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Inhibitory control in douc langurs (*Pygathrix nemaeus* and P. *cinerea*)

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Summary

Inhibitory control, defined as the ability to prevent pre-potent and unproductive actions, serves as a measure of cognitive skills in humans and non-human primates. Comparative research in this field revealed feeding ecology and aspects of social complexity, i.e. group size and fission-fusion dynamics, as reliable predictors for self-control in primates. Yet, these studies generally lack information on colobine species. Here we report the results of two self-control tasks conducted on folivorous and group-living red- and grey-shanked douc langurs. Altogether 17 captive animals were tested with a cylinder task and a middle-cup task. Both species revealed similar low levels of self-control, and, to the best of our knowledge, reached the lowest scores among all tested species in the cylinder task. Group size and fission-fusion dynamics cannot explain douc langurs' poor performances. Our results indicate that the intensity of social interactions within and between groups is more important for the development of inhibitory control than group composition. Douc langurs' poor self-control skills are in line with the performances of other folivorous primates promoting feeding ecology as good predictor for this cognitive skill.

Kiểm soát ức chế ở các loài Chà vá (*Pygathrix cinerea* và *P. nemaeus*)

Tóm tắt

Kiểm soát ức chế được định nghĩa là khả năng ngăn chặn các hành động bạo lực và không hữu ích. Khả năng này được xem như là một thước đo kỹ năng nhận thức ở người và thú linh trưởng. Những nghiên cứu so sánh trong lĩnh vực này cho thấy tập tính sinh thái dinh dưỡng cộng với sự phức tạp trong cấu trúc xã hội bao gồm: kích thước nhóm và tập tính tách nhập đàn là những chỉ thị đáng tin cậy để tìm hiểu khả năng tự kiểm soát ở các loài linh trưởng. Tuy nhiên, những nghiên cứu lĩnh vực này thường thiếu thông tin, dữ liệu trên các loài voọc. Dưới đây chúng tôi báo cáo kết quả thí nghiệm về khả năng tự kiểm soát được tiến hành trên loài khỉ ăn lá và sống theo đàn là voọc chà vá chân đỏ và chà vá chân xám. Tổng cộng 17 loài cá thể nuôi nhốt đã được thử nghiệm với một nhiệm vụ "xi lanh" và một nhiệm vụ với "cốc". Cả hai loài này cho kết quả ở mức độ thấp khả năng tự kiểm soát. Với sự hiểu biết của chúng tôi, cả hai loài đều đạt điểm số thấp nhất trong số tất cả các loài được thử nghiệm trong các nhiệm vụ tương tự. Quy mô nhóm và tập tính tách nhập đàn không thể giải thích màn trình diễn nghèo nàn của voọc chà vá. Kết quả cho thấy rằng cường độ các tương tác xã hội trong và giữa các bầy là quan trọng đối với sự phát triển của kiểm soát ức chế hơn so với thành phần cá thể trong bầy. Kỹ năng tự kiểm soát kém ở Voọc chà vá phù hợp với các loài linh trưởng chuyên ăn lá khác. Điều đó ủng hộ quan điểm sinh thái dinh dưỡng có thể dự báo tốt hơn về kỹ năng nhận thức này.

Introduction

Inhibitory control, also called self-control, is the capability of preventing pre-potent and unproductive behaviours (Hauser 1999) and serves as a measure of problem-solving skills in humans and nonhuman animals. In nonhuman animals, for instance, inhibitory control is required to prevent mating or feeding in the presence of higher-ranking conspecifics in order to avoid social conflict. Carnivores also require self-control when they pursue ambush predation strategies (MacNulty et al. 2007). Furthermore, inhibitory control is correlated with fitness in humans (Bezdjian et al. 2011; Mischel et al. 1989; Moffitt et al. 2011) and postulated to have positive influences on cognitive performances in primates (Amici et al. 2008; Schmitt & Fischer 2011; Wellman et al. 2011). Comparative analyses on self-control in 36 mammalian and bird species showed that self-control is widespread and this ability mostly strongly co-varies with absolute brain size (MacLean et al. 2014). In addition in primates, self-control was also positively correlated with dietary breadth but not with group size (MacLean et al. 2014). However, in another study conducted in several primates inhibitory skills were not related to variation in diet but to variation in social organization of the tested species, suggesting that social complexity is linked to inhibitory skills (Amici et al. 2008).

