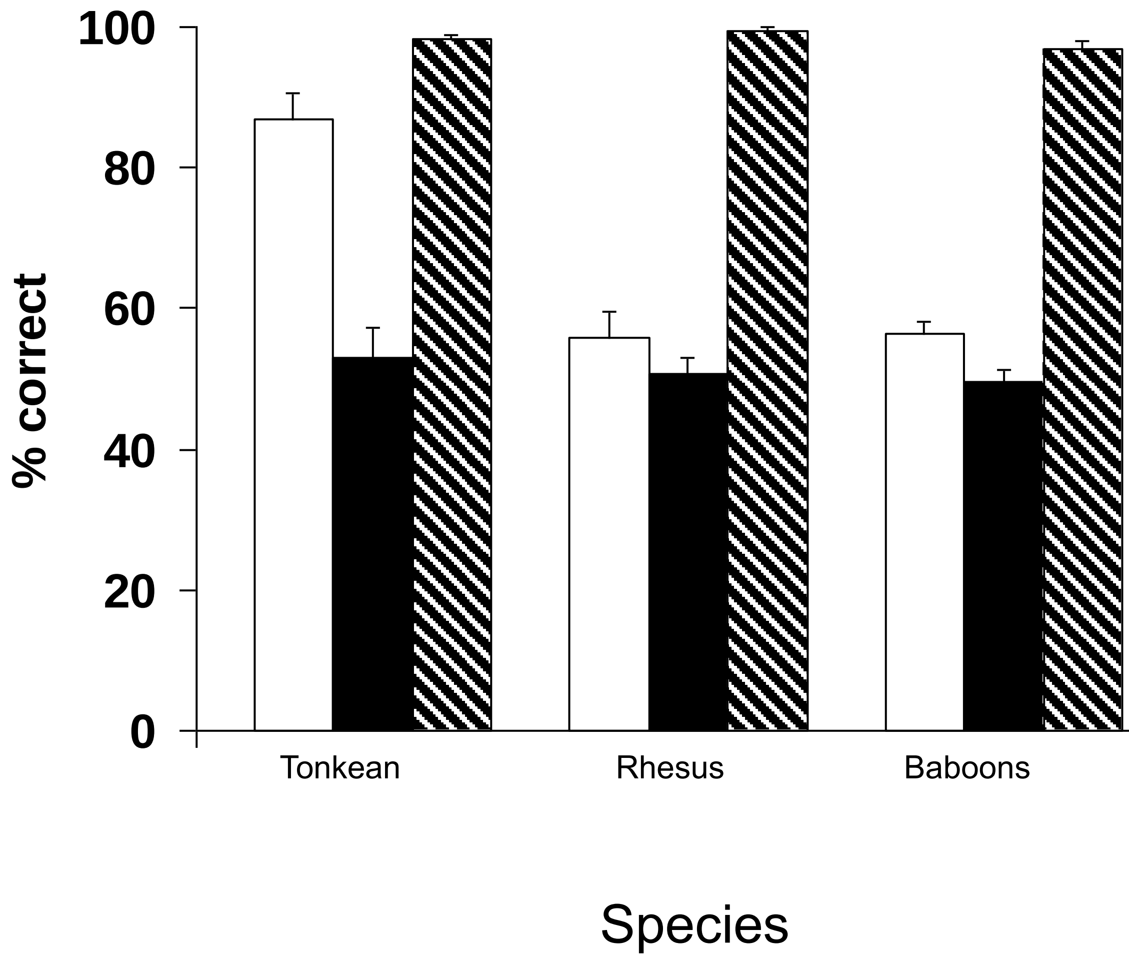

Figure 2

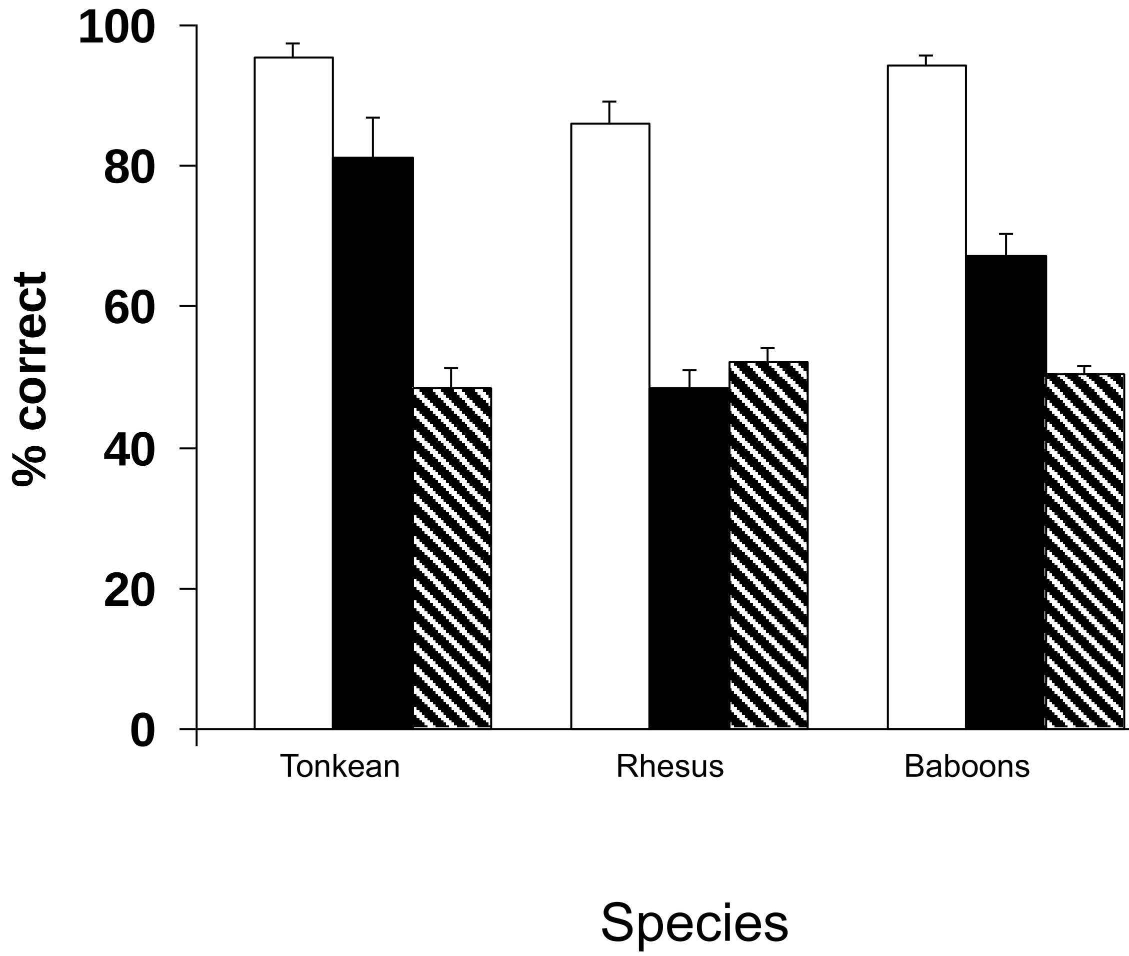

