

# **Inhibitory control in macaque species: validation of a task battery, individual differences in performance and effect of social tolerance**

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## Abstract

Living in a complex social environment requires primates to manage their emotions and inhibit impulsive behaviours. The cognitive processes that underpin these behaviours, crucial in many aspects of everyday life, are defined as inhibitory control. In animal studies, the various paradigms designed to measure inhibitory control often suffer from a lack of systematic validation. Moreover, striking individual variations in inhibitory control performances are often largely ignored and their causes rarely considered. Finally, little is known about the selective forces that shape the evolution of inhibitory control. It has been suggested that one route by which this ability can be enhanced is through selection on social tolerance. Hence the aim of this project was three-fold: 1- to develop a battery of inhibitory control tasks in non-human primates 2- to use this task battery to systematically investigate individual variability and its most common causes 3- on a broader evolutionary scale, to compare the inhibitory control skills in three species which differ in social tolerance style. For that purpose, we tested 66 macaques (28 *Macaca mulatta*, 19 *M. fascicularis* and 18 *M. tonkeana*) in a battery of touchscreen tasks assessing three main components of inhibitory control: *inhibition of a distraction* (using a Distraction task), *inhibition of an impulsive action* (using a Go/No-go task) and *inhibition of a cognitive set* (using a Reversal learning task). We found that all tasks were reliable and effective at measuring the inhibition of an impulsive and automatic response. We then demonstrated individual variations, sex and age differences in inhibitory control performances. Finally we demonstrated that the least tolerant species were poorer at controlling their emotions and impulses compared to other species. Overall, this project will help to get more insight into the multifaceted structure and the evolution of inhibitory control in primates.

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## Declaration

Whilst registered as a candidate for the above degree, I have not been registered for any other research award. The results and conclusions embodied in this thesis are the work of the named candidate and have not been submitted for any other academic award.

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## Dissemination of research from this thesis

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### **Articles and oral presentations:**

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### **Availability of the data set and online supplemental materials at:**

<https://github.com/Psychology-inhibitory-control/THESIS-INHIBITORY-CONTROL.git>

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# Chapter 1: General Introduction

## 1.1 Overview

To live in a complex social environment, animals need to manage their impulsive behaviours to maintain group cohesion and survival. For example, when a higher ranked social partner is present, an individual might benefit from withholding inappropriate behaviours, such as behaving aggressively, when competing over food or a mating partner. Such cognitive processes are defined as inhibitory control, the ability to override an impulsive, automatic or pre-learned response in order to maximise fitness benefits. A strong internal predisposition or an external distractor, tempting but counterproductive, irrelevant to the individual's goal, must be overridden in order to do what is more appropriate or needed. To cover the main domains of inhibitory control, we focus particularly on three of the most commonly described inhibitory processes in the literature: *distraction inhibition* (i.e., control of an emotional response to an internal or external distractor, in order to focus on a goal), *action inhibition* (i.e., inhibition of a prepotent, unwanted, reflexive motoric action) and *cognitive set inhibition* (i.e., inhibition of a pre-learned cognitive set to flexibly adjust behaviours). These crucial cognitive abilities have been studied in a wide range of fields (psychology, neurosciences, animal cognition) and have been tested in several animal classes such as insects, fishes, reptiles and mammals. Unfortunately, the common paradigms designed to measure inhibitory control often suffer from a lack of validity and reliability and have yielded mixed results. Therefore, the nature of inhibitory control, either defined as a common ability or a suite of distinct processes, is still debated. In addition, in animal studies, striking individual variations in

inhibitory control are often largely ignored. Performances of individuals are often pooled together implying that the performance of a sample of a population is representative of the whole species. At the individual and species levels, important causes of individual variations such as demographic factors (i.e. age, sex and rank) are rarely considered. Finally, the evolutionary processes shaping the variation in inhibitory control are still poorly understood. It has been suggested that one route by which social cognition can evolve is through selection on social tolerance. Tolerant social styles feature higher reconciliation rates, fewer conflicts, and more relaxed social relationships than despotic ones. It is possible that individuals living in a more tolerant social context might experience more diverse and complex social interactions and consequently would have better inhibitory control skills. Hence, the aim of this project was to first develop a battery of inhibitory control tasks in one species of macaque. Then, to use this task battery to systematically investigate intraspecies individual variability and its most common causes in macaques. Finally, adopting a comparative approach, to contrast the inhibitory control skills in three closely related macaque species which differ in their social tolerance style.

In the literature, there are still many debates about how to define and measure inhibitory control. To have a clearer picture, we first propose a definition of the three main components of inhibitory control (*inhibition of an action, inhibition of a distraction and inhibition of a cognitive set*). Then, we present a systematic review of a collection of papers measuring inhibitory control in non-human animals. Finally, based on species representativeness, sample size requirements and average animals' performances, we propose macaque species as an ideal model to develop a battery of inhibitory control tasks.

In chapter 2, we review the most common challenges encountered by researchers when developing valid and reliable measurements of inhibitory control. We introduce our strategy to tackle these challenges and how we developed a battery of tasks to test the three main components of inhibitory control. For this chapter, we used the model rhesus macaques (*Macaca mulatta*) to test the content validity, the reliability, and the contextual validity of a battery of common inhibitory control tasks. We first demonstrate the content validity of our three inhibitory control tasks, i.e. a prepotent response (dominant and automatic response to a stimulus) was generated by the test conditions. We then demonstrated temporal repeatability of the tasks by showing that the rank of the individual's performances within the group of subjects and within the same task, were repeatable over two time points. When looking at the contextual repeatability, we finally found consistency of performance between the *inhibition of a distraction* and the *inhibition of an action*, representing a response-driven basic form of inhibition, but not for the *inhibition of a cognitive set*. We argue that the *inhibition of a cognitive set* is a more cognitively demanding form of inhibition. This chapter gives a new insight in the multifaceted structure of inhibitory control. Besides, our findings highlight the importance of a systematic validation of cognitive tasks in animal cognition before applying a more thorough approach such as looking at individual differences.

In chapter 3, we adopt an intraspecific approach to explore the factors involved in individual variability of inhibitory control performances. We used the task battery validated in chapter 2 to investigate individual differences in three closely related macaque species (*Macaca mulatta*, *Macaca fascicularis*, *Macaca tonkeana*). In each species, we focus on demographic factors commonly associated with variation in inhibitory control

performances, i.e. sex, age and rank of the individuals. We first demonstrated individual variation in all components of inhibitory control in all three species. We then found an effect of sex and age on specific inhibitory control tasks, which was not consistent in all species. In rhesus macaques, males were more emotive and reactive than females in the *inhibition of a distraction* and they were more impulsive in the *inhibition of an action*. In Tonkean macaques, males were more perseverant in the *inhibition of a cognitive set*. On the contrary, female long-tailed macaques had worse performances in the *inhibition of a distraction*. Aged monkeys had impaired cognitive performances in the Reversal-learning task but only in rhesus macaques. We did not find an effect of the rank of the individuals in any of the inhibitory control tasks in any of the species. This chapter gives new insight into the individual variability of inhibitory control which is crucial to understand its evolutionary underpinnings.

In chapter 4, we adopt a comparative approach by looking at differences in inhibitory control performances in closely related macaque species with different degrees of social tolerance. Highly social tolerant species are supposed to live in more complex social environments than less tolerant species and thus would have developed higher cognitive abilities such as inhibitory control. Here, we compare performance of species characterised by low (*Macaca mulatta*), medium (*Macaca fascicularis*) and high social tolerance (*Macaca tonkeana*) in our battery of inhibitory control tasks. We find the best *inhibition a distraction* and *of a cognitive set* in the highly tolerant species and the worst performances in all domains of inhibitory control in less tolerant species. The picture was intermediate in the species with medium levels of social tolerance. They were the best in the *inhibition of an action* and had good performances in the *inhibition of a distraction*.

However, similarly to the low tolerant species, they still displayed emotional reactions toward pictures. Therefore, our data supports the hypothesis that low tolerant species have lower inhibitory control than other species. But the findings are not quite following a linear increase of inhibitory control performances from low to medium and high social tolerance, most probably reflecting a more diverse social complexity within the genus than previously acknowledged. More comparative research is needed to have a better understanding of the selective pressures driving the evolution of inhibitory control.

In the final chapter of this thesis, we highlight the key theoretical and practical implications of our findings. First, we demonstrated that inhibitory control is not a unitary ability, but a multi-dimensional construct consisting of separable processes. Depending on intra individual factors or on the inhibitory component tested results can vary drastically. Researchers must be cautious when inferring evolutionary underpinnings of inhibitory control, as all species are not equivalent models to test this ability. Then, we propose a framework to compare inhibitory control in several species which is crucial to better the evolution of this ability. Finally, as even closely related macaque species bred in captivity vary importantly in their inhibitory control capabilities they should not be managed identically. Thus in this final chapter we develop the important implications of our results on the welfare of macaque species.

Overall, this thesis highlights the importance of developing a valid and reliable battery of cognitive tasks. In addition, it demonstrates that precious information can be found when looking at individual variations within a species. Finally this study proposes social tolerance as one of the evolutionary factors shaping inhibitory control in non-human primates.

## 1.2 Definition of inhibitory control

Inhibitory control is defined as the ability to control impulsive behaviours in order to reach a more complex goal (Diamond, 2003; Macleod, 2007; Nigg, 2007). A strong internal predisposition or an external distractor, tempting but counterproductive, irrelevant to the individual's goal, must be overridden in order to do what is more appropriate or needed (Diamond, 2013; Dillon & Pizzagalli, 2007; Nigg, 2017). For instance, in the wild, stalking predators need to inhibit immediately pouncing on a prey (MacNulty, Mech & Smith, 2007). In social groups, low-ranking individuals should avoid mating or feeding in front of more dominant group mates to avoid injuries (Amici et al, 2018; Byrne & Bates, 2007). The inability to inhibit prepotent responses is responsible for disruptive anti-social behaviours (Weinerg-Wolf & Chang, 2019). Hence, inhibitory control allows animals to navigate a complex social environment and adjust behaviours which may otherwise become counterproductive or potentially harmful.

Inhibitory control is part of executive functions, a set of higher top-down cognitive processes that support goal-directed action (Banich et al., 2009; Friedman & Miyake, 2017; Nigg, 2007). The main inhibitory processes presented in the literature are the *inhibition of a distraction* (i.e., control of an emotional reaction in response to an internal or external interference), the *inhibition of an action* (i.e., a reflexive motoric action is withheld or withdraw) and the *inhibition of a pre-learned behaviour* (i.e., ability to flexibly adjust pre-learned behaviours in the context of dynamically changing goals; Diamond, 2013; Dillon and Pizzagalli, 2007; Nigg, 2017). Across fields, the term inhibition has been overextended (Friedman & Miyake, 2004) and various terminology have been used to refer to inhibitory related processes (self-control, response inhibition, behavioural inhibition, cognitive

control, interference control, self-regulation inhibition, etc.). Here we emphasise the discrimination between inhibitory control and self-control, which are terms that are often confused in the literature (see Beran, 2015). In a self-control task, there must be two options available, which are differentially preferred by the subject and there must be a cost for obtaining the preferred outcome (Beran, 2015). As it requires decisions, self-control is described as a more advanced cognitive ability within the umbrella term of inhibitory control (Beran, 2015, 2018). Delayed gratification tasks, which involve waiting for a better reward, are examples of self-control tasks (e.g. Miller et al., 2019).

In humans, inhibitory processes have been associated with intelligence and positive life outcomes (Duckworth and Seligman, 2005; Moffitt et al., 2011; Tangney, Baumeister & Boone, 2004). Deficit in inhibitory control has been associated with a greater risk of academic difficulties, poor social relationships, aggression, experimentation with and abuse of drugs, and unemployment (Duckworth et al. 2013). In animals, inhibitory control performances have been positively associated with brain size (Horschler et al., 2019; MacLean et al., 2014; Stevens, 2014), problem solving skills (Hauser et al., 2002; Müller et al., 2016; Vlamings et al., 2010), and fitness benefits (Ashton et al., 2018; Boogert et al., 2011; Shaw, 2017). Such inhibitory process, crucial in any individual's day to day life, is thus essential to respond to problems in a flexible manner which might be particularly important for rapidly changing social environments (Hauser et al., 2002; Müller et al., 2016; Vlamings et al., 2010).

Even though inhibitory control has been studied in a wide range of fields (e.g., in psychology, neurosciences, ethology, animal cognition) and has been tested in several animal classes such as insects, fishes, reptiles and mammals, the nature of inhibitory control is still debated. More than a general ability, researchers now propose inhibitory

control as a family of distinct components (Friedman & Miyake, 2017; MacLeod, 2007; Nigg, 2017).

### 1.3 Human research, the origins of inhibitory control tasks

The tasks currently used to measure inhibitory control were historically designed to study broad cognitive abilities such as problem solving in humans (Diamond, 2013). The Stroop task (Stroop, 1935) is one of the oldest tasks used in psychology to demonstrate a cognitive interference when incongruent stimuli are presented. This Stroop effect refers to the increased amount of time it takes to name the colour of a word when the colour of the letters and the word are incongruent (e.g., the word 'yellow' written in red characters). The Emotional Stroop task is a more recent variant of the Stroop task which does not involve a stimulus conflict but rather captures attention and slow response time due to the emotional valence of the stimulus. In this experiment researchers observe a longer naming latency to character colours of emotional words than to character colours of neutral words (Ben-Haim 2016). This task was then adapted with negative pictorial stimuli such as snake pictures (Constantine, MacNally & Hornig, 2001). The facial Emotional Stroop task has been later adapted using pictures of faces with positive or negative facial expressions (Isaac et al., 2012). This task is now used in inhibitory control research to measure the capacity of subjects to inhibit a distraction while doing a task.

Another common task used in inhibitory control human studies is the Wisconsin card sorting task. This experiment first described in 1948 by Grant and Berg was used to test cognitive reasoning. In this task subjects have to classify cards according to different criteria (colour, shape and numbers of items); the only feedback is whether the classification is correct or not. The classification rule changes during the session and the

participant needs to inhibit the interference of the pre-learned rule in favour of a new one (Diamond, 2013). This task is used in the inhibitory control field to measure the ability to inhibit a previously learned rule in favour of a new one.

Finally, the Go/No-go task is a common task used to study the inhibition of an impulsive motor action. In the Go/No-go task the subjects need to respond to frequent Go stimuli while withholding prepotent response to infrequently presented No-go stimuli (Diamond, 2013). In the stop signal task, often confused with the Go/No-go task the subject needs to respond to stimuli, but after the beginning of some trials, there is a "stop" signal, the response already initiated has to be stopped (Diamond, 2013). This task is commonly used in the inhibitory control field to measure the ability to inhibit a dominant motor response.

In human research inhibitory control is mainly studied because of its implication in psychopathologies. For instance, in developmental psychology, impairment in the Go/No-go task is associated with ADHD in children (Aron & Poldrack 2005; Duckworth et al. 2013), risk-taking behaviours in adolescents (Ivanov et al., 2008) or substance abuse disorder (Ahmadi et al., 2013). The variants of the Stroop task are widely adopted to study mood effect, depression and anxiety disorders (Duckworth et al. 2013; Isaac et al., 2012; Mitterschiffthaler et al., 2008). Finally, the Wisconsin Card sorting task was used to study frontal lobe dysfunction from traumatic brain injury (Gläscher, Adolphs & Tranel, 2019).

In developmental psychology, children are tested in simplified versions of these tasks (for review see Petersen et al., 2016). To study the development of executive functions in children, researchers use less complex tasks such as a simplified version of Go/No-go task using pictorial images (Petersen et al., 2016). Another common children task is the detour reaching task which was originally developed to study object

permanence in infants (Piaget, 1954). In this task the infants have to inhibit their tendency to reach directly for a visible reward through a transparent barrier. Infants of 6 to 11 months have great difficulty inhibiting reaching straight for the reward (Diamond, 1990). They gradually overcome this difficulty and execute detours around transparent barriers by the end of their first year (Diamond, 1990).

## 1.4 A review of the animal inhibitory control literature

In the human literature, inhibitory control tasks are well established and have been broadly used for more than 80 years (in neurosciences, in developmental psychology etc.; Diamond, 2013; Dillon & Pizzagalli, 2007; Nigg, 2017). However in the animal literature, the use of inhibitory control tasks, to specifically study this ability, is in its early stages. That is why, in this chapter, we wanted to have a clearer and up-to-date picture of the common tasks used to measure inhibitory control in non-human animals (we will use the term animals then after). For that purpose, we conducted a systematic review of the inhibitory control literature in animals. First, we wanted to investigate what were the most common tasks used to measure the three main components of this ability in animals. Then, we wanted to examine what were the most represented species in this field and what was the median sample size used in inhibitory control tasks. We were also interested in the average performances of each animal species. The overall aim of this review was to select the best animal model to study the three main components of inhibitory control.

### 1.4.1 Methods

We conducted a systematic review on a sample of 79 animal publications, published after 2000, using the following key words and terms in PubMed, Google Scholar and ISI Web of Science search engines: 'inhibitory control', 'response inhibition', 'motor

self-regulation', 'behavioural inhibition', 'cognitive control', 'executive function', 'attentional bias', 'self-control'. To review the methodology, we refined the search by adding the following terms: 'Detour task', 'reaching task', 'Cylinder task', 'barrier task', 'Go/No-go task', 'Reversal learning task', 'A-not-B task', 'Stroop task', 'Emotional Stroop task'. These papers include at least one task of inhibitory control in at least one animal species of (for more information and a list of the 79 papers used, see Appendix 1).

First, in each paper, we looked at the type of tasks used and in which domain of inhibitory control it could be categorised (i.e. *inhibition of a distraction, an action and a cognitive set*). We represented the frequency of testing of each domain of inhibitory control (in percentage). Then, we investigated each species' performances and more precisely their mean accuracy on a task (% of correct answer out of the total number of trials) in the A-not-B task, the Cylinder task, the Detour task, the Middle-cup-task and the Swing door task. We calculated the mean accuracy (M) for each class of animals, the standard error of measurement (S.E.M.) and the number of data points used in these calculations (N). For the cylinder task we represented the average performances for each species (out of 10 trials, except in 2 studies which were out of 7, Boogert et al., 2011, and out of 6 trials, Brucks et al., 2017). We finally investigated the number of times each species was used in a study (a study could test several species). We represented the median sample size used, the standard error (S.D.) and the number of data points used to calculate these values (N). For the visual representation of these data we used the graphic functions from the package 'ggplot2', version 3.3.5 (Wickham, 2016).

1.4.2 Results

1.4.2.1 Inhibitory control tasks in animals

Animal comparative studies have mainly focused on tasks of action inhibition (tested in 54% of the papers we selected, see Figure 1.1.).



Figure 1.1. Frequency of each type of inhibitory control components (action inhibition in blue, distraction inhibition in grey and cognitive set inhibition in orange) measured in our sample of reviewed papers (in percentage of the whole number of tasks mentioned). A paper can use different tasks.

These *inhibition of action* tasks, often adapted from simplified tasks for children, are mainly used because of their simplicity and ease of implementation (Kabadayi, Bobrowicz & Osvath, 2018). The most common inhibitory control task is the Cylinder task. In this task animals are habituated to reach for food from the sides of an opaque cylinder.

Subsequently the opaque cylinder is replaced by a transparent cylinder and the individuals must inhibit reaching directly for the food through the transparent barrier (for review see Kabadayi et al., 2018). One of the variants of the Cylinder task is the Swing door task. A reward is placed behind one of 2 doors but attempts to reach for it by pushing the door made the reward fall backward and out of reach. This task is similarly testing whether subjects can refrain from reaching the reward directly and instead open the non-baited door to grab the reward from behind (Amici et al., 2008; Vlamings et al., 2018). The reward can also be placed inside a transparent box (Brucks et al., 2017), behind a Plexiglas sheet (Amici et al., 2008) or inside a glass tube test when adapted for guppies (Lucon-Xiccato et al., 2020b). The cylinder task is a variant of the most general Detour task. In this Detour task, the reward is usually behind a fence (V or U shaped) or a transparent wall and the animal needs to move around this obstacle (Marshall-Pescini et al., 2015; Vernouillet et al., 2018). Another less common measure of the *inhibition of an action* is the middle cup task. Three cups are presented to the subject with only the cups from the extremities baited. The subject needs to inhibit directly reaching for the closest cup, the middle one. The Go/No-go task and its variant the Stop signal task are less frequent in animal research as extensive training is necessary. Finally, the Five-choice serial-reaction time task (5CSRTT), mainly used in rodents, measured how the subject learned to respond to a stimulus displayed at one of five random locations. Answering to a location that did not show the target is regarded as deficit in inhibitory control (Fletcher et al., 2007; Robbins and Crockett, 2010).

For the *inhibition of a cognitive set* (tested in 26% of the papers we selected, see Figure 1.1), researchers commonly use the Reversal learning task, a simplified version of the Wisconsin card sorting task. This task challenges both the ability to inhibit a previously

successful behaviour and the ability to produce a second behaviour to the same stimulus. In the Reversal learning task the subjects first learn a stimulus-reward contingency; once a pre-specified criterion is reached this first association is reversed. Subjects must then inhibit a prepotent response to previously correct stimuli and shift responses to a new stimulus-reward contingency (Bond, Kamil & Balda, 2007; Tapp et al., 2003). The A-not-B task (simplified version of the Reversal learning task, originated from Piaget's (1935) study on the development of object permanence in human infants. A reward is hidden in the same location multiple times and the subject will learn to find it here each time. Afterward, the reward is hidden in another location while the subject is watching. Then the animal needs to flexibly adjust its behaviour by inhibiting its previous knowledge and reach for the second location.

Finally, another task rarely used in animals to study *inhibition of distraction* (tested in 15% of the papers we selected, see Figure 1.1) is a variant of the Stroop task. In animals, the Stroop interference effect was mainly studied in non-human primates. For instance, in rhesus macaques, researchers used a numerical version of the Stroop task (Washburn, 1991). In another study, chimpanzees were tested with an incongruent association between a symbol and colour (Beran, Washburn & Rumbaugh, 2007). In a different chimpanzee study, subjects had to choose a stimulus based on its colour but the frame around the stimulus was from the alternative colour (Allritz et al., 2016, Hopper et al., 2021). The emotional Stroop task was also adapted for non-human primates. These tasks measured the inhibition of an emotional external distractor which interfered with the goal of the task. Researchers used negative stimulus like pictures of a veterinarian (Allritz et al., 2016), of an animal handler with gloves and a net (Boggiani, Addessi & Schino, 2018),

snakes (Shibasaki & Kawai, 2009), or of a threatening conspecific face (Bethell et al., 2012, 2016; Hopper et al., 2021; Howarth et al., 2021; King et al., 2012; Lacreuse et al., 2013).

The capacity of inhibiting behaviours in a social context (we called it social inhibition) has been somewhat neglected in the literature. When engaging in a task, individuals must assess the social context and inhibit inappropriate behaviours depending on the social status of other conspecifics present. For instance, in 3 non-human primate species, subordinate individuals wait for the dominant to leave to execute a behaviour, suppressing the prepotent response of eating when dominants are nearby (Amici, Call & Aureli, 2009). Social inhibition might be triggered by the presence of a human as well. For instance, lemurs inhibited approaching a reward in the presence of a competitive experimenter (Reddy et al., 2015). In another study, dogs had to inhibit their impulses to reach for a forbidden food while the owner was watching or not (Horschler et al., 2019). These tasks are measuring the inhibition of an impulsive action in function of the social context.

To summarise, in the animal literature, three main components of inhibitory control are studied: *inhibition of an action, of a distraction, and of a cognitive set*. However, researchers are often reusing the most common inhibitory control tasks: the Cylinder task, its variant the Detour task and the Reversal learning task.

#### 1.4.2.2 *Performances of animals in common inhibitory control tasks*

Animal performances are highly variable between tasks and species considered. In our sample of papers, the mean accuracy (% of correct responses) is quite variable depending on the task and the studied species (see Figure 1.2., Figure 1.3. and Appendix 2 for further details).

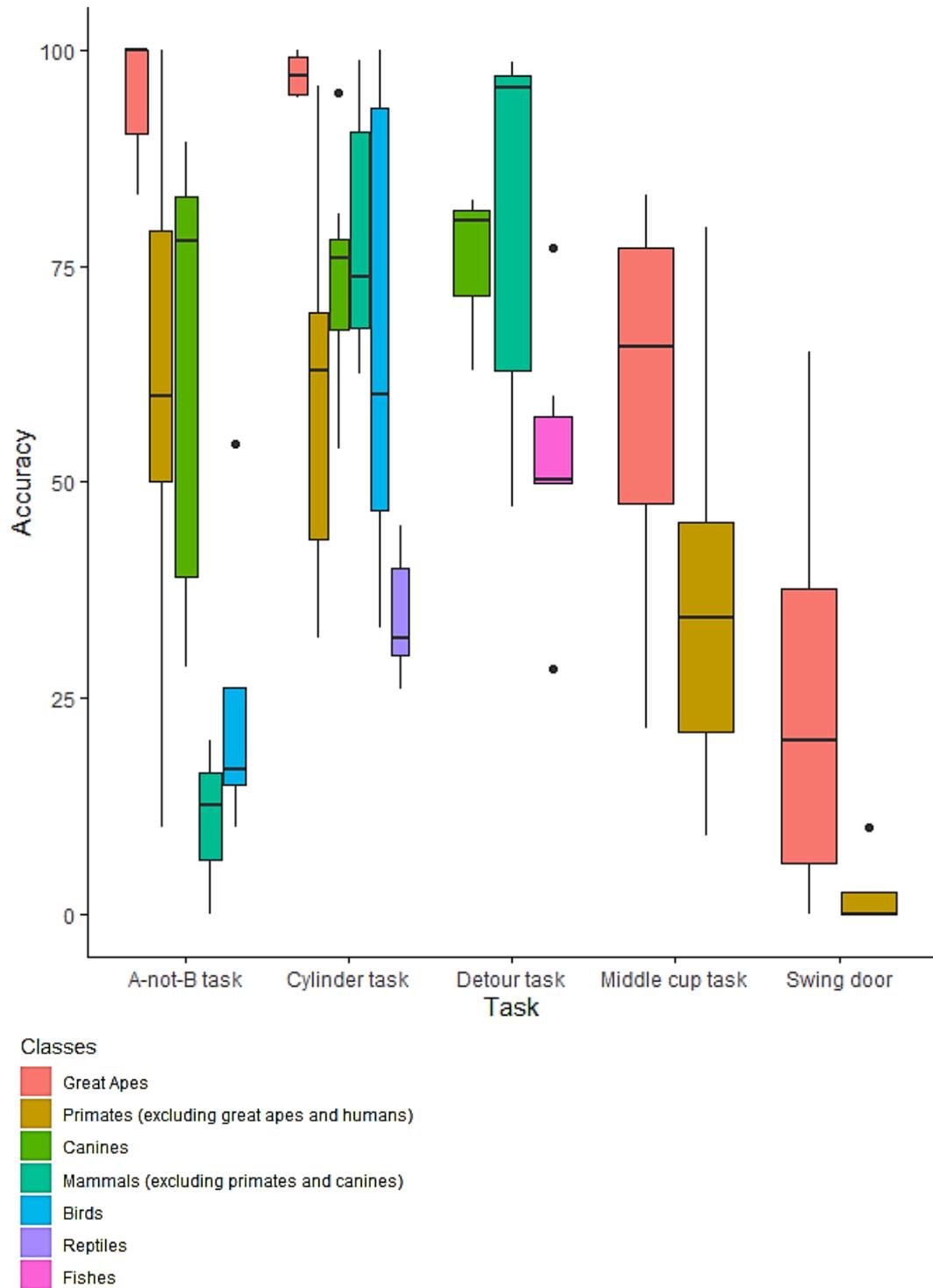


Figure 1.2. Mean accuracy (% of correct responses) per class of animal in the A-not-B task, cylinder task, the Detour task, the Middle cup task and the swing door task in our sample of papers (N = 113 task accuracy recorded). Error bars are represented. Not all animal classes have been tested in all tasks. Only non-human animals are represented.

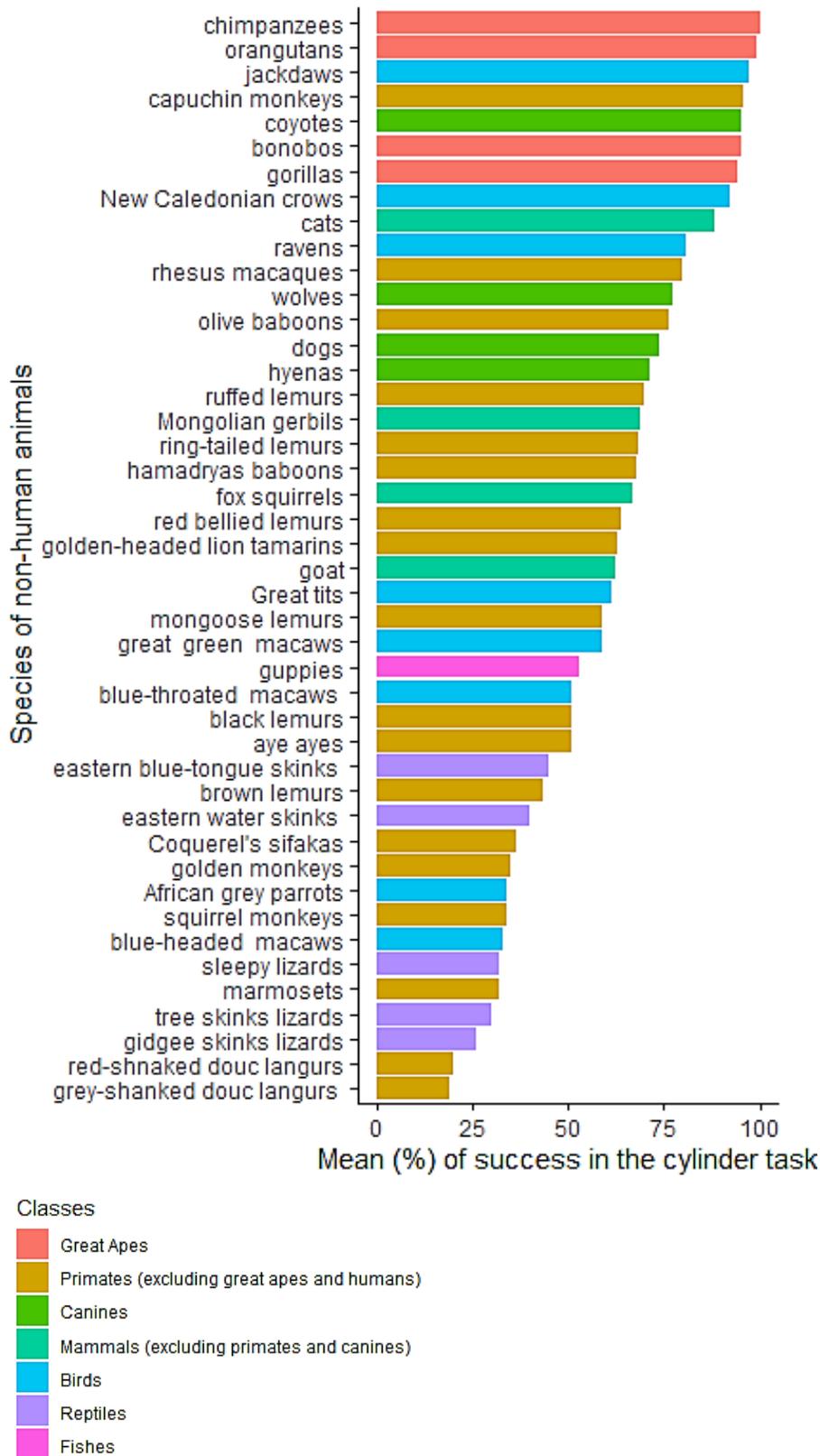


Figure 1.3. Performance in the cylinder task. Bars represent the mean percentage of correct trials. Error bars were not given for each species so they could not be represented.

For instance, great apes present the best performances in all the sampled tasks with a mean accuracy almost at ceiling in the cylinder task ( $M \pm S.E.M. (N) = 97.13 \pm 1.42 (4)$ ), see Figure 1.3, Figure 1.4, and Appendix 2) or in the A-not-B task ( $M \pm S.E.M. (N) = 95.21 \pm 2.47(8)$ ). However, in the swing door task, great apes seem to demonstrate poor performances ( $M \pm S.E.M. (N) = 22.90 \pm 6.65 (11)$ ), see Figure 1.3, Figure 1.4 and Appendix 2). The second-best performers seem to be the canines with for instance a mean accuracy in the cylinder task of 73.43% ( $M \pm S.E.M. (N) = 73.43 \pm 3.52 (12)$ ). The other primates (all excepted great apes and humans) always demonstrate worse performances than great apes (see Figure 1.3, Figure 1.4 and Appendix 2). Their performances are average in the A-not-B task ( $M \pm S.E.M. (N) = 60.92 \pm 6.36 (17)$ ) or the cylinder task ( $M \pm S.E.M. (N) = 53.61 \pm 5.06 (18)$ ) but the swing door task seem to be a rather difficult task as none of the 3 species (spider monkey, *Ateles geoffroyi*, long-tailed macaque, *Macaca fascicularis*, brown capuchin, *Cebus apella*) tested succeeded ( $M \pm S.E.M. (N) = 0 (3)$ ). Besides, birds seem to demonstrate low and spread performances in the A-not-B task ( $M \pm S.E.M. (N) = 24.48 \pm 10.13 (4)$ ) but average performances in the Cylinder task ( $M \pm S.E.M. (N) = 63.51 \pm 8.67 (8)$ ). Fishes seems to have average performances in the Detour task ( $M \pm S.E.M. (N) = 46.22 \pm 6.348 (8)$ ). Finally, mammals (excluding primates and canines) had poor performances in the A-not-B task ( $M \pm S.E.M. (N) = 10.83 \pm 5.83 (3)$ ). One of the studied species, the elephants (*Elephas maximus*) had a mean accuracy of 0 ( $N = 5$  elephants, Maclean et al., 2014).

Thus depending on the species a task can be either rather easy (reaching ceiling performances, mostly in great apes) or on the contrary impossible to achieve (falling to floor performance). Primates (excluding great apes and humans) seem to be one of the

best models to study inhibitory control as its average performances (without floor or ceiling effect) allows individual variability in the most common tasks.

1.4.2.3 Representativeness of the different animal species

Inhibitory control has been studied in a wide range of non-human species from insects, reptiles, fish, birds to mammals (see Figure 1.4).

