Comparing physical and social cognitive skills in macaque species with different degrees of social tolerance

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Abstract

Contemporary evolutionary theories propose that living in groups drives the selection of enhanced cognitive skills to face competition and facilitate cooperation between individuals. Being able to coordinate both in space and time with others and make strategic decisions are essential skills for cooperating within groups. Social tolerance and an egalitarian social structure have been proposed as one specific driver of cooperation. Therefore, social tolerance is predicted to be associated with enhanced cognitive skills that underpin communication and coordination. Social tolerance should also be associated with enhanced inhibition, which is crucial for suppressing automatic responses and permitting delayed gratification in cooperative contexts. We tested the performance of four closely related non-human primate species (genus *Macaca*) characterised by different degrees of social tolerance on a large battery of cognitive tasks covering physical and social cognition, and on an inhibitory control task. All species performed at a comparable level on the physical cognition tasks but the more tolerant species outperformed the less tolerant species at a social cognition task relevant to cooperation and in the inhibitory control task. These findings support the hypothesis that social tolerance is associated with the evolution of sophisticated cognitive skills relevant for cooperative social living.

Introduction

Living in social groups is challenging as it represents a continuous trade-off between facing competition and engaging in cooperative acts. Thus, living in groups should exert a selective pressure on the cognitive skills required for an individual to survive in its socially complex landscape. For instance, being able to coordinate with other individuals (both in space and time) and make strategic decisions are advantageous traits for cooperating successfully within groups. Social tolerance has been proposed as one specific aspect of group living that may facilitate the evolution of particularly good cooperative skills, and thus may have represented a major trigger in the evolution of human cognition (e.g.[1]). In a recent study, Hare and colleagues [1] found out that the more tolerant bonobo species (*Pan paniscus*) outperformed the more despotic chimpanzee species (*Pan troglodytes*) on a cooperative task. At the species level, tolerant social styles, which include higher reconciliation rates, fewer conflicts and more relaxed social relationships than despotic ones (see [2,3]), represent more egalitarian social systems that might provide room for negotiation and appear particularly prone to cooperation [1]. At the individual level, several studies have also now demonstrated that tolerance is indeed an important factor explaining the likelihood and success of cooperation in different animal taxa such as birds (e.g. [4-7]), carnivores (e.g. [8]) and non-human primates (e.g. [9,10]). In which case, social tolerance should be associated with enhanced socio-cognitive skills that enable better communication and coordination. Similarly, social tolerance should also be associated with better inhibition, which is crucial to allow the suppression of quick, reflexive responses and to permit delayed gratification in cooperative contexts [11,12].

The genus Macaca is the most successful primate radiation and represents a monophyletic group (descended from one ancestral species; see [2,3,13]). Twenty-three species of macaques are currently recognised (see [14,15]), which are distributed in South and East Asia (the only exception is the Barbary macaque which is found in North Africa). Macaques are mainly frugivorous, semi-terrestrial primates and inhabit a wide range of habitats. They share the same basic pattern of social organization in that they form multi-male, multi-female groups, which permanently contain both adult males and females with offspring. The adult sex ratio is biased toward females who constitute kin-bonded subgroups within their natal group while most males transfer between groups at maturation. However, macaque species differ both in their morphology and behaviour and in their styles of affiliation, aggression, dominance, nepotism, maternal behaviour and socialization (e.g. [16-19]). Therefore, Thierry [3,20] proposed classifying the different species of macaques along a 4-grade scale going from a despotic and nepotistic style of social relations to a more tolerant social style with open relations. Grade 1 species (i.e. less tolerant or despotic) display strong nepotism and steep dominance hierarchies with a low rate of tension-reducing contacts. Subordinates use the bared-teeth display to express submission, acknowledging their lower status relative to higher-ranking conspecifics [21]. In contrast, Grade 4 species (i.e. more tolerant or egalitarian) have less steep dominance hierarchies, lack formal indicators of subordination, and the bared-teeth display has a more affiliative role [16-19].