Figure 3

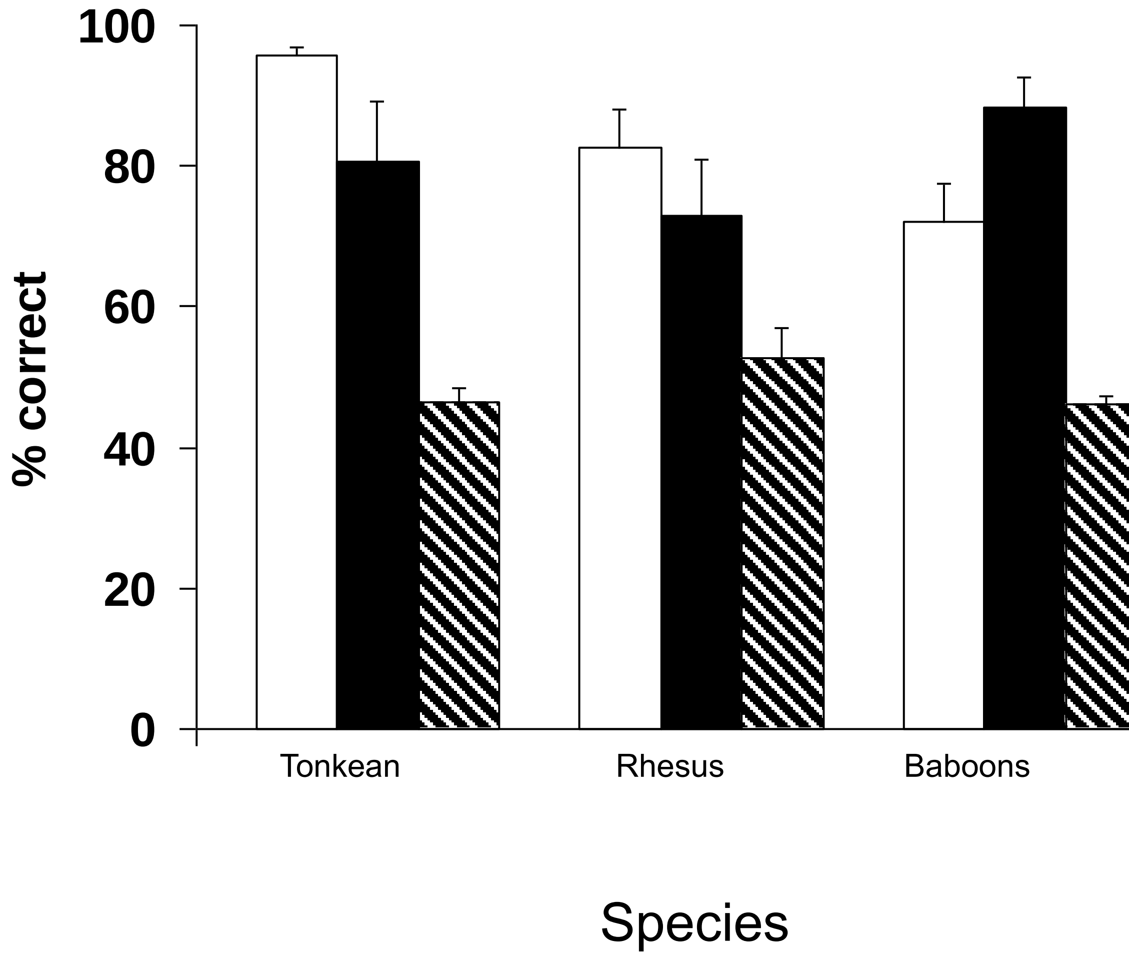

Figure 4