

Research



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Animal behaviour

Competition is crucial for social comparison processes in long-tailed macaques

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Humans modulate their self-evaluations and behaviour as a function of conspecific presence and performance. In this study, we tested for the presence of human-like social comparison effects in long-tailed macaques (*Macaca fascicularis*). The monkeys' task was to extract food from an apparatus by pulling drawers within reach and we measured latency between drawer pulls. Subjects either worked on the task with a partner who could access the apparatus from an adjacent cage, worked in the absence of a conspecific but with food moving towards the partner's side or worked next to a partner who was denied apparatus access. We further manipulated partner performance and competitiveness of the set-up. We found no indication that long-tailed macaques compare their performance to the performance of conspecifics. They were not affected by the mere presence of the partner but they paid close attention to the partner's actions when they were consequential for food availability. If social comparison processes are present in long-tailed macaques, the present study suggests they may only manifest in situations involving direct competition and would thus be different from social comparisons in humans, which manifest also in the absence of direct competition, for example in evaluative contexts.

1. Introduction

Human sensitivity to conspecifics results in sophisticated social comparison processes, where humans modulate their behaviour in response to people in their surroundings [1–4]. Social comparison is the utilization of conspecifics as comparison standards in order to ascertain how one fares along a particular dimension. A number of studies have shown that humans modulate their behaviour as a function of others' presence and performance [3]. In humans, social comparison is thought to be employed primarily for the purpose of self-evaluation and social comparison processes play a role in group formation and contribute to the gregarious nature of humans [2,5]. If this is the case, might a precursor to the social comparison process exist in gregarious animals that form socially complex groups?

Observational and experimental studies document various degrees of sensitivity to conspecific presence and performance in the wider animal kingdom. Several animal species are thought to assess conspecifics along fighting ability related dimensions. For example, roaring displays in stags present a chance for males to assess opponent strength—to assess

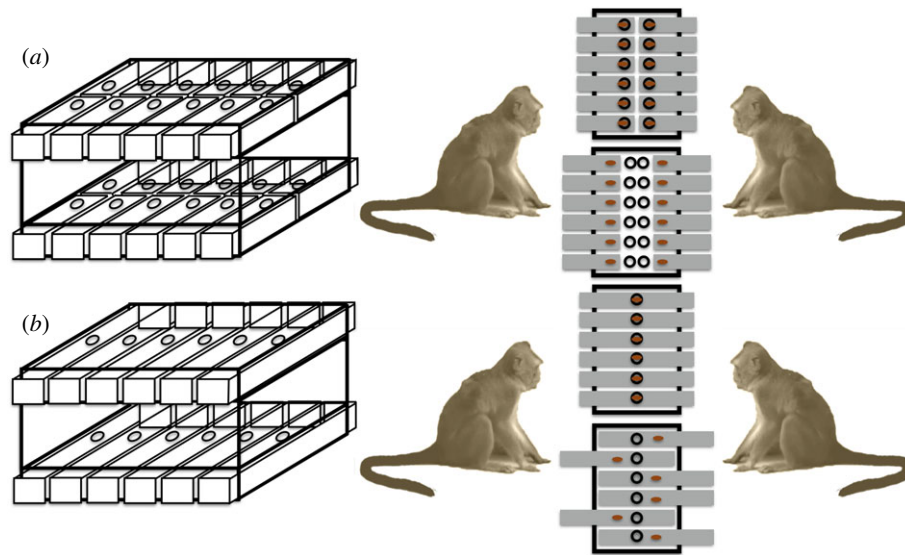


Figure 1. Schematic depiction of drawer-sets. (a) Co-action, (b) competition. Left column shows a side-angled 3-D view of both levels of drawers; right column shows a bird-eye view of starting position and position of drawers after having been pulled towards each side. The drawers were baited via a small opening (white circles) in the transparent ceilings covering each drawer level; raisins (brown oval symbols) were retrievable when drawers had been pulled to the respective side. (Online version in colour.)

whether escalation is advisable [6]. Chimpanzees are able to assess the relative difference in group size between their own and neighbouring rival parties and use this information to decide whether to retreat or attack [7]. In addition, experimental studies on inequity aversion [8,9] indicate that some species are sensitive to working effort and reward granted a conspecific relative to the self. Social comparisons with group members might also be useful to decide how to choose good or fair interaction partners in future encounters (see [10]). This said, the systematic study of human-like social comparison effects is a relatively new topic in animal cognition research [11,12].