Among non-human primates and along with great apes, baboons and capuchins, macaques possess an enhanced general intelligence compared to other mammals [22,23]. For decades, it has been reported that wild macaques are capable of innovative behaviours and use tools (see [24-26] and [27] for a recent review). Many experimental studies on macaque cognition have been performed and demonstrate that they have advanced understanding about objects and also about their spatial, numeral, and causal relations (e.g. [28-30]). In the social domain, macaques are able to follow gaze (either from a human demonstrator: e.g. [28,30-32], or from congeners: e.g. [33-35]; see also the review from [36]), understand the target of attention [37]) and seem capable of visual perspective taking (e.g. [38,39]), they can cooperate to solve a string-pulling task [40] but do not seem to show any indication of imitation in some social learning tests [29,30]. However, our knowledge on macaque cognition comes mostly from data or experimental studies in a limited number of macaque species, mainly belonging to Grade 1 and 2 (the less tolerant grades) on the social tolerance grade scale (but see recent findings in most tolerant macaque species [40-45]). As Call ([46], p.33) highlighted, it is however probable that macaques ‘whose social organization is more fluid may also show a different set of cognitive abilities’.

To our knowledge, data supporting a link between social tolerance and enhanced socio-cognitive skills, such as cooperative skills, across species is still scarce (e.g. see [1]). Direct comparative data on a large set of cognitive skills of several species differing in their social tolerance is lacking. To fill this gap, the main aim of this study was to test whether social style is associated with specific cognitive skills in different macaques species. For that purpose, we tested rhesus macaques (*Macaca mulatta*) and long-tailed macaques (*Macaca fascicularis*; grades 1 and 2: less tolerant macaque species) as well as Barbary macaques (*Macaca sylvanus*) and Tonkean macaques (*Macaca tonkeana*; grades 3 and 4: more tolerant macaque species) in a large and comprehensive cognitive task battery. We hypothesized that, while all macaque species should display similar skills in their understanding of the physical world, the more tolerant species would display more sophisticated skills in the social domain and especially those skills that enable cooperation. We therefore expected the more tolerant species to show better performance in tasks requiring inhibitory control crucial for delayed gratification (which might occur in cooperative contexts) and in communicative skills (e.g. non verbal communication to attract attention to an object) essential for coordination.

Material and Methods

Subjects and housing conditions

We tested four different species: rhesus, longtailed, Barbary and Tonkean macaques. A total of 39 adult macaques from 3 different European institutions were involved in this study: the Monkey Haven on the Isle of Wight (sanctuary, United Kingdom [UK]), the Parco Faunistico dell' Abatino in Rieti (sanctuary, Italy [IT]) and the Biomedical Primate Research Centre in Rijswijk (primate breeding centre, The Netherlands [NL], see Table 1 in ESM).

One group of rhesus (N=5 subjects, 2 females and 3 males) and one group of Barbary macaques (N=6 subjects, 4 females and 2 males) were housed in the UK. One group of Barbary (a subset of 5 subjects – 3 females and 2 males – from a group of 17 individuals) and 2 groups of Tonkean macaques (total N=10 subjects, group 1: 3 females, 4 males; group 2: 1 male, 3 females) were housed in IT. Six individuals from 6 different groups of rhesus (N=6 males) and one group (N=7 subjects, 7 females, from a group of 17 individuals) of longtailed macaques were housed in NL (see ESM for origins of the subjects). Subject ages ranged from 4 to 21 years old.

In the UK, the rhesus macaques were familiar with human presence and interactions, but they were all naïve to or had limited experience with behavioural studies or experiments. The Barbary macaques were involved in cognitive testing and were trained to participate in matching-to-sample tasks using a touch-screen (similar to [47] and see,[48]). They all had access to indoor and outdoor enclosures where testing areas were available.

In IT, the Barbary macaques were all raised in social groups and while familiar to human presence and interactions, they were all completely naïve to behavioural studies or experiments. The Tonkean macaque subjects were all raised in social groups and were familiar with human presence and interactions, but had various experiences with cognitive testing. One subject (Ninfa) was completely naïve to behavioural experiments while the other subjects had already taken part in previous cognitive studies (e.g. [43-45,49-51]). All subjects were naive to the present testing protocol. All groups were housed in enclosures approximately 500m^2 size and 5m high with access to indoor enclosures. The dedicated testing area was outdoor for the Barbary macaques and semi-outdoor for the Tonkean macaques.