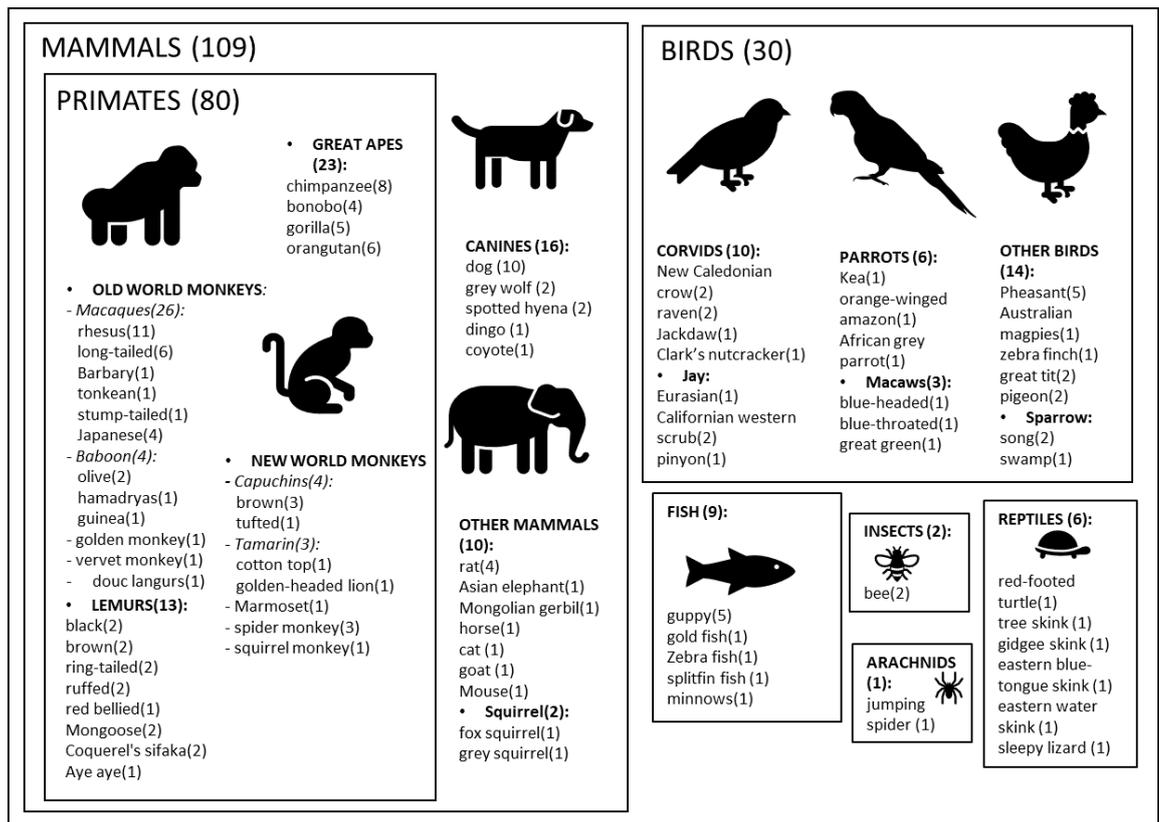


Figure 1.4. Animal species tested in inhibitory control tasks. The number indicates the occurrence of each species in a different article using at least one task of inhibitory control. The same article can use different species.

In our sample of papers, the primate order was the most represented taxon (with 31 different species). Particularly rhesus macaques (*Macaca mulatta*), were tested in 11 of the papers. Subjects from this species are probably more available to researchers as this model was and is still extensively used in cognitive, neuroscientific and biomedical research (Phillips et al., 2015). Chimpanzees (*Pan troglodytes*) are also well represented as

they appear in 8 of our sample of papers. The same representation bias for these 2 species was found in a meta-analysis of primate cognition studies (Many Primates et al., 2019a). Dogs (*Canis familiaris*) are also largely used in recent studies of inhibitory control with 10 studies in our sample of papers. It seems that the dog cognition field is benefiting from a recent enthusiasm from dog owners to participate in scientific experiments (Horschler et al., 2019). In less represented classes, the pheasants (*Phasianus colchicus*) are the most studied bird (used in 5 papers) and in fishes, guppies (*Poecilia reticulata*) were also used in 5 papers. The emergence of studies using this underrepresented species could be due to the practicality of rearing, testing and keeping a large number of these individuals. Overall, macaques seem to be the species the most used in research with potentially more data available about its cognition.

#### 1.4.2.4 Sample size in inhibitory control studies

In the inhibitory control studies we selected, the sample size seems to be low with a large dispersion (Median  $\pm$  S.D. (N) = 11  $\pm$  476.6 (216), see Figure 1.5. and Appendix 3 for further details). The number of subjects in our sample of papers ranges from one chimpanzee (Beran et al., 2007) to 7000 dogs (Horschler et al., 2019). The lower median of sample size is found in great apes studies (Median  $\pm$  S.D. (N) = 7.5  $\pm$  17.298 (40), see Figure 1.3 and Appendix 3). Primate studies (excluding great apes, Median  $\pm$  S.D. (N) = 10  $\pm$  5.77 (78)), mammal studies (excluding primates and dogs, Median  $\pm$  S.D. (N) = 11  $\pm$  13.38 (18)), parrot and corvid studies (Median  $\pm$  S.D. (N) = 8  $\pm$  4.02 (18)) also has a low median sample size. A similarly small median sample size was found in a Meta-analysis on animal physical cognition papers (Median = 7, Farrar et al., 2020). This low sample size is particularly

common in primate studies. In a meta-analysis of 574 primate cognition papers, Many Primates et al., 2019, also found a median sample size of 7.

On the other hand, we found the larger median sample size in birds' studies (excluding corvids and parrots, Median  $\pm$  S.D. (N) = 37  $\pm$  76.37 (19), see Figure 1.3 and Appendix 3). This large sample size in birds can be explained by large-scale inhibitory control studies in pheasants from breeding farms (for instance Langley et al., 2019, N = 341 pheasants studied). Studies in dogs also demonstrate a large median sample size with an important dispersion (Median  $\pm$  S.D. (N) = 30  $\pm$  1483.91 (22)). These results could definitely be explained by the accessibility of the species and the recent use of citizen science in dog research (see Hecht & Rice, 2015), which can help gather an important number of subjects (for instance N = 7000 dogs in Horschler et al., 2019).

To summarise, the inhibitory control field is characterised by the use of small sample size, particularly in great apes and other primates. Understudied species such as dogs, birds, fishes or insects can facilitate access to larger sample sizes. Macaque species seem to be a model with a good compromise between availability and testability.

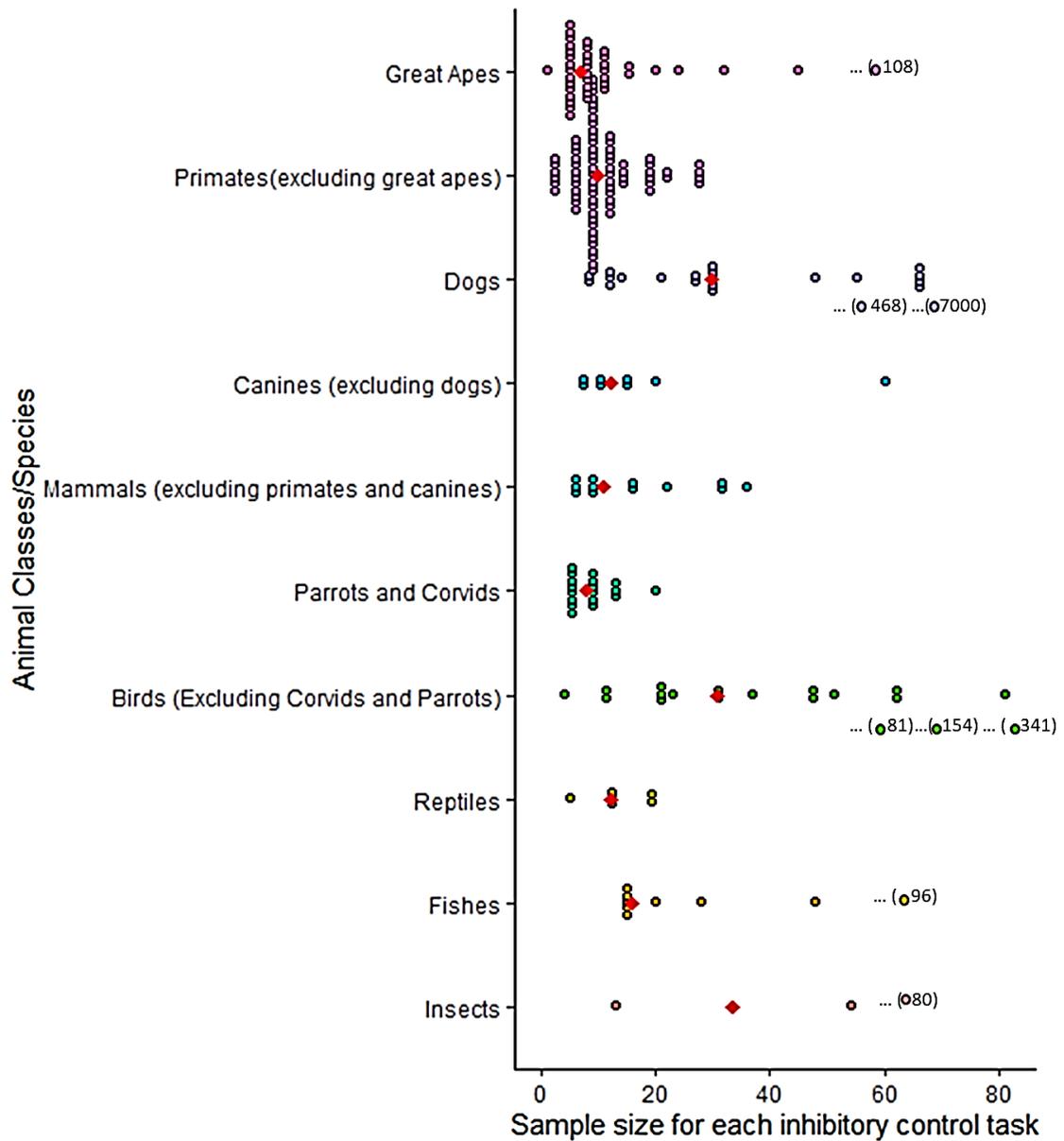


Figure 1.5. The distribution of the sample sizes from each inhibitory control task of our sample of papers for animal classes or species ( $N = 204$  different sample sizes collected). The red diamond indicates the median. ( $\circ N$ ) indicates an outlier not included for readability on this scale with  $N$  the sample size.

### 1.4.3 Conclusion

To cover all the domains of inhibitory control studied in the animal literature a study should investigate the three main components of inhibitory: *inhibition of an action, of a distraction, and of a cognitive set*. In addition, depending on the species considered a task can be either too easy or on the contrary impossible to achieve. Primates, particularly

macaques, seem to be one of the best models to study inhibitory control as its average performances (without floor or ceiling effect) allows individual variability in the most common tasks. In addition macaques are also well represented in the inhibitory control field which lead to more data available about its cognition. Finally, although the inhibitory control field suffers from small sample sizes, the choice of macaque species allows the testing of a good number of individuals. Overall, macaque species, broadly used in research, seem to be a model with a good compromise between availability and testability.

## 1.5 The macaques (*Macaca*)

### 1.5.1 Macaque ecology and societies

The macaque radiation (*Macaca*) is as old as the hominoid radiation, approximately 7 million years (Thierry, 2007). This genus of old-world monkeys has the widest geographical range among non-human primates; widespread throughout Asia with a single species inhabiting northern Africa (Mittermeier et al., 2013; Richard et al., 1989; Taub, 1977). Up to 23 species constitute the genus *Macaca* and are characterised both by a profound unity and a great diversity (Thierry, 2000; 2007). Macaques share the same basic pattern of social organisation as they form multi male multi female groups of up to 100 individuals (Thierry et al., 2004). While males emigrate when reaching maturity, females remain in their natal group forming kin-bonded matrilineal groups who maintain preferential relationships and support each other in conflicts (Thierry, 2007). The rank of females in the hierarchy remains quite stable thanks to kin-based alliances whereas the dominance status of males varies through their lifetimes depending on their competitive abilities (Thierry, 2007). Diets are comparable, with all macaques being mainly frugivorous (Mittermeier et al., 2013; Thierry et al., 2004).

Beyond these shared basic features, macaque species differ greatly both in their morphology and in their styles of affiliation, aggression, reconciliation, dominance, nepotism, maternal behaviour and socialisation (Balasubramaniam et al., 2012; Bernstein et al., 1983; de Waal & Luttrell, 1989; Thierry et al., 1985, 1994, 2000). Macaque species are characterised by their high degrees of sociality and contain species that represent a broad spectrum of social tolerance; from highly cooperative, tolerant species, to highly competitive, intolerant species (Thierry et al., 2004, 2007). In the more despotic species, there is a strict dominance hierarchy and individuals primarily interact with kin and conspecific with close ranking (Sueur et al., 2011; Thierry et al., 2004, 2007); conflicts are rare but severe and injuries are frequent mostly in subordinates (Linden et al., 2019; Ruehlmann, 1988; Thierry, 2000). In the more tolerant species, the hierarchy is less strict, individuals can interact with many social partners (Duboscq et al., 2013; Thierry, 2000). In these tolerant species, conflicts, although frequent, rarely involve biting or injuries but involve counter-aggression and more undecided outcomes (Thierry, 2000). The key differences and similarities in behaviour between this macaque species, is a precious source of information for researchers studying the evolutionary origins of human behaviour.

#### 1.5.2 [Macaque as an ideal model to study inhibitory control](#)

Within non-human primates, the macaque radiation, phylogenetically close to human, has been a popular model for behavioural and cognitive research and particularly to study human evolution (Cauvin et al., 2015; ManyPrimates et al., 2019a; Subbaraman, 2021). Macaques bred in captivity are common in research centres and breeding colonies (Cauvin et al., 2015; ManyPrimates et al., 2019a; Subbaraman, 2021). A greater availability, compared to other species of non-human primates, gives access to larger sample size (as

we demonstrated in 1.3.2.3). Besides, working with captive macaques allows for main confounding factors such as the rearing environment and the experience of the tested subjects. More practically, the use of experimental equipment is often difficult in wild conditions (Schubiger et al., 2020).

Furthermore, macaque species possess enhanced general intelligence (Reader & Laland, 2002) and can perform computerised testing (e.g., Gazes et al., 2013; Washburn 1994; Washburn, Harper & Rumbaugh, 1994). Macaque species possess the sensory abilities to perceive computerised stimuli and the motor skills to interact with a touch screen (Schubiger et al., 2020). This species has been tested in several inhibitory control tasks, for instance researchers have demonstrated the Stroop effect (interference effect of an incongruent stimulus, Lauwereyns et al., 2000) and the emotional Stroop effect in Japanese macaques (*Macaca fuscata*; Hopper et al., 2021). Barbary Macaques (*Macaca sylvanus*) have been tested in a modified version of the cylinder task and in cognitive flexibility tasks (Rathke & Fischer, 2020). Rhesus macaques have also been tested in Reversal learning tasks (Rayburn-Reeves & Beran, 2017) and in a stop task associated with emotional pictures (Vardanjani et al., 2021).

To summarise, captive macaque species, easily available to researchers, possess the necessary cognitive abilities to participate in research on inhibitory control. They have been tested on computerised tasks aiming at measuring the three main components of inhibitory control. Besides, their key similarities and difference in behaviours allow researchers to assess if differences in their social organisation might have provided a selective pressure during the evolution of each species. Thus this genus presents us with an ideal candidate to thoroughly study inhibitory control and the evolution of this ability.

## Chapter 2: Validating a Battery of Inhibitory Control Tasks

### 2.1 Overview

We have seen in the previous chapter that inhibitory control, a crucial ability in many aspects of everyday life, has been studied in a large variety of species. However, the various paradigms designed to measure inhibitory control often suffer from a lack of systematic validation and have yielded mixed results. Besides, the nature of this ability remains unclear, is it a general construct or a family of distinct sub-components? Therefore, the overarching aim of this second chapter was to develop a valid battery of inhibitory control tasks. We wanted to first demonstrate the content validity and the temporal repeatability of our selected tasks. Then we wanted to assess the contextual consistency of performances between these tasks to better understand the structure of inhibitory control. For this, we tested 21 rhesus macaques (*Macaca mulatta*, 12 males, 9 females) in a battery of touchscreen tasks assessing the three main components of inhibitory control: *inhibition of a distraction* (using a Distraction task), *inhibition of an action* (using a Go/No-go task) and *inhibition of a cognitive set* (using a Reversal learning task). All tasks were reliable and effective at measuring the inhibition of a prepotent response. However, while there was consistency of performance between *the inhibition of a distraction* and *the inhibition of an action*, representing a response-driven basic form of inhibition, this was not found for the inhibition of a cognitive set. This task battery provides us with a new insight into the structure of inhibitory control in a non-human primate. This ability seems to be composed of intertwined sub-processes, which might rely on other

cognitive constructs. Inhibitory control could be divided in sub-components, with on one hand, a cognitively low demanding process involving the inhibition of a prepotent, stimulus-driven response, and on another hand, a more controlled, deliberate inhibition of a mental state. It seems crucial that future studies focus on a better understanding of this ability given the importance of inhibition-related processes in successful day-to-day living.

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## 2.2 Challenges in measuring inhibitory control

From chapter 1, part 1.3.2, we know that the most commonly described inhibitory processes are: *distraction inhibition* (e.g., control of an emotional response to an internal or external distractor, in order to focus on a goal), *action inhibition* (e.g., inhibition of a prepotent, unwanted, reflexive motoric action) and *cognitive set inhibition* (e.g., inhibition of a pre-learned cognitive set to flexibly adjust behaviours; see Aron, 2007; Diamond, 2013; Dillon & Pizzagalli, 2007; Nigg, 2017). An important research question that has been a source of controversy in both neuropsychological and cognitive studies is to what extent these inhibitory processes can be considered unitary in the sense that they are reflections of the same underlying mechanism or ability (Dempster & Corkill, 1999; MacLeod, 2007; Miyake et al., 2000; Nigg, 2017). For instance, to support this unitary hypothesis, Duckworth and Kern (2011), in a large-scale meta-analysis (based on over 33,000 adult participants), demonstrated a moderate but significant convergence of several inhibition related measures such as the Go/No-go task (the subjects need to respond to Go stimuli

while inhibiting response to an unrewarded No-go stimuli) or the Stroop task (the subjects need to inhibit an interference from a distractor while doing a task). Similarly, in the animal cognition field, MacLean and colleagues (2017) found that the Cylinder task (a common inhibitory control task in which the animal needs to inhibit reaching directly for food through the transparent surface of a cylinder) and two Detour tasks (the subject needs to circumvent an obstacle to get a reward) loaded onto the same factor in a large-scale battery of cognitive tasks in 552 dogs (*Canis familiaris*). Maclean and colleagues (2014) also found a strong correlation in performances between the A-not-B task (the subject must inhibit a previously rewarded behaviour to learn a new reward-contingency) and the Cylinder task across 23 primate species.

In contrast, several authors have proposed that inhibition-related processes are instead a family of functions rather than a single unitary construct (Friedman & Miyake, 2004, 2017; Nigg, 2000, 2017). In humans, Friedman and Miyake (2004), using common inhibitory control tasks, found that two inhibitory factors: “prepotent response inhibition” and “resistance to distractor interference” were closely related, but both were unrelated to “resistance to proactive interference”, a form of *cognitive set inhibition*. In the animal cognition literature, several studies tested dogs (*C. familiaris*) in common inhibitory control tasks, including the Cylinder and the A-not-B. The authors found that the dogs’ performances in these tasks were not correlated (Bray et al., 2014; Brucks et al., 2017; Fagnani et al., 2016; Vernouillet et al., 2018). A similar result was also found in a study comparing wolves (*Canis lupus*) and dogs’ performances in a Cylinder task and in a detour paradigm (Marshall-Pescini, Virányi and Range, 2015). From these results, the authors concluded that inhibitory control would be context specific and of a diverse structure

(Bray, MacLean & Hare 2014; Brucks et al., 2017; Fagnani et al., 2016; Vernouillet et al., 2018).

However these mixed results and lack of correlation are difficult to interpret as evidence for separable inhibition-related processes for several reasons (Friedman & Miyake, 2004; Miyake et al., 2000). The first reason is that researchers often use these tasks and assume that they measure inhibitory control but without providing any justification of the choice of the task (Friedman & Miyake, 2004). Thus the content validity (defined as the degree to which a measurement is representative of the targeted construct, Haynes, Richard & Kubany, 1995) is rarely evaluated (Friedman & Miyake, 2004). According to Völter et al.(2018), to assess the content validity of a task, researchers should agree on features defining the ability of interest and look at characteristic responses' patterns. For instance, in inhibitory control tasks authors should demonstrate that a prepotent response (dominant and automatic response to a stimulus) have been triggered by the test conditions (Völter et al., 2018).

The second complication arises from the fact that common inhibitory control tasks tend to suffer poor repeatability, i.e. multiple exposures to the same task often lead to inconsistent individual's performance over time (Friedman & Miyake et al., 2004, Völter et al., 2018). Yet this test-retest reliability is necessary before considering the validity of a task (Biro and Stamps, 2015; Griffin, Guillette & Healy, 2015; Völter et al., 2018). In the animal cognition literature, the repeatability of inhibitory control measurements is rarely assessed, and the results are mixed. For instance, great tits (*Parus major*) demonstrated a significant repeatability of performances in successive Reversal learning tasks (Cauchoix et al., 2017). Similarly, Australian magpies (*Cracticus tibicen*) tested as juveniles in the

Cylinder task and reversal learning task repeated their performance as adults (Ashton et al., 2018). In a recent study, rhesus macaques demonstrated reproducibility in attention bias measurement (using threatening and neutral conspecifics pictures) several years apart (Howarth et al., 2021). However, the performance of robins (*Petroica longipe*) in the Cylinder task did not seem repeatable over a year (Shaw, 2017). This lack of valid and reliable cognitive measurements, often referred as the “replicability crisis”, is unfortunately a common issue in psychology experiments (for review see Lindsay, 2015).

A third difficulty is the task impurity problem, i.e. no tasks are pure measurement of a single cognitive process. Inhibitory control tasks often involve other cognitive (e.g. memory) or non-cognitive processes (e.g. personality) that are not directly relevant to the targeted function (Friedman & Miyake, 2004; Gärtner & Strobel, 2019; Miyake et al., 2000; Völter et al., 2018). For instance, the Cylinder tasks, one of the benchmark tests in large inter-species comparisons (MacLean et al., 2014, 2017), is the subject of vivid debates (for review see Kabadayi, Bobrowicz & Osvath, 2018; Shaw & Schmelz, 2017). Factors such as prior experience (Duque & Stevens, 2017; Kabadayi, Bobrowicz & Osvath, 2018; van Horik et al., 2018b, 2019; Vernouillet et al., 2018), can dramatically influence a subject’s performance on this Detour task. Various authors advocate to circumvent this task impurity problem by using a battery of tasks putatively measuring the same ability (but differing in other task demands) to reveal a common underlying cognitive construct (Cauchoix et al., 2018; Friedman and Miyake 2017; Many Primates et al., 2019; Shaw & Schmelz, 2017; Völter et al., 2018). If inhibitory control was a common ability, multiple tasks putatively measuring the same inhibitory process, should demonstrate cross-

contextual consistency in individuals' inhibitory performance (Shaw & Schmelz, 2017; Völter et al., 2018).

Therefore, the aim of this chapter was to validate a battery of inhibitory control tasks in non-human primates: (1) by assessing the content validity of three tasks covering the main domains of this inhibitory ability, (2) by demonstrating the necessary temporal repeatability of these tasks. Finally, we wanted to investigate the structure of inhibitory control by looking at the cross-contextual consistency between tasks. The goal here was to assess whether the main components of inhibitory control fall under the same common inhibitory ability or whether they are part of a family of distinct sub-components.

In this thesis we wanted to cover all aspects of inhibitory control, so we chose to study its main three domains cited in the literature (see chapter 1.3.1): the *inhibition of an action*, *of a distraction and of a cognitive set* (see Figure 2.1.). We did not want to use the overly represented Cylinder task as its validity has been repeatedly questioned in many species (for reviews see Kabadayi et al., 2016, 2017; Shaw & Schmelz 2017). So we selected three tasks of inhibitory control that are well-established and used in human and animal research, and which have been tested for validity and reliability in humans (Rana & Rao, 2013; Thomas, Rao & Devi, 2016; Wöstmann et al., 2013; Willoughby & Blair 2011). To investigate *the inhibition of a distraction*, we chose a Distraction task. In this task, a subject must inhibit a dominant and prepotent emotional response to a distractor (Allritz et al., 2016; Bethell et al., 2016; Howarth et al., 2021; Isaac et al., 2012; Stroop, 1935). To investigate *the inhibition of an action*, we chose a Go/No-go task. Here a subject learns to develop a prepotent motor response to frequently appearing target and must withhold it to less frequently appearing non target (Aron, 2007; Diamond, 2013; Dillon & Pizzagalli,

2007; Duckworth & Kern, 2011). Lastly, to assess *inhibition of a cognitive set*, we selected the Reversal learning task. In this task, a subject must inhibit a pre-learned rule to adopt a new set of rules (Bray et al., 2014; Jelbert, Taylor & Gray, 2016). We decided to use the touch screen technology as it is an extremely flexible tool which allows accurate recording of the subject's answer while controlling for important confounding factors (Kangas & Bergman, 2017). Thanks to this technology we could create our own inhibitory control tasks which were easily adapted to our subjects physical and motivational abilities. Thanks to a pilot study conducted in 7 macaques we could directly adjust all parameters of our tasks.

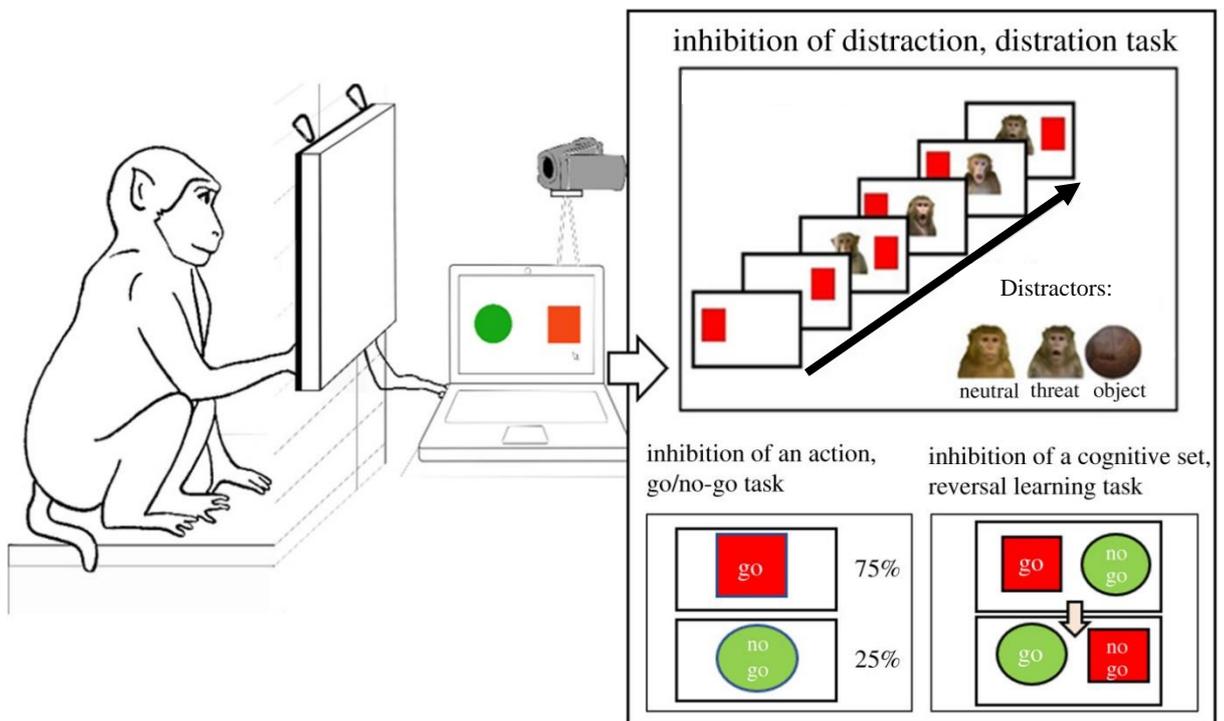


Figure 2.1. Schematic representation of the touchscreen apparatus and inhibitory control tasks procedure. The distraction task (inhibition of a distraction), the Go/No-go task (inhibition of an action) and the Reversal-learning task (inhibition of a cognitive set) are presented.

As outlined in the previous chapter, macaque species are an ideal model to study inhibitory control. We chose to develop our task battery on rhesus macaques (*Macaca mulatta*), as it is the most easily accessible species of macaque, and which have been thoroughly

studied in cognitive research. Rhesus species has been tested in several tasks of inhibitory control such as the emotional Stroop task or equivalents (Bethell et al., 2012, 2016; King et al., 2012; Lacreuse et al., 2013 Landman et al., 2014; Vardanjani et al., 2021), the middle cup task (Joly et al., 2017), the stop task (Liu et al., 2009) and the Reversal learning tasks (Rayburn-Reeves & Beran, 2017).

We first expected to demonstrate the content validity of our three inhibitory control tasks, i.e. a prepotent response (dominant and automatic response to a stimulus) was generated by the test conditions (see Figure 2.2). We further expected to demonstrate temporal repeatability of the tasks by showing that the rank of the individual's performances within the group of subjects and within the same task, would be repeatable over two time points (2 weeks apart, see Figure 2.2). On one hand, we did not want this interval to be too long to avoid dramatic changes in the internal and external states of the subjects (Bell, Hankison & Laskowski, 2009; Shaw & Schmelz, 2017). On the other hand, we did not want this interval to be so short that there would be an influence of carry over effects or shifts in emotion state (Bell, Hankison & Laskowski, 2009; Howarth et al., 2021). Finally, we expected that these 3 tasks would not demonstrate cross-contextual repeatability of the individuals' performances thus supporting the theory of the multifaceted structure of inhibitory control.

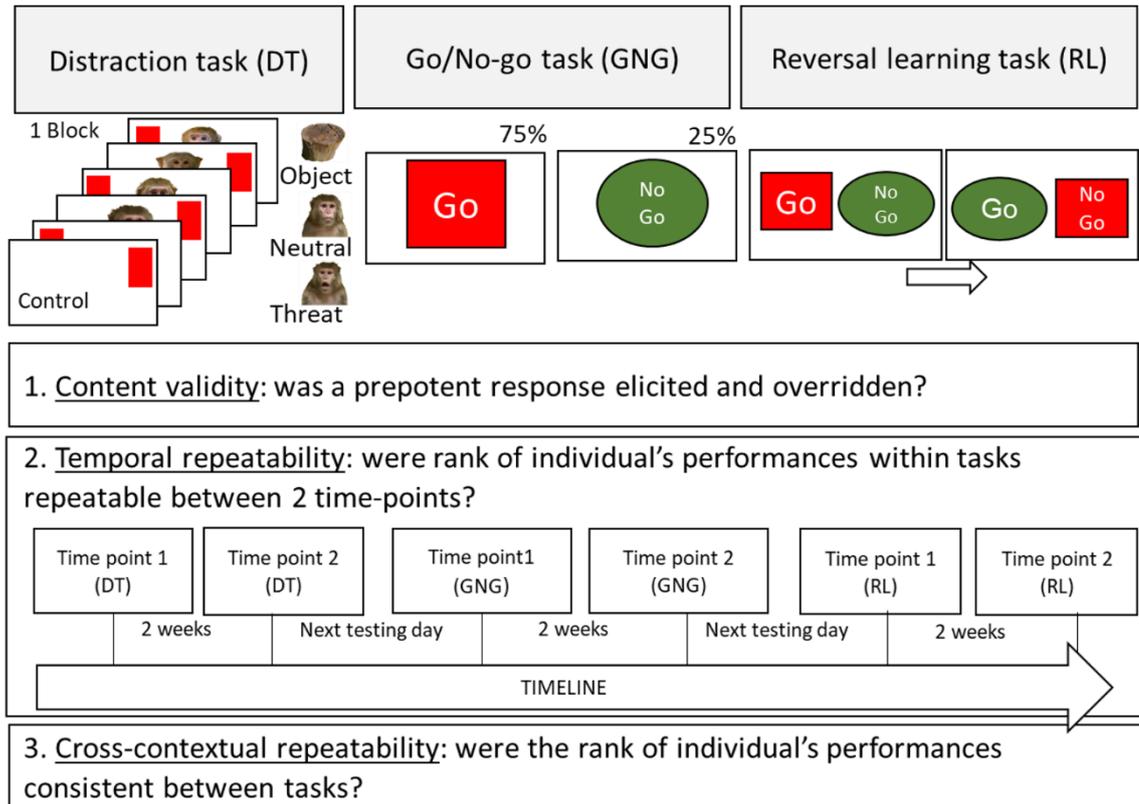


Figure 2.2. Schematic representation of the touchscreen tasks procedures and aims of the study. The Distraction task (inhibition of a distraction), the Go/No-go task (inhibition of an action) and the Reversal learning task (inhibition of a cognitive set) are presented. The aims of the study are also presented: 1. Content validity, 2. Temporal repeatability (with timeline) and 3. Contextual repeatability.

## 2.3 Materials & Methods

### 2.3.1 Subjects

All the adult rhesus macaques (*Macaca mulatta*) taking part in this study were from the breeding colony of the Medical Research Council's Center for Macaques (MRC-CFM) in Porton Down, United Kingdom (see Appendix 4 for Ethical approvals). Each group had access to an indoor free-roaming room (3.35 m × 8.04 m × 2.8m) and an adjacent caged area (1.5m×6.12m×2.8m), with a minimum total space of 3.5 m<sup>3</sup> /breeding animal in the largest groups. All rooms were temperature controlled (20 °C ± 5) with humidity at 55% +/-10. Each free-roaming area had a large bay window at one end facing outdoors and allowing a natural day-night cycle. At the other end of each room was an internal window

fitted with movable mirrors which the monkey could control using a handle, allowing them to view the activities outside their area. Rooms were enriched with climbing structures (platforms, poles, fire hose and ladders) and enrichment devices (food puzzles, boxes, plastic barrels and balls, and small plastic blocks attached to structures or walls). Subjects received a supply of fruit and vegetables, dried forage mix (cereal, peas, beans, lentils etc.), bread and boiled eggs, in the morning and afternoon, with enough food to last for a 24 h period. All subjects had access to water and food prior to and during the experiment. Eighteen of the subjects already participated in a behavioural study involving looking at pictures (Bethell et al., 2019b; Howarth et al., 2021) and all of them were familiar with basic training and clicker procedures. However, none of them had experience with touchscreen experiments. Thirty subjects (14 males, 16 females; aged from 3 to 17 years old, mean age in years  $M \pm S.D. = 8.10 \pm 4.05$ ,  $N = 30$ ) started the touch screen training phases (see Appendix 5) but only 21 (12 males and 9 females, aged from 3 to 17 years old, mean age in years  $M \pm S.D. = 8.9 \pm 4.41$ ) successfully completed the training and were able to take part in the experiment.

The subjects were housed in 14 different social groups with an average of 12 individuals per group. Hierarchy, calculated in each group using David's scores (David, 1987), was provided by the head of research of the facility (see Appendix 6 for rank calculations). Agonistic behaviours including threats, displacements, chases, and physical conflict were recorded to assess the hierarchy. The caretakers regularly monitored the groups, and David's scores were updated accordingly. Using video recordings of training and test sessions, a blind observer coded agonistic interactions between the tested individual and other conspecifics to verify the given ranks for each group (see Appendix 6).

If a male never lost, he was considered high ranking. If the female never lost against other females, she was considered high-ranking, otherwise she was considered low-ranking.