The current study was inspired by an experiment by Seta [13] in which human participants performed a simple manual task—pressing a sequence of buttons with four fingers. The task was carried out in the presence of a co-actor independently engaged in the same task. Acoustic feedback provided participants with information about the other person's performance. As the tasks were identical, subjects could attribute any apparent difference in co-actor performance to differing ability level. The experimenter manipulated the feedback such that co-actors appeared to be performing better, worse or equally well compared with the participant. Seta found that when paired with a slightly better performing partner, i.e. a performance that was within the capability of the participant, participants' performance increased compared with when working alone. Previous findings from a study that applied the co-action paradigm to long-tailed macaques (*Macaca fascicularis*) indicated that a certain level of competition might be necessary to draw subjects' attention to relevant aspects of the partner's behaviour and that simply working in parallel on two touchscreens is not sufficiently relevant for catching the monkeys' attention [12,14].

In the current study, we presented our monkeys with a hands-on task in which food items had to be extracted from an apparatus that could be accessed from two sides. We aimed to test whether long-tailed macaques are sensitive to a conspecific's task performance. Importantly, our definition of social comparison thus concerns whether someone

performs similar to/different from oneself rather than comparison of different pay-offs or experimenter treatment. To this end, we tested a group of monkeys in a co-action task where there was either direct food competition or no element of competition. We manipulated the designated partner's performance by changing the effort he had to apply to perform the task. In addition, we presented the monkeys with a social control condition in which the partner was present but not working at the task and a ghost control condition in which no partner was present but parts of the apparatus appeared to move on their own. Our specific questions were: (i) Do monkeys compare themselves with others and adapt their performance to the performance level of a co-actor? and (ii) Is performance change due to social presence of conspecifics or due to food disappearing from the monkey's reach? Reaction to the manipulation of partner performance in the co-action context would be an indication for the presence of classical social comparison processes. By contrast, the competition context should result in fast reaction times irrespective of partner performance. Furthermore, if disappearing food from subject's reach is the driving factor, we expect shorter latencies in competition ghost control compared with competition social control, co-action ghost control and co-action social control. If social presence is the driving factor we expect shorter latencies in social control compared with ghost control conditions.

2. Methods

We tested 10 long-tailed macaques (*Macaca fascicularis*) which were housed in a social group of 36 individuals at the German Primate Center (more details on subjects, procedure and analysis are provided in the electronic supplementary material). After familiarization with the set-up, subjects were tested in all test conditions in a within-subject design (order of condition counterbalanced across subjects). Subjects were tested with two versions of 'drawer' apparatus (figure 1) resulting in two contexts: competition (CO) and co-action (CoA). The task was to pull open drawers and extract food from the apparatus. During the test conditions, either subjects