In NL, the longtailed and rhesus macaques from the BPRC were all born in the centre and raised in social groups. The longtailed group (‘Haas’ group) had already participated in training and behavioural studies before (e.g. recently in [39,51,52]), and all animals were familiar with clicker procedures. All were clicker-trained to follow a trainer who held a target (a plastic shoe-horn) and to receive a reward while touching the shoe-horn presented against or through the fence of their cage. All rhesus macaques housed in the BPRC were familiar with the same training and clicker procedures, but were naive to previous behavioural studies and experiments. The study took place in their home cage in which monkeys were individually tested in a corridor with the experimental set-up placed directly in front. Each macaque was assigned to a social status category (see details of the methods used in ESM): i.e. categorised as either low, middle or high ranking (we divided the number of (sub)adult individuals in three equal categories, but when this was not possible, the additional individuals were allocated to the middle category, so that the number of high and low ranking individuals contained the same number of individuals).

All macaques in this study were housed in enriched enclosures, equipped with climbing structures and enrichment devices (food puzzles, boxes, etc.). They were fed daily with assorted fruits and vegetables, nuts, seeds and commercial monkey pellets. Water was available *ad libitum*. They all had access to food and water prior to and during the experiment. Furthermore, only those subjects voluntarily entering the area with the experimental setup participated in the study to ensure low stress levels.

Cognitive task battery

The Primate Cognition Test Battery (PCTB) was designed by Herrmann and colleagues [53] based on the theoretical framework of primate cognition proposed by Tomasello and Call [28]. It consists of 16 tasks examining skills of physical cognition and social cognition (see Table 2 in ESM). To our knowledge, the PCTB has been used in 4 different studies so far, investigating the heritability of cognitive performance in great apes [54], and comparing the performance of human children and apes [53], bonobos and chimpanzees [55], and baboons, longtailed macaques and great apes [30].

The 16 tasks of the battery are grouped into 2 domains (Physical or Social) with 3 scales each (Physical: Space, Quantities, Causality, and Social: Social Learning, Communication, Theory of Mind, see [53]). In the physical domain, the scale Space tests the monkeys’ ability to track objects in space. This scale consists of four different tasks: Spatial Memory, Object Permanence, Rotation, and Transposition (see Table 2 and methodological details in ESM). The Quantities scale, tests the monkeys’ abilities to understand quantities. This scale consists of two tasks: Relative Numbers and Addition Numbers (see Table 2 and methodological details in ESM). Lastly, in the Causality scale, the macaques’ understanding of the spatial-causal relationship between two objects is tested via four different tasks: Noise, Shape, Tool Use, and Tool Properties (see Table 2 and methodological details in ESM).

In the social domain, the Social Learning scale (only one task) aims at testing whether the monkeys’ imitate simple actions performed by a human to reach a food reward. For this task, a human demonstrator shows the subjects how to open three different plastic tubes, which contain a reward (Paper tube, Banana tube, Stick tube).

The Communication scale tests whether the subjects are able to understand communicative cues given by humans. This is done by using three different tasks: Comprehension, Pointing Cups, and Attentional State (see Table 2 and methodological details in ESM). Lastly, in the Theory of Mind scale, two different tasks are performed: Gaze Following and Intentions (see Table 2 and methodological details in ESM).

Testing procedures

The tests were performed when one animal was alone in front of the experimenter: the monkeys were usually tested through a priority of access model (the first individual to come is tested first) and left after they have finished a maximum number of trials. The testing apparatus and all materials used were identical for all species. For most of the experiments, it consisted of a sliding board made of white polyvinylchloride (70 cm x 45 cm, similar to [30], see ESM videos 1-5, 8), attached to a platform made of the same material by two drawer rails so that the sliding table could be moved horizontally. For most of the tasks, three blue opaque cups were used to cover or present the food reward (see ESM videos 1 and 2). Otherwise small brown plastic trays were used for the quantities task and functional and non-functional tools were presented for the Tool use tasks (see Material and Methods in ESM and videos 3 and 4). These were placed on the sliding table.

