Form 3

Abstract of Thesis

Name (Lorraine SUBIAS)	
Title	Experimental study of metacognition in free-ranging Japanese macaques: The influence of knowledge state, cost, stakes, and impulsivity on information-seeking behavior （餌付けニホンザルにおけるメタ認知の実験的研究：知識状態、コスト、報酬の価値、衝動性が情報希求行動に与える影響の検討）

Abstract of Thesis

Chapter 1: Current state of knowledge

Metacognition-the ability to monitor and control one's cognitive processes-is a hallmark of human cognition. However, over the past two decades, research has provided compelling evidence of metacognitive abilities in certain nonhuman primates. Definitions of metacognition vary, with some highlighting declarative metacognition involving language-based mind reading, while others emphasize procedural metacognition, which relies on epistemic feelings, such as the feeling of knowing, rather than concepts. Debates persist regarding whether animals lacking declarative metacognition can exhibit procedural metacognition and if it qualifies as "meta" cognition. The origins and functions of metacognition have been actively debated. While some propose it as a by-product of theory of mind, some compelling arguments suggest that metacognition may precede theory of mind and serve as a toolkit for managing thoughts and adjusting behavior.

Hampton proposes four criteria for demonstrating metacognition and stresses the importance of distinguishing between public and private mechanisms. Kornell further nuances this discussion by exploring direct and inferential cues. While it was initially believed that only direct-private cues constituted metacognition, human research has provided strong evidence that inferential cues can also influence confidence judgments. Metacognition has been investigated in several nonhuman primates, particularly great apes, rhesus monkeys (*Macaca mulatta*), and capuchin monkeys (*Sapajus apella*), using various methodologies, such as uncertainty responses, gambling tasks, confidence movements, and information-seeking paradigms. Methodological advancements and efforts to control alternative explanations have led to the consensus that apes and rhesus macaques possess the ability to monitor and regulate certain cognitive processes. Despite numerous studies, uncertainties remain regarding capuchin monkeys.

Significant gaps remain in our understanding of metacognition, particularly regarding its phylogenetic distribution and evolution. To progress in this area, it is essential to explore a broader range of species and conduct tests on free-ranging animals in their natural habitats. Certain species and questions prove challenging to investigate solely in laboratory settings, especially those related to evolutionary and ecological aspects of cognition within natural populations. Field studies can offer valuable insights into how the cognitive abilities of animals contribute to their survival. Japanese macaques (*Macaca fuscata*) are yet to undergo metacognitive testing. However, they are well suited for experimental studies on cognition in the wild, and their close phylogenetic relationship with rhesus macaques suggests that they may possess similar metacognitive abilities. The present thesis investigates information-seeking behavior in free-ranging Japanese macaques using the tubes task, aiming to 1) determine whether macaques appropriately seek information when ignorant and 2) how factors such as cost, stakes, and impulsivity influence their information-seeking behavior.

Chapter 2: Knowledge state, cost, and stakes influencing information-seeking behavior in free-ranging Japanese macaques

In Chapter 2, I explored the information-seeking behavior of free-ranging Japanese macaques regarding their awareness of ignorance. In humans, information seeking represents a facet of metacognition wherein individuals can optimize their task performance by adjusting their actions based

on the self-evaluation of their knowledge. To investigate this cognitive trait in nonhuman animals, researchers have employed the tubes task paradigm, in which a reward is concealed within one of several tubes, sometimes visible to the subject and sometimes not. The essence of this task lies in the subjects' capacity to inspect the contents of the tubes before making a selection, assessing their knowledge of the reward's location. The tubes task is easily implemented, even in natural environments, and has the advantage of requiring minimal training, as it capitalizes on the inherent foraging behavior of animals.

Ten adult macaques (nine males and one female) were subjected to a tubes task using four opaque tubes. Three parameters were manipulated: 1) the baiting process, categorized as either "obvious" (wherein the reward's placement within a tube was evident) or "ambiguous" (where the reward's location remained uncertain); 2) the effort required by the monkeys to look inside the tubes, varied by manipulating the height of the apparatus, modulating the task's difficulty level; denoted as either "low" (requiring minimal effort) or "high" (demanding greater effort); 3) the desirability of the reward, distinguished between high-quality (preferred food) and low-quality (less favored food). Subsequently, analyses were conducted to evaluate the effect of these parameters on the propensity of the monkeys to look inside the tubes before selection.