### 2.3.2 Apparatus

To minimise stress, all tests were conducted in the enclosure, with no isolation from the social group; meeting recent and important ethical considerations on animal welfare and cognition (Cronin et al., 2017; Jacobson et al., 2018). The macaques had free and voluntary access to the apparatus and were never restrained; at any point subjects could leave the experiment and return voluntarily. For the experimental task, the set up was customised to be transported from one cage to another (see Figure 2.3.). Outside the cage, a laptop was connected via USB and HDMI cables to a capacitive touchscreen (ELO 1590L, frequency of 60 Hz, 19" in diagonal, resolution 1280 x 1024 pixels). The program Elo touch solution 6.9.20 was used for calibration. The laptop screen duplicated the touchscreen display to be able to follow the experiment's progress. The touchscreen was attached to the cage bars and the position was adjusted to each individual. All experimental procedures including stimulus presentation and response collection were carried out using MATLAB (version R 2018b, using Psychtoolbox-3.0.15 functions), under Windows 10. The MATLAB scripts were specifically conceived for the needs of this study; an individual progression file allowed the experimenter to abort and come back to the same point of a running session (see online supplemental material for MATLAB CODE). If a trial was aborted the response latency was not recorded. The computer gave auditory feedback in response to the subject's performance. All sessions were videotaped with one digital video camera (Sony HDR-CX330EB). The rewards (dry raisins) for each correct answer were given by hand.



Figure 2.3. Apparatus used in the experiments. A laptop was connected to a touchscreen attached to the cage bars (a). Sessions were recorded thanks to a video camera. Individuals sat in front of the screen (b) and rewards (dry raisins for the tested individual) were given by hand.

## 2.4 General procedure

When the program for a specific task was launched, the experimenter entered the name of the individual. When more than one individual per cage was tested or when other individuals from the group were interacting with the touch screen, a research assistant was distracting the other macaques at the opposite side of the room. Every session was initiated by the subject touching a red cross located in the centre of the screen, starting the time recording. The session was aborted when another individual displaced the tested individual or interacted with the touchscreen. If the subject left the testing area or was not focusing attention on the screen the session was aborted. If the target was not touched within the specified time limit (see task descriptions below for specific time limit), the built-in timer of the program was paused, and a red cross appeared in the centre of the screen until the session was resumed by touching it. The response latencies above the time limits were not used in the analysis. If the subject stayed inactive for more than 5 min the

experiment was stopped and continued the next testing day, if the subject did not participate for three testing days in a row the subject was excluded from the task.

## 2.5 Inhibitory control tasks

For the task battery we chose three tasks covering the main domains of inhibitory control: *inhibition of a distraction*, *inhibition of an action* and *inhibition of a cognitive set* (see Figure 2.1).

The tasks were conducted in the same order as they were built upon the previous task (see Figure 2.2. for a visual presentation of the tasks and timeline): first a Distraction task (a target touching task with pictorial stimuli as distractors). This task was repeated (to assess temporal repeatability), for each subject, 2 weeks apart. Once this task was completed for the second time, the subjects were tested (the next testing day) on the Go/No-go task (a novel unrewarded stimulus was introduced). Once, the subjects were tested a second time on the Go/No-go task, they were tested on the Reversal learning task (built upon the previously rewarded and unrewarded stimuli). Finally they finished the experiment by being tested a second time on the Reversal learning task 2 weeks after. As in previous batteries of tasks in animals (Beran & Hopkins, 2018, Herrmann et al., 2007, 2010, Lacreuse, 2014, Maclean et al., 2017; Wobber et al., 2014), the order of tasks was the same for all subjects. Although this design cannot eliminate the possibility of order effects (i.e. the participation on a given task affects performance on subsequent measures), it ensures consistency across subjects, permitting direct comparisons of performances across time and tasks. Besides, we wanted our subject to have the same experience with inhibitory control testing as this ability can be learned (Diamond, 2013) and is directly influenced by previous inhibitory control testing (Radel, Gruet & Barzykowski, 2019).

### 2.5.1 Inhibition of distraction: Distraction task

The Distraction task we used is a variant of the Emotional Stroop task in which human participants name the colours of words that differ in emotional valence, with a longer response latency to negative words (Bar-Haim et al., 2007; Williams, Mathews & MacLeod, 1996). Instead of emotional words we used pictorial distractors presented at the same time as a target (as in Allritz et al., 2016 in chimpanzees and in Bethell et al., 2012) and looked at the distraction effect (i.e. the effect on the response latency) of three types of stimulus: objects, a neutral social stimulus and a threatening social stimulus.

Every session was initiated by the subject touching a red cross in the centre of the screen. Then the timer started, and the subject had to touch a target (a red rectangle of 10 x 13 cm) randomly displayed at the far left or right of the screen. When the subject successfully touched the target, a high-pitched chime was played, the timer was stopped, and the reward was given. After an inter-trial of 2000 ms with only a white background displayed, the next trial was presented. Such a trial without a distractor was considered as a “Control” trial. Two “Control” trials were followed by a block of four trials with pictures from the same categories (either four pictures of objects, neutral or threatening conspecific faces, see Fig. 1 and online for MATLAB codes and stimuli). Each block of pictures of the same category was seen 2 times per session. From the literature, it appeared that the Stroop effect was more pronounced with this block presentation of pictures (in humans Bar-Haim et al., 2007; McKenna & Sharma, 2004 and in chimpanzees, *P. troglodytes*, Allritz et al., 2016). The distractors were displayed at the centre of the screen at the same time as the regular target. The distractors were pictures of 16 x 18.5 cm with matching contrast and luminosity (function ‘Match colour’ in Adobe Photoshop

CS6). The category “Object” included a leather ball, a leather bag, a brown stone and a wooden log (see Figure 1.6.).



Figure 2.4. Objects presented to the rhesus macaques in the Distraction task (“Object” trials). We used a rock, a leather ball, a leather bag and a log of wood as stimuli.

The conspecific pictures were chosen to be as realistic as possible, depicting a frontal view of the face and the torso of four unknown adult rhesus macaques. The “Neutral” conspecific included four pictures of individuals with a neutral facial expression. The “Threatening” conspecific included four pictures showing a “open mouth threat” facial expression, frequently displayed by rhesus macaques (Bethell et al., 2016; Hinde & Rowell, 1962). Threatening stimuli (as well as positive stimuli see Hopper et al., 2021) have been shown to have an important distracting effect in macaques (Bethell et al., 2016; Howarth et al., 2021; Landman et al., 2014).

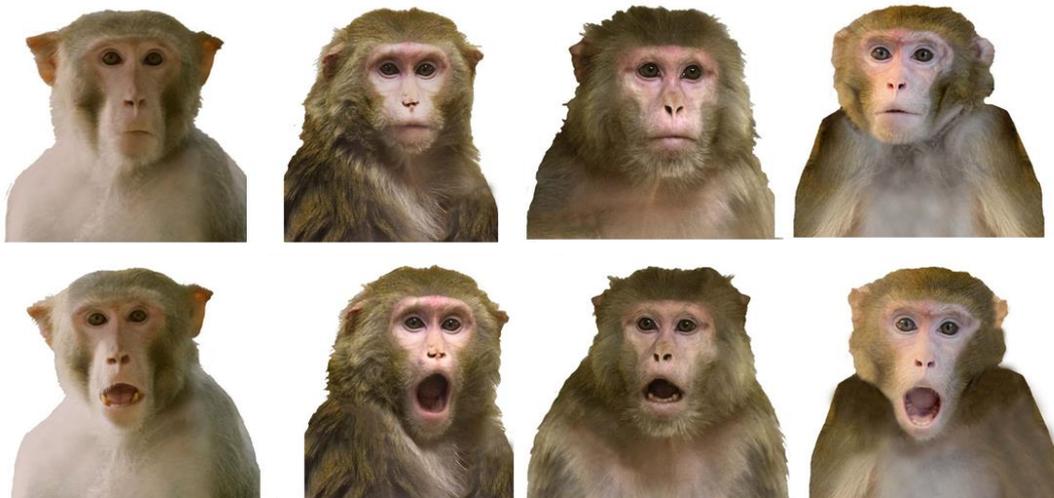


Figure 2.5. Stimuli used in the Distraction task in rhesus macaques. The first row displays neutral unknown conspecific faces (“Neutral” trials). The second row displays the same conspecifics but with a threatening facial expression (“Threat” trials).

The subjects were not rewarded to touch the distractors and the screen remained the same until the target on the side was touched. During a pilot study (N = 4 subjects, these data were not included in our analysis), we observed that the subjects were, for a long duration, intensely reacting to the pictures of their conspecifics' faces (lip-smacking, stares and threats) so we set up a maximum response time of 35 s (at the condition that the subject kept looking at the screen). This time period allowed the subject to display a behavioural response, overcome it, and continue the task. If the subject did not touch the target within 35 sec, the response latency was not taken into account in the analysis. Each block and trial were counterbalanced across subjects (see Fig. 1). Three sessions of 36 trials were repeated at time point 1 and time point 2 (average days between the time points  $M \pm S.D. = 12.91 \pm 2.84$ , N = 21; 216 trials total per individual). One male rhesus macaque was not willing to participate in further testing after this task.

### 2.5.2 Inhibition of an action: Go/No-go task

In the Go/No-go task the subjects need to respond to frequently presented Go stimuli while withholding a prepotent response to infrequently presented No-go stimuli (Dillon and Pizzagalli 2007; Duckworth and Kern 2011; Müller et al., 2012).

The apparatus and the general procedure were identical to the Distraction task. A "Go" (red rectangle of 16x18 cm) or a "No-go" stimulus (green circle of 16x16 cm) appeared randomly in the centre of the screen. The "Go" stimulus was preceded by a high-pitched sound (0.6 sec before the stimulus appeared) and the "No-go" stimulus a low pitch sound to help the subjects to anticipate the next trial. The "Go" stimuli appeared 75% of the 40 trials to elicit a prepotent response toward the screen. If the screen was touched outside the stimulus no sound was produced and the trial continued. The "Go" stimulus stayed on

the screen until it was touched. We set up a maximum response time (i.e. touching the “Go” stimuli) of 15 s after this the red cross appeared on the screen and the response latency was not recorded. From a pilot study conducted with a shorter response limit, we observed that the subjects frequently left the testing session as they were not rewarded on each “Go” trial. The “No-go” stimulus disappeared if not touched during 2000 ms and the subject received a reward. If the “No-go” stimulus was touched during this lapse of time, a blank white background appeared for 3000 ms (as a time out), an “incorrect” sound (with frequency 800, 1300, 2000 Hz) was produced and the reward was not given. At first, we fixed a success criterion for the subject’s performances at 80% of correct trials per session, but four macaques never reached this criterion. The performance was therefore measured after 5 sessions of 40 trials per time point (200 trials in total) for each monkey. These sessions were repeated at time point 2 (average days between the time points  $M \pm S.D. = 11.95 \pm 2.10$ ,  $N = 20$ , see Fig. 1).

### 2.5.3 Inhibition of a cognitive set: Reversal learning task

In the Reversal learning the subjects first learn a stimulus-reward contingency. Once a pre-specified criteria is reached this first association is reversed. Subjects must then inhibit a prepotent response to previously correct stimuli and shift responses to a new stimulus-reward contingency (as in Bond, Kamil & Balda, 2007; Tapp et al., 2003). We expected that the subjects would be able to learn a simple discriminant rule and successfully inhibit it.

At the beginning of the task, two stimuli, a “Go” rewarded stimulus (a red square of 15.34 x 15.34 cm) and a “No-go” unrewarded stimulus (a green circle of 15.34 cm of diameter), were displayed at the same time on the screen at counterbalanced locations (left or right of the screen). When the subject touched the “Go” stimulus, the usual “correct” sound

was played, the subject received a reward, and a new trial began. If the subject touched the incorrect stimulus the “incorrect” sound was played, the subject did not receive a reward and the two stimuli stayed on the screen until the correct stimulus was touched. If the background was touched nothing happened. We set up a maximum response time (i.e. touching the “Go” stimuli) of 15 s after this the red cross appeared on the screen and the response variables were not recorded. We set up this response limit to keep the subjects engaged with the task. From a pilot study we observed that this period of time allowed the subject to frequently receive a reward and to keep engaged with the task. A session consisted of 40 trials. Once a criterion of success was achieved (75% of correct trials out of 20 trials, i.e. the subjects touched the correct stimulus from the first attempt), the rule was reversed: the correct stimulus became the incorrect and the incorrect the correct. One male macaque was excluded from the study as he did not reach the first criterion. The reversed session was continued until the success criterion was reached again (75% of success for the whole session). Three sessions of the reversed paradigm were repeated at time point 2 (average days between the time points  $M \pm S.D. = 12.74 \pm 5.06$ ,  $N = 20$ ). One male subject could not participate in the second time point test as it was permanently removed from the facility.

## 2.6 Content validity

### 2.6.1 Analysis

To validate our battery of inhibitory control tasks our first aim was to assess the content validity of these tasks, for this we wanted to demonstrate that a prepotent response had indeed been triggered (Völter et al., 2018). In the Distraction task, we expected a prepotent response to be triggered by the pictorial distractors, which would increase the

response latency of the subjects in a trial with pictures. We expected a greater response latency when a picture was presented, particularly in the trials with the negative stimuli, compared to control trials with no picture (as in Allritz et al., 2016; Bethell et al., 2016, Howarth et al., 2021, in non-human primates). We also expected to demonstrate that the subjects would still be able to perform the task by overriding their prepotent response to the distractors, keeping a general high rate of success in the task (i.e. successfully touching the target within the time limit).

To assess the content validity of the Go/No-go task, we wanted to demonstrate that a prepotent response was triggered (an incorrect impulsive action toward the No-go stimulus). Therefore, we investigated the difference in response accuracy in the Go and No-go trials. We expected it to be lower on a No-go trial compared to a Go trial. We also expected the subjects to try to override their impulsive response in the No-go trial, with a greater response latency compared to a Go trial.

In the Reversal learning task, we expected an interference from the previously learnt rule while learning the new rule. We expected a lower probability of success in learning the reversed rule (Rule 2) compared to the first acquisition rule (Rule 1). However, we still expected that the subjects override this interference from the first rule with an overall high accuracy for the second rule. We used a Wilcoxon one sample test (function 'wilcox.test', package 'stats', version 3.6.2. R Core, Team, 2019), to check that the previous task did not reinforce the subjects' responses toward the red stimuli (even though the location and size were different).

All analyses were conducted in the R environment for statistical computing v.3.6.0 (R Core Team, 2019). We used linear mixed models and general linear models using the functions

'lme' from the R package 'nlme' v3.1-144 (Pinheiro et al., 2019) to analyse continuous variable (Harrison et al., 2018) and the function 'glmer' from the R package 'lme4' v1.1-21 (Bates et al., 2015) to analyse the binary variable (Bates et al., 2015). The dependent variables were the response latency to touch the target on a trial in the Distraction task and in the Go/No-go task (continuous). As the response latency data presented a skewed distribution, they were log transformed to meet assumptions of normality (Cauchoix et al., 2018; Fazio, 1990; Harald et al., 2010). We excluded latencies below 200 ms (time needed for stimulus perception and motor responses to occur, Harald et al., 2010; Whelan, 2008) and above the time limit. We also recorded the successful completion of a trial in the Go/No-go task and in the Reversal learning task (binary). For all tasks, the random factor included the individual's identity. We controlled for known influencing factors of inhibitory control by including the following explanatory variables into the models: the sex of the subject (Paul, Harding & Mendl, 2005; Sass et al., 2010), the age (in year, Tapp et al., 2003; Bray et al., 2014), the experience with pictures (for the Distraction task) and the rank of the subject (Johnson-Ulrich & Holekamp, 2020). To increase the power of the analysis we merged middle ranked individuals and low ranked individuals to have 2 categories of ranks : either low or high. We considered high ranking individuals the two subjects at the top of the hierarchy at the time of the testing (e.g. in mixed groups, the top-ranking male and the top-ranking female). We had a total of 16 individuals from the higher rank and five from the lower rank. We also controlled for the following task influencing factors: trial, session, time point and type of stimulus (type of picture, no picture vs any type of picture for the Distraction task, type of stimulus: Go vs No-go in the Go/No-go task and type of rule: acquisition or reversed rule in the Reversal learning task). The full model contained all probable explanatory variables (demographic and task determinants). Terms were

sequentially dropped from the full model, until the best fitted model contained only those terms that could not be removed without significantly reducing explanatory power (Bates et al., 2015; Harrison et al., 2018). We used the function 'anova' from the R package 'car' v3.0-6 (Fox & Weisberg, 2019) to compare each model by likelihood ratio test (given as :  $\chi^2$  Degree of freedom N = sample size)). Our significant threshold was  $p < 0.05$ . Visual inspection of residual plots did not reveal any obvious deviations from normality. We presented the mean  $\pm$  the standard error for each effect of the explanatory variable on the outcome. Data are available on an online repository (see online supplemental materials).

### 2.6.2 Results

#### ***Content validity, Distraction task***

There were no significant differences between each type of picture ('Threat', 'Neutral' or 'Object') in the overall performances but there was a significant difference in the mean response latency between the trials without pictures (control trial,  $M \pm SE = 3961.78 \pm 104.52$  ms,  $N = 21$ ) and with any type of picture (test trials,  $M \pm SE = 4496.52 \pm 111.17$  ms,  $N = 21$ , likelihood-ratio test,  $\chi^2_1 = 9.98$ ,  $N = 21$ ,  $p = 0.002$ ; see Fig. 2 and Appendix 7 for more details and for the presentation of the effects of the other explanatory variables).

This indicates that the response latency was higher when a picture was present, showing that the subjects were distracted. Nonetheless, when a picture was present the percentage of success on the task (to touch the target within the time limit) was still high (96%) showing that this prepotent response was overridden by the subjects. Thus, the interference from a distractor was inhibited in order to successfully complete the task, these results indicate the content validity of this first task.

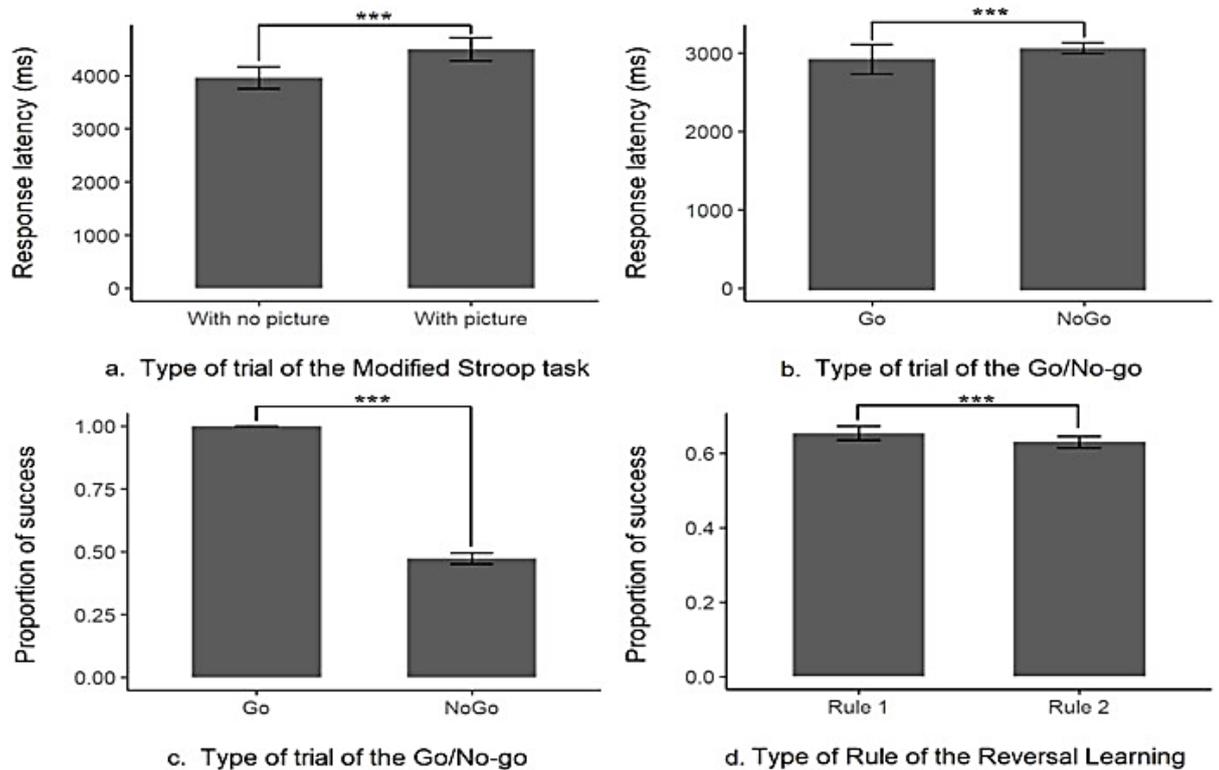


Figure 2.6. Content validity of the inhibitory control tasks. Distraction task: a. response latency the absence (With no picture) or in the presence of a picture (With picture); Go/No-go task: b. response latency or c. proportion of success in Go or No-go trials; d. Reversal learning task, proportion of success when first (Rule 1) or second rule learnt (Rule 2). \*\*\* indicates that  $p$ -value < 0.001

### Content validity, Go/No-go task

There was a significant difference in the mean successful completion of the task between the trials with the Go signal or the No-go signal (likelihood-ratio test ,  $\chi^2_1 = 3335.6$ ,  $N = 20$ ,  $p < 0.001$ , see Fig. 2 and Appendix 8). With only a mean of  $47.3 \pm 1.09\%$  ( $N = 20$ ) of correct answers when a No-go signal was presented (i.e. not touching the No-go stimulus), compared to a mean of success (i.e. touch the Go stimulus within the time limit) of  $99.8 \pm 0.04\%$  ( $N = 20$ , see Fig. 2) when it was a Go stimulus presented. This result is showing that a prepotent response, touching the target impulsively was triggered as the subjects, most of the time, made a mistake and touched the unrewarded No-go target associated with a time out. However, there was still a sign that the subjects tried to override their prepotent

response, the mean response latency on a No-go trial ( $M \pm SE = 3123.13 \pm 36.68$  ms,  $N = 20$ ) was significantly longer than the one in a Go trial ( $M \pm SE = 2881.81 \pm 91.69$  ms,  $N = 20$ , see Fig. 2, from the log-transformation of the response latency, likelihood-ratio test,  $\chi^2_1 = 600.73$ ,  $N = 20$ ,  $p < 0.001$ , see Appendix 9). Please refer to Appendix 8 and 9 for the effect of the other explanatory variables on the model. These results indicate that the subject had a prepotent response to touch any time of stimulus, but still tried to overcome this dominant response by slowing down their action toward the screen, this task is thus assessing the inhibition of a prepotent action.

### ***Content validity, Reversal learning task***

First, we found that the previous task did not influence the subjects' responses as they did not choose the red stimulus for the first trial above the chance level (chance level = 0.5, mean proportion = 0.53,  $p = 0.84$ ). There was a significant difference in the mean success in a trial if the rule was the first acquisition or the reversed rule (likelihood-ratio test, see Appendix 10 for more details on the other explanatory variables), the probability of success was significantly a little higher in the first rule ( $65 \pm 0.97$  % of success,  $N = 20$ ), compared to the reversed rule ( $63 \pm 0.78$  % of success,  $N = 20$ , see Fig. 2). These results indicate that the acquisition rule was interfering with the learning of the reversed rule, despite this interaction 100% of the remaining subject still managed to pass the 75% criterion of success for the second rule (see Table 1.1 for a summary of the main findings).

## **2.7 Temporal repeatability**

### **2.7.1 Analysis**

We wanted to assess the temporal repeatability (also known as test-retest reliability) of the individual's inhibitory performances. For this, we computed, from the response

variables (response latency and successful completion of the tasks), scores of inhibitory control. For the Distraction task we computed a *Distraction control score*, which is the standard method in Stroop task paradigms (as in Allritz et al., 2016; Bethell et al., 2016, 2019a; Howarth et al., 2021). *Distraction control score* represented, for each trial, the difference between the mean response latency in all trials without pictures minus the response latency in each trial. For a trial with a picture, a higher score would indicate better control of a Distraction (a shorter response latency). For the second task, the Go/No-go task, to quantify the individual's ability to inhibit its prepotent action, we calculated the *Action control score* as the mean percentage of trials when a No-Go was present, and the individual didn't touch it for each session (Verbruggen & Logan 2008). We took the last 3 sessions of each time point of each animal to have a comparable number of sessions between tasks. A higher score would indicate an individual is better at inhibiting the action. Finally, we calculated a *Rule control score* (as in Tapp et al., 2003; Wobber and Hare 2009), as the difference between the number of trials to reach the criterion of success for the first rule (75% of correct trials for the whole session) minus the number of trials to reach the same criterion for the reversed rule. A higher score would indicate that an individual is better at inhibiting a previous rule when learning a new one.

Once we had these inhibitory control scores, we wanted to assess the temporal repeatability (also known as test-retest reliability) of the individual's inhibitory control scores, i.e. if the rank of the performances of each subjects within the group were consistent over the two time points (as done in the meta-analysis of Cauchoix et al., 2018). We used the repeatability estimates (R) or Intraclass Correlation Coefficient (ICC) which indicates the amount of variation explained by inter-individual variation of performances

in the tasks relative to intra-individual variation (developed by Nakagawa and Schielzeth 2010). This estimate accounts for both consistency of performances from test to retest (within-subject change), as well as change in average performance of participants as a group over time (Vaz et al., 2013). This test thus assesses the repeatability of the rank of the subjects' performances within the group between the test and the retest and between contexts. We used the function 'rpt', from the 'rptR' package v.0.9.22 in R (Nakagawa and Schielzeth 2010; Stoffel, Nakagawa & Schielzeth, 2017; Vaz et al., 2013). We applied a restricted maximum likelihood function (with 1000 bootstrapping and 1000 permutations) and the individual identity was specified as a random intercept effect. The appropriate type of data distribution was adjusted in each model depending on the dependent variable under investigation ("Gaussian" for continuous variables, "Binomial" for binomial variables). We checked Gaussian models for normal distribution of the residuals using the function 'qqnorm' from the R package 'car' v3.0-6 (Fox & Weisberg, 2019). An individual's performance was considered as repeatable if the p-value from the Likelihood-ratio test was  $< 0.05$ . The decision for the qualification of the R estimates, either low, moderate, or high, was based on the work of (Cauchoix et al., 2018). In this meta-analysis, regrouping 44 studies across 25 animal species, the authors computed the repeatability of individual cognitive performances. They found a mean estimate for the temporal repeatability unadjusted of  $R = 0.18$ , 95% CI [0.09, 0.28], the R adjusted for test order and individual determinants was  $R_{adj} = 0.15$ , 95% CI [0.09, 0.21]. We considered that if  $R \leq 0.1$  the repeatability estimate is low, for  $0.1 < R \leq 0.3$ , it is moderate and for  $R > 0.3$  it is high.

Once the (R) estimates were calculated, we also needed to consider the influence of confounding factors on the temporal repeatability estimates. For this we calculated

adjusted estimates (estimates that adjust for confounding effects which remove fixed effect variance from the estimate, see Nakagawa and Schielzeth, 2010, Stoffell et al., 2017; as done in Cauchoix et al., 2018). Adjusted repeatability can be interpreted as the repeatability given that the level of the confounding factor is known (Nakagawa and Schielzeth, 2010). To calculate these adjusted estimates, we first needed to determine which factors had an effect on the individual's performances by fitting linear mixed models (LMM) and general linear mixed models (GLMM) (we used the same packages as for the content validity). The outcome variables were either the *Distraction control score*, the *Action control score* or the *Rule control score*. As before, we control for two types of confounding factors: individual determinants (age, sex, rank of the individuals, experience with pictures for the Distraction task), and test determinants (type of stimulus, time point, session and trial). Individual's identity was included as a random factor. The full model contained all probable explanatory variables (demographic and task determinants). We used the same model selection as before (see content validity) and the function 'anova' from the R package 'car' v3.0-6 to compare each model and our significant threshold was  $p < 0.05$ . Then, we calculated the adjusted repeatability,  $R_{adj}$ , by including confounding effects (identified by comparing GLMMs) into the repeatability function. Uncertainty in estimators was quantified by parametric bootstrapping and significance testing was implemented by likelihood ratio tests with a significance threshold of  $p < 0.05$  (Stoffell, Nakagawa & Schielzeth, 2010). We reported 95% confidence intervals (CIs) for parameter estimates based on 1000 bootstrapping and 1000 permutations. We reported the result for the adjusted repeatability from the "Link scale approximation".

## 2.7.2 Results

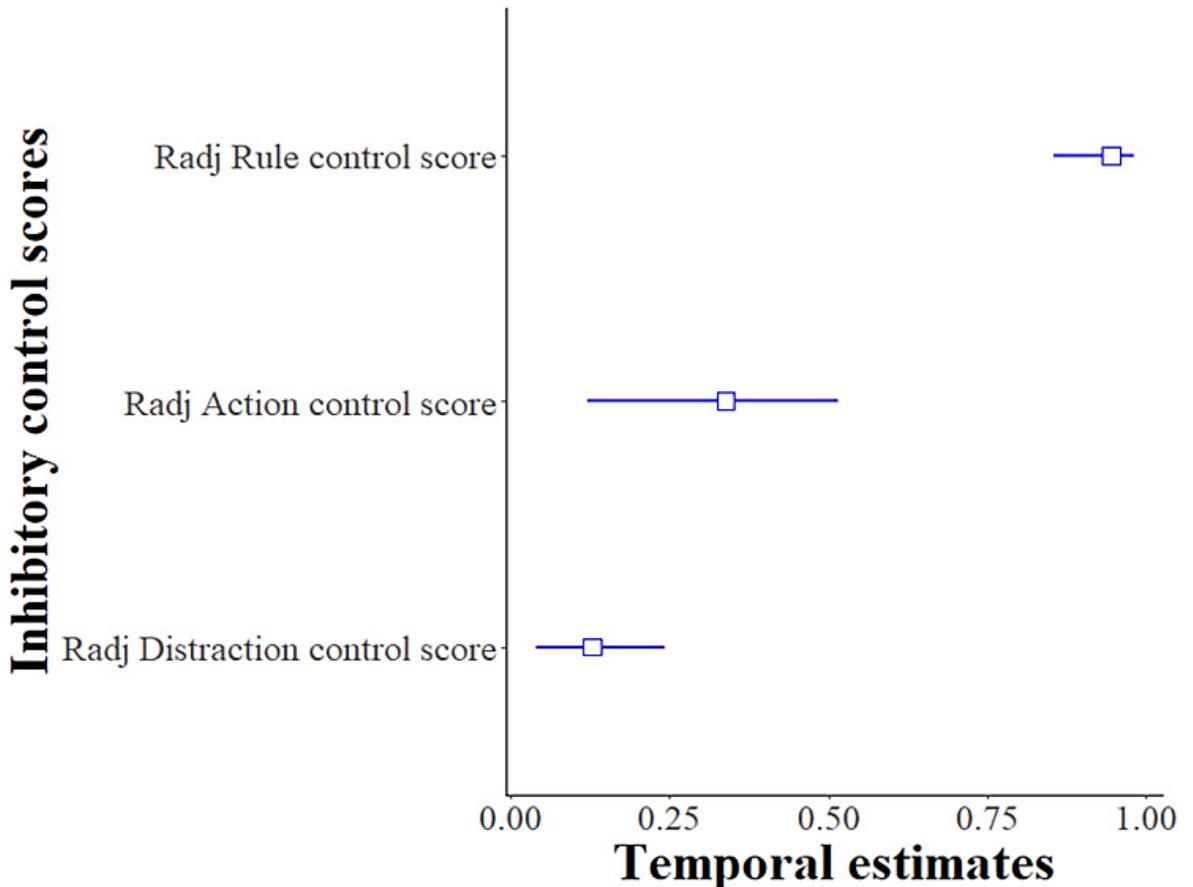
**Temporal repeatability, Distraction task**

Figure 2.7. Temporal repeatability  $R_{adj}$  (adjusted only for the Distraction control score) and 95% bootstrapped confidence intervals for inhibitory control scores. Y-axis presents the adjusted repeatability for each type of inhibitory control measurement: executive function (Executive function response latency), Distraction task (Distraction control score), Go/No-go (Action control score) and Reversal learning (Rule control score).

For the Distraction task, the *Distraction control score* per individual was moderately repeatable between sessions and the two time points ( $R = 0.282 \pm 0.095$ , 95% CI [0.093, 0.462],  $p < 0.001$ ). When testing for explanatory factors using LMMs, the model with the variables session, time-point and sex as fixed terms best explained the *Distraction control score* of the subjects (likelihood-ratio test comparing the best fitted model with the null model:  $\chi^2_5 = 119.61$ ,  $N = 21$ ,  $p < 0.001$ , see Appendix 11). Males had a lower *Distraction control score* (likelihood-ratio test,  $\chi^2_1 = 9.38$ ,  $N = 21$ ,  $p = 0.002$ , and this score increased as

the number of the session increased (likelihood-ratio test,  $\chi^2_1 = 14.02$ ,  $N = 21$ ,  $p < 0.001$ ) and at time point 2 (likelihood-ratio test,  $\chi^2_1 = 93.14$ ,  $N = 21$ ,  $p < 0.001$ ). When considering these confounding factors, the adjusted repeatability of the *Distraction control score* was lower than the unadjusted repeatability ( $R_{\text{adj}} \pm \text{SE} = 0.128 \pm 0.048$ , 95% CI [0.041, 0.241],  $p < 0.001$ ) but still repeatable (see Fig. 3). Thus, in this Distraction task, the rank of the subjects' performances within the group was repeatable over the two time points.

### **Temporal repeatability, Go/No-go task**

For the Go/No-go task, the *Action control score* per session per individual was highly repeatable between sessions and the two time points ( $R = 0.338 \pm 0.105$ , 95% CI [0.120, 0.514],  $p < 0.001$ ). When testing for confounding factors using GLMMs, none of the variables had a significant effect on the model of the *Action control score* of the subjects so the temporal repeatability estimates were not adjusted (likelihood-ratio test comparing the full model with the null model:  $\chi^2_7 = 6.85$ ,  $N = 20$ ,  $p = 0.44$ , see Appendix 12 and Fig. 3). Thus, in this Go/No-go task, the rank of the subjects' performance within the group was repeatable over the two time points.

### **Temporal repeatability, Reversal learning task**

For the Reversal learning task, the *Rule control score* per session per individual was highly repeatable between the sessions and the two time points ( $R = 0.944 \pm 0.033$ , 95% CI [0.855, 0.981],  $p < 0.001$ ). When testing for confounding factors using GLMMs, none of the explanatory variables had a significant effect on the models so the temporal repeatability estimates were not adjusted (likelihood-ratio test comparing the full model with the null model:  $\chi^2_7 = 3.59$ ,  $N = 20$ ,  $p = 0.61$ , see Appendix 13 for more details about the other

confounding variables). Thus, in this Reversal learning task, the rank of the subjects' performances, within the group, was repeatable over the two time points.

To summarise, the rank of the individual performances within the group for inhibitory control scores were consistent over time. While the adjusted temporal repeatability estimates were lower compared to the unadjusted ones, they were still repeatable (see Table 2.1. for a summary of the main findings).