Depending on the tasks, two or three openings (which allow pointing or retrieving of food or object) were made in the enclosure wire mesh. Each monkey had received a short period of training prior to testing: we presented one cup to the macaque on the platform. The subject had to stretch its arm, hand and fingers through the opening in the wire mesh to reach the cup, and was rewarded for this. This training was conducted up to a maximum of 10 times per subject. All monkeys passed the training. Throughout testing, the monkey choice was scored when it indicated (with whole hand or finger) to one of the locations or put a finger through one of the openings. When the monkeys indicated the correct location or object, they were given a small food reward. When they made incorrect responses they were always shown the location of the hidden food after each trial. The same desirable food items were used as rewards for most of the tasks (raisins, peanuts, pieces of fruits depending on the institution). All sessions were videotaped with two digital video cameras (Sony HDR-CX330EB).

Inhibitory control task

Each subject also participated in a set of additional tests as used by Herrmann et al. [53] and Schmitt et al. [30] to evaluate the inhibitory control of each individual. Previous studies from Call and colleagues showed that apes and human children had difficulty avoiding a middle cup when presented with 3 of them [56,57]. These difficulties seemed to be based on inhibitory control problems: subjects need to inhibit their tendency to choose the cup closest to themselves - here the middle one - in order to succeed. This task represents therefore a simple way to assess inhibitory control. Similar to the Spatial Memory trials (see ESM video 1), rewards were placed under two out of three cups while the subjects were watching. Only the two outer cups were baited, while the middle cup remained empty and untouched. If the subject first chose one of the outer cups it was allowed to make a second choice. If, however, it chose the middle cup first, no further choices were possible. A correct response was scored when the monkey chose the two outer cups in succession while skipping the middle cup.

The PCTB and inhibitory task were administered to all subjects by the same main experimenter (MJ) and in the same order. When needed, the second experimenter was a familiar human in each institution, *i.e.* a person who had been in regular contact with the monkeys during several months prior to the study.

Video and reliability analysis

Each trial within the cognitive battery and the inhibitory control task was videotaped for rating and analysis. Subjects' responses were coded live by MJ except for gaze-following trials, which MJ coded from videotape after the test. Two secondary observers (O_1 and O_2) independently scored all videotapes for a total of

4338 trials across all tasks for all macaque species. Inter-observer reliability was excellent (Kappa$_{MJ\text{-}O1}$= 0.98 with first observer who coded 3223 trials and Kappa$_{MJ\text{-}O2}$= 0.96 with second observer who coded 1115 trials).

Statistical analysis

The physical *vs.* social domain structure of the PCTB performance has been validated in two previous studies in great apes [53,54]. However, despite the use of large cohorts, the data did not support the scale subdivision for both domains (see [54]). We therefore opted for an analysis of the macaques' performance within each domain at a task level (and not a scale level) only (Table 2 in ESM). We followed the order of the tasks as described in the original study [53] and we presented the results following this order.

Within a domain, we calculated the proportion of correct answers per task and individual and the mean proportion for the whole macaque sample (see Table 3 in ESM). To evaluate whether the macaques understand a task and performed above chance level at a group level, we used a Wilcoxon-test and applied a Benjamini-Hochberg correction procedure to control for false discovery rate in multiple testing [58]. Within the physical domain, among the 39 tested macaques, only two individuals (longtailed macaques, NL) managed to retrieve a reward using a T-shaped tool (they had previously taken part in an experiment involving the use of a similar tool [52]). Within the social domain, none of the macaques succeeded in the social learning trials, the whole social learning task was therefore removed from the analysis. Both tasks were therefore not included in further analysis.

To study the relationship between the grade of social tolerance, the task, the sex, the age, the social status, the individual identity, and the probability of a correct answer in the physical domain, in the social domain and in the inhibitory control task, we used generalized linear mixed models (GLMMs) with binomial error structure and logit link function (see [59]).