The findings revealed that nine monkeys exhibited a significantly higher inclination to look when confronted with ambiguity regarding the reward location. Half of them demonstrated a tendency to reduce looking when the effort required was high but only when they possessed prior knowledge of the reward's location (in the obvious condition). Additionally, when a high-quality reward was at stake, the three individuals displayed an increased inclination to inspect the tubes despite being aware of the reward's location. These results challenge the notion that monkeys merely form associations between external cues (e.g., baiting process) and predetermined responses. Instead, they imply that monkeys possess an awareness of when looking is necessary and may exercise caution when highly desirable food is at stake.

Apart from metacognitive processes, an alternative explanation for the adaptive-seeking behavior of monkeys could be response competition. In the tubes task, the actions of inspecting and selecting a tube compete as the subject must opt for one over the other. It has been proposed that when monkeys possess knowledge about the reward's location, they feel a strong inclination to select the corresponding tube, opting for selection over inspection. Conversely, when they lack such knowledge, there is less inclination to select a tube in particular and, therefore, default to search their environment and look inside the tubes. Consequently, employing a more enticing reward should theoretically intensify the monkeys' motivation to select a tube in the "obvious" condition, resulting in reduced looking rates when a high-quality reward is involved compared to a low-quality one. Nonetheless, this effect was not observed, providing little support for the response competition hypothesis.

In conclusion, this study shows that free-ranging Japanese macaques exhibit adaptive information-seeking behavior in accordance with their knowledge state. Half of the subjects adjusted their behavior in response to the effort involved in seeking, while a minority also considered the desirability of the reward. The demonstrated flexibility in their information-seeking behavior parallels that observed in great apes and implies the presence of metacognitive capabilities in these macaques.

Chapter 3: Relationship between impulsivity and looking behavior in the tubes task

In Chapter 3, I conducted a complementary experiment to clarify an intriguing aspect of macaques' information-seeking behavior: unnecessary looking. In the tubes task described in Chapter 2, macaques showed higher content-checking behavior when unaware of a reward's location. However, they periodically inspected the tubes when aware, especially when a more appealing reward was involved. Analysis of the macaques' first look confirmed that they remembered which tube held the reward but looked nonetheless. Apes exhibited a similar behavioral pattern. It has been suggested that these unnecessary looks may constitute a metacognitive error (with the animal wrongly assuming they do not remember the reward location), or the animal may be cautious and check their knowledge before making their choice (the "passport effect"). However, some researchers argue that this explanation may be simpler: monkeys may look for the pleasure of looking at an appealing reward. Looking may result from an impulse, rather than

a controlled decision.

The study presented in Chapter 3 investigated whether the unnecessary tube-checking behavior observed in nine macaque subjects, previously tested for metacognition using the tubes task, could be solely attributed to impulsivity. To do so, I presented macaques with an “impulsivity test”: a piece of food of either low or high quality was placed inside a single tube in front of the subject. Owing to a transparent panel, the subject had to wait ten seconds before they could obtain food from the tube but could bend down at any time to peer inside the tube. The propensity of the macaques to look inside the tube in this situation was measured and compared with their looking behavior in the previous tubes task.

The findings revealed that the monkeys sometimes looked in the one-tube situation of the impulsivity test, and their looking behavior was affected by the quality of the reward. More specifically, the proportion of looks significantly increased as the reward quality improved. Nevertheless, when the reward quality was low, the macaques looked significantly less often in the impulsivity test than in the metacognition test. Moreover, the analysis revealed a strong and significant negative correlation in the proportion of looks between the two tasks—macaques displaying unnecessary tube inspections in metacognitive tests showed less impulsivity in looking. This intriguing result contradicts the notion that excessive looking in the tubes task is solely impulsive. Instead, I propose that impulsive individuals tend to look in the impulsivity test but prefer to directly grab a tube in the tubes task. This would mean, as proposed by the response competition hypothesis, that animals would need to refrain from selecting a tube to engage in information seeking. Further research is necessary to confirm this and clarify the relationship between impulsivity, inhibition, and information-seeking behavior.