A species' feeding ecology has long been assumed to have importantly shaped aspects of cognitive capabilities in primates (Call & Tomasello 1997; Clutton-Brock & Harvey 1980; Marshall & Wrangham 2007; Milton 1981). For example, feeding ecology influenced performances in an inhibitory control task in two New World monkeys: gummivorous marmosets (*Callithrix jacchus*) out competed closely related, but insectivorous, cotton-top tamarins (*Saguinus oedipus*) in a delayed gratification task. The marmosets waited longer for a larger reward rather than accepting immediate, smaller recompense (Stevens et al. 2005). Conversely, in a spatial discounting task, the tamarins travelled further for greater rewards whereas the marmosets preferred smaller, nearer rewards (Stevens et al. 2005). These behavioural patterns fit the feeding ecology of both species. That is, delayed sap discharge, requiring higher patience in gummivorous marmosets, explains their superior performance in a space-dependent inhibitory control task (Stevenson & Rylands 1988). Insectivorous tamarins, on the other hand, travel larger distances when foraging and, thus, performed better in a time-dependent inhibitory control task (Snowdon & Soini 1988). Similarly, chimpanzees (*Pan troglodytes*), which generally rely on small, distributed food patches and fluctuating fruit resources, showed stronger inhibitory skills in a delayed gratification task than bonobos (*Pan pansicus*) that live in environments with more stable and reliable food sources, suggesting that the different feeding ecologies of chimpanzees and bonobos strongly influence foraging effort and ultimately led to the development of different cognitive abilities (Rosati et al. 2007).

According to the social brain hypothesis evolutionary brain enlargement in group-living mammals was driven by the necessity to develop adequate social manipulation skills, allowing individuals to keep track of complex social relationships (Byrne & Bates 2007). Indeed, comparative analyses revealed positive correlations of mean group sizeand the number of grooming partners with neocortex volume among several mammal species (Barton & Dunbar 1997; Dunbar 1995; Dunbar & Bever 1998; Kudo & Dunbar 2001; Shultz & Dunbar 2006). The neocortex, a part of the mammalian brain, is important for higher cognition (Carlson, 1986) and is suggested to have evolved along with the increasing cognitive requirements of sociality (Dunbar & Shultz 2007; Pérez-Barbería et al. 2007). Comparing seven primate species on five inhibition tasks, Amici et al. (2008) revealed a positive correlation between self-control and the degree of fission-fusion dynamics, the latter being a recognised aspect of social complexity. However, in a larger comparative study, group size, another proxy of social complexity, did not predict performances of 23 primate species in two inhibition tasks (MacLean et al. 2014).

Although studies investigating primate cognition have become more numerous in the last decades, the majority of Old World monkey studies were performed on Cercopithecinae. To this day, knowledge of cognitive capacities in the Colobinae subfamily remains sparse. Here we report the first investigation of inhibitory control skills in endangered red- and grey-shanked douc langurs (*Pygathrix nemaeus* and *P. cinerea*). Red- and grey-shanked doucs are endemic to evergreen and semi-deciduous forests of Indochina. They are diurnal, arboreal and predominantly folivorous, occasionally feeding on seeds, buds, flowers and fruits (Ha Thang Long 2009; Lippold & Vu Ngoc Thanh 2008; Moore & Ali 1984; Nadler 2008; Stevens et al. 2008; Ulibarri 2013; Workman & Covert 2005). Both species live primarily in one-male family groups with on average 13.5 and 8.5 individuals in red- and grey-shanked doucs, respectively (Nadler & Brockman 2014). On a daily basis, one-male units can congregate to larger groups with up to 50 individuals in red-shanked doucs (Lippold 1998) and up to 88 individuals in grey-shanked doucs (Ha Thang Long 2009). These fission-fusion patterns can differ with seasonality (Ha Thang Long 2009; Lippold 1998).

