Do metacognitive performances of Japanese macaques (Macaca fuscata) correlate positively with inhibitory control?

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Research Article

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Abstract

Metacognition is the ability to monitor and control cognitive processes. It enables awareness of what one does (or does not) know and is associated with consciousness. Potential metacognitive abilities have been revealed in some primate species. This study investigated how nine Japanese macaques’ impulsivity to look inside a tube containing a reward of varying quality correlated with their tube-checking behaviour in metacognition testing. In a tube task, apes and macaques showed higher tube content-checking behaviour when unaware of which tube held a reward. Intriguingly, even when aware of the reward’s location, they periodically inspected the tubes, especially when a more appealing reward was at stake, akin to humans verifying their knowledge (the passport effect). Some critics argue that this behaviour can be explained by lower-order processes such as a lack of inhibition. Results indicated that impulsivity to look increased as reward quality improved. However, macaques displaying unnecessary tube inspections in metacognitive tests showed less impulsivity. This result counters the notion that excessive looking in the tube task is solely due to a lack of inhibition. Inhibitory control seems crucial for the emergence of metacognition, making it a vital question to address.

INTRODUCTION

Metacognition allows one to be aware of what one does (or does not) know. Investigating metacognition in non-human animals can provide valuable insights into the mechanisms and origins of consciousness. Introduced by Call and Carpenter (2001), the tube task has been used, and positive results have been reported in several species, mainly apes and macaques (Call 2010; Gazes et al. 2023; Hampton et al. 2004; Marsh 2014; Mars and Macdonald 2012; Rosati and Santos 2016; Subias et al. 2023). However, there is some dispute about whether success in the tube task reflects metacognition. Carruthers and Williams (2019) proposed that looking in the “unknown” condition could be explained in terms of first-order questioning attitudes (or, more simply, curiosity). They define curiosity as an affective emotion-like motivating state that takes the form of a question, like “Where is the food?” This questioning attitude drives the animal to search to satisfy his curiosity.

A counter-argument is that subjects sometimes look in the “known” condition. In a previous experiment (Subias et al. 2023), we tested ten free-ranging Japanese macaques (Macaca fuscata) using a four-tube apparatus and a protocol similar to that used by Call (2010) to test apes. We tested an “obvious” condition in which the subject knows which tube contains the reward and an “ambiguous” condition in which they do not know. Japanese macaques showed a metacognitive-like response by looking inside the tubes significantly more often after ambiguous baiting compared to obvious. Interestingly, the monkeys still looked in the obvious condition in 44% of trials, and their first look was always directed toward the tube containing food. This observation suggests that monkeys implicitly remember the reward’s location. The same was observed with apes and rhesus macaques, who also tend to look approximately 50% of the time in the “known” condition when looking inside the tubes does not require too much effort (Call 2010; Gazes et al. 2023; Hampton et al. 2004). Also, like apes, some Japanese macaques tended to
decrease unnecessary looks (i.e., looking in the “known” condition) whenever the cost of looking increased, and some subjects tended to increase unnecessary looks when a preferred food was at stake.

If Carruthers and Williams (2019) were correct in their assertion that looking behaviour in the tube task stems from curiosity sparked by the inability to recall the food's location, why do apes and monkeys look even when they know the food's location? Call has proposed the “passport effect” as an explanation, likening it to humans checking their passports before travelling. This suggests that apes and macaques verify that the reward remains where they remember it. Alternatively, this behaviour could result from difficulty in suppressing foraging tendencies. Perner (2012) suggested that looking at a reward could be inherently pleasurable, with a more attractive reward being even more enticing. This could account for instances in which apes and monkeys look despite knowing which tube holds the reward and why their interest intensifies when a more appealing reward is at stake. Using a highly preferred reward may make it harder to resist looking, whereas increasing the effort required to look could make resistance easier. Despite its relevance, this explanation has never yet been explored.

The present study tested whether monkeys looking in the obvious condition reflects a desire to confirm their knowledge (passport effect) or a lack of inhibition (impulsivity). Nine Japanese macaques previously tested on the tube task were tested for their impulsivity to look. We investigated to what extent they looked inside a single tube containing food using two types: low- and high-quality rewards. Contrary to the tube task used to test metacognition, we used only one tube and forced the monkeys to wait ten seconds before retrieving the reward.

In this task, monkeys always witness baiting and have only one possible choice; therefore, looking inside the tube is unnecessary. First, we assessed the participants’ impulsivity to looking inside the tube. If monkeys were driven to look at the reward, we predicted they would look more when using high-compared to low-quality rewards. Second, if monkeys looked in the tube task’s obvious condition solely to look at the reward, we expected a positive correlation between monkeys’ looking frequencies in the impulsivity test and the tube task for low- and high-quality rewards.