Models were fitted with trial response (correct/incorrect) as the outcome variable and the following explanatory variables: *Tolerance degree* (less tolerant – rhesus and longtailed macaques; or more tolerant – Barbary and Tonkean macaques), *Task* (physical domain: 9 levels, social domain: 5 levels; for each domain, the reference level was the first task in which the macaques were tested), *Sex* (male or female), *Age* (in years), and *Social Status* (defined as Low, Medium or High). For the social domain, we considered also the interaction *Tolerance* x *Task* as the nature of the tasks may predict a different outcome according to the social tolerance degree. *Individual Identity* nested within *Species* within *Tolerance degree* was fitted as a random factor in all models to control for multiple observations of the same individuals (avoiding pseudoreplication, see for instance [60]) and therefore control for any variation in tendency to perform certain acts and respond in a particular way

[61, 62].

We fitted GLMMs using the function glmer from the package lme4 [63] for R 3.2.3 [64]. We estimated the parameters by Maximum Likelihood (ML) and using a Laplace approximation. This is in line with best practice when fitting Generalized Linear Mixed Models for our datasets similar to ours [59]. To assess the overall significance of the models, we compared them to the null model including only the intercept and the random variables by performing a likelihood-ratio test comparing the log-likelihoods of both models [65]. Significant effects were considered only if the model with predictors was more informative than the null model (i.e. if the likelihood- ratio test was significant). Initially all explanatory variables and the two-way interactions were fitted in a maximal model. Non-significant interactions and main terms were then dropped sequentially to simplify the model. We present here the simplified models with their predictors. Estimates and their standard error are given, alongside odds ratios, z-scores and p-value ($\alpha = 0.05$), as measures of the effect of each predictor on the occurrence of a correct answer in a trial.

Results

Inhibitory control task

The overall mean proportion of correct answers of the macaques in the inhibitory control task was 0.26 ± 0.35 and not significantly different from a random choice (N=39, chance level=0.33, z=-1.046, p= 0.29; see Table 3 in ESM). Macaques belonging to the less tolerant species performed significantly below the chance level (N=18, mean proportion= 0.11 ± 0.23, z= -2.199, p= 0.0.028: see Table 4 in ESM) while macaques of the tolerant species did not (N=21, mean proportion= 0.31 ± 0.38, p>0.05).

These results were supported by the model with the variable *Tolerance degree* as a fixed term (likelihood-ratio test comparing the full model with the null model: $\chi2 = 5.5$, df = 1, p=0.019, see Table 1 summarizing the results). A strong effect came from the social tolerance degree: individuals belonging to more tolerant species were more likely to show inhibitory control. Looking more closely at the performance in the Inhibitory Control task, less tolerant species chose first a correct outer cup but then chose the closest, i.e. the middle cup, as a second choice and therefore did a mistake by not inhibiting their action in 85% of the failed trials. The picture was slightly different for the more tolerant species: while they had overall fewer fails (31% of success compared to 11% for the non tolerant), when failing, they chose first an outer cup in 64% of the trials (non significantly different from a random choice). So this confirmed that this task is quite difficult for our monkeys, and that less tolerant species had particularly poor inhibitory control skills.

Physical Domain

All macaques performed significantly above chance level in 5 out of the 9 tasks: Spatial Memory (N=39, chance level=0.33, mean proportion= 0.56 ± 0.28, z=-3.06, p= 0.002), Object permanence (N=39, chance level=0.33, mean proportion= 0.57 ± 0.16, z=-5.05, p<0.0001), Rotation (N=39, chance level=0.33, mean proportion= 0.44 ± 0.17, z=-2.60, p=0.009), Relative Numbers (N=39, chance level=0.5, mean proportion= 0.70 ± 0.18, z=-4.86, p<0.0001) and Tool properties (N=38, chance level=0.5, mean proportion= 0.56 ± 0.13, z=-2,61, p<0.009).