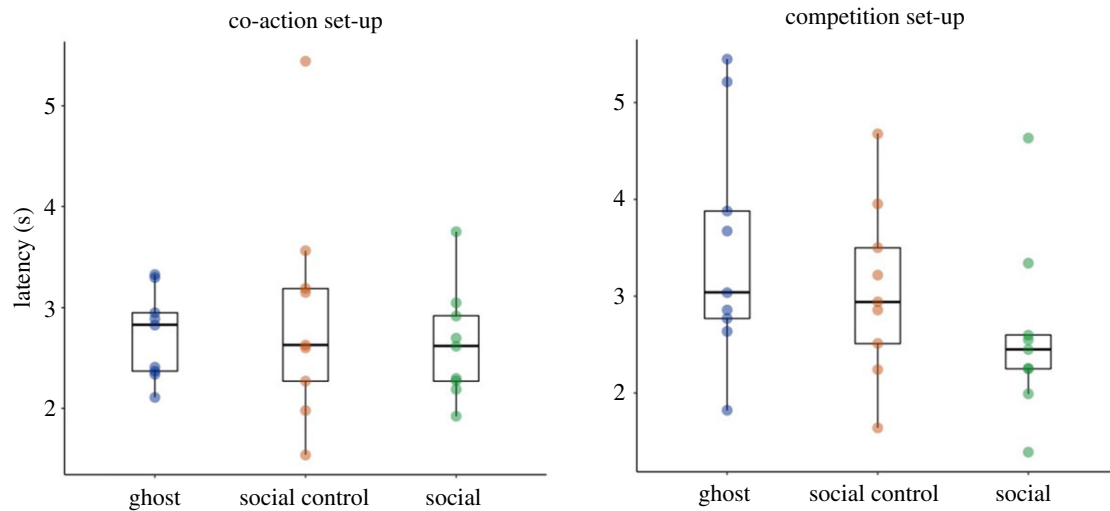


Figure 2. Average latencies between pulls for each individual in the different test conditions in co-action and competition set-ups. Black horizontal lines indicate means per condition; vertical lines indicate 95% confidence intervals.

Table 1. Results for individual predictors for pull latency in CO set-up (full model: $\text{latency} \sim \text{condition} + \text{trial} + (1 + \text{condition} + \text{trial} \parallel \text{subject ID})$).

term	estimate	s.e.	CI _{2.5}	CI _{97.5}	χ^2	d.f.	p-value
intercept	1.050	0.095	0.866	1.226			
competition ^a	-0.225	0.066	-0.352	-0.088	12.05	2	0.002
ghost ^a	0.119	0.091	-0.054	0.292			
trial	-0.081						

^aCondition was dummy coded with social control condition as the reference category. The indicated test refers to the overall effect of condition.

were paired with a partner who was working on the apparatus from an adjacent cage, or they worked alone while the partner's access was blocked (social control condition), or worked alone with no partner present but parts of the apparatus moved toward the partner's side (ghost control condition). We additionally manipulated the speed of partner pulling by attaching weights to drawers such that for half of the social trials the partner was slowed down.

We coded latencies between drawer pulls to assess if subjects' behaviour changed as a function of condition. We used linear mixed models [15] to analyse the data. As the effect of the weight manipulation diminished during the study, we included the partners' actual pulling latencies in each trial as predictor in the model, instead of weight condition (see electronic supplementary material). We first tested if partner ID and performance had an effect on subject performance (full model included partner performance and partner ID as fixed predictors of interest and trial number as fixed control predictor). We then tested for the effect of disappearing food and social presence (full model included condition (ghost, social control, CoA/CO) as fixed predictor variable and trial number as fixed control predictor). In a separate analysis, we compared test conditions with a baseline condition where subjects worked in the absence of a next-door partner. We analysed the data separately for CoA and CO set-up.

3. Results

(a) Effect of partner performance and partner identity

We tested if partner performance and partner identity affected subjects' behaviour. Model comparisons revealed

no such effect for either of the two set-up conditions (CoA: $\chi^2 = 3.36$, d.f. = 2, $p = 0.19$; CO: $\chi^2 = 4.43$, d.f. = 2, $p = 0.11$).

(b) Effect of disappearing food and social presence

(i) Co-action

Figure 2 provides an overview of mean drawer pull latencies per condition. We compared CoA, ghost and social control condition to test for the influence of social presence of a partner and of food disappearing from the subject's reach. The full and null model were not different, indicating that for CoA set-up neither factor had a systematic influence on subjects' pull latencies ($\chi^2 = 4.1$, d.f. = 2, $p = 0.13$).

(ii) Competition

Figure 2 gives an overview of mean drawer pull latencies per condition. Model comparison revealed the full model was significantly different from the null model ($\chi^2 = 12.05$, d.f. = 2, $p < 0.01$, conditional $R^2 = 0.47$). The negative coefficient of the trial estimate indicates that response latencies decreased with increasing trial number (see table 1 for detailed summary of the full model). Pairwise comparisons (table 2) revealed a significant difference between CO and social control condition (latencies in CO condition < social control) and between CO and ghost condition (latencies in CO condition < ghost control).

(c) Comparison with baseline

For co-action, we compared subjects' performance in baseline–social control, baseline–ghost and baseline–CoA

Table 2. 95% family-wise confidence intervals for pairwise multiple comparisons in CO set-up.

	estimate	lower boundary	upper boundary
ghost–social control	0.120	−0.094	0.333
competition–social control ^a	−0.225	−0.378	−0.071
ghost–competition ^a	0.344	0.148	0.540

^aA significant difference between the compared conditions (both $p < 0.001$).

conditions. None of the comparisons was significant. For competition, we compared subjects' performance in baseline–social control, baseline–ghost and baseline–CO conditions. We found a significant difference only between baseline and CO ($z = -2.81$, $p = 0.01$).