**METHOD**

**Subjects**

The tests were conducted on nine Japanese macaques belonging to a free-ranging macaque group in Awajishima, Hyôgo Prefecture, Japan (34°14’41.5”N, 134°52’59.6”E). This group was artificially provisioned by the Awajishima Monkey Center in 1967. Wheat and soybeans were provided three times daily. At the time of the study, the group size was estimated at 126.

The participants included eight males and one female, all adults (> seven years old; Electronic Supplementary Material Table S1). All nine had previously been tested for metacognition using the tube task (Subias et al. 2023). The impulsivity tests were conducted daily from June to July 2023, from 9:30
a.m. to 5 p.m., in the feeding area, where all the subjects ranged freely. They were free to participate by approaching and manipulating the apparatus.

**Testing location and Apparatus**

A four-tube and a one-tube apparatus were used (Electronic Supplementary Material S2) at two testing locations that were established to test metacognition (Subias et al. 2023). Three subjects were tested exclusively at location 1, one at location 2, and the remaining five at both locations, depending on the opportunity (Electronic Supplementary Material Table S1).

**Procedure**

The experiment was conducted in two steps: first, a titration procedure using a four-tube apparatus that served to establish a height at which the subject would be willing to look inside a set of tubes, even though they already knew which tube contained the reward (Electronic Supplementary Material S3). Second, the “impulsivity to look” test using the one-tube apparatus.

**Impulsivity to look test**

The subjects were familiar with this procedure and had already learned to obtain food from the tubes; therefore, no training was required. After titration, the monkeys were immediately tested using the one-tube apparatus.

The apparatus was placed against the wire mesh of the hut (tube perpendicular to the subject) behind a transparent screen. The screen prevented the subjects from reaching the tube while allowing them to look inside it. The experimenter presented the reward to the subject for approximately three seconds and placed it inside the tube. After a 10 s delay, the experimenter removed the screen, allowing the subject to retrieve the reward from the tube. A new trial was initiated immediately thereafter.

We tested two conditions:

*Low-quality reward*: Monkeys’ less preferred food was used as a reward: a piece of sweet potato or carrot, depending on the individual.

*High-quality reward*: Monkeys’ most preferred food was used as a reward: a peanut.

Each subject underwent 12 consecutive trials under both conditions. Four subjects were tested on the “low-quality reward” condition first and the “high-quality reward” condition second, while the other five subjects experienced the opposite order (Electronic Supplementary Material Table S1). Participants were randomly assigned to one group. After testing a subject in one condition (low or high quality), we waited a minimum of one week before testing the same subject in the second condition to minimise the impact of learning in the second session.

**Behaviour scoring**
Looking behaviour was assessed during the 10-minute waiting time of each trial. A “look” was scored when the subjects lowered their heads to align their eyes with the tube opening. Looking proportions were calculated by dividing the number of trials in which monkeys had looked by the total number of trials. Looking proportions in the tube task were assessed similarly in a previous study (Subias et al. 2023). Sessions were recorded on videotape. The experimenter first watched and scored the monkeys’ behaviours in real time and then checked them using the recordings.

Data analysis

To compare looking proportions between low- and high-quality conditions of the impulsivity test, we used a paired t-test. The effect size (Cohens’d) was calculated. Because our data did not always follow a normal distribution and the sample size was small, we assessed whether there was a correlation between monkeys’ looking proportions in the impulsivity test and the tube task using Spearman’s correlation test.

As one subject, Yubisashi, did not differentiate between obvious and ambiguous conditions in the tube task, he was excluded from the analysis when looking for a correlation in look proportions between impulsivity and the tube task but was included in the other analyses.

Using video recordings, a second observer scored 20% of the analysed trials again. The inter-observer reliability was excellent (Cohen’s kappa = 0.8). All analyses were performed using RStudio 4.1.0.

RESULTS

Impulsivity to look

All nine monkeys made at least one look in at least one condition during the 10 s waiting time, which confirms that monkeys have some drive to look at an appealing reward. The proportions of the subjects are listed in Table 1.
Table 1
Individuals’ looking proportion.