The widespread, temporally stable distribution of the douc langurs' main food source indicates a relaxed feeding competition as is generally assumed in folivorous species (Sterck et al. 1997; Wrangham 1980). This kind of feeding ecology predicts relatively low social skills and high impulsivity. However, their social organisation predicts the opposite. Social skills and self-control are presumably enhanced in group-living primates, particularly those with significant fission-fusion dynamics (Amici et al. 2008; Aureli et al. 2008; Barrett et al. 2003). Aside from the general lack of knowledge on cognition in douc langurs, the contradictory predictions on their self-control skills based on feeding ecology and sociality make them relevant and interesting subjects.

To assess self-control capabilities in red- and grey-shanked douc langurs, we tested 17 captive animals of the Endangered Primate Rescue Center (EPRC) in Vietnam with the cylinder task (MacLean et al. 2013) and the middle-cup task (Call 2001). In the former, subjects are required to perform a detoured side-approach to obtain a reward situated behind a transparent barrier, inhibiting their impulse for a direct frontal approach. In the latter, subjects that observe baiting of two flanking cups must suppress their temptation to pick an empty, central cup. To the best of our knowledge, to date, only one study has investigated inhibitory control in a folivorous colobine species (Tan et al. 2013). In this study, golden snub-nosed monkeys (*Rhinopithecus roxellana*) showed low self-control skills, comparable to those of other folivorous primates (MacLean et al. 2014). Interestingly, their large group sizes and fission-fusion dynamics could not explain poor self-control performances (Tan et al. 2013). Based on these findings, we predict that (I) red- and grey-shanked douc langurs will also show low levels of inhibitory control; and (II) that no differences in self-control skills will occur between both species, as they are closely related and share similar social and ecological environments.

Material and Methods

Study site and subjects

Our study was conducted in the EPRC in Cuc Phuong National Park, Vietnam, from April to June 2015. The park is located in the Nho Quan District of Ninh Binh Province, 120 km south of Hanoi (Wright et al. 2008). The EPRC houses about 160 primates of 15 different Indochinese primate taxa, 4 listed as ‘CriticallyEndangered’, 9 as ‘Endangered’ and 2 as ‘Vulnerable’ (Nadler 2014).

Eight red-shanked douc langurs, including four males (6 to 19 years) and four females (7 to 17 years), and nine grey-shanked douc langurs, with eigh males (6 to 19 years) and one female (6 years), were examined. At the EPRC, animals are housed in chain-link out door enclosures measuring about 10.0 m x 5.5 m x 3.5 m (length x width x height). Enclosures are equipped with natural tree branches and bamboo poles. Douc langurs are provisioned with water ad libitum and fresh leaf bundles three times a day. Additionally, monkeys are provided with pieces of sweet potato once a day.

Experimental design

All primates were completely naïve to cognitive experiments. Experiments took place in the animals’ enclosures. Monkeys were either tested in the morning between 9.30am and 10.30am or in the afternoon between 1.30pm and 2.30pm. During testing, the experimenter and the subject were separated by the enclosure’s mesh. Rewards were offered as small pieces (ca.1 cm x 1 cm) of sweet potato. All animals participated voluntarily in the experiments. If a monkey would not participate in a session, e.g. would not approach the cylinder/sliding table or would not try to receive the reward, the test was terminated and repeated another day.

Cylinder task

In this task, we use the same apparatus and experimental design as suggested in MacLean et al. (2012; 2014).

Apparatus

Two plastic cylinders, one opaque and one transparent, were used in our study. Both cylinders had the same measurements (width = 23 cm, diameter = 13 cm) and were each attached to small wooden boards. The boards were necessary for stabilisation to keep the cylinders from rolling away when manipulated by the animals during the trials.

Procedure

At first, animals were trained to reach for a reward hidden in the centre of an opaque cylinder. The cylinder was baited beyond subject's reach, but the subject could watch the baiting process. The baiting was alternately performed from the right or left side of the cylinder. Afterwards, the cylinder was placed in reach of the monkey so that it could try to retrieve the reward. After successfully conducting five consecutive training trials, subjects were confronted with the experimental transparent cylinder. Test trials were accomplished in the same way as described for the training trials, however, the opaque cylinder was now replaced by the transparent cylinder. A trial was correct if an animal did not attempt to retrieve the reward directly and thereby pushed frontal against the cylinder with its hands. A trial was also rated as successful if an animal clearly used a hand only to pull the cylinder closer in order to secure it for easier access to the sides. Altogether, ten test trials were conducted in this experiment. In both conditions, training and test trials, animals could retrieve the rewards regardless of performance.