	<b>Content validity:</b> - prepotent response - overridden	<b>Repeatability of performances over 2 time points</b>	<b>Contextual repeatability</b>
<b>Distraction task</b>	- Response latency longer when pictures presented - But still high success	Moderate (R = 0.282) Adjusted for sex, session and time point (R <sub>adj</sub> = 0.128)	With the Go/No-go task
<b>Go/No-go task</b>	- Success on No-go trials lower than Go trials - Response latency longer for No-go trials	High (R = 0.338) Not adjusted	With the Distraction task
<b>Reversal learning task</b>	- Probability of success lower for the reversed than for the acquisition rule - But still high success	High (R = 0.944) Not adjusted	With no other tasks

Table 2.1. Summary table presenting the main findings of the study. All tasks have demonstrated content validity, whereby a prepotent response was elicited and overridden. All individual's performances were repeatable over 2 time points. The individual's performances were consistent between the Distraction task and the Go/No-go task but there was no consistency with the Reversal learning task.

## 2.8 Contextual repeatability between each task

### 2.8.1 Analysis

Once we had demonstrated the content validity and the temporal repeatability of our measurements, we were able to look at the cross-contextual consistency of the individual's performances between the different tasks. We estimated contextual repeatability of our tasks by comparing individual performances on different tasks that putatively measure inhibitory control (as done in the meta-analysis of Cauchoix et al., 2018). We thus wanted to look at the consistency between the ranks of the subject's performance between each pair of tasks. We use the same repeatability test as before to assess the repeatability of the rank of the subjects' performances within the group between contexts. As before, we used LMMs and GLMMs to look for confounding factors in order to adjust the contextual repeatability when two tasks were analysed. In the models, the inhibitory control score was the dependent variables and one of the 4 types of tasks, the sex, the age, the rank, the session, and the time point were the independent variables. Each score was centred and scaled using the function 'scale' from the package 'base', in R v3.6.3 (R Core Team, 2019) to allow comparison between the scores of different units. As before, the decision for the qualification of the R estimates was either low ( $R \leq 0.1$ ), moderate ( $0.1 < R \leq 0.3$ ), or high ( $R > 0.3$ ).

### 2.8.2 Results

The contextual repeatability between the *Distraction control score* and the *Action control score* ( $R = 0.166 \pm 0.067$ , 95% CI [0.041, 0.305],  $p < 0.001$ ), between the *Distraction control score* and the *Rule control score* ( $R = 0.212 \pm 0.085$ , 95% CI [0.049, 0.38],  $p < 0.001$ ) and between the *Action control score* and the *Rule control score* ( $R = 0.138 \pm 0.077$ , 95% CI

[0.003, 0.303],  $p = 0.01$ ) were moderate (see Appendix 14 for a summary of the unadjusted contextual repeatability for all the inhibitory control scores).

The adjusted contextual repeatability (Table 2.2 summarises all the adjusted contextual repeatability estimates), between the *Distraction control score* and the *Action control score* when controlling for session and time point, remained repeatable and moderate ( $R_{adj} \pm SE = 0.17 \pm 0.066$ , 95% CI [0.045, 0.306],  $p < 0.001$ , see Appendix 15). However, between the *Action control score* and the *Rule control score* when controlling for sex, the performances between the tasks were not repeatable anymore. ( $R_{adj} \pm SE = 0.101 \pm 0.066$ , 95% CI [0.000, 0.24],  $p = 0.07$ , see Appendix 16). Similarly, between *Distraction control score* and the *Rule control score* when controlling for sex ( $R_{adj} \pm SE = 0.09 \pm 0.058$ , 95% CI [0.000, 0.22],  $p = 0.07$ , see Appendix 17) the performances between the tasks were not repeatable after adjustments. The other scores did not have any confounding variables, so the contextual estimates were not adjusted.

To summarise, we found, for the inhibitory control scores, when adjusted for confounding factors, that the contextual repeatability was only significant between the *Distraction* task and the *Go/No-go* (see Table 1.1. for a summary of the main findings).

Contextual $R_{adj}$ for the scores	Distraction control	Action control	Rule control
Distraction control	1	-	-
Action control	✓ 0.170 ( $p < 0.001$ )***	1	-
Rule control	0.09 ( $p = 0.07$ )	0.101 ( $p = 0.07$ )	1

Table 2.2. Contextual adjusted repeatability estimates of the scores of inhibitory control. Distraction control score (Distraction task), Action control score (Go/No-go task), Rule control score (Reversal Learning task). The tick mark indicates that the individual's performances are significantly repeatable between tasks \*\*\*  $p < 0.001$

## 2.9 Discussion

The aim of this second chapter was to first validate a battery of inhibitory control in non-human primates by assessing the content validity and temporal repeatability of three tasks covering the main domains of inhibitory control. Then, using this battery of tasks, we wanted to investigate the structure of inhibitory control by looking at the contextual consistency of subjects' performances between these tasks. First, we found a response pattern characteristic of inhibitory control in each of the 3 tasks, an indicator of content validity. A prepotent response (an interference from a pictorial distractor, a dominant motoric response, and a pre-learned rule) was inhibited by the subjects to successfully achieve the goal of the task. We then confirmed that the performances of the subjects were repeatable across 2 time points, thus validating the test-retest reliability of our tasks. Finally, our results gave an insight of the structure of inhibitory control by demonstrating that the individual performances between the Distraction task and the Go/No-go tasks, even after adjustments for confounding factors (session and time point), were also consistent, indicating that these tasks seem to capture the same cognitive process.

However, after adjustment, the individual performances between the Reversal learning task and the other tasks of inhibitory control were not consistent, interestingly indicating the absence of a common underlying ability (see Table 1.1 for a summary of the main findings).

The first step in validating a battery of inhibitory control measurement was to demonstrate their content validity. Looking closely at the pattern of response, our results indicated that a prepotent response was generated from the test conditions. In other research studies, using the Reversal learning task and motor inhibition tasks, in dogs (Bray, MacLean & Hare 2014; Brucks et al., 2017; Marshall-Pescini, Virányi and Range, 2015; Vernouillet et al., 2018), wolves (Marshall-Pescini, Virányi and Range, 2015) or in pheasants (van Horik et al., 2018a,b, 2019), the tasks were similarly producing a prepotent response. The same pattern of response was found in the Distraction tasks in non-human primates (Allritz et al., 2016; Bethell et al., 2016; Howarth et al., 2021; Landman et al., 2014). Unfortunately, this inhibitory pattern of response is rarely systematically investigated. For example, the Cylinder task has been used in a large comparative study, of more than 36 species, to draw conclusions about the evolution of inhibitory control (Maclean et al., 2014). However, the content validity of this task has been recently challenged (Kabadayi, Bobrowicz & Osvath, 2018; Shaw & Schmelz, 2017). Thus, to first demonstrate the content validity of a cognitive task seems a crucial step in order to both justify its use and draw evolutive conclusions from it.

Another method to look at the validity of a task is to use neurosciences to infer the mechanisms of a cognitive ability from its neural underpinnings. Hence, another way to assess the validity of an inhibitory control task would be to compare inhibitory

performances of healthy subjects to performances of subjects with lesions of the frontal cortex, region that is crucial for inhibitory control (e.g. Cook, Spivak & Berns, 2016). For instance, a neuroscientific study demonstrated the validity of the Stop signal test and the Go/No-go task by matching performance of patients with specific brain lesions to performances of healthy subjects (Thomas, Rao & Devi, 2016). In animal research, targeted brain lesions or electrophysiology have been used to study neural mechanisms of inhibitory control. For instance, lesions of the prefrontal cortex induced impairment in the performance of common marmosets on a detour reaching task (Wallis et al., 2001). Similarly in monkeys, electrical stimulation of these regions induced changes in the Go/No-go performances (Sakagami et al., 2001). Due to important ethical considerations, less intrusive paradigms including fMRI, PET-scans or EEG technologies have been adopted in animals (Cook et al., 2016; Sakagami et al., 2001). For instance, Cook et al., 2016, using fMRI on awake dogs performing a Go/No-go task, precisely localised frontal brain regions underpinning response inhibition. It would be interesting to use modern imaging techniques to look more precisely at the neural underpinnings of inhibitory control in awake trained macaques.

Another critical step was to make sure that these tasks were repeatable over time. A lack of temporal repeatability can be detrimental in subsequent assessment of validity (Friedman & Miyake, 2017; Paap & Oliver, 2016). As expected, we found moderate and significant, temporal estimates. Our mean estimate of  $R = 0.40$  is higher than mean estimates found in common cognitive tasks in animals (from the meta-analysis of Cauchoix et al., 2018, the mean estimate is  $R = 0.18$ ). In the animal cognition literature, inhibitory control temporal estimates are ranging from very low ( $R = 0.012$ ) to very high values ( $R =$

0.975) (Ashton et al., 2018; Cauchoix et al., 2017, 2018; Howarth et al., 2021); our range of estimates is similarly diverse (from  $R = 0.128$  to  $0.944$ ) but still significant as expected. The confirmation of the temporal repeatability of any cognitive measurements seems also a crucial step before establishing the validity of any tasks.

Once we established the content validity and temporal repeatability of our measurements, we evaluated the cross-contextual consistency of the inhibitory control tasks. We first found that all the unadjusted estimates were significant. These results were similar to the ones obtained in Australian magpies which obtained a Spearman rank order correlation estimate of  $r = 0.433$  between the Cylinder task and the Reversal learning task (Ashton et al., 2018). Similarly, in a large interspecies study, Maclean et al.(2014), found that performance on the A not B and Cylinder task was strongly correlated ( $r = 0.53$ ). However, using the data from the study of Maclean et al.(2014), looking from an individual difference perspective, Völter and colleagues (2018), did not find any correlation between the inhibitory control tasks. When controlling for confounding factors, the adjusted repeatability between the Distraction task and the Go/No-go task were lower but still significant, this could indicate a common underlying ability. The decrease in the value of the adjusted contextual estimates were similar to the one found in Cauchoix and colleagues (2018). This could be because the confounding factors, that vary between individuals, reduce the between-group variance and thus the repeatability (Nakagawa and Schielzeth, 2010). These results confirm the importance of controlling for confounding factors when assessing contextual repeatability.

Surprisingly, the adjusted contextuality estimates between the Reversal learning task and the two other tasks of inhibitory control were not significant. It seems that the

Distraction tasks (*inhibition of a distraction*) and the Go/No-go (*inhibition of an action*), share a common underlying inhibitory ability, i.e. to inhibit an impulsive, unconscious response to a stimulus. However, between the Reversal learning task (*inhibition of a cognitive set*) and the other tasks no clear pattern emerges that would support the notion of a common cognitive ability. These results reproduce the same pattern found in human research, with correlation between two inhibition-related functions: the “resistance to distractor interference” (similar to our definition of Distraction inhibition) and “prepotent resistance interference” (similar to our definition of action inhibition) but not with “resistance to proactive interference” (similar to our definition of cognitive set inhibition; Friedman & Miyake, 2004). Interestingly, similar results were also demonstrated in several studies in canids, specifically designed to understand the structure of inhibitory control. Authors found a lack of correlation between the Detour task or Cylinder task (*inhibition of an action*) and the A-not-B task (*inhibition of a cognitive set*; Bray, MacLean & Hare 2014; Brucks et al., 2017; Fagnani et al., 2016; Marshall-Pescini, Virányi and Range, 2015; Vernouillet et al., 2018). Thus, the inhibition of an external distractor and the inhibition of a prepotent motor response seem to share the same underlying inhibitory ability but not the inhibition of a previously learned rule. It is possible that the inhibition of an impulsive and prepotent, stimulus driven response, relies more on cognitively low demanding construct, such as a simple bottom-up inhibitory control function (Nigg, 2017). On the contrary, in the learning of a new rule, it could be required, in addition to inhibitory control, to employ a higher deliberate cognitive ability, a top-down function, relying on mental representations (e.g. working memory or set shifting, Dillon, 2007, Nigg, 2017). These results are at odds with the hypothesis that all three inhibition-related functions are measuring some common ability. Thus, our results provide a new insight in favour of the

multifaceted structure of inhibitory control in a non-human primate. It would be difficult to broaden our interpretation to other species because of the potential species-specific differences in the nature of inhibitory control. Inhibitory control could be a general construct in some taxa but a family of independent components in other taxa.

Understanding the structure of inhibitory control is particularly crucial as impairments in inhibitory control have been associated with several psychopathologies. For instance, in children suffering from ADHD, it is still unclear if it is inhibitory control as a general ability which is impaired or only some independent components (Gaultney, 1999; Nigg 2001). Consistent with this last view, there is some evidence that individuals with ADHD are impaired on tasks measuring response inhibition, whereas it remains unclear if these patients are also impaired in cognitive inhibition tasks (Gaultney et al., 1999; Nigg, 2000). However, we need to be cautious in the comparison of results between studies using different types of contextual validity analysis. On one hand, some studies used correlations analysis (Bray et al., 2014; Duckworth & Kern, 2011; Fagnani et al., 2016; Vernouillet et al., 2018); which focuses on the strength of association between two means of performances (Liu et al., 2016; McGraw & Wong, 1996). On the other hand, some authors used repeatability estimates or intraclass correlation based on variance analysis (Ashton et al., 2018; Cauchoix et al., 2018; Shaw, 2017). Unlike correlation, in this agreement analysis, the emphasis is on the degree of concordance between individual performances (Koo & Li, 2016; Liu et al., 2016; McGraw & Wong, 1996). Furthermore, repeatability analysis, unlike correlation, allowed researchers to control for confounding factors (such as individual or temporal determinants, Nakagawa & Schielzeth, 2010; Vaz et al., 2013). It is thus possible to have two sets of scores that are highly correlated, but not

repeatable (Zaki et al., 2013). We can thus look for patterns between results of different studies, but we should be careful in making stronger assertions.

Moreover, the interpretation of the repeatability estimates must be drawn carefully because it assumes that inhibitory control performances on each cognitive test is independent of other idiosyncratic task demands (e.g., learning, problem solving), or individual characteristics (e.g. motivation, personality traits; see Cauchoix et al., 2018; Griffin, Guillette & Healy, 2015; Kabadayi, Bobrowicz & Osvath, 2018). For example, motivation to get a reward is an important confounding factor. If the reward is visible, it strongly affects the subject's ability to inhibit its response (Brucks et al., 2017; Kabadayi, Bobrowicz & Osvath, 2018). As in the inhibitory control field, this task impurity problem is particularly strong, we should be careful to label any common factor inhibitory control (or a suite of inhibitory control abilities) as it remains unclear what the shared variance represents (Friedman & Miyake, 2004; Völter et al., 2018). These results are in line with the claim that the nature of inhibitory control is not unitary but are more likely a collection of sub-components intertwined with other cognitive processes that may or may not be engaged on specific contexts that require inhibition (Beran, 2018; Diamond, 2013; Dillon & Pizzagalli, 2007; Friedman & Miyake, 2004; Nigg, 2017).

To minimise this task impurity problem, a measurement of another influencing construct, e.g. a memory task (known to tap mostly in memory ability) should ideally be incorporated in a battery of inhibitory control tasks. In this way, researchers could compare the performances in the inhibitory control tasks and the memory task to try to disentangle the different constructs involved. In addition, we could incorporate measures of behaviours characteristic of other involved constructs (Cauchoix et al., 2018). For

example, an eye tracker could be used to record the rate of gaze switching direction between stimuli to control for attention. Similarly, the occurrence of facial expression or body scratches could be used to assess the emotional arousal or stress of the subjects. Once the effect of confounding factors is clearer, researchers could focus on a broader approach of inhibitory control looking at the factors influencing its evolution, such as species' social life or ecology.

Another limitation we faced, common when working with primates, is the low sample size which might decrease the power of our analysis and thus lead to unreliable results (Koo & Li, 2016; Paap & Oliver, 2016; Völter et al., 2018). A small sample can prevent a researcher from detecting existing effects or lead to the finding of spurious effects (Many Primates et al., 2019; Shaw & Schmelz, 2017; Völter et al., 2018). A small sample size can also limit the ability to generalise from a sample to the entire population of species (Many Primates et al., 2019). On the contrary, Smith and Little, 2018, argue that a small sample size produces results that are robust and readily replicated if the individual participant is treated as the replication unit. From the literature review of the first chapter of this thesis (see 1.3.2.2), we found a median sample size of 11 animals per inhibitory control studies. Our sample size with 21 subjects seems to be relatively acceptable for inhibitory control studies but to have more reliable results it would be interesting to replicate this study with a larger sample. Unfortunately in animal cognition, researchers are confronted with a limited access to large animal species, often kept in captivity (such as primates and large mammals) and the necessity of the "Reduction" of the number of subjects used in animal research imposed by the Institutional Animal Care and Use Committee. Researchers must then balance between ethical and methodological requirements. One solution to replicate

our study to a larger sample size would be to use, for instance, a large-scale collaborative project across laboratories or field sites (e.g. ManyPrimates et al., 2019a,b).

### Conclusion

To conclude we develop a valid and reliable battery of inhibitory control tasks in one species of macaque. The next step would be to adopt an intra species approach to look in more detail at individual variations in macaque inhibitory control performances and influencing factors explaining these variations. According to a growing number of authors, it is crucial to understand individual variability in a cognitive process to better apprehend its evolution (Boogert et al., 2018; Jelbert et al., 2016; Sauce & Matzel, 2013; Shaw & Schmelz, 2017; Thornton & Lukas, 2012). As Darwin pointed out, individual variations ‘afford materials for natural selection to act on’ (Darwin, 1859). Indeed, investigating individual differences is essential to our comprehension of how natural selection sifts individual differences leading to evolutionary changes (Boogert et al., 2018). Studying individual variation seems to be a compulsory step before being able to look at potential evolutive factors affecting inhibitory control.

## Chapter 3: Individual Differences and Influencing Factors of Inhibitory Control

### 3.1 Overview

We have seen in the first chapter that inhibitory control, the ability to override a dominant response, is crucial in many aspects of everyday life. However, in animal studies, striking individual variations are often largely ignored and their causes rarely considered. Hence, our aims were to use the battery of inhibitory control tasks validated in the previous chapter to systematically investigate individual variability in macaque inhibitory control. Then, we wanted to investigate the most common causes of individual variation (age, sex and rank) and determine if these factors had a consistent effect on three main components of inhibitory control (*inhibition of a distraction*, *inhibition of an action*, *inhibition of a cognitive set*). We tested three species of macaques (28 rhesus macaques, *Macaca mulatta*; 18 Tonkean macaques, *Macaca tonkeana* and 20 long-tailed macaques, *Macaca fascicularis*) using our battery of validated touchscreen tasks. We found individual variation in performance of all inhibitory control components in all species. Then, we found an effect of age and sex on inhibitory control, varying as a function of the task and the species. In rhesus macaques, males were less in control of a distraction and more emotive than females in the *inhibition of a distraction task*, they were also more impulsive in the *inhibition of an action* task. In Tonkean macaques, males persevered more than females in the *inhibition of a cognitive set*. On the contrary, female long-tailed macaques had worse performances in the *inhibition of a distraction* task. In addition, only in rhesus macaques was age associated with an impairment in cognitive performance in the reversal-learning

task. The rank of the subjects did not influence any inhibitory control performance in any species or in any task. Our findings highlight the crucial importance of taking into account individual differences in comparative studies. Basic factors such as sex and age can have a drastic impact on individuals' performances. This study adopts a novel approach for animal behaviour studies and gives new insight into the individual variability of inhibitory control which is crucial to understand its evolutionary underpinnings.

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## 3.2 Introduction

Even though inhibitory control performances may be stable within an individual, confounding factors, frequent in animal cognition, can also influence performances differently across individuals and tasks (Schubiger et al., 2020). It is hardly imaginable to obtain a pure measure of inhibitory control within a single task (Völter et al., 2018). A large proportion of the observed variation may reflect non-cognitive or cognitive individual differences or idiosyncratic task requirements with only a small proportion of the variation actually capturing changes in the studied process (Friedman & Miyake 2017; Gärtner & Strobel 2019; Jelbert et al., 2016; Schubiger et al., 2020; Shaw & Schmelz 2017).

While in human psychometric research, individual differences in cognition have been studied since the early twentieth century (Boogert et al., 2018; Carroll and Maxwell, 1979; Deary et al., 2010; Shaw & Schmelz, 2017), research on non-human animals'

cognition has, until recently, tended to minimize the importance of variation among individuals (Boogert et al., 2018; Shaw & Schmelz, 2017). Performances of individuals are often pooled together implying that the performance of a sample of a population are representative of the whole species (Boogert et al., 2018; Herrmann et al., 2010; Shaw & Schmelz, 2017; Thornton & Lukas, 2012; Völter et al., 2018). Besides, studies often focus on a subset of high-performing individuals to draw conclusions on the presence or absence of a cognitive capacity in a species (Boogert et al., 2018; Thornton & Lukas, 2012). In inhibitory control research, large comparative studies have demonstrated high variability in inhibitory control between species (Amici et al., 2018; Maclean et al., 2014); however, striking individual variations are usually ignored and considered as mere 'noise' around the population mean (Shaw & Schmelz, 2017; Thornton & Lukas, 2012). Nonetheless, over the last decade, researchers have started to focus on intra- and inter-individual variations in cognitive abilities and the factors generating individual differences (for review see Boogert et al., 2018, Shaw and Schmelz, 2017; Thornton & Lukas, 2012; Völter et al. 2018). Increasingly, authors are recognizing that valuable information can be lost when focusing only on group-level performances (Shaw & Schmelz, 2017). Several studies put a great effort in casting light on individual differences in animal cognition (Boogert et al., 2018; Herrmann et al., 2010; Sauce & Matzel, 2013; Thornton & Lukas, 2012); however, only a handful of them have systematically examined individual differences in inhibitory control, and the findings are contradictory. For instance, in guppies (*Poecilia reticulata*), researchers reported individual differences in two measures of *inhibition of action*. In these tasks, subjects needed to inhibit reaching directly for a prey through a transparent glass tube (Lucon-Xiccato et al., 2020a; 2020b; Montalbano et al., 2020) or through a transparent cylinder (Montalbano et al., 2020). Similarly, pheasants (*Phasianus colchicus*)

displayed a great individual variability in a response inhibition task in which the subjects were required to adjust their movement while pursuing a moving target (Meier et al., 2017). Dogs also demonstrated individual differences in common inhibitory control tasks such as the Detour task (Brucks et al., 2017). However, another study in pheasants did not demonstrate a stable individual variation using common detour-reaching tasks (van Horik et al., 2018a,b). Similarly, in a meta-analysis, Völter et al., 2018, re-analysed, from an individual difference perspective, two large comparative studies (Amici et al., 2018 and Maclean et al., 2014). These studies measured the *inhibition of action* (a detour-reaching task) and the *inhibition of a cognitive set* (the A-not-B task in which the subjects are required to inhibit a previously rewarded behaviour to learn a new reward contingency) in several species. From the first study (Maclean et al., 2014), the researchers extracted and re-analysed performances of 15 species, and from the second study, they re-analysed performances of six primate species (Amici et al., 2018). The authors did not find consistent individual differences between these tasks of inhibitory control. To the best of our knowledge, only one study in rhesus macaques demonstrated individual difference in distraction inhibition (using an attentional bias task, a variant of our Distraction task; Howarth et al., 2021). These contradictory findings could indicate a need for a more systematic analysis of individual differences across all the main components of this crucial ability.

Even though some authors put great efforts in studying individual difference in inhibitory control, the causes of these variations are seldom investigated and remain largely unknown (Thornton & Lukas, 2012 ). Yet, recent studies have started to look at the factors influencing inhibitory control variability (Ashton et al., 2018; Johnson-Ulrich &

Holekamp, 2020; Lucon-Xiccato & Bisazza, 2014; Lucon-Xiccato et al., 2020; Thornton & Lukas, 2012; van Horik et al., 2018a). At the time scale of an individual's life, individual variation in inhibitory performances can be influenced by several factors, such as the characteristics of an individual (e.g. age, sex or rank). Inhibitory control develops from early life to adulthood through neurogenesis and experience (Nigg, 2017), and demonstrates a high plasticity (Bedard et al., 2002; Nielson et al., 2002). Cognitive abilities are predicted to improve with experience over an individual's lifetime (for a review see Burkart et al. 2016). For instance, researchers found that in chimpanzees, age had a positive effect on individual performance in a physical cognitive task (a causality task and a repeated spatial memory task; Lacreuse et al., 2014). Similarly, older chimpanzees and bonobos performed better in physical tasks such as locating a reward with changing location (Herrmann et al., 2010). Later in life, inhibitory control abilities get impaired while ageing (Bedard et al., 2002; Nielson et al., 2002). This impairment in performances has been particularly demonstrated in a common task of *inhibition of a cognitive set*, the Reversal learning task (Jelbert et al., 2016). In human research, it has been demonstrated that performances of older people are impaired while switching to a new rule (Fjell et al., 2017; Kramer et al. 1994). This result was also found in older dogs (*Canis familiaris*, older rats (*Rattus norvegicus*, Schoenbaum et al., 2002) or older non-human primates (Bonté, Kemp & Fagot 2014, Itoh et al., 2001, Smeltzer & Teichroeb 2020; Tsuchida, Kubo & Kojima 2002), whereby these animals showed less flexibility in reversing a previously learned rule. The factor age has also an influence in a common measurement of *inhibition of action*, the Go/No-go task, in which subjects need to respond to frequently presented stimuli while withholding prepotent response to infrequently presented non-target. Several studies,

using this task, found that older people were less able to control an impulsive action (Nielson et al., 2002; Kubo-Kawai & Kawai, 2010).

Variation in inhibitory control is also influenced by the sex of the subject. Human studies demonstrated that women outperform men on Go/no-go tasks (in this task subjects need to respond to frequently presented stimuli while withholding prepotent response to infrequently presented non-target; Sjoberg & Cole, 2018; Yuan et al., 2008). In animals, male guppies had worse performances than females in an *inhibition of action* task, the transparent tube task, in which males attempted to attack the prey inside a transparent tube twice as often as females (Lucon-Xiccato et al., 2020). Female guppies were also better at reversing a pre-learned rule (Lucon-Xiccato & Bisazza, 2014). This sex difference is particularly strong in one measurement of *distraction inhibition*, the emotional Stroop task (an emotional pictorial stimulus interferes with the goal of a task; Paul et al., 2005), with men having an attentional bias toward threatening stimuli (Sass et al., 2010; Smith & Waterman, 2005). In animal research, few studies looked at sex differences. For example, Howarth and colleagues (2021), demonstrated a stronger attention toward social stimuli in male rhesus macaques compared to females. However, Boggiani and colleagues (2018), found no sex difference in the distractive effect of a threatening stimulus in capuchins monkeys (*Sapajus apella*).

Finally, the structure of the social environment where an individual interacts is also an important factor influencing variations in cognitive abilities (Dunbar & Shultz, 2007; Humphrey, 1976). The social intelligence hypothesis (Dunbar & Shultz, 2007; Humphrey, 1976), postulates that the demands associated with a complex social life, with differentiated social relationships, generate selection for increased brain size and higher

cognitive performances, such as inhibitory control (e.g. Wascher et al., 2018). In a more complex environment, individuals may tune their social behaviours in relation to the identity of the social partner with whom they interact (Amici et al., 2008, 2009; Aureli & Schino, 2019; Byrne & Bates, 2007; Wascher et al., 2018). Such skills are particularly adaptive in societies where dominance hierarchies determine access to food and mates (Amici et al., 2008; Byrne & Bates, 2007; Menzel & Halperin, 1975). Research on non-human primates suggests that living in social systems, with steeper dominance hierarchies, may be associated with better inhibitory control skills (Amici et al., 2008; 2009). A subordinate individual may frequently inhibit his impulsive behaviours (reaching for food or a mating partner) in the presence of more dominant individuals to avoid conflicts (Amici et al., 2008, 2009, 2018; Byrne & Bates, 2007). Johnson-Ulrich & Holekamp, 2020, have demonstrated that lower ranked hyenas (*Crocuta Crocuta*) living in larger groups have better inhibitory control skills than higher ranked conspecifics in a common task of *inhibition of action*, the Cylinder task (subject needs to inhibit reaching directly for food through the transparent surface of a cylinder). To the best of our knowledge, this rank effect on inhibitory control has only been studied in one study using a Cylinder task (Johnson-Ulrich & Holekamp, 2020) but this social factor could potentially affect all the components of inhibitory control. To summarize, depending on the task, individual's characteristics (age, sex and rank) can have a strong influence on variations of inhibitory control skills, but this hasn't been examined systematically.

Besides, it is still unclear if individual factors such as sex and rank are consistently influencing the different inhibitory processes. For example, if the factor age influences one measure of inhibition of action it should equally influence one measure of inhibition of a

cognitive set if inhibitory control is one common ability. However, the findings are mixed. In dogs, Bray and colleagues (2014), found that age influenced dogs' performances in the Cylinder task but not in the A-not-B task. Contrarily, in the same species, researchers found an effect of age on performances in a modified version of the A-not-B task but not in the original A-not-B task nor in the Cylinder task (Vernouillet et al. 2018). The same study found no effect of the sex for the A-not-B task, but they found a higher score for females in the Cylinder task. Hence, the influence of different factors on the three main components of this ability remains unclear.

Therefore, the aim of this third chapter was threefold: (1) to systematically demonstrate individual variability in the three main components of inhibitory control in three species of macaques, (2) to investigate the most common causes (age, sex and rank) of these individual variations, and (3) to determine if these influencing factors have coherent effects on the three main components of inhibitory control.

We have seen in chapter 1 (see 1.4) that macaques (*Macaca* genus) represent an ideal model to study inhibitory control. Besides, macaques are also an interesting model to investigate in further details factors influencing this ability. These species live in large multi-male multi-female complex social groups (Maestriperi, 2010) characterised by a defined hierarchy (Thierry, 2000). Macaques also present sex differences in social behaviour, anatomy and biology (Kulik et al., 2015; Wallen & Hassett, 2009). Finally, in captivity macaque groups are often composed of infants, adult individuals, and aged individuals (in captivity individuals can live up to 25 years old; Mittermeier et al., 2013). Macaque species are thus an ideal model to study the effect of sex, age and rank on inhibitory control performances. To have a more complete approach of factor influencing

inhibitory control in macaque species we used three macaque species in this chapter: rhesus macaques (*Macaca mulatta*), long-tailed macaques (*Macaca fascicularis*) and Tonkean macaques (*Macaca tonkeana*).

To investigate the factors influencing the main components of inhibitory control (*inhibition of a distraction, of an action and of a cognitive set*) we used the battery of tasks developed in chapter 1. We expected individual variability in the inhibitory control performances for the three tasks and for the three species. We hypothesised that the different factors would all have the same effect in the three species of macaque and consistently on the three main components of inhibitory control. More specifically, we predicted that the females would have better inhibitory control performances than males. We expected that as subjects grow older, they will get more experience and will have better inhibitory performances. Then, as they get in the old age class, they will have an impairment in their performances. Finally, we predicted that lower ranked individuals would have better inhibitory control than higher ranked conspecifics.

### 3.3 General methods

#### 3.3.1 Subjects and housing conditions

We tested three different species: rhesus, long tailed and Tonkean macaques. A total of 66 adult macaques from two different institutions were involved in this study: 21 rhesus macaques were from the breeding colony of the Medical Research Council Centre for Macaques (MRC-CFM) in Porton Down United Kingdom (UK) (the same subjects used in chapter 2, see 2.3.2 for more details about the subjects). Seven rhesus macaques, 20 long-tailed macaques and 18 tonkean macaques were from the Centre of Primatology of the

University of Strasbourg (abbreviated as CPUS), France (FR). In Strasbourg, this study was approved by the Animal Welfare and Ethical Review Body of the CPUS (see Appendix 4).

The rhesus macaques from the CPUS (N = 7 subjects, 5 females and 3 males, aged from 2 to 25 years old) were raised in social groups from 3 to 5 individuals consisting of one dominant male and several females and younglings. They lived in cages, measuring 16.5 to 33 m<sup>2</sup> for the indoor area and 14 to 29 m<sup>2</sup> for the outdoor area. Cages were enriched with climbing devices. Tested subjects were naive to previous behavioural studies and cognitive experiments except two subjects which did touch screen experiments in their youth.

The long-tailed macaques from the CPUS (N = 20, 12 females, 8 males, aged from 7 to 21 years old) were all born in the centre and raised in social groups. The subjects were taken from 8 mixed groups of 2 to 13 individuals with one dominant male and several females and younglings. One group was constituted of only males and one group of only females. They lived in cages, measuring 16.5 to 33 m<sup>2</sup> for the indoor area and 16.5 to 23 m<sup>2</sup> for the outdoor area. Cages were enriched with climbing devices. Tested subjects were naive to any previous clicker training procedures and behavioural studies and experiments.

The Tonkean macaques from the CPUS (N = 18, 6 females, 12 males, aged from 4 to 23 years old) were all born in the centre and raised in social groups. The subjects were taken from two groups. Four subjects tested were from a group of five males. In this group, subjects had free access to an approximately 1364 m<sup>2</sup> wooded outdoor area, connected to a 20m<sup>2</sup> heated indoor area. Tested subjects were familiar with basic training and clicker procedures and they already took part in behavioural studies and experiments. They all had access to touch screen modules when they were young but were never tested with

pictures (see Ballesta et al., 2020). Fourteen subjects were from a group of 21 to 23 individuals. In this group, subjects had free access to an approximately 3700 m<sup>2</sup> wooded outdoor area, connected to a 20m<sup>2</sup> heated indoor area. All subjects have free access to touch screen modules (see Ballesta et al., 2020). They were exposed to pictures of familiar conspecifics, but they have never been tested with pictures of unknown or threatening conspecifics. At the CPUS, all animals were provisioned with commercial monkey pellets seven days a week, in addition to a supply of fresh fruit and vegetables once a week. Water was available ad libitum.

To ensure low stress levels only subjects voluntarily interacting with the experimental setup participated in the study and were free to leave the testing area. They were never isolated from other members of their group. The subjects were not tested in the same week as a veterinary procedure. The subjects had to undergo the same training procedure as the rhesus macaques from the MRC (see chapter 2.3.1) to learn to use the touchscreen (see Appendix 5) which took approximately 2 to 8 weeks depending on the individual. The Tonkean macaques did not spontaneously interact with the touch screen in a new context and needed training. The rank of each individual was calculated using David's scores (see Appendix 18) for rhesus, long tailed and tonkean macaques (from the small group). As in chapter 2, to increase the power of our analysis, the subjects were considered as either high or low ranking. We considered high ranking individuals the two subjects at the top of the hierarchy at the time of the testing (e.g. in mixed groups, the top-ranking male and the top-ranking female). The rank of the individuals from the large group of Tonkean macaques was automatically calculated in real-time using the modules installed in their enclosure (see Ballesta et al., 2020). Ballesta and colleagues (2020),

demonstrated that the calculation of the ranking they developed, using displacements occurring in the modules, was highly correlated with traditional behavioural observations (using agonist interactions as we did).

See Table 3.1 below for a detailed description of the subjects and Figure 3.1 for a visual representation of the ages for the different macaque species.

			rhesus macaques	long-tailed macaques	Tonkean macaques
<b>Total number</b>			28	20	18
<b>Sex</b>		Male	16	8	12
		Female	12	12	6
<b>Age</b>		average	10	13.8	11
		S.D	5.7	2.9	5.6
		Min	2	7	4
		Max	25	21	23
<b>Ranking</b>	High	Male	13	6	5
		Female	8	5	0
	Low	Male	2	2	7
		Female	5	7	6

Table 3.1. Description of the sex, the age and the ranking of the subject rhesus, long-tailed and Tonkean macaques. Average, S.D. (standard deviation), minimum and maximum of the values are given.