Their performance was not significantly different from a random choice in the tasks Transposition (N=39, chance level=0.33, mean proportion= 0.40 ± 0.22, z=-1.48, p= 0.138), Addition Numbers (N=39, chance level=0.5, mean proportion= 0.60 ± 0.21, z=-1.934, p=0.052), Noise (N=39, chance level=0.5, mean proportion= 0.50 ± 0.21, z= -0.876, p=0.379), and Shape (N=39, chance level=0.5, mean proportion= 0.53 ± 0.18, z=-1.57, p= 0.116).

The presented model with the variables *Tolerance degree* and *Task* as fixed terms explains the performance of the macaques in the tasks relevant to the physical domain (likelihood-ratio test comparing the full model with the null model: χ2 = 102.6, df = 9, p < 0.0001, see Table 2 summarizing the results for each predictor). The results show that only the tasks affected the probability to succeed in a trial: for the macaques, the Transposition task was the most difficult to solve compared to the Spatial Memory task. Conversely performance on the task Relative Numbers was higher than in the Spatial Memory task. There was no effect from the social tolerance degree: individuals belonging to more tolerant species had a comparable understanding of the physical domain tasks as less tolerant species (see Table 2).

Social Domain

Within the social domain, the macaques did not perform differently from chance level in the tasks requiring a choice between 2 options (Comprehension: N=38, chance level=0.5, mean proportion= 0.54 ± 0.14 and Intentions: N=34, chance level=0.5, mean proportion= 0.52 ± 0.18, $p>0.05$). They produce communicative gestures to get a food reward in less than half of the trials (Pointing Cups task: N=34, mean proportion= 0.39 ± 0.34), responded poorly in the Attentional State task (N=34, mean proportion= 0.11 ± 0.19) and follow the gaze of the experimenter in less than 4 out of the 9 trials (N=36, ± 2 trials).

The model with the variables *Tolerance degree* and *Task* as fixed terms and their interaction best explained the performance of the macaques in the tasks relevant to the social domain (likelihood-ratio test comparing the full model with the null model: $\chi 2 = 139.8$, df = 9, $p < 0.0001$, see Table 3 summarizing the results for each predictor). The interaction between *Tolerance degree* and *Task* predicted a different pattern of success in a trial. More tolerant species were more likely to succeed in the Pointing Cups task compared to less tolerant species, but there were no differences between the more tolerant and less tolerant species in the Comprehension, Attentional State, Gaze Following or Intentions tasks.

Discussion

In summary, our findings demonstrate that socially tolerant macaques display better inhibitory control and enhanced skills in the production of communicative cues than less tolerant macaques, but perform similarly in the physical domain. Our data corroborate the idea that living in a social and tolerant environment may be associated with better capacity for cooperation, such as better control of reflex responses and production of communicative cues. Individuals belonging to the less tolerant species were less able to inhibit an automated response compared to those living in a more tolerant social landscape. This capacity is particularly crucial for cooperation as it may enable the individual to wait in order to get a benefit from an interaction with a conspecific (see [9,10]).

Our results demonstrate that social tolerance is associated with a modular set of cognitive skills and not overall enhanced abilities in the social domain *per se*. Both tolerant and less tolerant macaques displayed similar performance in the physical domain while there were differences in the performance within a task of the social domain. Our data therefore do not support a domain-general intelligence hypothesis with social tolerance degree as a predictor (but see support for the hypothesis with degree of sociality as a predictor in e.g. birds [66], social carnivores [67] and non-human primates [68]). Our results are also congruent with the findings of a study investigating seven non-human primate species differing in their phylogenetic relatedness and socio-ecological characteristics [69]. This study showed that an interaction between species and domain best explained the performance of the tested monkeys and apes in a battery of cognitive tests, supporting the hypothesis that domain-specific cognitive skills undergo different evolutionary pressures in different species in response to specific ecological and social demands. This is also on par with the findings within the Pan genus and differences in the cognitive skills in both physical and social domain between the more tolerant bonobo and the extractive forager chimpanzee [55].