Middle-cup task

In this task, we use the same experimental design as proposed in Herrmann et al. (2007) and Amici et al. (2008).

Procedure

Three cups were aligned on a sliding table in front of the animal and two rewards were placed under the two outer cups, while they were out of the monkeys' reach. Afterwards, animals were free to choose among the cups. If the subject chose one of the baited cups it was allowed a second choice. If the animal took the unbaited cup for its first or second choice, the trial was over. A trial was correct, if the monkey chose both baited cups in succession. Altogether, four trials were conducted in this experiment per animal. In this task, animals require self-control to refrain from the tendency of choosing the cup closest to them, which would always be the middle cup.

Data Analysis

All experiments were videotaped. After each trial, the results were announced audibly to the camera and later rechecked when analysing the tapes. Individual success rates were calculated for each inhibitory control task. On the species level, Mann-Whitney U tests were calculated to control for differences in the performances of red- and grey-shanked doucs for both tests. We used Wilcoxon tests to compare individual performances in both tests. The influence of age on monkeys' performances was examined with a Spearman correlation, since age was not normally distributed (Shapiro: $W = .78$, $p < .01$). The same statistical test was used to examine correlations between number of training trials and performance in the cylinder task (Shapiro: $W = .83$, $p < .01$). For both tasks, a second observer scored 24% of test sessions (in total 4 out of 17 sessions per task) to assess inter-observer reliability, which was excellent with an agreement of 100%. All statistical analyses were conducted using R (R Core Team 2014).

Results

In the cylinder task, red- and grey-shanked doucs reached mean success rates of 0.20 ± 0.19 and 0.19 ± 0.25, respectively, and did not differ in their performances (Mann Whitney: $U = 32.5$, $p = 0.77$) (Fig. 1). The number of training trials an individual required before participating in the experimental phase did not correlate with individual's performance in this task (Spearman: $rs = -0.24$, $p = 0.34$).

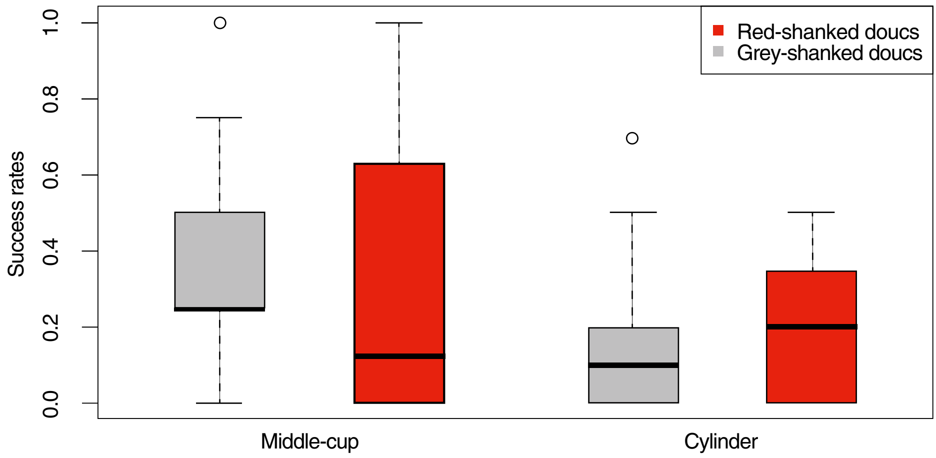

Fig.1. Success rates of red and grey-shanked doucs in the inhibitory control tasks. The bold line across the boxes represents the median. Boxes show the inter-quartile range of scores from the 25th percentile to the 75th percentile. Maximum and minimum values are presented through whiskers and outliers through emty circles.

In the middle-cup task, red-shanked doucs reached a mean success rate of 0.31 ± 0.35 and grey-shanked doucs reached a mean rate of 0.42 ± 0.31. Again no interspecific differences in performances was detected (Mann Whitney U: U = 45, p = 0.39). Age was not correlated with animals' performances in both experiments (Spearman: cylinder task: rs = 0.22, p = 0.41; middle-cup task: rs = -0.11, p = 0.69) (Fig. 2).