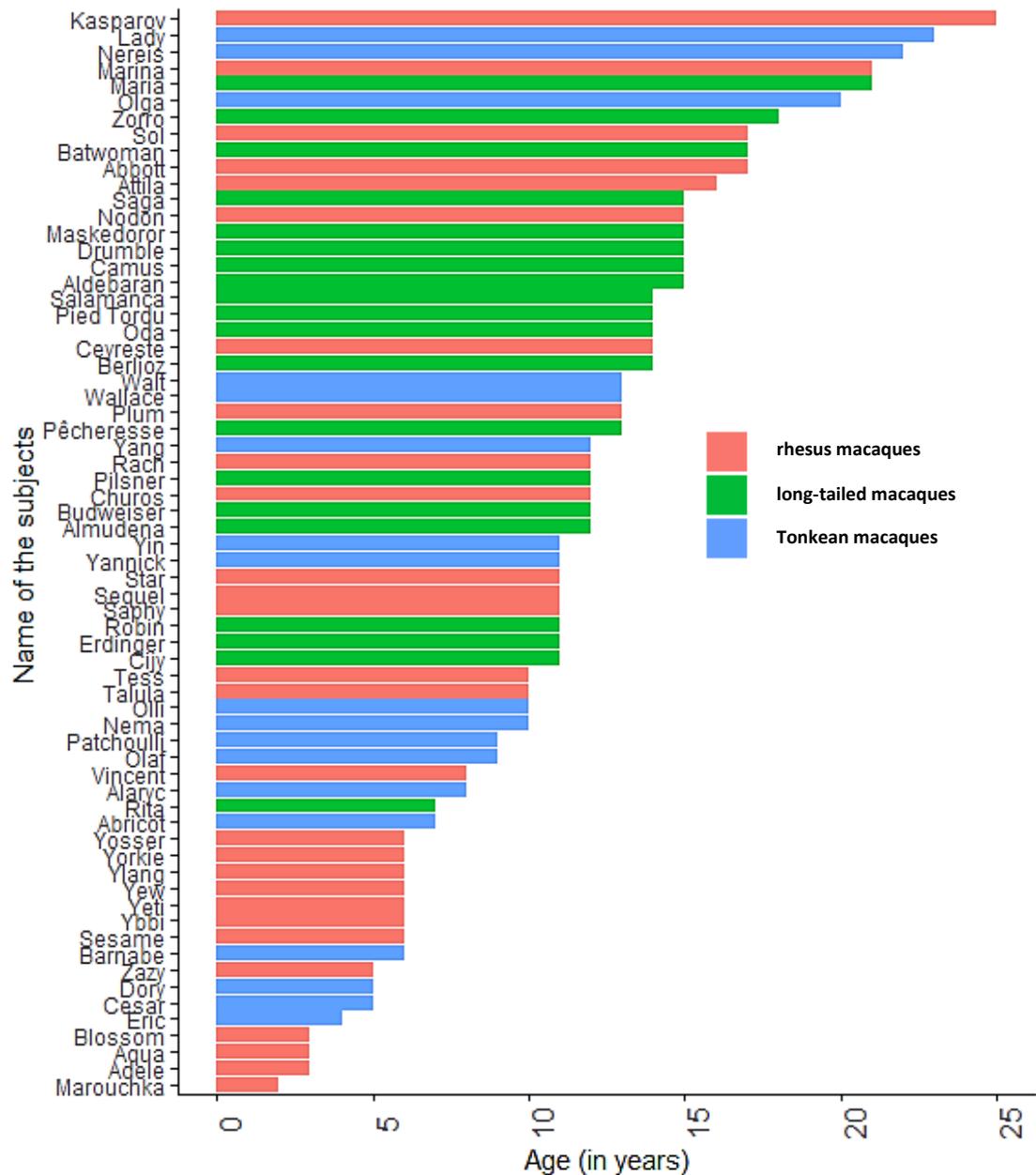


Figure 3.1. Repartition of the age of the subjects for rhesus, long-tailed and Tonkean macaques. The age (in year) is given for each individual.

### 3.3.2 Apparatus and procedures

As before, all tests were conducted in the enclosure, with no isolation from the social group. All species of macaques had free and voluntary access to the apparatus and were never restrained; at any point subjects could leave the experiment and return voluntarily.

We used the same experimental setup and procedures presented in chapter 2.3.3 (except

that the subjects were tested in only one time point). The laptop, touchscreen and camera were transported from one cage to another. The touchscreen was attached to the cage bars and the position was adjusted to each species and to each individual. As before, all experimental procedures were carried out using MATLAB. When more than one individual per cage was tested or when other individuals from the group were interacting with the touch screen, research assistants were distracting the other macaques at the opposite side of the cage. The subject initiated or restarted a session by touching a red cross. The session was paused if the subject exceeded the time limit. The session could also be aborted if the subject was not focusing its attention on the task or if other conspecifics interacted with the touchscreen. The rewards (dry raisins) for each correct answer were given by hand.

### 3.3.3 General analysis

As in chapter 2, to study the relationship between the outcome variables of inhibitory control (see each task for specific outcomes) and the different categories of explanatory variables, we used linear mixed models (LMM, for repeated continuous outcomes) or general linear mixed models (GLMM, for binomial outcomes). We wanted to study the effect of influencing factors on each species of macaque, so we analysed their performances separately. For the individual characteristics, models for each species were fitted with the same variables as before: sex (male or female), age (in years) and rank. To increase the power of our analysis, each macaque was assigned to a social status category (see Appendix 18): i.e. categorised as either low or high ranking. Because of the potential interaction between sex and rank, we decided to analyse the rank effect separately per sex. Due to our limited sample size, we were able to conduct the rank analysis separately only on female rhesus macaques (5 high ranked and 8 low ranked females), long-tailed

macaques (5 high ranked and 7 low ranked females) and only in male Tonkean macaques (5 high ranked and 7 low ranked males). The factor institution was added for rhesus macaques as we tested individuals from two different locations (MRC and CPUS). For the rhesus macaques from the MRC we used the data collected at time point 1 (see Figure 2.2.). The last explanatory variable category was experimental factors to control for habituation and learning: trial number, session number and the type of stimulus depending on the experiment. The random factor of the individual identity remained in all models to account for repeated measures of individuals (see online supplementary materials for the dataset generated during the study).

As in chapter 2 (see 2.6.1), we used LMM and GLMM using the functions ‘lmer’ and ‘glmer’ from the R package ‘lme4’ v. 1.1-21 (Bates et al., 2015). For binomial models' convergence, we used bound optimization by quadratic approximation (BOBYQA) with a set of 100 000 iterations (Powell, 2009). The models were fitted using the maximum-likelihood (ML) function. We used the functions ‘hist’ and ‘qqnorm’ (from the package ‘stats’ v. 3.6.2, R Core Team, 2019) to visually check for the normal distribution of the residuals. For binomial or Poisson distribution, we used the function ‘simulateResiduals’ (from the package ‘DHARMA’, Hartig, 2020). Models were compared by the likelihood ratio test using the function ‘anova’ from the R package ‘car’ v. 3.0-6 (Fox & Weisberg, 2019). Significant effects on the models were considered if the model with the predictor was significantly different from the model without it.

We applied backward reduction to analyse the contribution of each variable on the models (Field et al., 2012). Initially, all explanatory variables and interaction were fitted in the maximal model. Non-significant interaction and terms on the model ( $p > 0.05$ ) were

dropped sequentially in p-value decreasing order to simplify the model. Once an optimum model was obtained with only variables having a significant effect on the model, we compared the effect of each variable by comparing the optimum model and the model without this variable. We presented the model with all the predictors. Our significant threshold was  $p < 0.05$ .

To study individual differences, we used the repeatability estimates (R) which provide a way of assessing individual differences by quantifying the amount of variation explained by inter-individual variation of performances in the tasks relative to intra-individual variation (developed by Nakagawa & Schielzeth, 2010; e.g. used in Cauchoix, 2018; Bethell et al., 2019b; Howarth et al., 2021; Lucon-Xiccato et al., 2019, 2020a,b). We used the function 'rpt', from the 'rptR' package v. 0.9.22 in R (Nakagawa & Schielzeth, 2010; Stoffel et al., 2017). We applied a restricted ML function, and the individual identity was specified as a random intercept effect. We estimated 95% CI with 1000 bootstraps and 1000 permutations. The appropriate type of data distribution was adjusted in each model regarding the dependent variable investigated ('Gaussian', 'Poisson' or 'Binomial'). This function showed whether the individual macaques' performances were significantly repeatable across trials and sessions as expected for individual differences. An individual's performance was considered as repeatable and significant if the p-value from the likelihood ratio test was less than 0.05. We then adjusted the repeatability models with the significant factors obtained from the LMM and GLMM analysis to obtain the adjusted repeatability,  $R_{adj}$ . The adjusted repeatability is an estimate that adjusts for confounding effects by removing fixed effect variance from the estimate (Cauchoix, 2018; Stoffel et al., 2017).

### 3.4 Inhibition of a distraction: Distraction task

We used the same Distraction task than in chapter 2 (see 2.5). As before, we used pictorial stimuli presented at the same time as a target (see Allritz et al., 2016 in chimpanzees and Bethell et al., 2012 with rhesus macaques) to look at the distraction effect (i.e. the effect on the response latency) of each kind of stimulus (an object, a neutral social stimulus and a threatening social stimulus) on the performances of the three species. Several studies have demonstrated that macaques perceive, at first, pictorial stimuli of conspecifics as real individuals. For example, naive rhesus monkeys typically react to pictures of conspecifics with retreat, threat responses and vocalisations (Rosenfeld & Van Hoesen, 1979, Sackett, 1965, for review see Fagot et al. 2010). As in chapter 2, we used 3 categories of stimuli. The category “Object” included the same leather ball, leather bag, brown stone and wooden log as before (Figure 2.4.). For each species, the conspecific pictures were also chosen to be as realistic as possible, depicting a frontal view of the face and the torso of four unknown adult macaques. The “Neutral” conspecific included, for each species, four pictures of individuals with a neutral facial expression (see Figure 3.2. and 3.3.). The “Threatening” conspecific also included for each species, four pictures showing a “open mouth threat” facial expression (see Figure 3.2. and 3.3.). Each subject was tested in 3 sessions of 36 trials.

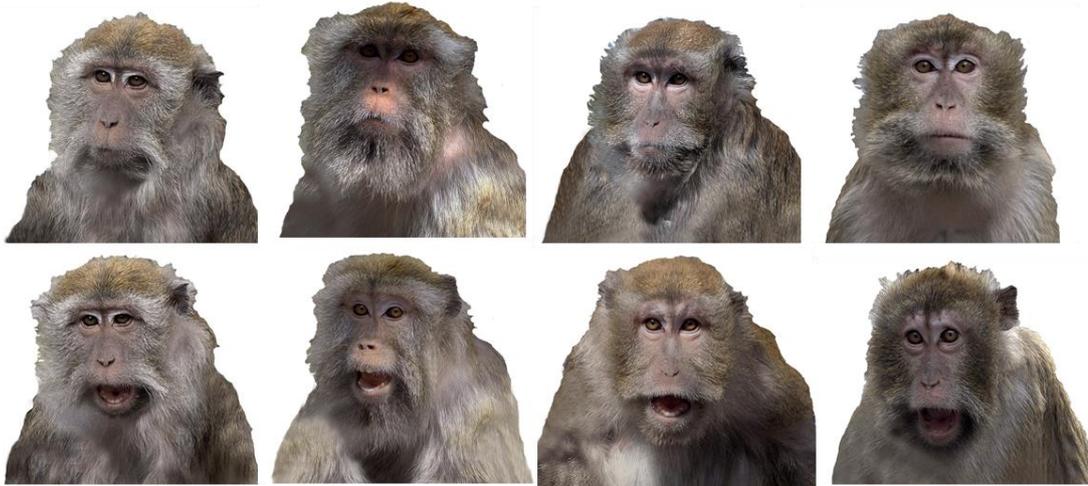


Figure 3.2. Stimuli used in the Distraction task for long-tailed macaques. First row displays neutral unknown faces of conspecifics (“Neutral” trials). The second displays the same conspecifics but with a threatening facial expression (“Threat” trials).

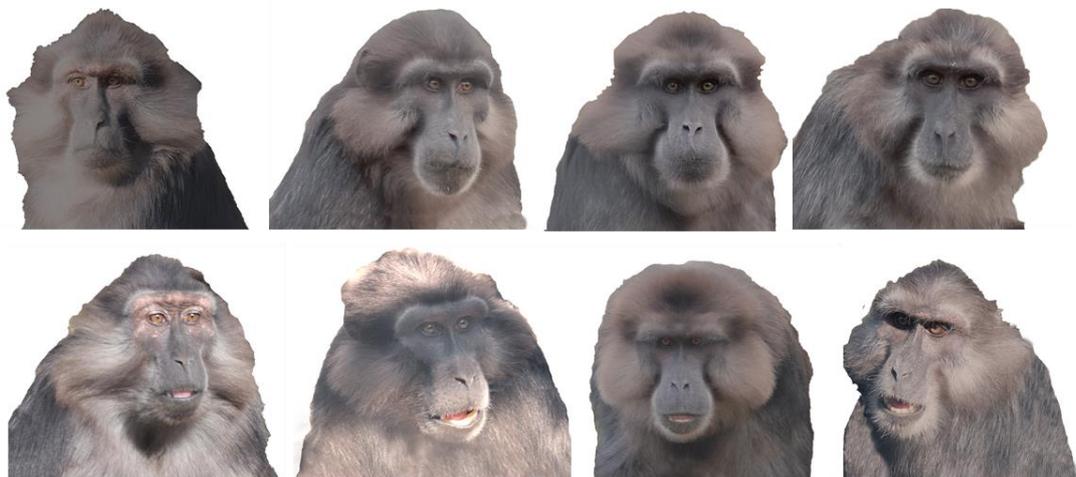


Figure 3.3. Stimuli used in the Distraction task for Tonkean macaques. First row displays neutral unknown faces of conspecifics (“Neutral” trials). The second displays the same conspecifics but with a threatening facial expression (“Threat” trials).

In this task individuals need to inhibit their response to a distraction (pictures of an object, a neutral or threatening conspecific’s face) while performing a task. We hypothesised that in this task, the attentional bias would be stronger in males compared with females (Paul et al., 2005; Sass et al., 2010; Smith & Waterman, 2005). We also hypothesised that low-ranking individuals would be less distracted by the pictures as they are supposed to have better inhibitory control skills (Johnson-Ulrich & Holekamp, 2020). More experienced

individuals will have better control over a distraction (Lacreuse et al., 2014; Hermann et al., 2010) but old individuals will have an impairment in their inhibitory abilities (as in Kabadyi et al., 2018; Bonté et al., 2014, Itoh et al., 2001, Smeltzer & Teichroeb 2020; Tsuchida et al., 2002).

### 3.4.1 Analysis

We analysed the effect of individual and task determinants on performances of inhibition of a distraction in each of the three species of macaque. As done in chapter 2 (see 2.7.1), for the Distraction task, we computed a *Distraction control score*, representing the difference between the mean response latency in “Control” trials for each individual (baseline) minus the response latency in one trial with. A higher score would indicate better control of a distraction, as the subject’s reaction to the stimuli interfered less with the goal of the task. As the distribution of the residuals for the Distraction control score was not satisfyingly following a normal distribution, we applied the following transformation (as advised in Field et al. 2012; Tabachnick et al. 2007 for moderately negatively skewed distribution): *normalised Distraction control score* =

$$\sqrt{(\max(\text{Distraction control score} + 1)) - \text{Distraction control score}}$$

We computed LMMs with normalised Distraction control score as the outcome, demographic (age, sex and institution for the lowest grade) and experimental factors (trial, session and type of picture) as explanatory variables. Type of picture was nested within the individual identity. For rhesus and Tonkean macaques, we also looked at the influence of experience with pictures on their performances on the Distraction task.

We used the function ‘contrasts’ from the package ‘stats’ v.3.6.2 (R Core Team, 2019) to look at the difference between “Control” trials and other trials with the different

types of pictures (“Object”, “Neutral”, and “Threat”). To verify our results we also used the post-hoc test Tukey's Honest Significant Difference test (Tukey HSD test, function ‘glht’, package ‘multcomp’, version 1.4-18, Hothorn, 2008) to analyse the difference between each type of picture (Haynes, 2013). For this, we use the function ‘glht’ from the R package ‘multcomp’ v1.4-13 (Hothorn et al., 2008). We considered an effect to be truly significant only if we found the same result in the linear models and in the post-hoc test. We excluded latencies below 200 ms (time needed for stimulus perception and motor responses to occur; Harald et al., 2010; Whelan, 2008) and above 35 sec (Harald et al., 2010; Whelan, 2008).

Besides, we recorded the number of times each subject totally withheld their response (which can be assimilated as freezing behaviour), reaching the time limit, while still focusing their attention on the screen (Bethell et al., 2019a). We used GLMM with a Poisson distribution and the same explanatory variables as before to look at the effect of these factors (tolerance, sex, age and type of picture) on the number of responses withheld. Finally, we recorded the number of facial expressions displayed by the subjects toward each type of trial (lip-smacking, teeth chattering and bared teeth). Unfortunately we did not have enough data per sex, age and rank to conduct a reliable statistical analysis.

### 3.4.2 Results

In each species, the factor session had a significant effect on subjects’ performances (for rhesus macaques:  $\chi^2_1 = 12.232$ ,  $N = 28$ ,  $p < 0.001$ , for long-tailed macaques:  $\chi^2_1 = 72.995$ ,  $N = 20$ ,  $p < 0.001$ , for Tonkean macaques:  $\chi^2_1 = 12.472$ ,  $N = 18$ ,  $p < 0.001$ ). In all species, individuals were less distracted by the stimuli as they got habituated through sessions (and this decrease started during the second session). We wanted to look at the strongest

distractive effect, so we looked at the macaque's performances at their first session (as in Allritz et al., 2017).

### Distraction control score

#### *Rhesus macaques*

When looking at session 1, the factor institution did not have a significant effect on the rhesus macaques' performances ( $\chi^2_1 = 0.292$ ,  $N = 28$ ,  $p = 0.589$ ) so we pooled all the individuals together. There was a main significant effect of the sex of the subjects on their Distraction control score ( $\chi^2_1 = 5.268$ ,  $N = 21$ ,  $p < 0.05$ , see Table 3.2.), females had a higher distraction control score ( $M = -320.53$  ms,  $S.D. = 5462.56$ ,  $N = 12$ ) than males ( $M = -2302.66$  ms,  $S.D. = 6935.3$ ,  $N = 16$ , see Figure 3.4. for rhesus macaques).

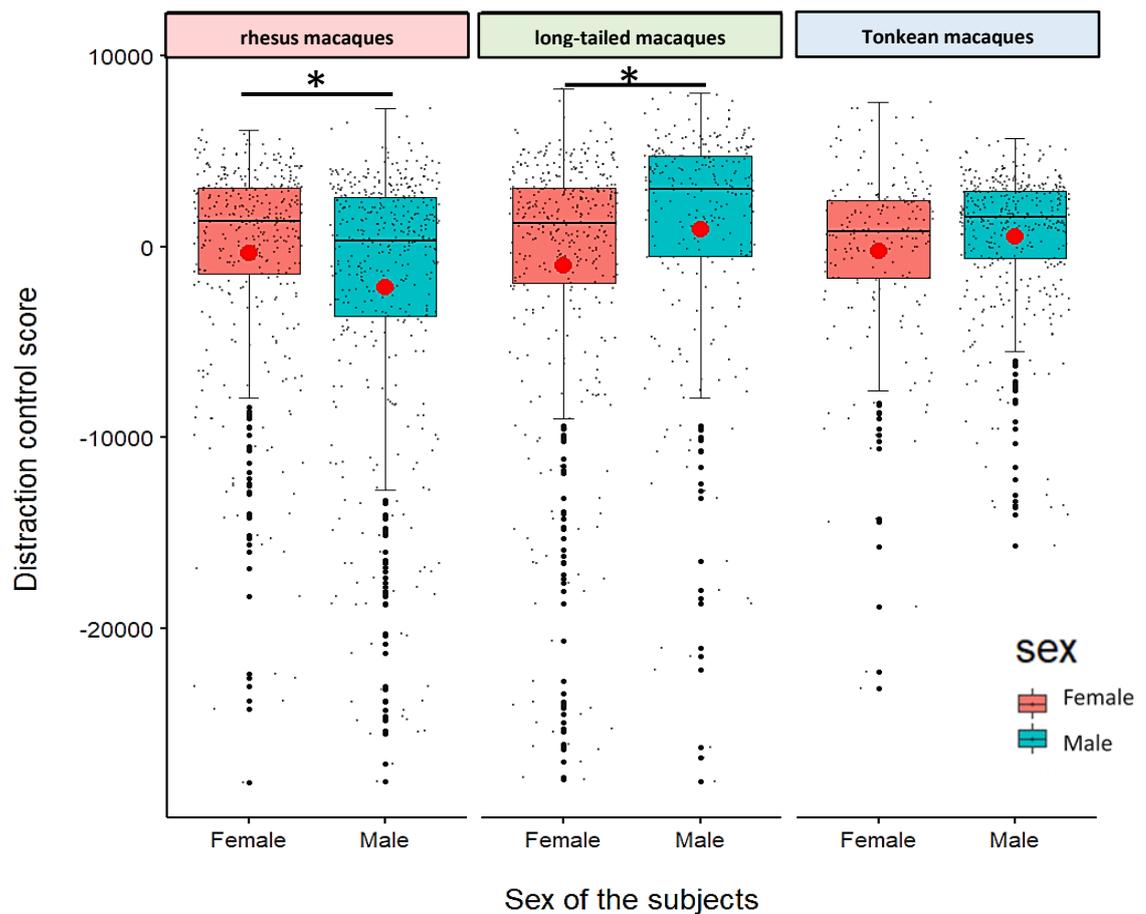


Figure 3.4. Distraction control score (not normalized) between species (low, medium and high tolerance) and sex, for session 1 of the Distraction task. There was a main significant difference between sexes in rhesus and long-tailed macaques. The red dot represents the mean. Horizontal lines represent the 25th, 50th and 75th percentile and error bars are represented. \*  $p < 0.05$  (from the analysis of the models).

The same sex difference was found in both institutions (see Figure 3.5).

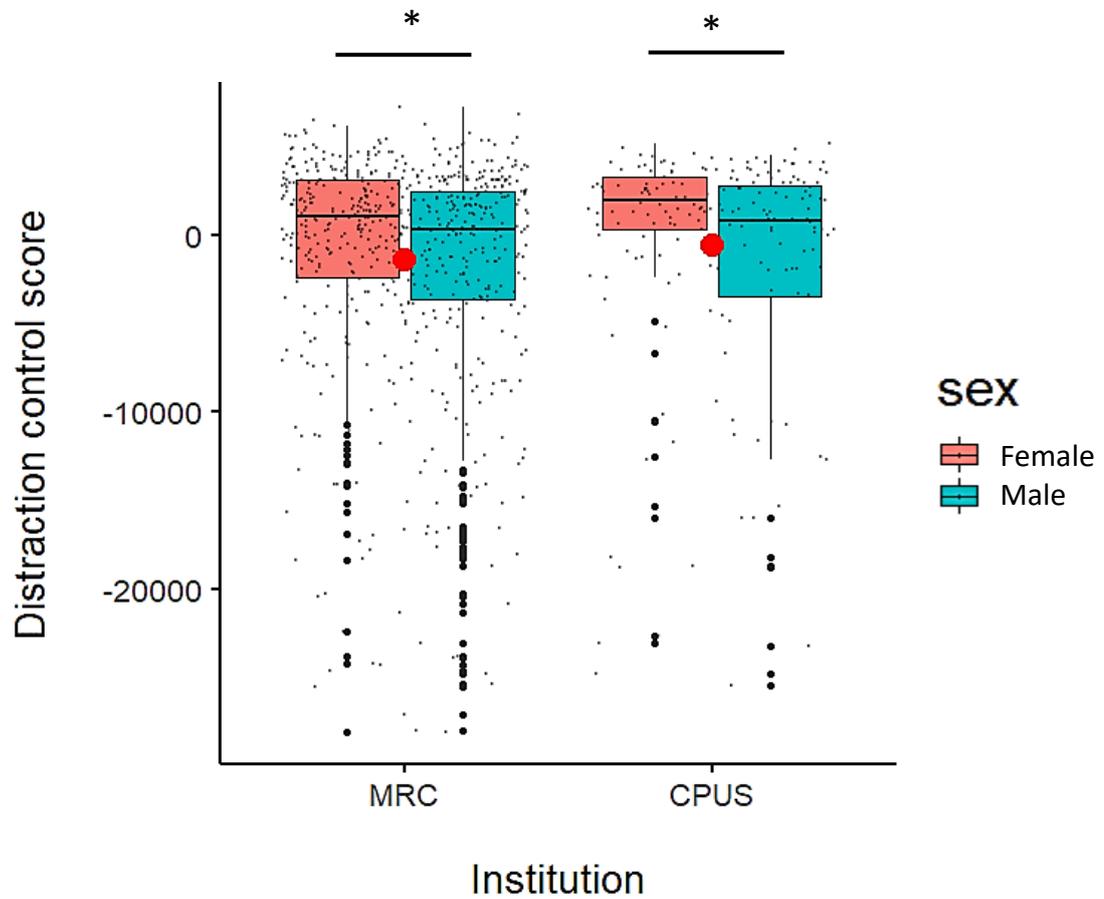


Figure 3.5. Distraction control score between female and male rhesus macaques for session 1 and between two institutions (MRC and CPUS). Males had a lower distraction control score than females, as they were more distracted by pictures. The red dot represents the mean. Horizontal lines represent the 25th, 50th and 75th percentile, and the whiskers extend to 1.5 interquartile range.  $*p < 0.05$  (from the analysis of the models).

This result means that, in general, the pictorial stimuli distracted the females less than males (Table 3.2.).

Predictors		Estimate	Std. Error	t value	Pr(> t )
<b>(Intercept)</b>		91.172	4.239	21.506	0
<b>age</b>		0.212	0.356	0.594	0.558
<b>sex</b>	male vs female	8.041	3.688	2.181	0.039*
<b>type of picture</b>	control vs neutral	-9.990	3.278	-3.047	0.003*
	control vs object	-1.376	2.093	-0.657	0.513
	control vs threat	5.646	2.153	2.623	0.010*
<b>trial</b>		2.860	2.130	1.343	0.183
<b>Experience with pictures</b>		-4.783	4.013	-1.192	0.244
<b>Institution</b>	CPUS vs MRC	-2.534	4.570	-0.555	0.584
<b>ranking in females</b>	high vs low	-0.015	3.125	-0.005	0.996

Table 3.2. Results of the LMM for the normalised distraction control score (Distraction task) for session 1 in rhesus macaques. Explanatory included age, sex, type of picture, trial, institution (Centre of Primatology of the University of Strasbourg or MRC) and ranking (analysis only conducted in females). All full models included the individual ID nested in the type of picture as a random factor. The estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), standard error, t-value and p-value are represented. \*  $p < 0.05$ .

For rhesus macaques, the factor type of picture had a significant effect on the Distraction control score ( $\chi^2_2 = 15.782$ ,  $N = 28$ ,  $P < 0.01$ ). When looking at the LMM result (Table 3.2.), the Distraction control score for the trials with a threatening conspecific face (results are given not normalised here,  $M = -2727.18$  ms,  $S.D. = 8009.51$ ) and with a neutral conspecific face (results are given not normalised here,  $M = -2087.51$  ms,  $S.D. = 6924.78$ ) were lower than Distraction control scores of “Control” trials ( $M = -35.71$  ms,  $S.D. = 4893.36$ ). When looking at results of the Tukey HSD test (Table 3.3.) we found the same results ( see Figure 3.6., for a visual presentation for the rhesus macaques).

Type of picture	Estimates	Std. Error	z value	Pr (> z )
Control - Neutral	-9.990	3.278	-3.048	0.012*
Object - Neutral	-4.231	3.475	-1.218	0.615
Threat - Neutral	2.748	3.547	0.775	0.866
Object - Control	5.759	3.227	1.785	0.2801
Threat - Control	12.738	3.307	3.852	<0.001***
Threat - Object	6.979	3.506	1.990	0.1911

Table 3.3. Result of the Tukey HSD test comparing the normalised Distraction control score in rhesus macaques for session 1, for each type of picture: Control (no picture presented), Neutral (a picture of a neutral conspecific face presented), Threat (a picture of the face of a threatening conspecific is presented), Object (a picture of an object). \*  $p < 0.05$ , \*\*\*  $p < 0.001$

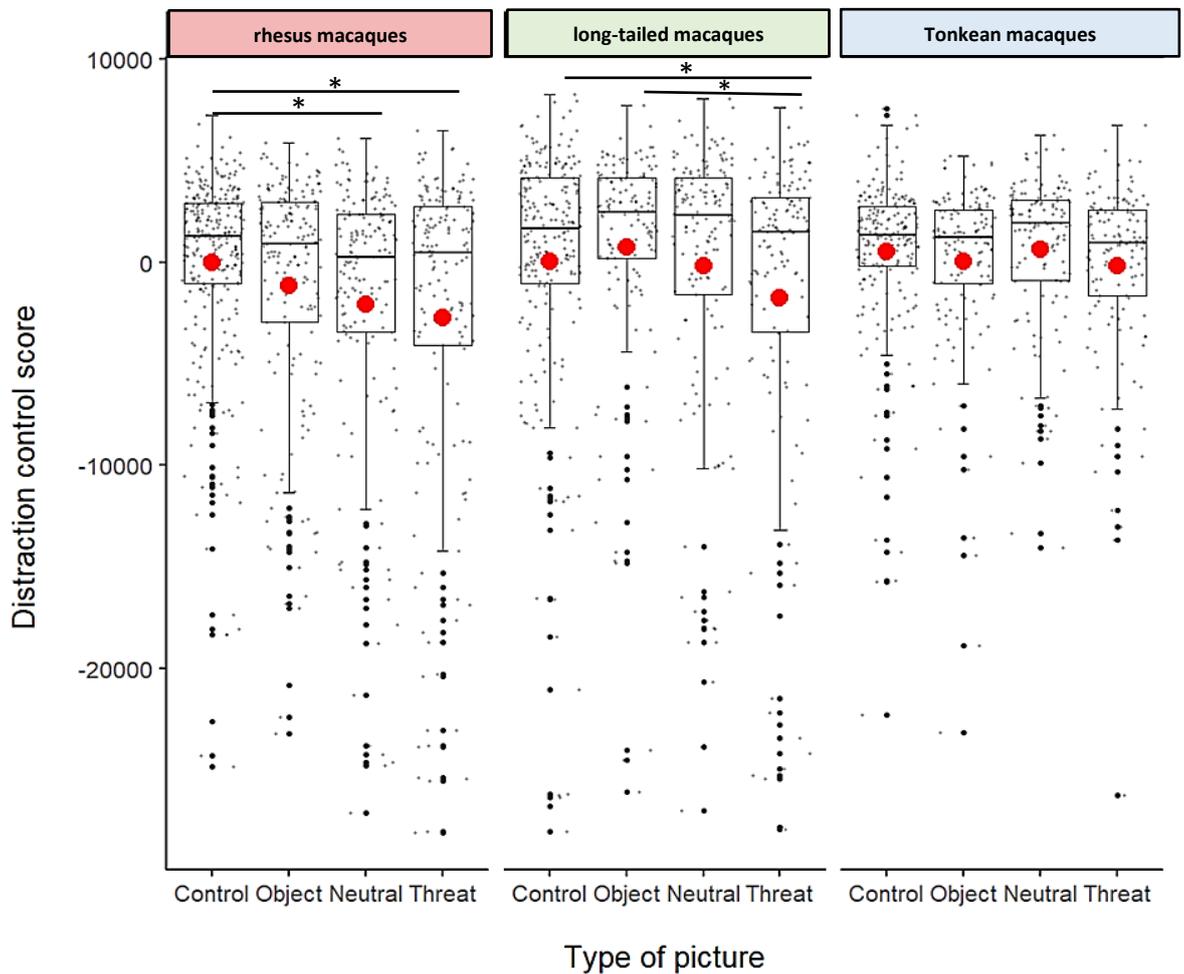


Figure 3.6. Distraction control score in the Distraction task for the session 1 in rhesus, long-tailed and Tonkean macaques for each type of picture (“Control”: no picture, “Object”: picture of an object, “Neutral”: picture of a conspecific neutral face and “Threat”: picture of a conspecific threatening face). In rhesus macaques, the Distraction control score for the “Control” trials was higher than the scores for the “Neutral” and “Threat” trials. In long-tailed macaques, the Distraction control score was higher for the “Object” and “Control” trials compared to the “Threat” trials. In Tonkean macaques, the type of picture did not have a significant effect on the Distraction control score. Red dots represent the mean. Horizontal lines represent the 25th, 50th and 75th percentile and the whiskers represents the error bars. \*  $p < 0.05$  (from the analysis of the models).

The other explanatory factors: age, experience with pictures, trials and institution and ranking (in females) did not have a significant effect on the models (see Table 3.2.).

When looking at each sex separately, from the Tukey HSD test, there was no difference between each types of pictures in female rhesus macaques (see Appendix 19.a). However there was a difference in males (see Figure 3.7. below and Appendix 19.b), with males having a higher distraction score in the “Control” trials (M = - 80.75 ms, S.D. = 5052.49) compared to trials with “Object” trials (M = -2238.07 ms, S.D. = 6572.36), “Neutral” conspecific trials (M = - 3520.99 ms, S.D. = 7587.82) and “Threatening” conspecific trials (M = - 4578.38 ms, S.D. = 8690.98).

Concerning individual differences between individuals, rhesus macaques exhibited significant repeatability of their distraction control score for session 1 ( $R = 0.114$ ,  $CI = [0.041, 0.199]$ ,  $p < 0.001$ ). This result demonstrates an individual variation in their distraction task performances (see visual variation in performances in the Figure 3.6.). When adjusting for the following confounding factors sex and type of picture, the macaques' performances were still repeatable ( $R_{adj} = 0.094$ ,  $CI = [0.031, 0.184]$ ,  $p < 0.0001$ ). This result demonstrates an individual variation in the distraction task performances even when taking into account confounding variables.