4. Discussion

In this study, we tested whether monkeys compare themselves with others based on human-like social comparison processes. Assimilation of own performance to the performance of a similar comparison standard would be an indication of such social comparisons [3,13,16,17]. We tested for the role of partner performance and competition on monkeys' behaviour in a co-active food extraction task.

Our findings do not provide support for the notion that the monkeys' performance was influenced by partner performance level. The monkeys increased their feeding speed when food disappeared out of reach when they competed directly with a conspecific (CO condition). They decreased their feeding speed when the food items moved out of reach in the ghost control condition. It seems that disappearing food mattered to the subjects; however, the missing effect for social control versus ghost control condition as well as the reversed direction of the effect for ghost (they pulled slower in ghost than CO condition) indicate that social presence probably also played a role.

The monkeys differentiated between the two drawer set-ups: unlike in the CO set-up, in the CoA set-up behaviour did not change according to social presence or moving food items. Comparisons with baseline revealed that subjects' performance differed significantly from baseline only in the partner CO but none of the other test conditions. Hence, the monkeys were not affected by the mere presence of the partner or by mere environmental changes of the test set-up (moving drawers in the CoA condition). They paid close attention to the partner's actions, however, when they were consequential for the subject's own food availability. This pattern indicates that CO is crucial for the monkeys' attention to test partners.

At first sight, our results seem to contradict two previous studies reporting social comparisons in non-human primates [11,12] and previous findings on social facilitation effects in macaques (for an overview, see [18]). However, such differences might rely on methodological details, including task type, trial duration, partner orientation and distance, choice of comparison standards and response measure. Importantly, the field of comparative social comparison research is still in its infancy and it is important to explore scope and limits of different approaches. For example, longer exposure to the comparison standard might be necessary for social comparisons to manifest [13].

Another potentially important point is that long-tailed macaques are very despotic and hierarchical [19], with subordinate individuals normally not feeding from a high-quality food source in such close proximity to higher ranking individuals. Social tolerance might play an important role for the occurrence of social comparison effects in co-active tasks. To address this possibility, a systematic study of several macaque species ranging from highly despotic to very tolerant would be an interesting and informative project for future research. Unfortunately, our available sample size did not allow us to additionally test for effects of rank and bond strength between subject–partner dyads or sex-composition of the dyads. In humans, similarity of self and comparison standard is an important factor for social comparisons [20,21]. We would thus welcome replications of this study with other non-human primate groups to allow, at some point in the future, a meta-analysis where such additional factors can be considered.

In this study, we adapted the classic study by Seta [13] to a set-up that is feasible for testing non-human primates. We found no indication that long-tailed macaques compared their performance with and adapted it to the performance level of conspecifics. Competition was necessary to elicit sufficient attention to the co-actor, a necessary prerequisite for social comparisons. By contrast, humans also compare themselves with others in the absence of direct competition, for example, in evaluative situations (which could be considered *indirectly* competitive) or out of social motivations such as conforming to group norms. Whether this divergence between human and non-human primates reflects differences in the engagement of social comparison proper or is merely an effect of differences in the attention given to conspecifics remains to be tested in future research.

Ethics. This non-invasive behavioural study was approved by the ethics committee of the Animal Welfare Body of the German Primate Center (permit number E4-17). As confirmed by the Lower Saxony State Office for Consumer Protection and Food Safety, these experiments do not constitute a procedure according to the animal welfare legislation (§7, Abs. 2 TierSchG); therefore, a permit was not required (LAVES Document 33.19-42502-04).

Data accessibility. Data are available on Dryad: <http://dx.doi.org/10.5061/dryad.47j2q8b> [22].

Authors' contributions. S.K. designed and coordinated the study, collected and analysed the data and drafted the manuscript. R.T. collected data and contributed to the manuscript. T.M. and T.B. contributed to the development of the research question as well as to the manuscript. J.F. contributed to study design and substantially contributed to the manuscript. All authors gave final approval for publication. All authors agree to be held accountable for the content of this paper.

Competing interests. The authors have no competing interests.

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