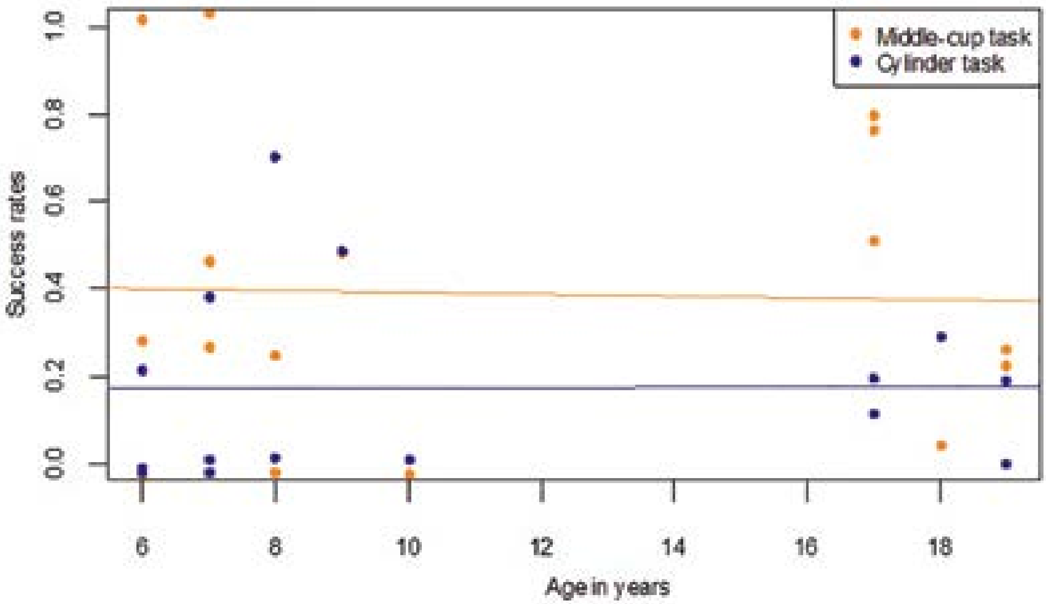

Fig.2. Success rates of all individuals incorrelation to their age in the inhibitory control tasks. In both experiments, no correlation was found between age and performance.

Individual performances did not differ between both experiments (Wilcoxon: Z = -1.96, p> 0.05).

Discussion

In our study, we present the first data on self-control in red- and grey-shanked douc langurs contributing to the under studied field of cognition in colobines. The two species demonstrate similar low levels of inhibitory control in both tasks. In comparison to other primates (MacLean et al. 2014), they exhibit rather low levels of inhibitory control, which are nevertheless comparable to those of other folivorous primates. Age did not influence animals' performance and individuals did not differ in their scores between both tasks. Interestingly, in the cylinder task red- and grey-shanked doucs scored below all so far tested bird and mammal species. Altogether, since langurs are folivorous our results support the increasing body of empirical studies suggesting that feeding ecology strongly influences inhibitory control skills.

Our findings also indicate that group size and fission-fusion dynamics do not appear to have a strong influence on the development of this cognitive skill. Both species live in groups which regularly split and reassemble - a social system which is commonly regarded as cognitively demanding, including complex interactions and behaviours such as competition and cooperation among conspecifics, frequent monitoring of group movements and tracking of group members (Dunbar 2009). Yet, these demands neither led to the acquisition of enhanced self-control in douc langurs nor in golden snub-nosed monkeys, which share a similar social system (Kirkpatrick & Grueter 2010). For the latter, Tan et al. (2013) posit that their loose associations in assembled groups and rare inter-unit interactions represent a specific type of fission-fusion dynamics that does not require enhanced inhibitory skills. This would also explain douc langurs' poor self-control. In comparison to species of the Cercopithecinae, colobine species like red- and grey shanked douc langurs exhibit rather low levels of social interactions, i.e. grooming or aggression, in their daily activity patterns (Kavanagh 1978; Oates & Davies 1994; Poirier 1974). Furthermore, red- and black-shanked doucs seemingly lack female dominance hierarchies (Rawson 2009; Ruempler 1998). Detecting and understanding social hierarchies, however, constitutes an important cognitive capability and its presence has been suggested to increase social complexity (MacLean et al. 2008). Moreover, the fact that douc langurs regularly congregate to large groups, is contradictory to the assumption that self-control increases with group size and degree of fission-fusion (Amici et al. 2008). Also, in the majority of studies investigating inhibitory control in primates, other mammal species and birds, larger group sizes and frequent fission-fusion dynamics were not linked to increased self-control (MacLean et al. 2014; Stevens 2014; Tan et al. 2013; Vernouillet et al. 2016).With our study we contribute to this literature, as group size and fission-fusion dynamics can not explain douc langurs' poor self-control. The intensity of social interactions within and between groups appears more important for the development of this cognitive skill than group composition.