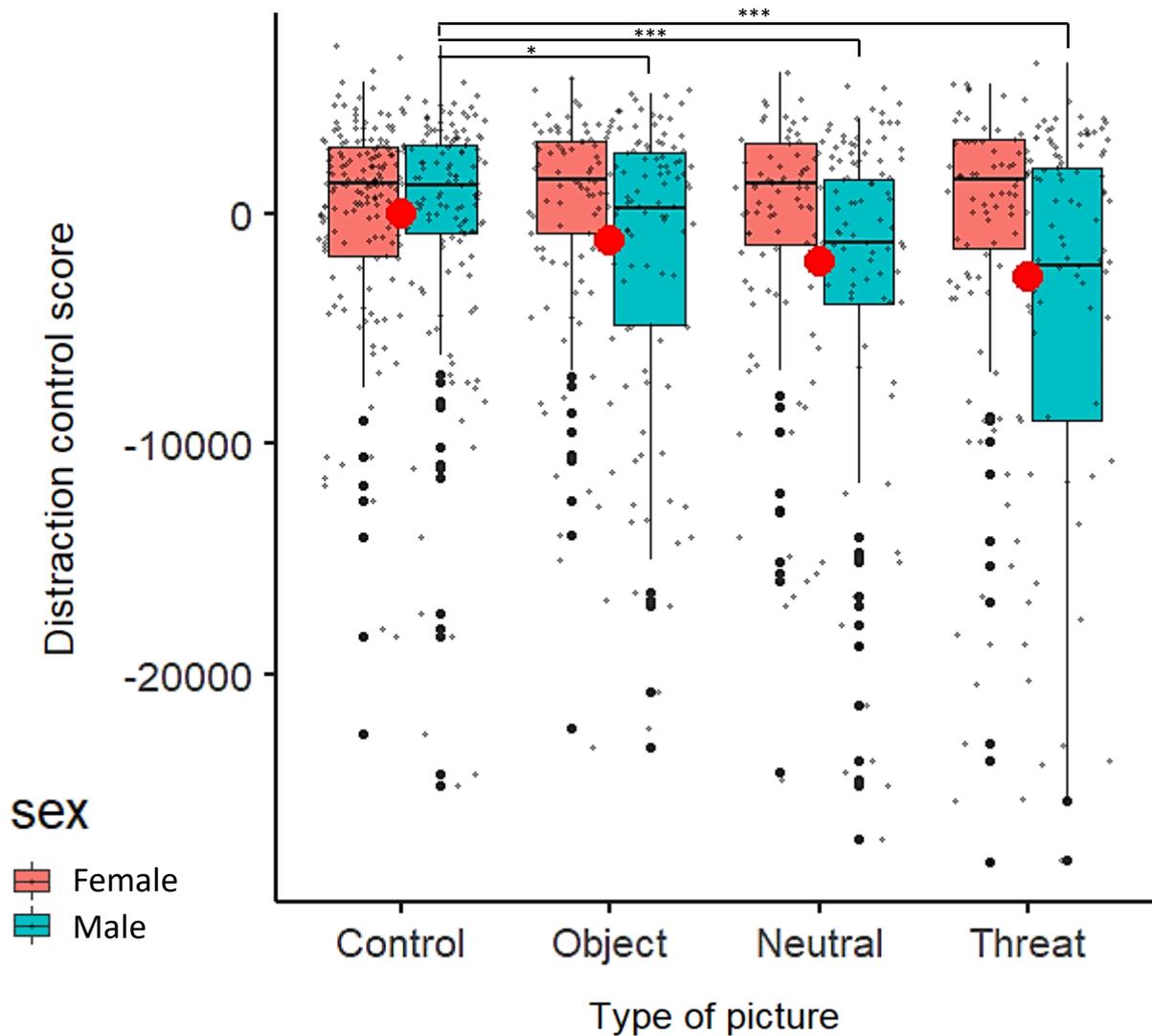


Figure 3.7. Distraction control score in the Distraction task for the session 1 in rhesus macaques for each sex and for each the type of picture (“Control”: no picture, “Object”: picture of an object, “Neutral”: picture of a conspecific neutral face and “Threat”: picture of a conspecific threatening face). Only in males the distraction control score was lower in presence of a conspecific face (neutral and threatening facial expression) or an object compared to the control trials. Red dots represent the mean. Horizontal lines represent the 25th, 50th and 75th percentile and the whiskers represent the error bars. \*  $p < 0.05$ , \*\*\*  $p < 0.001$  (from the analysis of the models).

*Long-tailed macaques*

In long-tailed macaques, when looking at session 1, there was a significant main effect of the sex of the subjects ( $\chi^2_1 = 4.906$ ,  $N = 20$ ,  $p < 0.05$ ), females had a lower distraction control score ( $M = -1004.93$  ms,  $S.D. = 7954.37$ ,  $N = 12$ ) than males ( $M = 886.39$  ms,  $S.D. = 6295.77$ ,  $N = 8$ , see Table 3.4. and Figure 3.4. above). This result means that males were

less distracted by the pictorial stimuli in general and were even faster when a picture was presented.

Predictors		Estimate	Std. Error	t value	Pr(> t )
<b>(Intercept)</b>		95.181	11.727	8.117	0.000
<b>age</b>		-0.055	0.863	-0.064	0.950
<b>sex</b>	male vs female	-10.981	5.101	-2.153	0.044*
<b>type of picture</b>	control vs neutral	-0.911	2.133	-0.427	0.671
	control vs object	-4.235	2.191	-1.932	0.058
	control vs threat	7.132	2.208	3.231	0.002*
<b>trial</b>		-0.104	0.114	-0.911	0.363
<b>ranking in females</b>	high vs low	3.532	1.832	1.928	0.078

Table 3.4. Results of the LMM for the normalized distraction control score (distraction task) for session 1 in long-tailed macaques Explanatory included age, sex, type of picture, trial, institution and ranking (analysis only conducted in females). All full models included the individual ID nested in the type of picture as a random factor. The estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), standard error, t-value and p-value are represented. \*  $p < 0.05$ .

For long-tailed macaques, the factor type of picture had a significant effect on the Distraction control score ( $\chi^2_2 = 10.424$ ,  $N = 20$ ,  $P < 0.05$ , see Figure 3.6.). When looking at the LMM results (Table 3.4.), the Distraction control score for the “Threatening” stimulus ( $M = -1761.12$  ms,  $S.D. = 8104.41$ ) was higher than the Distraction control score (not normalised) for “Control” trials ( $M = 45.57$  ms,  $S.D. = 6409.01$ ). We also found that the Distraction control score for the trials with “Objects” (results are not normalised here,  $M = 746.97$  ms,  $S.D. = 5451.42$ ) were lower than Distraction control scores of trials with pictures of a conspecific’s face ( $M = -934.5$  ms,  $S.D. = 7212.198$ , see Appendix 20). When looking at results of the Tukey HSD test (Table 3.5.), we can also see that the “Threatening”

stimulus had the most distracting effect, with a lower Distraction control score than “Control” trials and “Object” trials.

Type of picture	Estimates	Std. Error	z value	Pr (> z )
Control - Neutral	-1.075	3.236	-0.332	0.987
Object - Neutral	3.323	3.569	-0.931	0.787
Threat - Neutral	8.039	3.592	2.238	0.112
Object - Control	-2.248	3.320	-0.677	0.905
Threat - Control	9.115	3.339	2.730	0.032*
Threat - Object	11.363	3.65	3.109	0.010*

Table 3.5. Result of the Tukey HSD test comparing the normalised Distraction control score in Long-tailed macaques for session 1, for each type of picture: Control (no picture presented), Neutral (a picture of a neutral conspecific face presented), Threat (a picture of the face of a threatening conspecific is presented), Object (a picture of an object). \*  $p < 0.05$

The factors age, trial and rank (in females) did not have an effect on the individual’s performances (see Table 3.4.).

When looking at each sex separately (see Figure 3.8.), from the Tukey HSD test, there was no difference between the different types of pictures in males in long-tailed macaques (see Appendix 21.a). However females had a higher distraction score in the “Control” trials ( $M = -189.7$  ms,  $S.D. = 5602.47$ ) compared to trials with a “Threatening” conspecific ( $M = -3038.87$  ms,  $S.D. = 8955.49$ ; see Figure 3.8. and Appendix 21.b).

Concerning individual differences in long-tailed macaques, there was a significant repeatability of their distraction control score for session 1 ( $R = 0.086$ ,  $CI = [0.033, 0.147]$ ,  $p < 0.001$ ). This result demonstrates an individual variation in their distraction task performances (see visual variation in performances in the Figure 3.6. above). When adjusting for the following confounding factors sex and type of picture, the macaques' performances were still repeatable ( $R_{adj} = 0.078$ ,  $CI = [0.026, 0.139]$ ,  $p < 0.001$ ). This result demonstrates an individual variation in the distraction task performances even when taking into account confounding variables.

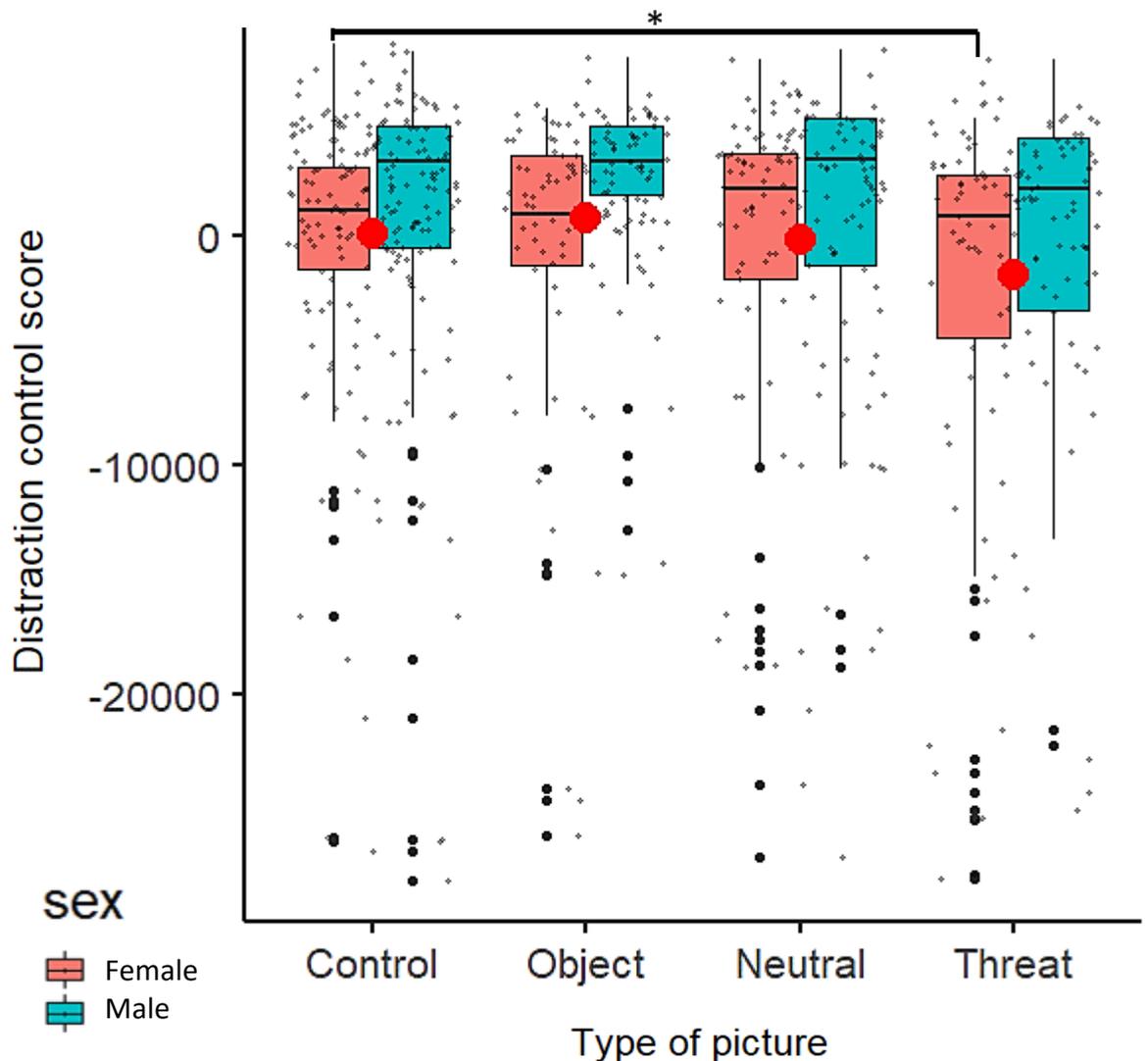


Figure 3.8. Distraction control score in the Distraction task for the session 1 in long-tailed macaques for each sex and each type of picture (“Control”: no picture, “Object”: picture of an object, “Neutral”: picture of a conspecific neutral face and “Threat”: picture of a conspecific threatening face). Only in females the distraction control score was lower in presence of a conspecific threatening face compared to the control trials. Red dots represent the mean. Horizontal lines represent the 25th, 50th and 75th percentile and the whiskers represent the error bars. \*  $p < 0.05$  (from the analysis of the models).

#### Tonkean macaques

In Tonkean macaques, when looking at session 1, there was no significant main effect of any of the explanatory variables (age, sex, type of picture, trial, experience with pictures and ranking) on the Distraction control score (see Table 3.6.).

Predictors		Estimate	Std. Error	t value	Pr(> t )
<b>(Intercept)</b>		84.896	5.987	20.579	14.179
<b>age</b>		-0.068	0.242	18.301	-0.283
<b>sex</b>	male vs female	-2.070	3.010	18.412	-0.688
<b>type of picture</b>	control vs neutral	-1.962	1.597	-1.229	0.224
	control vs object	1.096	1.592	0.688	0.494
	control vs threat	2.254	1.607	1.403	0.166
<b>trial</b>		0.088	0.080	1.098	0.273
<b>Experience with pictures</b>		4.548	2.881	18.046	1.579
<b>ranking in females</b>	high vs low	-0.036	1.261	1357.000	-0.029

Table 3.6. Results of the LMM for the normalized distraction control score (distraction task) for session 1 in Tonkean macaques Explanatory included age, sex, type of picture, trial, institution and ranking (analysis only conducted in females). All full models included the individual ID nested in the type of picture as a random factor. The estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), standard error, t-value and p-value are represented.

When looking at results of the Tukey HSD test (Table 3.7.), we found the same absence of significant effect of any type of picture in the Distraction control score for Tonkean macaques (Figure 3.6.).

Type of picture	Estimates	Std. Error	z value	Pr (> z )
Control - Neutral	0.603	2.451	0.246	0.995
Object - Neutral	3.080	2.623	1.174	0.643
Threat - Neutral	4.206	2.647	1.589	0.384
Object - Control	2.476	2.448	1.011	0.742
Threat - Control	3.603	2.461	1.464	0.459
Threat - Object	1.127	2.638	0.427	0.974

Table 3.7. Result of the Tukey HSD test comparing the normalised Distraction control score in Tonkean macaques for session 1, for each type of picture: Control (no picture presented), Neutral (a picture of a neutral conspecific face presented), Threat (a picture of the face of a threatening conspecific is presented), Object (a picture of an object).

When looking at each sex separately (see Figure 3.9.), from the Tukey HSD test, there was no difference between the different types of pictures in females in Tonkean macaques (see Appendix 22.a). However there was a difference in males (see Figure 3.9. and Appendix 22.b), with males having a lower distraction score in trials with a threatening conspecific ( $M = -568.62$  ms,  $S.D. = 5050.93$ ) compared to trials with a neutral conspecific ( $M = 976.12$  ms,  $S.D. = 3495.62$ ).

Concerning individual differences, Tonkean macaques exhibited significant repeatability of their Distraction control score for session 1 ( $R = 0.034$ ,  $CI = [0.001, 0.079]$ ,  $p < 0.01$ ). This result demonstrates an individual variation in their distraction task performances (see visual variation in performances in the Figure 3.6.). The estimate was not adjusted as there were no confounding factors.

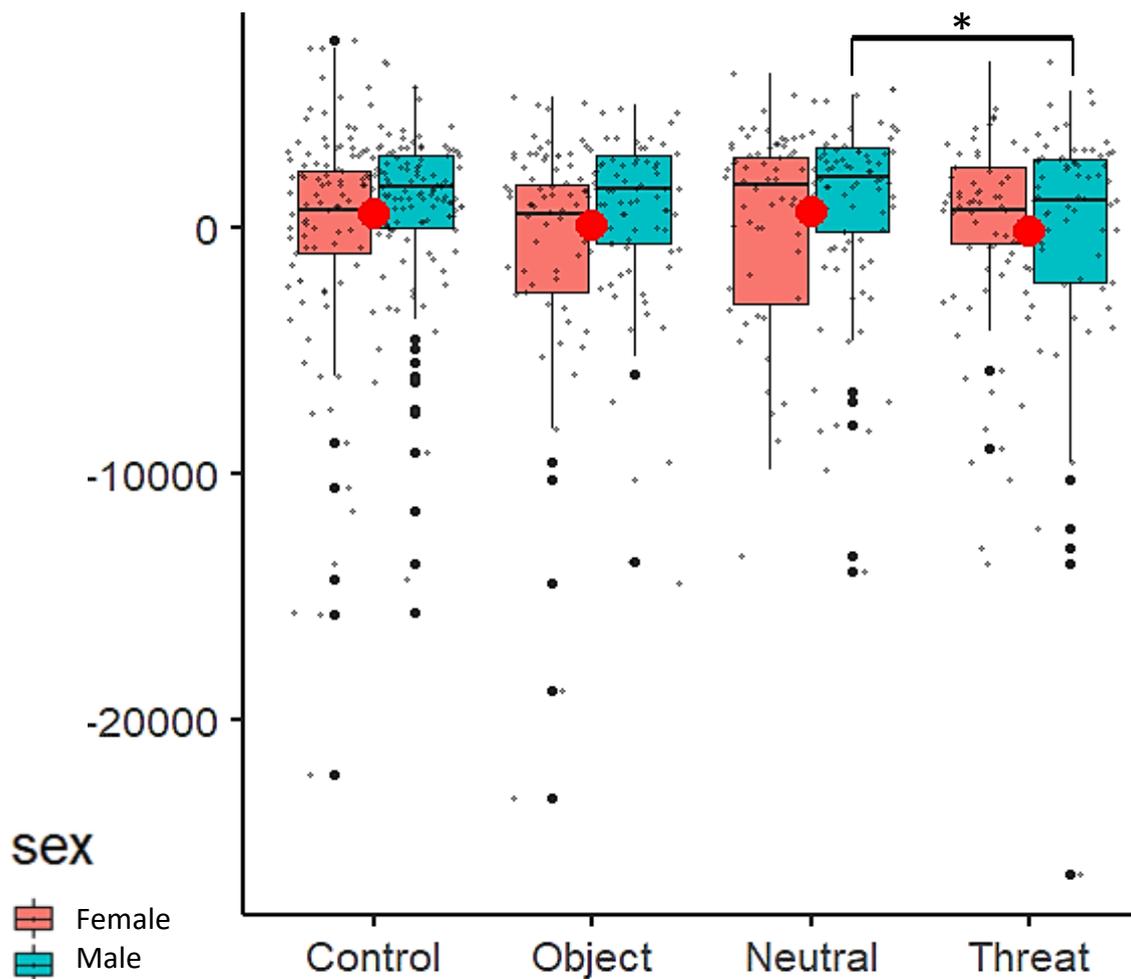


Figure 3.9. Distraction control score in the Distraction task for the session 1 in Tonkean macaques for each sex and for each type of picture (“Control”: no picture, “Object”: picture of an object, “Neutral”: picture of a conspecific neutral face and “Threat”: picture of a conspecific threatening face). Only in males, the distraction control score was lower in presence of a threatening conspecific face compared to a neutral face. Red dots represent the mean. Horizontal lines represent the 25th, 50th and 75th percentile and the whiskers represent the error bars. \*  $p < 0.05$  (from the analysis of the models).

### Response withheld

#### *Rhesus macaques*

From the analysis of the models, we did not find any main significant effect of the age, the sex or the rank (in females) on their number of response withheld in rhesus macaques (see Appendix 23). When looking at the number of responses withheld, individuals exhibited significant repeatability of their number of responses withheld for session 1 ( $R = 0.29$ ,  $CI = [0.092, 0.461]$ ,  $p < 0.001$ ). When adjusting for the type of picture, the macaques'

performances were still repeatable ( $R_{adj} = 0.321$ ,  $CI = [0.118, 0.509]$ ,  $p < 0.001$ ). This result demonstrates an individual variation in the distraction task performances.

#### *Long-tailed macaques*

In Long-tailed macaques, from the analysis of the models we did not find any main significant effect of the age, the sex, type of picture or the ranking (in females) on their number of response withheld (see Appendix 23). When looking at the number of responses withheld, individuals exhibited significant repeatability of their number of responses withheld for session 1 ( $R = 0.448$ ,  $CI = [0.205, 0.645]$ ,  $p < 0.001$ ). There were no confounding factors, so the estimate was not adjusted. This result demonstrates an individual variation in their distraction task performances.

#### *Tonkean macaques*

In Tonkean macaques, from the analysis of the models, we did not find any main significant effect of the age and the sex or the type of picture on their number of response withheld (see Appendix 23). The rank analysis could not be conducted in males, as they did not withhold any responses. When looking at the number of responses withheld, individuals did not exhibit a significant repeatability of their number of responses withheld for session 1 ( $R = 0$ ,  $CI = [0, 0.063]$ ,  $p = 1$ ). This result demonstrates no individual variation in their distraction task performances (no males withheld their response while only 4 females did it).

When looking at each species separately, there was no difference between each type of pictures in the number of response withheld in long-tailed macaques ( $\chi^2_2 = 10.725$ ,  $N = 20$ ,  $P = 0.09$ ) and Tonkean macaques ( $\chi^2_2 = 7.443$ ,  $N = 18$ ,  $P = 0.190$ ). On the contrary rhesus macaques were more distracted by pictures in general (withholding more their responses

compared to “Control” trials;  $\chi^2_2 = 24.019$ ,  $N = 28$ ,  $P < 0.001$ ) and particularly by “Neutral” and “Threatening” stimuli (Table 3.8.).

Type of picture	Estimates	Std. Error	z value	Pr (> z )
Control - Neutral	-1.658	0.545	-3.040	0.0115*
Object - Neutral	-0.264	0.332	-0.796	0.850
Threat - Neutral	0.330	0.287	1.153	0.645
Object - Control	1.394	0.560	2.493	0.057.
Threat - Control	1.989	0.533	3.728	0.001***
Threat - Object	0.595	0.311	1.910	0.212

Table 3.8. Result of the Tukey HSD test comparing the number of response withheld, for each type of picture in rhesus macaques: Control (no picture presented), Neutral (a picture of a neutral conspecific face presented), Threat (a picture of the face of a threatening conspecific is presented), Object (a picture of an object). \*  $p < 0.05$ , \*\*\*  $p < 0.001$

### Emotional reactions

#### Rhesus macaques

Regarding the number of facial expressions produced by rhesus macaques in response to conspecific stimuli, eight macaques (seven males and 1 female) expressed a submissive facial expression ‘bared teeth’ toward the threatening stimulus, five macaques to the neutral stimulus (four males, one female) and none towards the objects or the control stimulus. Four of them have been previously exposed to threatening pictures in the past. Unfortunately we did not have enough data in each category (sex, age and rank) to conduct a reliable statistical analysis.

#### Long-tailed macaques

Regarding the number of facial expressions produced by long-tailed macaques in response to conspecific stimuli, one female expressed a submissive facial expression ‘bared teeth’ toward the threatening stimulus, three macaques to the neutral stimulus (one male, two females) and none towards the objects or the control stimulus. Unfortunately we did not

have enough data in each category (sex, age and rank) to conduct a reliable statistical analysis.

#### *Tonkean macaques*

None of the macaques from Tonkean macaques emotionally reacted to the stimuli, even the individuals that have never been exposed to pictures before.

#### 3.4.3 Discussion

As expected, we found a significant individual variation in the *inhibition of a distraction* for rhesus, long-tailed and Tonkean macaques prior to habituation. In rhesus macaques, the threatening and neutral conspecific were the most distracting type of stimulus. As hypothesised, only in rhesus macaques, we found that males were more distracted by pictorial stimuli than females regardless of the type of pictorial stimulus. In long-tailed macaques, the threatening conspecific was the most distracting stimulus; surprisingly the subjects were faster for a picture of an object. Contrary to what we expected, the long-tailed females were more distracted than the males and particularly for the threatening stimulus. In Tonkean macaques, there was no sex differences, and the pictures had no distracting effect. When looking at each sex separately we found that Tonkean males were more distracted by a threatening face compared to a neutral conspecific. Rhesus macaques' performances were similar in the two institutions, previous experience with pictures did not change performances in rhesus and Tonkean macaques (see Table 3.18. at the end of the chapter for a summary of the results).

We first found individual differences in the performances of *inhibition of a distraction*, even when considering confounding factors. Another study in rhesus macaques demonstrated similar individual differences in distraction inhibition (using an

attention bias task with threatening or neutral conspecifics; Howarth et al., 2021). In this study they found surprisingly similar repeatability estimates in distraction measurements compared to our findings (ranging from 0.12 to 0.26 in Howarth et al., 2021; while our estimates ranged from 0.11 to 0.29). It would be interesting to re-analyse, from an individual difference perspective (as did Völter et al. 2018, for the Cylinder task and the A-not-B tasks), datasets from other studies on the *inhibition of a distraction* (e.g. Allritz et al. 2016). Demonstrating individual differences in a task seems to be a crucial step before considering using this task in further comparative studies.

All species demonstrated better control of their emotional reaction to the stimuli as trials and sessions increased through habituation (as in King et al., 2012; Bethell et al., 2019b). Similarly, a study looking at attentional bias toward threatening stimuli in rhesus macaques demonstrates a decrease in the distracting effect over time (Howarth et al., 2021). In our study, rhesus and long-tailed macaques emotionally reacted to the pictures of conspecifics (freezing behaviour, fear and submissive facial expression). None of the Tonkean macaques appeared to react to the pictures, even the four individuals never exposed to pictures before. Similarly, in other studies, rhesus macaques also reacted at first with vocalisations, threats, and retreats to the first presentation of slides of conspecifics' faces (Rosenfeld & Hoesen, 1979; Sackett, 1965). Pictures of a snake also strongly capture the attention of laboratory-breed Japanese macaques (Shibasaki & Kawai, 2009). However, authors reported that this behaviour did not persist, as macaques realised that the stimuli were only pictures. In their model of picture perception, Fagot et al. (2010) described a first phase of confusion between the picture and reality, but after repeated exposure, the animal could then consider the picture as equivalent to the represented

object or process the picture and the object as independent. It is possible that in our study, rhesus and long-tailed macaques first confused the picture of conspecifics and reality (the subjects only reacted to conspecifics faces not objects); emotionally reacting to them but after repeated exposure to the stimulus, they considered the pictures as either equivalent or independent of the reality. Several studies have demonstrated using eye-tracking technology that non-human primates and particularly macaques process faces similarly than humans (Dahl et al., 2009). It would be interesting to use an eye-tracker to look at the pattern of subject's exploration of their conspecific faces after habituation. As an additional project we tested ten of our tonkean macaque subjects using the Digitrack technology (Lio et al., 2019; see Appendix 24). A blurred image was presented on a touch screen, the subject could explore the image by sliding a finger over the screen to unblurred the desired parts. Lio and colleagues (2019), demonstrated that this method was strongly correlated to eye-tracking methods and provides a proxy for eye movements and attention. The data need to be analysed but the data looks promising as it seems that subjects tended to focus their attention on social stimuli and eye regions (see Appendix 24).

Thirteen of the rhesus macaques in the MRC have been previously exposed to pictorial stimuli (threatening and neutral conspecific's faces, 2 years before this study; Bethell et al., 2019b; Howarth et al., 2021). This previous exposition to picture did not influence the subject's performances. It is possible that their exposition to the picture during these past experiments was too short to go past the confusion phase or that their memory of the picture is limited.

As expected, we found, in rhesus macaques, that males had lower performances in the inhibition of a distraction compared to females. In proportion, males also displayed more frequent emotional responses to the picture than females (8 males out of 14 males reacted to the pictures whereas only two females out of 12 reacted). In Tonkean macaques, this difference was only found when looking at the males separately with a higher distraction provoked by the threatening conspecific face compared to a neutral face. In the literature, better inhibitory control skills in females were also found in the Go/No-go task (Sjoberg & Cole, 2018; Yuan et al., 2008) and in other tasks of inhibition of an action such as the Cylinder task (Montelbano et al., 2020) and the tube task (Lucon-Xiccato, 2020a; Montelbano et al., 2020). Concerning the distraction task, this sex difference was found in human research, with men being more distracted by pictures than women (Sass et al., 2010; Smith & Waterman, 2005). One study in rhesus macaques demonstrated that males had an attentional bias toward social stimuli (neutral and threatening conspecifics' faces) compared to females (Howarth et al., 2021). In rhesus and Tonkean macaques, males and females may face different selective pressures on *inhibition of a distraction*, which can lead to different fitness consequences (Jones et al., 2003; Lucon-Xiccato et al., 2020b; Miletto et al., 2017). For instance, female guppies had better performances at the Reversal-learning task (Lucon-Xiccato & Bisazza, 2014) at the Cylinder task and at the tube task (Lucon-Xiccato et al., 2020). The authors proposed that this sex difference could be explained by a selection in males for high persistence and reduced inhibition in the mating behaviour. Regarding the Distraction task, this attentional bias toward pictorial stimulus in non-human primates could be explained by a higher level of vigilance needed from males at the top of the hierarchy. For instance, Watson et al. 2015, found that rhesus macaque's vigilance, while drinking from a waterhole, was higher in

males compared to females. This difference could be explained by the higher volatility of dominance ranking in male rhesus macaques compared to females (who exhibit inherited dominance ranks; Holekamp & Smale, 1991). Males would need to be more vigilant about others' behaviours to maintain their social ranking. Similarly, a study in marmoset (*Calitrix jacchus*) demonstrated a higher vigilance to the surroundings in males compared to females (Koenig, 1998). Male marmoset had also a particularly elevated emotional reactivity compared to females which affected their attention in a cognitive task (Schubiger et al., 2015). It is thus possible that male non-human primates, predominantly high ranking, need to be more vigilant and reactive to threatening stimuli as they monitor their family group to detect predators and contestants (Koenig, 1998) .

Difference in hormones levels could explain this sex difference in this Distraction task. For instance, in human research, testosterone level was associated in males with a greater attention toward negative social cues (van Honk et al., 1999; Watson et al., 2015; Wirth & Schultheiss, 2007). In animals, male rhesus macaques' testosterone level significantly increased watching time of video clips which depicted fights between unfamiliar conspecifics (Lacreuse et al., 2010). However, the effect of testosterone on attentional bias toward negative stimuli was not found with pictorial stimuli in rhesus macaques (King et al., 2012). In another study, testosterone level was associated with a greater impulsivity in male rats (Bayless et al., 2013) and greater non-contact aggression in rhesus macaques (Barrett et al., 2002). Hence, higher testosterone levels could explain a higher arousal to emotional stimuli in our male subjects. It has also been demonstrated that alpha males have higher level of the cortisol than low-ranking males in rhesus macaques (Higham et al., 2013; Milich et al., 2018), in Japanese macaques (Barrett et al.,

2002) and in baboons (*Papio cynocephalus*; Gesquiere et al., 2011). In humans, researchers have demonstrated a link between anxiety, cortisol level and higher attention to threatening cues (Bradley & Linda, 2007). High glucocorticoid stress-responsiveness was associated with longer response latency and freezing reactions toward “angry” human faces (Roelofs et al., 2007). People with higher anxiety had inhibitory control deficits in the Emotional Stroop task (Richard et al., 1992; Zhang et al., 2019). Conversely, attentional bias for threat may also be a causal factor in the etiology and maintenance of anxiety (Macleod et al., 1986). It is possible that in our sample, males, predominantly alpha males (13 high-ranking individuals out of 15 males), had higher anxiety levels associated with higher cortisol and testosterone levels which made them more emotionally reactive in the Distraction task.

One important factor we did not control for in our study is recent stressful experiences. In chimpanzees (Allritz et al., 2016) or in rhesus macaques (Bethell et al., 2012; Howarth et al., 2021) recent veterinary procedures strongly influence the attentional bias of the subjects toward threatening stimuli. After a stressful experience, chimpanzees were slower to respond when a threatening stimulus was presented (Allritz et al., 2016). However, following a veterinary health check, rhesus macaques showed an initial vigilance toward the threatening stimuli followed by a stronger avoidance (Bethell et al., 2012, 2016). It could be possible some of our subjects that had a recent stressful experience were faster to respond to the target to avoid the threatening stimulus. At the CPUS, rhesus macaques were frequently anaesthetised to collect LCR and blood samples (at least once a month, all the group were collected at the same time) and were supposed to live in a more stressful environment than rhesus macaques from the MRC. However we

found similar performances in both groups in this Distraction task. It would be interesting to include the number of days since a recent stressful experience in our analysis to understand more precisely the effect of stress on subjects' performances.

For the first appearances of the pictures, the threatening stimulus was the most distracting in all the species. This result showed that the emotional content of the picture is important. This attentional bias toward threatening stimuli was similarly found in chimpanzees, using pictures of a veterinarian (Allritz et al., 2016) and in rhesus macaques, using pictures of a threatening conspecific (Bethell et al., 2012; 2016; Howarth et al., 2021). This prioritisation of attention to threat has been proposed as an evolutionary adaptation (Kawai et al., 2016). Our results could then be explained as a survival mechanism as it would be more adaptive to focus more on a threat as it appears. This attentional bias for threatening stimuli may provide a fitness benefit to improve ability to defend against or escape danger (Ohman & Mineka, 2001). Besides, macaques, and particularly males, were making fear-related or submissive facial expressions toward conspecific faces and mainly toward threatening faces. Similarly, emotional response to threatening stimuli on a screen was also found in chimpanzees with an increasing heart rate when pictures of aggressive conspecifics appeared (Boysen & Berntson, 1989), and with changes in skin temperature in viewing emotionally negative videos (Parr, 2001). This emotional reaction could demonstrate that some of our subjects confused the pictures with real individuals, processing them as a threat. It would be interesting to redo the same task but with positive facial expression e.g. lip smack. Indeed, Hopper and colleagues (2021) demonstrated that positive stimuli had the most distracting effect in long-tailed macaques (even more than negative stimuli). Another potential confounding effect that we did not control for is the

identity of the conspecific's faces presented. A study in capuchin monkeys demonstrated that females had an attentional bias toward pictures of female conspecifics over male conspecifics (Schino et al., 2020). However, Howarth and colleagues (2021) did not demonstrate a clear gender bias attention (depending on the sex of the conspecific presented) in rhesus macaques. In another study, crested macaques (*Macaca nigra*), were better at discriminating higher ranking familiar faces (Micheletta et al., 2015). It would be interesting to look at the effect of the sex and the rank of the individual presented on our subjects' performances in this Distraction task.

Surprisingly, contrary to what we found in rhesus and Tonkean macaques, female long-tailed macaques were more distracted than males and particularly by the threatening pictures. Females also emotionally reacted to their conspecific's faces (three long-tailed macaques out of four which reacted were females). A study found similar findings in long-tailed females which were more novelty-averse than male (Montgomery et al., 2005). Compared to the other species, in long-tailed macaques, there was a high proportion of high-ranking females, which could also explain this difference (5 high-ranking females for 6 high-ranking males). Researchers described high-ranking long-tailed females as more emotionally reactive and aggressive than low ranking females (Shively et al., 1995).

It is also possible that the faster response of males toward pictures of objects might have biased this sex difference. It is well established that long-tailed macaques are a species of macaques particularly attracted to new objects. This species uses tools for feeding (e.g. cracking open shells, see Beck, 1980; Gumert et al., 2011, Luncz et al. 2019), hygiene, communication, play, self-directed and self-hygiene behaviour (Mazumder & Kaburu, 2020; Leca et al., 2021; Zuberbühler et al., 1996). Interestingly, researchers

demonstrated that males and females showed differences in the way they chose and manipulated tools (Mazumder & Kaburu, 2020; Gymert et al., 2011). In another study, males were more involved in tool use and manipulated objects more frequently than females (Mazumder & Kaburu, 2020). It is possible that this sex difference in manipulative behaviours have biased the results; the new objects presented could have been particularly interesting for the male long-tailed macaques.