<table>
<thead>
<tr>
<th></th>
<th>Low-quality reward</th>
<th>High-quality reward</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gaara</td>
<td>0.17 (2/12)</td>
<td>1.00 (12/12)</td>
</tr>
<tr>
<td></td>
<td>(level2)</td>
<td>(level2)</td>
</tr>
<tr>
<td>Gattsu</td>
<td>0.08 (1/12)</td>
<td>0.17 (2/12)</td>
</tr>
<tr>
<td></td>
<td>(level2)</td>
<td>(level3)</td>
</tr>
<tr>
<td>Kikuhime</td>
<td>0.08 (1/12)</td>
<td>0.00 (0/12)</td>
</tr>
<tr>
<td></td>
<td>(level3)</td>
<td>(level3)</td>
</tr>
<tr>
<td>Manta</td>
<td>0.33 (4/12)</td>
<td>0.92 (11/12)</td>
</tr>
<tr>
<td></td>
<td>(level2)</td>
<td>(level3)</td>
</tr>
<tr>
<td>Paku</td>
<td>0.67 (8/12)</td>
<td>0.42 (5/12)</td>
</tr>
<tr>
<td></td>
<td>(level4)</td>
<td>(level4)</td>
</tr>
<tr>
<td>Puriko09</td>
<td>0.33 (4/12)</td>
<td>0.75 (9/12)</td>
</tr>
<tr>
<td></td>
<td>(level2)</td>
<td>(level2)</td>
</tr>
<tr>
<td>Spot</td>
<td>0.00 (0/12)</td>
<td>0.33 (4/12)</td>
</tr>
<tr>
<td></td>
<td>(level2)</td>
<td>(level2)</td>
</tr>
<tr>
<td>Tim</td>
<td>0.00 (0/12)</td>
<td>0.58 (7/12)</td>
</tr>
<tr>
<td></td>
<td>(level2)</td>
<td>(level1)</td>
</tr>
<tr>
<td>Yubisashi</td>
<td>0.58 (7/12)</td>
<td>0.58 (7/12)</td>
</tr>
<tr>
<td></td>
<td>(level1)</td>
<td>(level1)</td>
</tr>
<tr>
<td>GROUP</td>
<td>0.25 (27/108)</td>
<td>0.53 (57/108)</td>
</tr>
</tbody>
</table>

The upper brackets indicate the number of trials in which the monkey looked inside the tube divided by the total number of trials. Lower brackets indicate the heights at which the apparatus was set (see Electronic Supplementary Material S3 for details).

**Reward quality effect on looking**

On average, monkeys looked significantly more often when using a high- than low-quality reward (Fig. 1, \( t (8) = 2.31, p = 0.049 \)), with a large effect size (\( d = 0.941 \)).

**Figure 1** Comparison of looking proportion between low- and high-quality reward. x represents the average value
Thus, our first hypothesis was supported. Monkeys showed a greater tendency to look when the reward quality increased. This suggests that, in the previous tube task, the increased looking behaviour induced by using a more appealing reward might be due to a lack of inhibition.

**Impulsivity to look and looking in the tube task**

The monkeys who looked more frequently in the obvious condition of the tube task did not show the highest impulsivity when looking inside a single tube containing a reward (Table 2). Contrastingly, the monkeys who looked at the highest rate in the tube task were those who looked at the lowest rate in the impulsivity test, at least when using a low-quality reward (Fig. 2).

<table>
<thead>
<tr>
<th></th>
<th>Low-quality reward</th>
<th>High-quality reward</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gaara</td>
<td>0.57 (12/21)</td>
<td>0.85 (17/20)</td>
</tr>
<tr>
<td>Gattsu</td>
<td>0.57 (21/37)</td>
<td>0.76 (28/37)</td>
</tr>
<tr>
<td>Kikuhime</td>
<td>0.60 (12/20)</td>
<td>0.95 (19/20)</td>
</tr>
<tr>
<td>Manta</td>
<td>0.44 (7/16)</td>
<td>0.88 (15/17)</td>
</tr>
<tr>
<td>Paku</td>
<td>0.17 (4/23)</td>
<td>1.00 (25/25)</td>
</tr>
<tr>
<td>Puriko09</td>
<td>0.48 (12/25)</td>
<td>0.88 (21/24)</td>
</tr>
<tr>
<td>Spot</td>
<td>0.52 (12/23)</td>
<td>0.95 (21/22)</td>
</tr>
<tr>
<td>Tim</td>
<td>0.63 (15/24)</td>
<td>0.92 (22/24)</td>
</tr>
<tr>
<td>Yubisashi</td>
<td>1.00 (12/12)</td>
<td>1.00 (12/12)</td>
</tr>
<tr>
<td>GROUP</td>
<td>0.56 (120/220)</td>
<td>0.92 (198/219)</td>
</tr>
</tbody>
</table>

Extracted from Subias and colleagues (2023) investigating information-seeking in Japanese macaques using a tube task (a four-tube apparatus). It shows the number of trials in which subjects looked inside the tubes before choosing divided by the total number of trials. "Obv." and "Amb." indicate obvious and ambiguous baiting, respectively.