Feeding ecology seems to be a better predictor for inhibitory skills than social complexity. Douc langurs' poor results in the two self-control tasks align with the low performances of other folivorous primates in the same or similar experiments, e.g. for the cylinder task: Coquerel's sifakas (*Propithecus coquereli*), 36% (MacLean et al. 2014) and golden snub-nosed monkeys, 35% (Tan et al. 2013); for the middle-cup and plexiglas hole task: gorillas (*Gorilla gorilla*), 21% and 42%, respectively (Amici et al. 2008).The reliance on food sources that are spatially and temporally highly abundant and easy to harvest unlikely engenders inter- and intragroup competition (Isbell & Young 1993; 2002; Sterck et al. 1997; Wrangham 1980). Additionally, leaf-eating does not demand complex foraging strategies where animals have to show patience, e.g. gummivores waiting for gum to exudate or carnivores stalking on their prey, or temporal and spatial orientation, e.g. frugivores which need to know about the maturing of fruits and the position of fruit trees.

However, dietetic categorisations of primate species as "pure" folivores, frugivores or gummivores have been recently criticised (Sayers 2012) and should be treated with caution. For example, most folivorous primates include small amounts of fruits, seeds or flowers in their diets. For harvesting these different food types other feeding strategies and cognitive abilities are required. Furthermore, many studies have identified folivores as very selective feeders primarily foraging high-quality foods that are often temporally and spatially dispersed (Chapman et al. 2003; Glander 1982; Kirkpatrick 1999; Oates 1994; Snaith & Chapman 2007; Yeager & Kool 2000). Thus, the cognitive demands of a folivorous species might be therefore more complex than formerly assumed. Nevertheless, our results contribute to the empirical body of literature suggesting that folivorous species possess lower self-control than species with other main food sources, and that inhibitory capacities highly depend on a species' feeding ecology.

Strikingly, in the cylinder task, douc langurs did not just reveal poor inhibitory skills but they also scored below all 31 tested mammal and bird species examined in the study by Maclean et al. (2014). As all of our individuals successfully passed a training phase with an opaque cylinder, a general lack of understanding how to retrieve the rewards can be excluded. Moreover, the number of training trials subjects required to advance to the testing trials did not predict the outcome. Hence, douc langurs' errors in the cylinder task may have been driven by their principal lack of self-control. Yet, although douc langurs' feeding ecology predicts low levels of self-control, their performance was even outcompeted by another colobine species, the golden snub-nosed monkeys which share a similar ecological environment but scored almost twice as high in the same task (Tan et al. 2013). Since golden snub-nosed monkeys have larger brains then douc langurs (Isler et al. 2008) and absolute brain size predicted performance in self-control tasks across primates (MacLean et al. 2014), the combination of both factors may explain the difference in performance between these species.

Conclusion

This study provides a first insight into inhibitory skills in captive red- and grey-shanked douc langurs in two different tasks. Both species revealed similar low levels of self-control, and, to the best of our knowledge, reached the lowest scores among all tested species in the cylinder task. Their poor self-control skills are in line with the performances of other folivorous primates and suggest that feeding ecology influences performance in this cognitive skill. A large group size and fission-fusion dynamics, both aspects of social complexity, cannot explain douc langurs' performances. Future research on cognition should therefore focus on colobine species, as comparative studies generally lack this important subfamily.

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