Neither the age of the subjects nor their rank had an effect on their distraction inhibition. In the literature, these factors are rarely considered in primate studies using pictures as distractors (Allritz et al., 2016; Bethell et al., 2012, 2016). One study looked at the effect of age and rank on attentional bias but did not find any significant effect (Howarth et al., 2021). It is possible that the absence of effect could be due to a true absence of influence of these factors on the *inhibition of a distraction*. Is it also probable that a small sample size, reduced the range of age and rank differences between individuals and thus decreased the power of the statistical analysis.

In rhesus macaques, the groups born and bred in two different institutions were similarly strongly emotionally reactive toward pictures. This attentional bias was particularly strong in males in both locations. Is it possible that this pattern of behaviour in rhesus macaques could be generalised to other captive groups around the world. Similarly, in several articles, rhesus macaques living in different environments demonstrated consistent patterns of behaviours such as patterns of impulsivity or aggression (Berman, 1980; Judge & de Waal, 1997; Thierry, 2007). In this sense, Thierry and Iwaniuk (2000) proposed a phylogenetic model regrouping seven constant traits of social behaviours in macaques independently of the environment. These results were

supported by a meta-analysis in nine macaque species living in different conditions (Balasubramaniam et al., 2012). In this study, both steepness and counter aggression showed evidence of phylogenetic signals (Balasubramaniam et al., 2012). It is thus possible that emotional reactivity and impulsivity could be part of a behavioural pattern in rhesus macaques; it would be interesting to test this phylogenetic association in several groups of rhesus macaques across institutions.

### 3.5 Inhibition of an action: Go/No-go task

In the Go/No-go task, as before, the subjects need to respond to frequently presented stimuli while withholding prepotent response to infrequently presented no-go stimuli (Dillon & Pizzagalli, 2007). Each subject was tested in 5 sessions of 40 trials. We predicted that more experienced monkeys, with improved inhibitory control skills, would be better at controlling their impulsive actions (as in Herrmann et al., 2010; Kabadayi et al., 2017, 2018; Lacreuse et al., 2014). Their *inhibition of an action* will then decrease in aged monkeys with the impairment of executive function (Kabadayi et al., 2018; Bonté, Kemp & Fagot 2014, Itoh et al., 2001, Smeltzer & Teichroeb 2020; Tsuchida, Kubo & Kojima 2002). Besides, males will be more impulsive than females, indeed researchers demonstrated that they were less capable of controlling a dominant response (Sjoberg & Cole, 2018; Yuan et al., 2008). Finally, low-ranking individuals, which must frequently inhibit both feeding and aggression in the presence of higher-ranking conspecifics, were predicted to have better inhibitory control skills (Johnson-Ulrich & Holekamp, 2020).

#### 3.5.1 Subjects

The same subjects who completed the distraction task participated in the Go/no-go task except two rhesus macaques who were not willing to continue the experiment.

### 3.5.2 Analysis

We analysed the effect of individual and task determinants on performances of inhibition of an action in each of the three species of macaque. For the second task, the Go/Go-go task, to quantify the individual's ability to inhibit its prepotent action, we recorded the success in a trial when a No-go stimulus was present. A higher probability of success for No-go trial would indicate an individual better at inhibiting an action. As before, we used GLMM models comparison and we controlled for the factors age, sex, trial, session, institution (for rhesus macaques) and ranks. We also used the Wilcoxon test (function 'wilcox.test', package 'stats', version 3.6.2, R Core Team, 2019) to compare species performances to the chance level (> 50 % of probability of success) for the last session.

### 3.5.3 Results

#### *Rhesus macaques*

In rhesus macaques, the institution did not have a significant effect on the probability of success on a No-go trial ( $\chi^2_1 = 2.026$  N = 28,  $p = 0.155$ ), so we pooled all the individuals together. Any of the other factors we controlled influenced this score (age, sex, trial, session and institution, see Table 3.9.). In females, the rank did not have a significant main effect on the probability of success ( $\chi^2_1 = 0.070$  N = 12,  $p = 0.792$ ). When looking at each sex separately, we found that the females only had a better accuracy on a No-go trial over sessions as their accuracy increased with the number of the sessions ( $\chi^2_1 = 4.624$  N = 12,  $p = 0.032$ ).

Predictor	Estimate	Std. Error	z value	Pr(>  t )
<b>(Intercept)</b>	-0.042	0.374	-0.112	0.911
<b>age</b>	-0.003	0.030	-0.100	0.920
<b>sex (males)</b>	0.084	0.325	0.260	0.795
<b>trial</b>	-0.003	0.005	-0.684	0.494
<b>session</b>	0.037	0.043	0.864	0.387
<b>institution (CPUS)</b>	-0.513	0.409	-1.255	0.209
<b>rank (high in females)</b>	0.191	0.724	0.264	0.791

Table 3.9. Results of the GLMM for the accuracy on a No-go trial (Go/No-go task) in rhesus macaques. Explanatory included age, sex, trial, session; institution (Centre of Primatology of the University of Strasbourg vs MRC) and rank (analysis only conducted in females). All full models included the individual ID as a random factor. The estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), standard error, t-value and p-value are represented.

As the individuals increased their performances over sessions, we wanted to see the difference between species at their peak performance, i.e. last session of the task. We found that the rhesus macaques did not have performances above chance level for the last session (Wilcoxon test,  $V = 80.5$ ,  $P = 0.5322$ ,) with a mean performance of ( $M = 0.538$ , S.D. = 0.217).

Concerning individual differences, rhesus macaques exhibited significant repeatability in the Go/No-go accuracy performance ( $R = 0.123$ ,  $CI = [0.052, 0.195]$ ,  $p < 0.0001$ ) on a No-go trial, across trials and sessions. These results mean that there are individual variations in the accuracy and in the response latency in the Go/No-go task. None of the confounding factors had a significant main effect on the probability of success so we did not adjust the R estimates.

#### *Long-tailed macaques*

In long-tailed macaques, we found a significant effect of the number of the session on the proportion of success on a No-go trial ( $\chi^2_1 = 9.061$ ,  $N = 20$ ,  $P < 0.01$ ), with a better accuracy as sessions increase. Any of the other factors we controlled for influenced our subjects'

scores (age, sex and trial Table 3.10.). The rank in females did not have a significant main effect on the probability of success in a No-go trial ( $\chi^2_1 = 2.425$ ,  $N = 12$ ,  $p = 0.119$ ).

Predictor	Estimate	Std. Error	z value	Pr(> t )
<b>(Intercept)</b>	0.372	0.590	0.630	0.529
<b>age</b>	-0.005	0.042	-0.108	0.914
<b>sex (males)</b>	-0.100	0.247	-0.406	0.685
<b>session</b>	0.144	0.048	3.009	0.003
<b>trial</b>	-0.008	0.006	-1.325	0.185
<b>rank (high in females)</b>	-0.456	0.280	-1.629	0.103

Table 3.10. Results of the GLMM for the accuracy on a No-go trial (Go/No-go task) in Long-tailed macaques. Explanatory included age, sex, session, trial and rank (analysis only conducted in females). All full models included the individual ID as a random factor. The estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), standard error, z-value and p-value are represented.

At the last session, long-tailed macaques had performances above chance level (Wilcoxon test,  $V = 179.5$ ,  $P < 0.001$ ) with a mean performance of ( $M = 0.725$ ,  $S.D. = 0.180$ ).

Concerning individual differences, long-tailed macaques exhibited significant repeatability in the Go/N-go accuracy performance ( $R = 0.036$ ,  $CI = [0.005, 0.077]$ ,  $p < 0.0001$ ) on a No-go trial, across trials and sessions. Session had a significant main effect on the probability of success, so we used this factor to adjust the estimate which remained significant ( $R_{adj} = 0.035$ ,  $CI = [0.005, 0.067]$ ,  $p < 0.001$ ). These results mean that there are individual variations in the accuracy in the Go/No-go task.

#### *Tonkean macaques*

In Tonkean macaques, none of the factors we controlled for influenced the inhibition of action of our subjects (age, sex, session and trial, see Table 3.11.). We found a significant effect of the number of the session on the proportion of success on a No-go trial ( $\chi^2_1 = 15.297$ ,  $N = 18$ ,  $P < 0.001$ ), with a higher accuracy as the number of the session increased. Males' rank did not have a significant main effect on the probability of success ( $\chi^2_1 = 2.425$ ,  $N = 12$ ,  $p = 0.798$ ).

Predictor	Estimate	Std. Error	z value	Pr(>  t )
<b>(Intercept)</b>	0.032	0.616	0.052	0.959
<b>age</b>	-0.029	0.034	-0.854	0.393
<b>sex (males)</b>	-0.273	0.394	-0.693	0.488
<b>session</b>	0.197	0.051	3.857	0.000
<b>trial</b>	0.008	0.006	1.368	0.171
<b>rank (high in females)</b>	0.125	0.492	0.256	0.798

Table 3.11. Results of the GLMM for the accuracy on a No-go trial (Go/No-go task) in Tonkean macaques. Explanatory included age, sex session, trial and rank (analysis only conducted in males). All full models included the individual ID as a random factor. The estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), standard error, z-value and p-value are represented.

At the last session, Tonkean macaques had performances above chance level (Wilcoxon test,  $V = 134.5$ ,  $P < 0.01$ ) with a mean performance of ( $M = 0.667$ ,  $S.D. = 0.206$ ).

Concerning individual differences, Tonkean macaques exhibited significant repeatability in their accuracy on a No-go trial ( $R = 0.077$ ,  $CI = [0.022, 0.14]$ ,  $p < 0.0001$ ) across trials and sessions. Session had a significant main effect on the probability of success, so we used this factor to adjust the estimate ( $R_{adj} = 0.081$ ,  $CI = [0.023, 0.136]$ ,  $p < 0.0001$ ). These results mean that there are individual variations in the accuracy and in the response latency in the Go/No-go task.

#### 3.5.4 Discussion

As expected, we found a significant individual variation in the *inhibition of an action* in all three species of macaques. Tonkean and long-tailed macaques increase their performances through sessions and had performances above chance level in the last session. Only female rhesus macaques learned through sessions. There was no difference in age, sex or institution (for rhesus macaques; see Table 3.18. at the end of the chapter for a summary of the results).

We first found that macaques exhibit strong individual variations in inhibiting an impulsive action in their accuracy on a No-go trial. For instance, in the last session, three rhesus macaques were above 80% of success (i.e. not touching the no-go stimulus significantly above chance) and 5 below 50% of success. If the task was too easy for all the individuals, we would not have detected variation in individual accuracy. These results demonstrate the importance of designing a task difficult enough to reveal differences between individuals (a signature limit of performances, Völter et al., 2018).

As expected, long-tailed and Tonkean macaques learned through sessions and performances above chance level in this reward association task. Similar studies demonstrated advanced cognitive abilities in macaque species tested in their understanding of spatial, numeral and causal relations (Amici et al., 2010; Schmitt et al., 2012). Surprisingly, only females in rhesus macaques learned through sessions. This sex difference could be found in the way subjects learn to respond to the task, with females learning how to inhibit their action more efficiently over time. Human studies demonstrated that women outperform men on No-go trials, indicating greater inhibition (Sjoberg & Cole, 2018; Yuan et al., 2008). However, other human studies found no sex difference in the performances in the Go/No-Go task, but interestingly; they found differences in the pattern of regional brain activation (Li et al., 2009). It is possible that in our study a difference in brain activation could explain the better performance in females, which could be verified, for instance, by a PET-scan. Similarly, a study in guppies also demonstrated sex differences in tasks of *inhibition of action*: the Cylinder and the tube task (Lucon-Xiccato et al., 2020a,b), with a similar sample of 14 females and 14 males. Authors suggested that this sex difference in guppies might be due to a specific mating system,

with a reduced behavioural inhibition in males (Lucon-Xiccato et al., 2020b). In the literature, sex difference in spatial cognition have been also described in rhesus macaques, with females having either better (Herman et al., 2007) or worse performance than males (Lacreuse et al., 2005). However, to the best of our knowledge, we did not find any research on sex differences in a more general form of cognition. In addition, a study in marmoset (*Calitrix jacchus*) demonstrated that males had a particularly elevated emotional reactivity compared to females which affected their attention in a cognitive task (Schubiger et al., 2015). Similarly, in another study in marmosets, males were more attentive to their surroundings than the test apparatus in front of them compared to females (Koenig, 1998). It is possible that in our study male rhesus macaques were more impulsive and were less focused on the task which made the learning of the Go/No-go task more difficult for them.

Contrary to our results, some studies found that more experienced primates were better at several cognitive tasks (Herrmann et al., 2010; Lacreuse et al., 2014). Unfortunately, to the best of our knowledge, the factor age has not been analysed for the Go/No-go task in the animal literature. An explanation for our absence of age difference could be that the simple variant of the task we chose was too difficult for the more experienced individual to show cognitive improvement. The small sample size in our study compared with sample size in human research can also be an explanatory factor for this lack of age effect.

Unfortunately, to the best of our knowledge, the effects of the rank were not investigated on the Go/No-go task. Researchers only investigated it in spotted hyenas in the Cylinder task (Johnson-Ulrich & Holekamp, 2020). We would potentially need to

increase the sample size to reveal this rank effect, or it might also be specific to the Cylinder task.

In rhesus macaques, there was no difference in the *inhibition of an action* between institutions, groups in both locations had bad performances (as seen in the Distraction task, in the paragraph 2.3.3). This consistency in performances could be due to a consistent pattern of impulsivity in rhesus macaques in general (Balasubramaniam et al., 2012; Berman, 1980; Judge & de Waal, 1997; Thierry, 2007). It would be interesting to test other rhesus macaques in other institutions to confirm this phylogenetic association.

### 3.6 Inhibition of a cognitive set: Reversal-learning task

For the Reversal-learning task, individuals were required to inhibit a response that was previously successful. As before, the subjects were tested in sessions of 40 trials until they reached the criterion of success (75% of success over 20 trials). We expected that females would be better at this task as demonstrated in a study in guppies using the Reversal learning task (Lucon-Xiccato & Bisazza, 2014). We also hypothesised that adult subjects will be better at reversing a rule as they have better cognitive capabilities (Herrmann et al., 2010; Lacreuse et al., 2014) and will make less perseverative errors (i.e. the repetition of a response toward the wrong stimulus even if the reward-stimulus contingency has changed). However, we expected that aged individuals will have an impairment in their *inhibition of cognitive set* performances (Bonté, Kemp & Fagot 2014, Itoh et al., 2001, Smeltzer & Teichroeb 2020; Tsuchida, Kubo & Kojima 2002). We finally hypothesised that low-ranking individuals would be more efficient in this task as they are supposed to have better inhibitory control skills (Johnson-Ulrich & Holekamp, 2020).

### 3.6.1 Subjects

The same subjects that completed the Go/No-go task participated in the Reversal-learning task. One individual from the rhesus macaques never learnt the acquisition rule and one individual from the long-tailed macaques never learnt the reversed rule.

### 3.6.2 Analysis

We analysed the effect of individual and task determinants on performances of *inhibition of a cognitive set* in each of the three species of macaque. As a measurement of inhibitory control, we recorded a number of trials to learn the rules. We also recorded the number of perseverative errors (number of taps when the wrong stimulus is displayed). To approach a normal distribution of the residuals the number of perseverative errors were log transformed (Tabachnick et al., 2007). As before, we compared LMM and we controlled for the factors age, sex, rank, institution (in rhesus macaques) session and rule (acquisition or reversed rule). Individual identity was included as a random factor.

### 3.6.3 Results

#### **Number of trials to learn the rules**

##### *Rhesus macaques*

In rhesus macaques, the factor age had a main significant effect on the number of trials to learn the rule ( $\chi^2_1 = 5.099$ ,  $N = 28$ ,  $p < 0.05$ ) with a higher number of trials as the subjects get older (see Table 3.12. and Figure 3.10.). The factor institution did have a significant main effect on the number of trials to learn a rule in rhesus macaques ( $\chi^2_1 = 5.099$ ,  $N = 28$ ,  $p = 0.024$ , when comparing the model with age and institution and the model with age only). However when the model with the factor institution was compared to the null model there was no significant effect ( $\chi^2_1 = 01.878$ ,  $N = 28$ ,  $p = 0.171$ ). It is probable that the factor

age and institution interacted. So we did the same analysis with only individuals from the MRC and we found the same effect of age ( $\chi^2_1 = 5.923$ ,  $N = 21$ ,  $p < 0.05$ ). Including or excluding the 7 rhesus macaques from the CPUS did not change the results so we kept them in the analysis. The individuals needed as many trials to learn the reversed rule compared to the acquisition rule ( $\chi^2_1 = 1.088$ ,  $N = 28$ ,  $P = 0.267$ ).

Predictors	Estimate	Std. Error	t value	Pr(> t )
<b>(Intercept)</b>	75.979	25.187	3.017	0.004
<b>age</b>	5.092	2.105	2.419	0.019*
<b>sex (male)</b>	-6.499	23.159	-0.281	0.780
<b>rule (reversed)</b>	-23.879	22.291	-1.071	0.289
<b>Institution (CPUS)</b>	67.072	28.551	-2.349	0.023*
<b>Rank (high ranking) in females</b>	27.857	49.785	0.560	0.581

Table 3.12. Results of the LMM for the number of trials to learn the rules (Reversal learning task) in rhesus macaques. Explanatory variables included age, sex, rule (reversed versus acquisition rule), location (Centre of Primatology of the University of Strasbourg vs MRC) and rank (analysis only conducted in females). All full models included the individual ID as a random factor. The estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), standard error, t-value and p-value are represented.

In females, rank did not have a significant main effect on the number of trials to learn a rule ( $\chi^2_1 = 0.885$ ,  $N = 28$ ,  $p = 0.347$ ).

As this score was only composed of two data points per individual (one for each rule) we could not run a repeatability analysis.

#### Long-tailed macaques

In long-tailed macaques, we looked at the number of trials to learn the acquisition rule compared to the reversed rule. Individuals needed more trials to learn the reversed rule compared to the acquisition rule ( $\chi^2_1 = 4.2036$ ,  $N = 18$ ,  $P < 0.05$ ). The factor age and sex did not have a significant effect on the models (see Table 3.13., Figure 3.10.). In females,

rank did not have a significant main effect on the number of trials needed to learn a rule ( $\chi^2_1 = 1.232$ ,  $N = 20$ ,  $p = 0.267$ ).

Predictors	Estimate	Std. Error	t value	Pr(> t )
<b>(Intercept)</b>	52.382	46.200	1.134	0.270
<b>age</b>	1.042	3.407	0.306	0.763
<b>sex (male)</b>	-21.920	20.465	-1.071	0.296
<b>rule (reversed)</b>	34.972	16.466	2.124	0.046*
<b>Rank (high ranking) in females</b>	-29.00	25.464	-1.139	0.277

Table 3.13. Results of the LMM for the number of trials to learn the rules (Reversal learning task) in Long-tailed macaques. Explanatory variables included age, sex, rule (reversed versus acquisition rule) and rank (analysis only conducted in females). All full models included the individual ID as a random factor. The estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), standard error, t-value and p-value are represented.

#### Tonkean macaques

Tonkean macaques needed more trials to learn the reversed rule compared to the acquisition rule ( $\chi^2_1 = 10.238$ ,  $N = 18$ ,  $P < 0.01$ ). The factors age and sex did not have a significant effect on the models (see Table 3.14., Figure 3.10.). In males, rank did not have a significant main effect on the number of trials to learn a rule ( $\chi^2_1 = 0.028$ ,  $N = 18$ ,  $p = 0.967$ ).

Predictors	Estimate	Std. Error	t value	Pr(> t )
<b>(Intercept)</b>	50.594	43.572	35.579	1.161
<b>age</b>	-0.735	2.457	35.441	-0.299
<b>Sex (male)</b>	-3.761	28.445	35.441	-0.132
<b>rule (reversed)</b>	77.778	22.573	3.446	0.001*
<b>Rank (high ranking) in females</b>	-6.745	40.404	-0.167	0.869

Table 3.14. Results of the GLMM for the accuracy on a No-go trial (Go/No-go task) in Tonkean macaques. Explanatory included age, sex, rule (reversed versus acquisition rule) and rank (analysis only conducted in males). All full models included the individual ID as a random factor. The estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), standard error, t-value and p-value are represented.

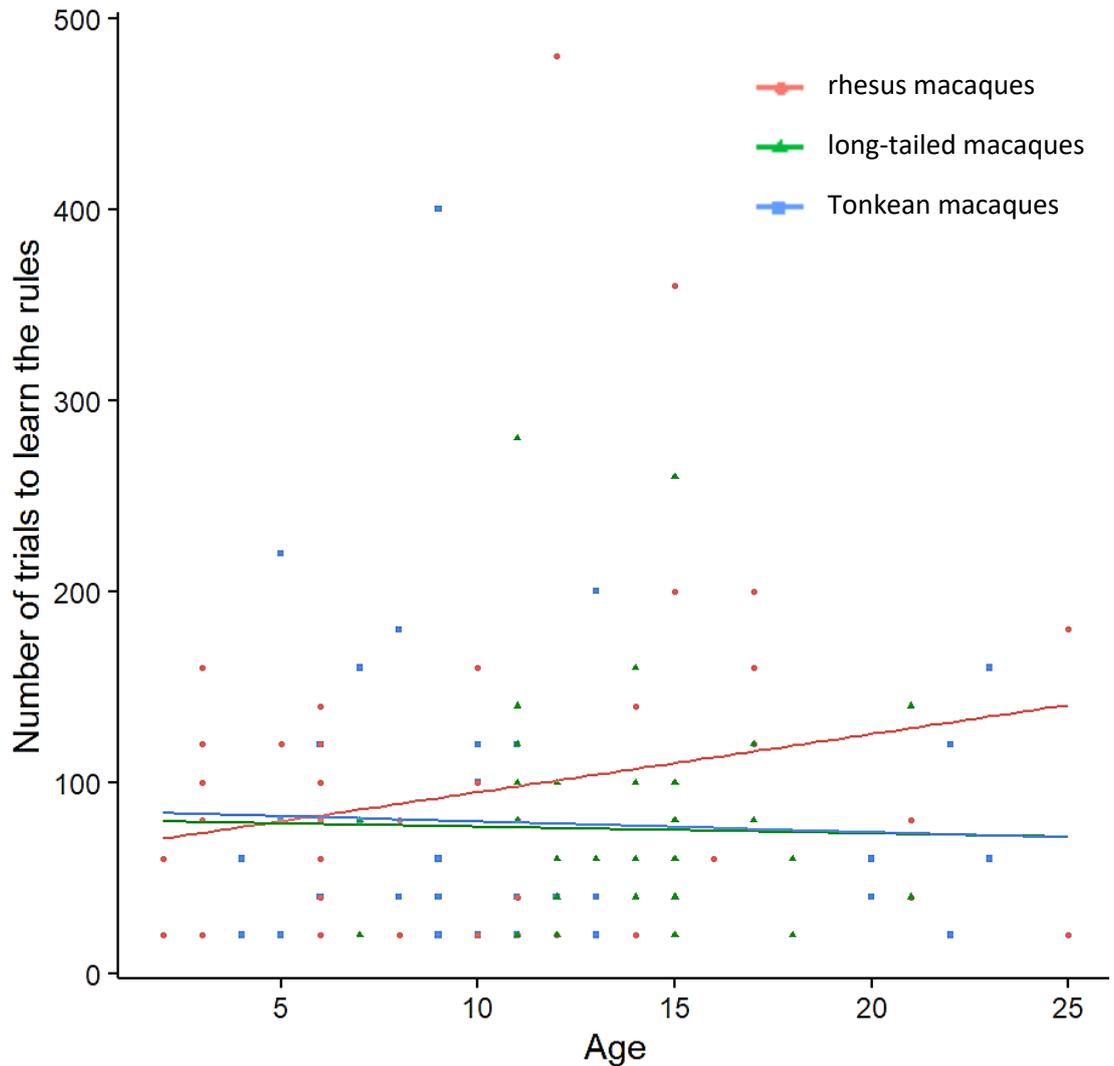


Figure 3.10. Number of trials learn each rule (reach the criterion of success for the acquisition phase and the reversal phase) depending on the age in the Reversal learning task in rhesus, long-tailed and Tonkean macaques. Older monkeys needed more trials to learn both the rules only in rhesus macaques. Each point represents an individual score, and the lines represent the regression lines for each species.

**Perseverative errors**

We now look at the number of perseverative errors (number of times and individuals persisted on the wrong answers before switching to the correct answer) in each species.

*Rhesus macaques*

In rhesus macaques (Table 3.15.), we found that there was a significant difference between the acquisition rule and the reversed rule ( $\chi^2_1 = 5.424$  , N = 18, P < 0.05), subjects made

more perseverative errors in the reversed rule compared to the acquisition rule. There was also a main significant effect of the number of the session ( $\chi^2_1 = 11.539$ ,  $N = 25$ ,  $P < 0.001$ ), the number of perseverative errors decreased as the number of the session increased. The variables age and sex did not have a significant effect on the models. Finally, there was a significant main effect of the institution on the number of perseverative errors, rhesus macaques from the MRC made more perseverative errors than rhesus macaques from the CPUS ( $\chi^2_1 = 12.11$ ,  $N = 25$ ,  $P < 0.001$ ). We ran the analysis for each institution separately and we find similar results in both institutions with an effect of rule and session and no effect of age and sex.

Predictors	Estimate	Std. Error	t value	Pr(> t )
<b>(Intercept)</b>	1.791	0.073	24.627	0.000
<b>age</b>	-0.001	0.005	-0.240	0.812
<b>sex (male)</b>	0.055	0.057	0.966	0.345
<b>rule (reversed)</b>	0.069	0.031	2.259	0.024*
<b>session</b>	-0.034	0.008	-4.382	0.000***
<b>Institution (CPUS)</b>	-0,256	0,074	-3,468	0,002**
<b>Rank (high ranking) in females</b>	-0.008	0.008	-0.106	0.918

Table 3.15. Results of the LMM for the number of perseverative errors (Reversal learning tasks) in rhesus macaques. Explanatory included age, sex and rank (analysis only conducted in females). All full models included the individual ID as a random factor. The estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), standard error, t-value and p-value are represented. \*  $p < 0.05$  \*\*  $p < 0.01$  \*\*\*  $p < 0.001$

In females, rank did not have a main significant effect ( $\chi^2_1 = 0.011$ ,  $N = 28$ ,  $p = 0.916$ ).

Concerning individual differences, rhesus macaques exhibited significant repeatability in the number of perseverative errors across trials and sessions ( $R = 0.078$ ,  $CI = [0.03,$

0.131],  $p < 0.0001$ ). When adjusting for session and location the performances were still repeatable ( $R = 0.045$ ,  $CI = [0.013, 0.083]$ ,  $p < 0.001$ ). These results mean that macaques exhibited stable individual variations in their performances between trials and session, even when we considered the confounding factors.

#### *Long-tailed macaques*

In long-tailed macaques, there was a main significant effect of the number of the session ( $\chi^2_1 = 7.305$ ,  $N = 20$ ,  $P < 0.05$ ); the number of perseverative errors decreased as the number of the session increased (Table 3.16. ). When comparing models, age and sex did not have a main significant effect on the long-tailed performances. There was no difference between the number of perseverative errors between both rules ( $\chi^2_1 = 2.261$ ,  $N = 20$ ,  $P = 0.123$ ). In females, rank did not have a main significant effect on their performances ( $\chi^2_1 = 1.124$ ,  $N = 20$ ,  $p = 0.289$ ).

<b>Predictors</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
<b>(Intercept)</b>	1.674	0.228	7.357	0.000
<b>age</b>	0.005	0.016	0.285	0.779
<b>sex (male)</b>	-0.083	0.098	-0.852	0.405
<b>rule (reversed)</b>	0.054	0.036	1.518	0.129
<b>session</b>	-0.037	0.013	-2.744	0.006**
<b>Rank (high ranking) in females</b>	-0.111	0.102	-1.086	0.303

*Table 3.16. Results of the LMM for the number of perseverative errors (Reversal learning tasks) in Long-tailed macaques. Explanatory included age, sex and rank (analysis only conducted in females). All full models included the individual ID as a random factor. The estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), standard error, t-value and p-value are represented. \*  $p < 0.05$  \*\*  $p < 0.01$*

Concerning individual differences, long-tailed macaques exhibited significant repeatability in the number of perseverative errors across trials and sessions ( $R = 0.118$ ,  $CI = [0.05, 0.206]$ ,  $p < 0.0001$ ). When adjusting for the session the performances were still repeatable

( $R = 0.115$ ,  $CI = [0.045, 0.197]$ ,  $p < 0.0001$ ). These results mean that macaques exhibited stable individual variations in their performances between trials and session, even when we considered the confounding factors.

*Tonkean macaques*

In Tonkean macaques there was a main significant effect of the sex of the individuals; males made more perseverative errors than females ( $\chi^2_1 = 6.8604$ ,  $N = 18$ ,  $P < 0.01$  see Table 3.17.). There was also a significant difference between the acquisition rule and the reversed rule ( $\chi^2_1 = 8.6257$ ,  $N = 18$ ,  $P < 0.01$ ); the subjects made more perseverative errors in the reversed rule compared to the acquisition rule. There was finally a main significant effect of the number of the session ( $\chi^2_1 = 11.539$ ,  $N = 18$ ,  $P < 0.001$ ); the number of perseverative errors decreased as the number of the session increased. The variable age did not have a significant effect on the models. In males, the rank did not have a main significant effect on their performances ( $\chi^2_1 = 2.472$ ,  $N = 18$ ,  $p = 0.116$ ).

Predictors	Estimate	Std. Error	t value	Pr(> t )
<b>(Intercept)</b>	1.267	0.140	9.020	0.000
<b>age</b>	0.005	0.007	0.664	0.515
<b>sex (male)</b>	0.239	0.086	2.785	0.012*
<b>rule (reversed)</b>	0.116	0.040	2.902	0.004*
<b>session</b>	-0.036	0.010	-3.426	0.001**
<b>Rank (high ranking) in males</b>	-0.133	0.079	-1.689	0.120

Table 3.17. Results of the LMM for the number of perseverative errors (Reversal learning tasks) in Tonkean macaques. Explanatory included age, sex and rank (analysis only conducted in males). All full models included the individual ID as a random factor. The estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), standard error, t-value and p-value are represented. \*  $p < 0.05$  \*\*  $p < 0.01$

Concerning individual differences, Tonkean macaques exhibited significant repeatability in the number of perseverative errors across trials and sessions ( $R = 0.081$ ,  $CI = [0.028, 0.146]$ ,

$p < 0.0001$ ). When adjusting for session, rule and sex the performances were still repeatable ( $R = 0.059$ ,  $CI = [0.016, 0.115]$ ,  $p < 0.0001$ ). These results mean that macaques exhibited stable individual variations in their performances between trials and sessions, even when we considered the confounding factors.

#### 3.6.4 Discussion

To summarise, we found individual variation in the *inhibition of a cognitive set* for the number of perseverative errors in the three species. In rhesus macaques, older individuals had worse cognitive performances as they needed more trials to understand both rules. In this species, subjects needed as many trials to learn the acquisition than the reversed rule but made more perseverative errors in the reversed rule. In rhesus macaques, individuals from the CPUS, learnt the rules with fewer trials and made less perseverative errors compared to the individuals from the MRC. In long-tailed and Tonkean macaques, individuals needed more trials to learn the reversed rule compared to the acquisition rule. Long-tailed macaques persevered more in the reversed rule than in the acquisition rule. In Tonkean macaques, males made more perseverative errors than females (see Table 3.18. at the end of the chapter for a summary of the results).

We first found inter-individual variation in the number of perseverative errors across trials and sessions even when considering confounding factors. This indicates that some individuals were consistently more perseverant than others were. This variability in performance was also found in a study in dogs using the A-not-B task (a simplified reversal-learning task), which found that more than half of the dogs experienced difficulties in this task (Vernouillet et al., 2018). This result indicates that this task was sensitive enough to reveal individual variations.

We also demonstrated, in rhesus macaques, that older individuals needed more trials to learn the rules than younger ones, both in the acquisition phase and in the reversion phase. Contrary to previous studies (Herrmann et al., 2010; Lacreuse et al., 2014), more experienced individuals did not have better cognitive performance. This impairment in cognitive abilities in older macaques could have been due to age-related decline in executive function, however we had only a few aged individuals in our sample (only five individuals were more than 20 years old). Surprisingly, it seems that even middle-aged individuals experienced this impairment in executive functions. In a previous study we showed this age impairment in the Reversal learning task in middle-aged rhesus monkeys (the older individuals were 17 years old; Loyant et al., 2021). Interestingly, one study in chimpanzees showed age-related decline in cognitive flexibility (with an increased number of trials to reach criterion) already observed at middle age (Lacreuse et al., 2018). In a study with rhesus macaques, researchers compared executive function between young adults (5 to 9 years old), middle-aged macaques (12 to 19 years old) and aged macaques (20 to 30 years old). They found similar results with an impairment in cognitive flexibility beginning at middle age (Moore et al., 2006). In this direction, recent data in humans showed that age-related changes in cognition, particularly in executive function, might occur much earlier than expected (Gunning-Dixon & Raz, 2003). When looking at the Wisconsin card-sorting task, a benchmark task to study cognitive flexibility, not only individuals of advanced age are less efficient at this task, but so are those of middle age (Rhodes, 2004). Executive function may be the earliest domain of cognitive function to show impairment in normal ageing (Moore et al., 2006; Gunning-Dixon, 2003). Deficits in executive functions occur at an age as early as 40 (Gunning-Dixon, 2003) which could correspond to the middle-age in the monkeys of our study.

An explanation proposed for this age impairment in inhibitory control is a decline in the functioning of a region critical for inhibitory control, the prefrontal cortex. This decline is associated with an impairment in the dopamine system (West, 1996). Interestingly, many aspects of age-related cognitive deficits, such as distractibility and impaired memory could be due to a failure in inhibitory mechanisms and particularly an inability to inhibit irrelevant information (Hasher & Zacks, 1988). In humans, there is evidence of a U-shaped model of the inhibitory control performances, as this ability develops slowly during childhood and decreases with age (Christ et al., 2001; Hasher & Zacks, 1988). It would be interesting to test immature macaques of less than 3 years old and more aged macaques (more than 20 years old) to compare their performances with adult macaques.

In our study, long-tailed and Tonkean macaques did not exhibit this age impairment. As this age impairment of cognitive abilities was also found in other macaque species such as Japanese macaques (Itoh et al., 2001, Darusman et al., 2014; Tsuchida et al., 2002) and long-tailed macaques (Darusman et al., 2013), we cannot conclude that this age impairment is species specific. This absence of difference in other species could be due to lower sample size in these species of our study, which would decrease the probability to find an effect. Specifically in long-tailed macaques in which the majority of the individuals were from the adult class of age (see Figure 3.1.). It would be interesting to test more individuals from long-tailed and Tonkean macaques to try to replicate this age impairment in executive function. In Barbary macaques, there was no age impairment in an inhibitory control task assessing cognitive flexibility, but researchers found a decrease in motivation with age (Rathke & Fischer, 2020). It would be interesting to look at the

motivation effect (increase in response latency for example) of our older individual to try to replicate these results.