We agree with Amici et al. [69] and encourage the use of selecting multiple basic tasks that address an array of cognitive skills belonging to a wide range of domains and systematically administer them to multiple species. By doing this, we may more easily detect some domain-specific effects that would otherwise be missed. We consider this to be a first step to first identify differences among wisely chosen species of interest, refine the theoretical framework and then use more elaborated designs to test advanced cognitive skills.

While the PCTB provided a great opportunity to test multiple basics skills in a standardised way, we observed an overall quite poor performance of the macaques, especially in the social domain. The PCTB was initially designed to test human children and great apes (see [53]). So for macaques which have a lower general intelligence than great apes (see [23]), the battery tasks are probably far more challenging. Moreover, while Herrmann and colleagues tested an impressive sample of chimpanzees and bonobos providing a good picture of cognitive performance of great apes in the PCTB, we have only data from a small number of individuals in two species of monkey (13 longtailed macaques and 5 olive baboons [30]) published so far. Another particular caveat here is that the social context might not be ecologically relevant for our tested subjects. Whether our findings in the social domain would still hold true when animals are tested with conspecifics is unknown. Some recent experiments testing the functions of such mechanisms with live conspecifics are encouraging though. In the domain of social communication, Micheletta et al. [34] showed that strong positive bonds between individuals improved gaze-following responses in a tolerant macaque and therefore highlight the importance of species' social style in shaping primate cognition. Similarly a high level of inter-individual tolerance seems to be crucial for the initiation of a pair up in macaques in order to solve a cooperative task [40]. The present results add to our understanding of the cognitive performance of Old World monkeys and offer insight into the evolution of cognitive performance in non-human primates in general.

A recent large study demonstrated that within the primate order, diet breadth was a better predictor of species differences in self-control (see [70]) than social complexity (measured using the social group size). While the authors tested an impressive sample of 23 non-human primate species (309 subjects) in two straightforward tasks with only few test trials (1 to 10 in A-not-B task and cylinder task, respectively [70]), it could be argued that social group size is not an accurate proxy for social complexity. By taking a finer proxy parameter reflecting the social landscape, such as social tolerance degree, we may better predict the selective pressure acting on social cognition. While social complexity can be clearly defined (see e.g. [71]), how to measure it remains a difficult task (see e.g. [72]). For instance, macaques have different relationships within their groupmates depending on the sex, rank, age and kin relationship with other individuals, and tolerant macaques form strong bonds with non-kin as well as kin (i.e. friendships, see e.g. [73,74]). Using a more accurate measure of social complexity is clearly an important goal for future studies and the social landscapes of many species may actually be more complex than described so far.

Altogether, our data suggest that tolerant macaques are equipped with enhanced cognitive abilities which could enable better cooperation and communication in comparison to less tolerant species. As previously hypothesised, the selection of tolerance against aggression may have led to psychological, behavioural, physiological and morphological phenotypic changes (see also [75]). This framework offers an interesting avenue to further investigate those characteristics and gain important insight into the evolutionary roots of human cooperation and cognition.

Ethics

This study was carried out after receiving approval by an EU Ethics committee (for grant approval, EU FP7 Marie Curie Project No. 623908), by the University of Portsmouth, UK, regulated by the Department of Psychology Animal Ethics Committee (Approval of project by the Animal Welfare and Ethical Review Body, AWERB, No. 4015B) and by the BPRC's Ethics Committee (DEC 756). All aspects of the study were covered by these ethical approvals. Subjects were never food deprived for the cognitive tasks conducted in this study. Cognitive testing required subjects to break from their social group and enter the testing area voluntarily. All subjects were kept to normal daily husbandry schedules predetermined by the institutional staff throughout the data collection period. The data collection took place between December 2014 and December 2015.

Data accessibility

Data are available in the ESM.

Competing interests

We declare we have no competing interests.

Author's contributions

MJ conceived and designed the study, collected the data, carried out the statistical analyses, wrote and drafted the manuscript. ADM participated in the data collection in IT and helped draft the manuscript. JM helped in the statistical analyses and helped draft the manuscript. JAL coordinated the data collection in NL and helped draft the manuscript. EHMS coordinated the data collection in NL and helped draft the manuscript. BMW helped in conceiving the study and helped draft the manuscript. All authors gave final approval for publication.