Chapter 4: General discussion

This research revealed that free-ranging Japanese macaques appropriately seek information when ignorant; in the tubes task, they tend to look inside the tubes when unaware of which one contains a reward but select a tube without looking when aware. This observation was consistent with previous findings in rhesus macaques. Further, findings reveal for the first time that macaques can be sensitive to the cost they have to pay to look inside tubes and, to a lesser extent, to the quality of the reward at stake. Specifically, they tended to decrease unnecessary looking when the cost was high but increased it when the stakes were high, a flexibility reminiscent of what has been observed in great apes. While unnecessary looking behavior may stem from a desire to view the reward, further investigation revealed that subjects who engaged the most in unnecessary looking during the four-tubes task did not look as much when facing a single tube. Therefore, the number of tubes is an important factor. Although additional testing is required to confirm this finding, it is unlikely that unnecessary looking in the tubes task results solely from an impulsive desire to view the reward. This observation supports the hypothesis that macaques look inside the tubes during the tubes task to gain knowledge.

Overall, macaque behavioral patterns are not consistent with alternative explanations such as associative learning or response competition. Instead, the results suggest that wild Japanese macaques are aware of their lack of knowledge, an ability that appears to be shared by members of different branches of Cercopithecidae. Additionally, this study showed that the tubes task could be implemented in the wild while controlling for various factors, providing useful data for comparisons between laboratory-housed and free-ranging animals. By confirming that wild Japanese macaques possess metacognitive abilities similar to those of rhesus macaques, this study opens the door for further investigation of this species in wild settings, which could significantly enhance our understanding of metacognition, notably regarding its functions and evolution.

様式 7

論文審査の結果の要旨及び担当者

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論文審査の結果の要旨

メタ認知とは、自分の知識や記憶や思考を、自ら評価する能力である。自分が知っていることと知らないことを区別して行動することで、個体は課題を効果的に解決することができる。本論文は、ヒト以外の動物を対象としたこれまでのメタ認知研究のレビューと野生ニホンザルを対象とした野外実験の成果をまとめて、霊長類の意識の進化的起源について議論したものである。

第1章では、メタ認知を実証的に検証するための方法論とそれぞれの長所と短所について広範なレビューを行っている。Escape反応パラダイムや情報希求パラダイムなどは、動物が持つメタ認知の能力を実証的に検討できる優れた実験手法であるが、実験手続きを手がかりとした連合学習や反応競合などのメタ認知以外の要因で行動が説明できる可能性があることを指摘している。

第2章と第3章では、野生ニホンザルを対象に情報希求パラダイムに基づいたチューブ課題を実施した。調査地は淡路島モンキーセンター（兵庫県洲本市）であり、実験は2022年から2023年にかけて実施した。10頭の対象個体のうち9頭は、報酬がどのチューブに入っているかわかりにくい条件では、選択する前に情報を得ようとチューブの中を覗く行動を頻繁に行っていた。さらに、報酬となる餌の価値を変化させたり、チューブの探索にかかるコストを変化させたりした実験を行うことで、サルの覗き込み行動が連合学習や反応競合といった対立仮説では十分に説明できないことを示した。これらの結果は、自分の知識が不十分な場合には情報を求めて行動を変化させること、つまり野生ニホンザルが自らの知識の状態を評価する能力（メタ認知）を有していることを示す有力な証拠であった。第3章では、同じ個体を対象に、衝動性を測るテストを行った。報酬が提示された時、入手できないことが明らかであっても、サルは報酬を求める衝動を抑えられないときがある。解析の結果から、衝動性の低い個体ほどメタ認知に由来する行動を頻繁に示していたことが示唆され、抑制機能とメタ認知の出現に関連がある可能性が議論されている。

第4章では総合論議がなされており、解釈の妥当性やサンプリングバイアスの危険性を慎重に議論している。本論文により得られた結果を系統発生と関連付けて議論することで、霊長類のメタ認知の機能と進化について有用な知見を提供している。

本論文の特徴は、様々な認知実験を繰り返し経験した実験動物ではなく、類似の実験を経験したことがない野生動物を対象とした野外実験を行った点にある。これは、霊長類のメタ認知

の進化に生態学的な妥当性があることを示唆するものであり、関連分野に貢献する優れた成果であると評価できる。審査の結果、本論文は博士（人間科学）の学位を授与するにふさわしいと判定した。