**Figure 2** Correlation between the proportion at which monkeys looked inside the tubes in the tube task when they knew the reward location (x-axis) and their looking proportion in the impulsivity test (y-axis).
Graph a. displays the result when using a low-quality reward, and Graph b. when using a high-quality reward. Each dot represents an individual.

The correlation between looking proportions in the tube task and the impulsivity test was strong and statistically significant in the low-quality reward condition (Fig. 2a: \(r_s=-0.76, N=8, p=0.027\)). In the high-quality reward condition, the correlation is moderate and not significant (Fig. 2b: \(r_s=-0.60, N=8, p=0.118\)). No positive correlation was found; therefore, the second hypothesis was rejected.

**DISCUSSION**

The main goal of this study was to assess whether monkeys’ looking behaviour in the tube task could be explained by a desire to look at the reward (or a lack of inhibition). We found that Japanese macaques tended to look inside a single tube that they knew contained food they could not immediately reach, and they tended to look even more when a higher-quality reward was at stake. Alone, this result suggests that the possible “passport effect” observed in our monkeys in the tube task (Subias et al. 2023) might come from a lack of inhibition. However, the macaques’ looking proportion in the impulsivity test was not positively correlated with the proportion in the tube task. Contrastinglly, we identified a strong negative correlation among the eight monkeys who performed in a metacognitive-like way when tested on the tube task. Those who made the highest rate of unnecessary looks were those who showed the best aptitude to inhibit looking inside a tube containing a reward. The correlation became weak and non-significant when a highly preferred reward was at stake; nevertheless, we never observed the opposite trend.

If the monkeys’ unnecessary look in the tube task cannot be explained by difficulty in inhibiting looking at a reward, then the question remains: Why do macaques look half the time even though they know which tube holds the reward? The passport effect is the only alternative explanation. However, our results suggest that using an overly attractive reward could interfere with macaques’ ability to engage in metacognition.

Thus, Japanese macaques showed less inhibitory control when presented with attractive rewards. However, subjects with weaker inhibitory control abilities did not look into the tube very often when tested for metacognition in a previous tube task. These results suggest that looking behaviour in the tube task was influenced not only by a lack of inhibitory control but also by the passport effect.

The present study has limitations. The correlation was calculated using only eight subjects, and each monkey was tested only once on 12 trials for both conditions. Although we adjusted the apparatus height before each testing session to ensure that it was set up at a height at which monkeys would be willing to look, even when they did not need to, the monkeys’ motivation to look inside the tubes can vary greatly from day to day. We could find different results if we tested them again, or the correlation’s direction could change with a larger sample size. These results should be reproduced to reach stronger conclusions.

Despite its limitations, our study is the first to assess how inhibition capacity correlates with metacognitive performance observed in non-humans, and we believe our findings will bring new
perspectives on the subject. In a recent study, Kuhn (2022) emphasised the importance of inhibition in various domains that require metacognition, such as theory of mind, understanding false belief, reasoning, and belief revision. Given the importance of inhibition and how a lack of inhibitory control could invalidate some of the arguments raised against response competition or the curiosity account, providing more data investigating the relationship between metacognition and inhibition is crucial to progress in this debate.

Declarations

Funding

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Competing interests

The authors have no relevant financial or nonfinancial interests to disclose.

Ethics statement

The study was conducted in accordance with the Regulations of the Osaka University Animal Experiment Committee. This study was approved by the Animal Experimentation Committee of the Graduate School of Human Sciences at Osaka University, Japan (No. R3-2-0).

Data availability

All data analysed in this study are included in the published article and its supplementary information files.

Author contributions

L.S. designed and conducted the experiments, collected and analysed the data, and wrote the first draft; K. Y. supervised the work, helped in the setup of the testing locations and building of the apparatus, and edited the manuscript; N.K. supervised the work, helped with the data analysis, and edited the manuscript.

References


**Figures**

![Box plot comparing look proportion between low- and high-quality reward](image)

**Figure 1**

Comparison of looking proportion between low- and high-quality reward. x represents the average value
Figure 2

Correlation between the proportion at which monkeys looked inside the tubes in the tube task when they knew the reward location (x-axis) and their looking proportion in the impulsivity test (y-axis). Graph a. displays the result when using a low-quality reward, and Graph b. when using a high-quality reward. Each dot represents an individual.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryTableS1.docx
- SupplementaryMaterialS2.docx
- SupplementaryMaterialS3.docx