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Table 1. Impact of Tolerance degree, social status and individual identity on the probability of a correct answer in the inhibitory control task

Predictor variable	**Estimate**	**SE**	**Odds ratio** **(95% CI)**	**z**	**P**
Intercept	-2.046	0.872	-	-2.347	0.0189*
Tolerance degree					
Low	0	0	1		
High	2.272	0.879	8.643 (1.587-47.061)	2.58	0.0098**

Estimates represent the change in the dependent variable relative to the baseline category of each predictor variable, and indicate the magnitude and direction of the effect of each condition on the likelihood of correct answer. Individual identity (estimated variance component = 2.46, SD = 1.57) nested within Species within Tolerance degree (estimated variance component < 0.001, SD < 0.001) was included as a random factor.

Table 2. Impact of Tolerance degree, task and individual identity on the probability of a correct answer in the tasks relevant to the physical domain

Predictor variable	**Estimate**	**SE**	**Odds ratio** **(95% CI)**	**z**	**P**
Intercept	0.227	0.199	-	1.142	0.253
Tolerance degree					
Low	0	0	1		
High	0.063	0.105	1.065 (0.867-1.308)	0.600	0.548
Task					
Spatial Memory	0	0	1		
Object Permanence	0.059	0.217	1.060 (0.693-1.622)	0.272	0.786
Rotation	-0.475	0.216	0.622 (0.407-0.950)	-2.196	0.028*
Transposition	-0.689	0.217	0.502 (0.328-0.769)	-3.168	0.002**
Relative Numbers	0.569	0.211	1.766 (1.168-2.672)	2.695	0.007**
Addition Numbers	0.184	0.225	1.201 (0.773-1.868)	0.815	0.415
Noise	-0.278	0.229	0.757 (0.483-1.186)	-1.216	0.224
Shape	-0.122	0.229	0.885 (0.564-1.387)	-0.534	0.593
Tool Properties	0.006	0.206	1.006 (0.672-1.506)	0.029	0.977

Estimates represent the change in the dependent variable relative to the baseline category of each predictor variable, and indicate the magnitude and direction of the effect of each condition on the likelihood of correct answer. Individual identity (estimated variance component = 0.05, SD = 0.23) nested in Species within Tolerance degree (estimated variance component < 0.001, SD < 0.001) was included as a random factor.

Table 3. Impact of Tolerance degree, Task and individual identity on the probability of a correct answer in the tasks relevant to the social domain

Predictor variable	Estimate	SE	Odds ratio (95% CI)	z	P
Intercept	0.364	0.184	-	1.981	0.047*
Tolerance degree					
Low	0	0	1		
High	-0.331	0.246	0.718 (0.443-1.163)	-1.345	0.179
Task					
Comprehension	0	0	1		
Pointing Cups	-1.974	0.407	0.139 (0.063-0.308)	-4.854	<0.001 **
Attentional State	-17.92	25.248	<0.001 (-)	-0.707	0.740
Gaze Following	-0.780	0.239	0.458 (0.287-0.732)	-3.267	0.001**
Intentions	-0.067	0.287	0.935 (0.532-1.642)	-0.233	0.816
Tolerance x Pointing Cups	2.138	0.487	8.481 (3.268-22.012)	4.394	<0.001 **
Tolerance x Attentional State	16.150	25.348	-	0.637	0.765
Tolerance x Gaze Following	0.339	0.318	1.404 (0.752-2.621)	1.065	0.287
Tolerance x Intentions	-0.03	0.370	0.969 (0.469-2.002)	-0.084	0.933

Estimates represent the change in the dependent variable relative to the baseline category of each predictor variable, and indicate the magnitude and direction of the effect of each condition on the likelihood of correct answer. Individual identity (estimated variance component = 0.11, SD = 0.32) nested in Species within Tolerance degree (estimated variance component < 0.001, SD < 0.001) was included as a random factor.