As expected, we also found that male Tonkean macaques made more perseverative errors than females. This sex difference is also present in other species, for instance, female guppies were also better at reversing a pre-learned rule compared to male guppies (Lucon-Xiccato & Bisazza, 2014). Another study found this sex difference in perseverative behaviour (Lucon-Xiccato et al., 2020b). In this study males attempted to attack the prey inside a transparent tube twice as often as females. In the large group of Tonkean macaques we tested, the males were mostly at the top of the hierarchy. It is possible that this bias toward high-ranking males negatively affected the male Tonkean macaques' performances as high-ranking individuals are supposed to be more impulsive (Johnson-Ulrich and Holekamp, 2020).

Furthermore, it was more difficult for long-tailed and Tonkean macaques to learn the reversed rule. Subjects needed more trials to learn the reversed rule and long-tailed macaques made more perseverative errors in the reversed rule. They probably encountered more difficulty learning the second rule as it contradicted their initial learning. Similarly, macaque's studies demonstrated difficulties to learn a new rule in the reversal phase (as in Lai et al., 1995 and Tsuchida et al. 2002). These results demonstrated the interference of the first learnt rule on the learning of the second rule. However, these results were not found in rhesus macaques. This species needed a high number of trials to learn the acquisition and the reversed rule. It is possible that this task was too difficult for rhesus macaques and that they reached the criterion of success by chance rather than by understanding.

Finally, in this task rhesus macaques bred in the MRC had worse performances than species bred in the CPUS. They needed more trials to learn the rules and were more perseverant. The groups in the two institutions were bred in captivity in similar conditions (similar cages with similar type of enrichment, majority of the groups with one males and several females). However, in the CPUS two individuals out of six doing the task have been trained (when they were young) on cognitive tasks requiring memory and learning. It could be possible that their experience brought a bias in the data, explaining the better performances of the individuals from CPUS. In the literature, training and prior experience with behavioural experiment is one of the most described confounding factors of inhibitory control (Duque & Stevens, 2017; Kabadayi et al., 2018; van Horik et al., 2019; Vernouillet et al., 2018, see Appendix 29). Experienced individuals can have an advantage in physical understanding of the task (i.e., object permanence, spatial relationship, transparency; Duque & Stevens 2017; Kabadayi et al., 2017, 2018). For instance, a study demonstrated that New Caledonian crows trained to track rewards moved by a human demonstrator were more likely to pass the A-not-B test (Jelbert et al., 2016). These birds were performing at a similar level than non-human primates in opposition with the results obtained by MacLean and colleagues (2014). In pheasants, learning, type of training and prior experience with transparent surfaces have been demonstrated to greatly improve inhibitory control performances (van Horik et al., 2018b, 2019). Therefore, these results cast light on the importance to be cautious when interpreting inter-species comparative studies as intra-specific differences are a crucial factor to take into consideration.

### 3.7 Summary of the findings

Inhibitory control	Task outcome	Factors	Rhesus macaques	Long-tailed macaques	Tonkean macaques	
<b>Control of emotions</b>  <i>Distraction task</i>	<i>Distraction control score</i>	Individual differences	✓	✓	✓	
		Type of picture	More distracted by threatening and neutral conspecifics	More distracted by threatening conspecifics, objects faster	No effect	
		Sex	Males more distracted than females  (all types of stimuli)	Females more distracted than males  (more threatening face)	Females = Males but males more distracted by threat. than neutral conspecifics	
		Age/Rank	No effect	No effect	No effect	
	<i>Number of response withheld</i>	Individual differences	✓	✓	✓	
		Type of picture	More distracted by conspecifics faces	No effect	No effect	
		Sex/Age/Rank	No effect	No effect	No effect	
	<i>Emotional reactions toward pictures</i>	Sex	2 females  10 males (conspecific)	3 females 1 male (conspecific)	No reaction	
	<b>Control of an action</b>  <i>Go/No-go task</i>	<i>Accuracy on a No-go trial</i>	Individual differences	✓	✓	✓
			Sex	Only females learnt through sessions	No effect	No effect
Age/Rank			No effect	No effect	No effect	

Inhibitory control	Task outcome	Factors	Rhesus macaques	Long-tailed macaques	Tonkean macaques
<b>Control of a cognitive set</b>  <i>Reversal learning task</i>	Number of trials to learn	Sex/Rank	No effect	No effect	No effect
		Age	Older individuals needed more trials	No effect	No effect
	Perseverative error	Rule	No difference reversed/acquisition rule	Greater number of trials/acquisition rule	Greater number of trials/acquisition rule
		Individual differences	✓	✓	✓
		Sex	No effect	No effect	Males more perseverative
		Age/Rank	No effect	No effect	No effect
		Rule	More perseverant in the reversed/acquisition rule	No difference between rules	More perseverant in the reversed/acquisition rule

Table 3.18. Summary of the results for the three tasks (Distraction, Go/No-go and Reversal learning tasks) and their outcomes. Results are presented for rhesus, long-tailed and Tonkean macaques and for the factors age, sex and rank considered. Individual differences are also presented.

### 3.8 General discussion

The aim of this chapter was threefold: (1) to investigate individual variability in inhibitory control skills in three species of macaques; (2) to replicate, depending on the task, in each species, the most common effects of individual and group determinants (age, sex and rank) on inhibitory control performances; and (3) to demonstrate the effect of these factors on the three main components of inhibitory control. We first demonstrated individual variations in all components of inhibitory control in all three species. We then found an effect of sex and age on specific inhibitory control tasks and not consistently in all species. Males had worse inhibitory performances than females in but not consistently across the different tasks. In rhesus macaques, males were more distracted and more emotive and they were more impulsive in the *inhibition of an action* task. In Tonkean macaques, males were more perseverant in the *inhibition of a cognitive set*. On the contrary, female long-tailed macaques had worse performances in the *inhibition of a distraction*. Aged monkeys had impaired cognitive performances in the *inhibition of a cognitive set* only in rhesus macaques. We did not find an effect of the rank of the individuals in any of the inhibitory control tasks and in any of the species.

#### Individual differences in all tasks and species

Firstly, we found that the three macaque species showed consistent individual variations in all three components of inhibitory control. These individual differences were similarly demonstrated in several inhibitory control tasks. For example, individual differences were found in guppies using a variant of the detour-reaching task (Lucon-Xiccato et al., 2020a; 2020b; Montalbano et al., 2020) and in pheasants using a response inhibition task (Meier et al., 2017). Dogs also demonstrated individual differences in common inhibitory control tasks such as the Detour task (Brucks et al., 2017). Besides, a study in rhesus macaques

demonstrated individual differences in a Distraction task (Howarth et al., 2021). Until recently, individual variations have been largely ignored, considered as ‘noise’ around the population mean and only high performing individuals were considered (Boogert et al., 2018; Shaw & Schmelz, 2017; Thornton & Lukas, 2012). However, many authors are recognizing that valuable information can be lost when focusing only on group-level performances (Shaw & Schmelz, 2017). Before considering large comparative studies, further studies should therefore first systematically investigate individual differences in inhibitory control. These tasks, by demonstrating individual variation in performance, are avoiding the floor and ceiling effect (i.e. the task being too difficult or too easy), a common problem in cognitive tasks, particularly important in inhibitory control studies (Shaw & Schmelz, 2017; Völter al., 2018, see chapter 1.3.1.3). These effects induce low variability between subjects which can reduce the strength of correlations (Biro & Stamps, 2015; Koo and Li 2016; Nakagawa & Schielzeth 2010; Paap & Oliver 2016). Thus, the battery of tasks we developed successfully triggered individual differences in three species of macaques.

#### [Toward a multifaceted structure of inhibitory control](#)

We also found that the individual characteristics (age and sex) influence the different components of inhibitory control inconsistently in the three macaque species. Age only influenced performances in the *inhibition of a cognitive set* and only in rhesus macaques. Sex influenced performances in the *inhibition of a distraction* in rhesus and long-tailed macaques, in the *inhibition of an action* in rhesus macaques and in the *inhibition of a cognitive set* in Tonkean macaques. Other studies also demonstrated this inconsistency of the effect of the different factors influencing the different inhibitory control tasks. For example, Bray and colleagues (2014) found that the factor age only influenced dog's performances in the *inhibition of action* (Cylinder task) but not *the inhibition of a cognitive*

set (A-not-B task). However, Vernouillet and colleagues (2018) found an effect of age on the inhibitory performances only in a modified version of the A-not-B task with barrier (mixing *inhibition of action* and of a *cognitive set*) but not in the *inhibition of a cognitive set* alone (A-not-B task) nor in the *inhibition of an action* (Cylinder task). Inconsistent performances and contradictory effect of the influencing factors between the inhibitory control tasks could be explained by the task impurity problem (i.e. no tasks are pure measurement of a single cognitive process but relies on a mixture of cognitive processes, see chapter 2.2). It could be possible that the three tasks are not equally measuring inhibitory control with for instance a large influence of memory or flexibility in the Reversal learning task (Izquierdo et al., 2017). It is also possible that the inconsistent effect of age and sex on the different components of inhibitory could be due to the multi-faceted structure of inhibitory control, divided in independent components, as proposed by several authors (Duckworth & Kern, 2011; Friedman & Miyake, 2004; Macleod, 2007; Nigg, 2017). Supporting this idea, in chapter 2 we found the consistency of performance between the *inhibition of a distraction* and the *inhibition of an action*; this was not found for the *inhibition of a cognitive set* which strengthens the hypothesis of a multi-faceted structure of inhibitory control.

The different factors did not influence the different species consistently. It is possible that the effect of age is species specific. However, Comrie et al., 2019, found the effect of cognitive ageing in rhesus macaques and bonnet macaques (*Macaca radiata*) in a memory task (in an object recognition memory task and in an object-reward association task). Besides, cognitive ageing was also found in long-tailed macaques (Darusman, et al., 2013) so this age effect is probably not species specific. Interestingly, these results demonstrate

that all macaque species are not equivalent models of cognitive ageing and highlight the value of cross-species comparison. However, it is also possible that this absence of age effect could be due to our lower sample size in long-tailed and Tonkean macaques compared to rhesus macaques with a smaller age spread.

We did not find any effect of the social rank on inhibitory control performance across all tasks and species. Similarly, the social ranking did not influence cognitive performances in any of the Primate Cognition Task Battery in ring-tailed and ruffed lemurs (Fichtel et al., 2020) or in olive baboons and long-tailed macaques (Schmitt et al., 2012). This absence of effect could be due to our relatively small sample size, a common limitation when working with primates, which might have decreased the power of our analysis (Paap & Oliver, 2016). The only paper demonstrating rank difference (using continuous ELO rating ranks) in inhibitory control tested 62 hyenas on a Cylinder task (Johnson-Ulrich & Holekamp, 2020). However, individual's rank did not affect attentional bias toward pictures in a large sample of rhesus macaques (66 and 43 individuals in two different studies, Howarth et al., 2021). In this study they use three different classes of ranking: low, middle and high. It would be interesting to replicate our study with a larger sample size and to use continuous values of rank measurements such as ELO rating instead of categorical ranking.

#### Phylogenetic basis of basic forms of inhibitory control?

In rhesus macaques, only for the tasks of *inhibition of a distraction* and of *inhibition of an action*, we found similar performances between the groups of rhesus macaques from the two institutions. It is possible that these tasks, reflecting a more basic form of inhibitory control compared to the *inhibition of a cognitive set* (see chapter 2.8.2), are less influenced by other factors such as previous experience with cognitive tasks. Similar patterns of

behaviours have been demonstrated for aggressivity and reactivity (Balasubramaniam et al., 2012; Berman, 1980; Judge & de Waal, 1997; Thierry et al., 2007). It could be possible that these simpler forms of inhibitory control (*inhibition of a distraction* and of *inhibition of an action*), as a more direct measurement of impulsive behaviour, are more phylogenetically conserved.

*Are these tasks valid in long-tailed and Tonkean macaques?*

This task battery has been validated in rhesus macaques from the MRC (see chapter 2) and have been used here to test inhibitory control in rhesus macaques from another institution, in long-tailed and Tonkean macaques. In animal cognitive literature, common tasks are often extensively used in many animal species before being validated in these species. For instance, the Cylinder task, a common but not systematically validated task of inhibitory control, have been used to compare inhibitory performances in distant species such canids (Bray et al., 2014; Fagnani et al., 2013; Johnson-Ulrich et al., 2018, Maclean et al., 2014; Marshall-Pescini et al., 2015) primates (Maclean et al., 2014), birds (Maclean et al., 2014; Kabadayi et al., 2016; van Horik et al., 2018a,b), fishes (Lucon-Xiccato et al., 2020a,b; Santacà et al., 2019) and reptiles (Szabo et al., 2020).

We have seen in chapter 2.6, that to demonstrate the content validity of our tasks we should demonstrate that a prepotent behaviour (a distraction, an impulsive action or a pre-learned behaviour) has been overridden in order to reach a goal. In the Distraction task, a distraction should be elicited by the stimuli and overridden to complete the task. In this task, in rhesus macaque, we found a strong distractive effect of the stimuli on the subject's response latency (see Appendixes 25 and 26 for a detailed presentation of the results and see also chapter 2.3.3). Similar results were found in long-tailed macaques,

with also a strong distractive effect elicited by the threatening stimulus on the Distraction control score (see Appendixes 25, 26 and chapter 1.4.2.3.2). However, in Tonkean macaques, the picture is less clear. In general the presence of a picture did not significantly influence their response latency (see Appendixes 25 and 26). When looking at the Distraction control score (see 3.4.2), only males reacted to threatening conspecific's pictures with a longer response latency compared to neutral pictures. Still, this task was successfully demonstrating a sex difference even though it had not been validated beforehand. It would be interesting to try to validate this task in both sexes of Tonkean macaques by designing an experiment in which the subjects exhibit a stronger reaction toward the stimulus (e.g. by using videos or positively valenced stimuli as in Hopper et al., 2020).

For the *inhibition of an action* task, we compared the accuracy in the Go and No-go trials (see chapter 2.6.2). No-go trials should elicit a prepotent response and thus subjects should have a lower accuracy in this type of trials. Similar results were found in the new group of rhesus macaques at the CPUS (see Appendixes 25 and 27), long-tailed macaques tailed (see Appendix 25) and Tonkean macaques (see Appendixes 25 and 27) with a significant main effect of the type of trial (Go or No-go) on the subject's accuracy (see Appendix 27). All three species were less accurate on No-go trials demonstrating a prepotent action toward the No-go stimulus.

For the *inhibition of a cognitive set*, we compared the accuracy between the acquisition and the reversed rule (see 2.6.2). If a prepotent response was elicited, then the previous learnt rule should distract the subject while learning a new rule. Subjects should demonstrate a better accuracy in the acquisition rule compared to the reversed rule. For

the accuracy on a trial, we found in 2.6.2., a significant difference in the mean success in a trial if the rule was the first acquisition or the reversed rule in rhesus macaques (see Appendix 25 and 28). In long-tailed (see Appendix 25 and 28) and Tonkean macaques (see Appendix 25) we also found a significant main effect of the type of rule on the accuracy with a lower accuracy on the reversed rule (see Appendix 28). However, when looking at the number of trials to learn the rules, the distracting effect of the new rule was only found in long-tailed and Tonkean macaques (see 2.5.3), rhesus macaques needed as many rules to learn the acquisition rule and the reversed rule. Depending on the measurement, a task could be considered as valid or not.

To summarise, our newly developed battery of inhibitory control tasks elicited a prepotent response and is thus adequately measuring inhibitory control in three species of closely related macaques. However, the results are to be taken with caution as the prepotent response was demonstrated in only male Tonkean macaques in the distraction task. Besides this, content validity also depended on the measurement chosen in the Reversal learning task.

The next objective would be also to test for test-retest repeatability in long-tailed and Tonkean macaques. Finally, it would also be interesting to re analyse the contextual validity of these task in long-tailed and Tonkean macaques to see if, as in rhesus macaques, performances in the *inhibition of a cognitive set* were not consistent with performance in the *inhibition of a distraction* and of *an action*.

#### Other factors that can explain individual differences

Many intricate factors can also influence inhibitory control performances (see Appendix 29 for a non-exhausting list of influencing factors). For instance, the motivation of the

subjects can strongly influence their performances (Brucks, Marshall Pescini, Range 2018; Duque & Stevens 2017; Schubiger et al., 2020; Shaw & Schmelz 2017). Either in the wild or in captivity, if the experiment is voluntary, only the most motivated individuals from a group will be willing to interact with the experimental setup (Schubiger et al., 2020). To control for these transient variabilities, subjects can for instance, be fed ad libitum (to minimise variability in food motivation). This motivation factor can also be itself affected by factors which might seem trivial such as the salience of the reward (see Appendix 29). The more a reward is visible and the less the subject is going to be able to inhibit its response (Brucks et al., 2017; Kabadayi et al., 2017, 2018). For instance, authors suggested that difference in reward visibility might explain difference in performances in the Detour task and in the A-not B (Bray et al., 2014; Brucks et al., 2017a; Fagnani et al., 2016; Marshall-Pescini et al., 2015; Vernouillet et al., 2018). Hence the need to provide carefully detailed methods and use similar protocols to improve the validity of interspecies comparison.

The personality of a subject is also strongly influencing his performances in cognitive tasks (see Appendix 29, Griffin et al., 2015; Boogert et al., 2018; Schubiger et al., 2020, see Table S5). Here we refer to personality as stable individual differences of behaviour that are repeatable across time and/or contexts (Réale et al., 2007). In humans, it has been demonstrated that anxious people have an attentional bias toward negative stimuli (MacLeod et al., 1986; Bar-Haim et al., 2007). Non-human primates which had recently experienced a traumatic experience showed a similar bias toward threatening stimulus (Allritz et al., 2016; Bethell et al., 2012, 2016, for review see Crump et al., 2018). This attentional bias was also linked to measurement of fearful temperament in rhesus

macaques (Bethell et al., 2019a). In both zebrafishes and guppies, bolder individuals showed greater inhibitory control skills when tested in a variant of the Cylinder task (Lucon-Xiccato et al., 2020b). Personality is thus an important factor to take into consideration when testing for inhibitory control. Researchers can, for instance, assess these personality traits beforehand, using standardised behavioural procedures and include this factor in the analysis (as in Madden et al., 2018; Lucon-Xiccato et al., 2020).

Another factor which we could not control was the number of individuals surrounding the tested subject during the tasks. Most of the time, high-ranking individuals were alone in front of the screen whereas low ranking individuals were surrounded by other conspecifics. For a side study, a research assistant coded the number of individuals surrounding a tested individuals from videos taken at the MRC (individuals always alone, partially alone, partially surrounded and always surrounded). The research assistant found that the presence of surrounding conspecifics did influence subject's performances in the distraction task ( $\chi^2_{1} = 5.24$ ,  $N=20$ ,  $P < 0.05$ ). Subjects were less distracted if they were constantly alone (coded as 0) or constantly surrounded with conspecifics (coded as 4, see Figure 3.11.). No effect of the conspecific's presence was found in the Go/No-go task. In the Reversal learning task there was also an effect of the conspecifics' presence ( $\chi^2_{1} = 148.16$ ,  $N=19$ ,  $P < 0.001$ ), the subjects needed more trials to learn the rules as the presence of conspecifics increased. Similarly, in another primate study, under social presence, baboons were less able to inhibit a learned action in favour of a new one and were also less able to take advantage of previous experience (Huguet et al., 2014). In another study, chimpanzees exhibited greater self-control when alone than when tested alongside a conspecific (Evans et al., 2012). These findings explain why inappropriate

behaviours are not easily suppressed in primates acting in social contexts and indicate a greater demand for cognitive control in social groups (Huguet et al., 2014). It would be interesting to repeat this analysis for all the species we tested to look for a similar effect of the conspecific's presence on inhibitory control performances.

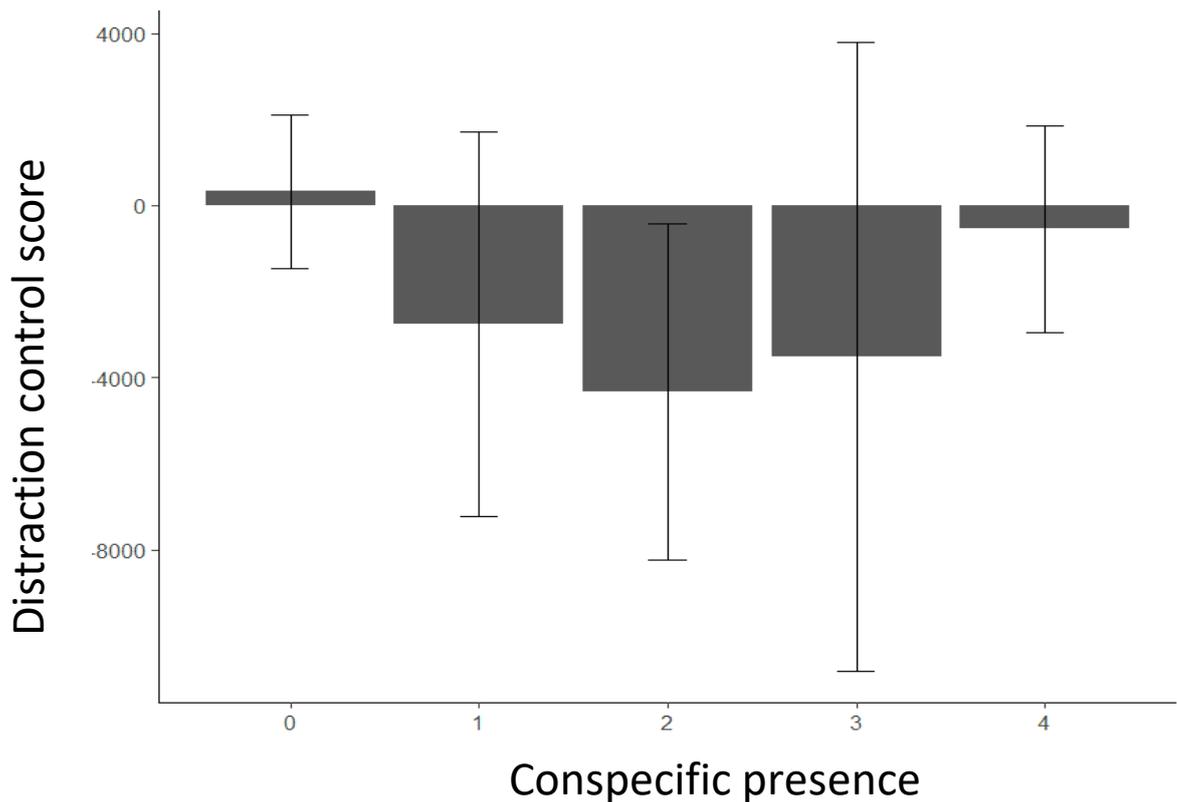


Figure 3.11. Distraction control score depending on conspecifics' presence for the session 1, first block of the Distraction task. 0 : 100% of the time alone, 1 : 100-75% of the time alone, 2 : 50-75% of the time alone or 50-75% of the time with one or more conspecifics, 3 : 75-100% with conspecifics, 4 : 100% with one or more conspecifics. Standard errors are presented.

In our study, we did not consider other important components of the social environment which could also explain variation in inhibitory control (Schubiger et al., 2020). For instance, the size of a social group has also been used as a proxy for social complexity (Bergman & Beehner, 2015; Kappeler *et al.*, 2019). Living in larger groups may be more cognitively demanding due to an increase in the number of interactions between groupmates (Bergman & Beehner, 2015). It has been demonstrated with the Cylinder task

in spotted hyenas that developing in a larger group generates better inhibitory control skills (Johnson-Ulrich & Holekamp, 2020). This result was also found in Australian magpies with the Cylinder task and the Reversal-learning task (Ashton et al., 2018). However, MacLean et al. 2013, using the Cylinder task with six species of primates did not find an effect of the group size on their performances. It would be interesting to include in our analysis the size of the group in which our subjects developed.

Recently a study demonstrated that the complexity of a social system (calculated from indexes of social diversity, individual's behavioural variations and patterns of interactions between individuals) increases with the degree of tolerance among macaques (Rebout et al., 2021). Besides, it has been suggested that enhanced cognitive abilities, such as inhibitory control, evolved as a response to the complexity of social life (Powell et al., 2017). Species characterised by higher social tolerance would develop more diverse relationships, and thus would need to employ more inhibitory strategies (Wascher et al., 2018). As the three species studied in this chapter differ in their social tolerance (Thierry, 2007), the next chapter of this thesis is going to look at social tolerance as an evolutionary factor of inhibitory control in macaque species.

## Chapter 4: Inhibitory Control and Social Tolerance

### 4.1 Overview

Living in a complex social environment requires primates to manage their emotions and inhibit impulsive behaviours. Such cognitive processes are defined as inhibitory control. To date, little is known about the selective forces that favour the evolution of inhibitory control. It has been suggested that one route by which social problem solving can evolve is through selection on social tolerance. Our hypothesis was that species characterised by higher social tolerance live in more complex groups, with more diverse relationships, and therefore need to employ more inhibitory strategies. Hence the aim of this project was to compare the inhibitory control skills in three closely related macaque species which differ in their social tolerance style, from despotic to more relaxed relationships. For that purpose, we tested 66 macaques (28 *Macaca mulatta*, low tolerant species; 19 *M. fascicularis*, medium tolerant species; and 18 *M. tonkeana*, high tolerant species) using the battery of touchscreen tasks validated in chapter 1, which test the *inhibition of a distraction, an action, and a pre-learned cognitive set*. Overall we found that the least tolerant species had the worst inhibitory control performances in all three tasks; this species was the most impulsive and emotive. Intermediate species on the tolerance spectrum had the best performances in the inhibition of an action but average performances in the *inhibition of a distraction and a cognitive set*. Highly tolerant species had the best performances in *the inhibition of a distraction and of a cognitive set* but there was no clear difference with the other species in the inhibition of an action task. Our results

demonstrate that low level of social tolerance is associated with reduced inhibitory control performance compared to species with the highest degree of social tolerance. The picture is mixed for the species with the intermediate level of tolerance, showing average performances compared to other species. Social organisation seems to influence inhibitory control skills when looking at both ends of the tolerance scale. An individual living in a highly tolerant social organisation would need to employ more inhibitory strategies to navigate in a more complex social context. Overall this project will help to get more insight into the evolution of inhibitory control in primates.

## 4.2 Introduction

Inhibitory control is crucial in a complex social environment to help animals control their impulsive behaviours and manage their emotions when interacting with conspecifics. For example, in the presence of a higher ranked conspecific, an individual needs to inhibit aggressive behaviours when competing over food or a mate (Amici et al., 2008; Byrne & Bates, 2007). Hence, inhibitory control allows to flexibly respond to an animal's social environment and adjust behaviours becoming counterproductive or potentially harmful (Marshall-Pescini et al., 2015).

Having a better understanding of animal inhibitory control is crucial to apprehend the evolutionary underpinnings of this ability, particularly if the selective pressures acting on this ability can be identified. To date, we know little about the selective forces that affect the evolution of inhibitory control. Ecological factors (Maclean et al., 2014 ; Amici et al., 2008), brain size (Maclean et al., 2014; Stevens, 2014) or social pressures (Johnson-Ulrich & Holekamp, 2020; Asthton et al., 2018) seem to shape inhibitory control skills (MacLean et al., 2014). However, some of the evolutionary factors proposed have been

challenged by recent studies (Beran, 2018; Jelbert, Taylor & Grey, 2016; Kabadayi et al., 2017). As inhibitory control is crucial in the social life of primates, it would be particularly interesting to understand which aspect of their social environment would have influenced its evolution. It has been suggested that the organisation of the social environment is an important factor for the evolution of socio-cognitive skills such as inhibitory control (Byrne 1996; Byrne & Bates, 2007, Schubiger et al., 2020).

On one hand, the Machiavellian intelligence hypothesis suggests that in a despotic society, social manipulation and deception would lead to the development of richer socio-cognitive skills, such as inhibitory control (Byrne 1996; Byrne & Bates, 2007). An individual living in a more competitive social environment would need to constantly inhibit inappropriate behaviours, such as feeding or mating, in the presence of higher ranked conspecifics (Byrne 1996; Byrne & Bates, 2007). On the other hand, the social intelligence hypothesis (Dunbar, 1998; Humphrey, 1976) postulates that the demands associated with a complex, more cooperative social life generates selection for increased brain size and higher cognitive performances, such as inhibitory control (Wascher et al., 2018). In complex social conditions, the inhibition of impulsive behaviours and emotions are crucial for forming and maintaining stable social relationships (Amici et al., 2008, 2018; Aureli & Schino, 2019; Byrne & Bates, 2007; Wascher et al., 2018). Skills such as cooperation or coalition, requiring a high degree of inhibitory control, are particularly adaptive in societies where dominance hierarchies determine access to food and mates (Amici et al., 2008, 2018; Byrne & Bates, 2007). Animals may tune their social behaviours in relation to the social context or the identity of the social partner with whom they interact (Amici et al., 2008, 2018; Aureli & Schino, 2019; Byrne & Bates, 2007; Dunbar, 2007; Wascher et al.,

2018). The more complex a society is, the more often an individual would need to employ inhibitory strategies as they monitor and engage in diverse social events occurring around them such as remembering, tracking and managing relationships (Amici et al., 2008).

Several definitions of social complexity have been proposed. Freeberg and colleagues (2012), suggested that complex social systems are those in which individuals frequently interact in many different contexts with many different conspecifics. Other authors suggested that social complexity could be related to complex social behaviours such as consolation (de Waal & Aureli, 1996) and the ability to form complex alliances (Connor, 2007). Bergman & Beehner (2015), defined social complexity as the number of differentiated relationships that individuals have with conspecifics. In complex societies, one individual may treat every conspecifics differently based on their identity, their kinship, the social context or their life history (Bergman & Beehner, 2015; Shultz and Dunbar, 2007). More particularly in despotic species, individuals will treat their close kin differently from the rest of the group, but the rest of the group are treated the same (Bergman & Beehner, 2015; Shultz and Dunbar, 2007). In such asymmetrical societies, the number of differentiated stable interactions is often lower than the size of the group (Bergman & Beehner, 2015; Shultz and Dunbar, 2007). In contrast, in tolerant species, the number of differentiated relationships often approaches the size of the group with a greater diversity of responses (Shultz and Dunbar, 2007). For instance, depending on the social context, tolerant species have developed a higher rate and diversity of post-conflict behaviours such as reconciliation (Thierry, 2000) and consolation (de Waal & Aureli, 1996). Such post-conflict behaviours have been described as a marker of higher social complexity (Aureli et al. 2012; Bergman & Beehner, 2015; Kappler et al., 2019 Shultz and Dunbar,

2007). Thus, an individual living in a more tolerant society, characterised by more relaxed relationships, would have more opportunities to develop diverse and complex relationships. Interestingly, a recent study developed a social complexity index (closely related to the system uncertainty). This index was calculated using three factors: the social diversity in a group (the number of individuals, their age and sex), the flexibility in behavioural interactions (according to social situations) and the patterns of interactions between individuals (Rebout et al., 2021). Taking the example of macaque societies, the researchers demonstrated that the complexity of a social system increased with social tolerance. More particularly they demonstrated that the rhesus macaques' societies were less complex than the Tonkean macaques's societies.

Therefore, according to the social intelligence hypothesis, an individual living in a more tolerant society, defined as more complex, would need to employ more inhibitory strategies while engaging in more diverse relationships (Bergman & Beehner, 2015; Fischer et al., 2017). Similarly, one study testing four different macaque species demonstrated that the more tolerant macaque species outperformed the less tolerant ones in one simple inhibitory control task (the middle cup task, Joly et al., 2017). As the inhibitory control task used in these studies was a basic task using only a few trials it would therefore be interesting to replicate these results using a more robust battery of inhibitory control tasks.

The macaque radiation is an ideal taxon for such a comparative study. As we saw in chapter 1, this genus shares the same basic pattern of social organisation as they form multi-male multi-female groups organised in kin-bonded subgroups. Beyond these shared basic features, macaque species differ greatly both in their morphology and in their styles

of affiliation, aggression, dominance, nepotism and maternal behaviour (Balasubramaniam et al., 2012). Therefore, Thierry and colleagues (2004, 2007), proposed a classification of their social styles along a four-grade scale mainly based, among other criteria, on patterns of aggression and reconciliation; from despotic and nepotistic style of social relationships to a more tolerant style with more open relationships. For example, grade 1 (less tolerant), is characterised by steep dominance hierarchies, frequent unidirectional conflicts of high intensity aggression, conspicuous submission signals and strong preference for kin partners. By contrast, grade 4 (more tolerant or egalitarian), is characterised by less steep dominant hierarchies, relatively low degree of kin preference and more bidirectional conflicts characterised by lower intensity, more uncertainty about the outcome and frequent reconciliations. Grades 2 and 3 have intermediate degrees of social tolerance depending on the behaviour considered. For instance, grades 1 and 2 use the silent bared teeth to express submission, in grade 3 it may either have a positive meaning or also express submission, in grade 4 it signals peaceful intentions (Thierry, 2000).

Hence, the aim of this chapter was to explore the influence of social tolerance degrees on inhibitory control skills using the battery of tasks we developed beforehand (see chapter 2). We chose to base our hypothesis on Joly and colleagues' study (2017), which demonstrated that species with higher social tolerance had better inhibitory control skills than low tolerant species. Our main hypothesis is that the more tolerant species, living in more complex social environments, will outperform the less tolerant species in the main components of inhibitory control: *inhibition of a distraction*, *inhibition of action* and *inhibition of a cognitive set*. For our project, we tested 66 macaques from three

different species with different social tolerance degrees: rhesus macaques (*Macaca mulatta*, grade 1: less tolerant macaque species, we will refer to this species as the low tolerant species), long-tailed macaques (*M. fascicularis* grade 2: species with intermediate level of social tolerance, we will refer to this species as the medium tolerant species), and Tonkean macaques (*M. tonkeana*; grade 4: highly tolerant macaque species, we will refer to this species as the high tolerant species). We hypothesised that the more tolerant a species is, the better inhibitory performances this species will have in all three domains of inhibitory control.

## 4.3 Materials and methods

### 4.3.1 Subjects

We tested the same 28 rhesus macaques (from the CPUS and the MRC), 20 long-tailed and 18 Tonkean macaques as in Chapter 3 (see 3.5.1, for subjects and housing conditions).

### 4.3.2 Apparatus and procedures

We used the same general procedure and the same apparatus as in chapters 2 and 3 (see 2.3.2 and 3.3.2). Subjects had free and voluntary access to the apparatus and were never restrained. All tests were conducted in the enclosure, with no isolation from the social group. The experimental setup was transported from one cage to another and adjusted for each individual. As before, all experimental procedures were carried out using MATLAB. To avoid interruption, research assistants distracted non tested individuals at the opposite side of the cage. The session was paused if the subject exceeded the time limit and restarted if the subject touched a red cross. The session could also be aborted if the subject was not focusing its attention on the task or if other conspecifics interacted with the touchscreen. The rewards (dry raisins) for each correct answer were given by hand.

### 4.3.3 General statistical analysis

We applied the same method of analysis as in chapter 3. The outcome variables, analysed separately for each task, were the inhibitory control performances of all macaque species pooled together. As we demonstrate in chapter 3 that the factors sex and age influenced inhibitory control performances, we decided to include them as general controlling factors in this comparative analysis. We also fitted the models with tolerance degrees (high, medium or low). In the lowest tolerant species individuals from two different institutions were tested. Thus, we included the factor institution when we analysed the subjects' performances in this species. The last explanatory variable category was experimental factors to control for habituation and learning: trial number, session number and the type of stimulus depending on the experiment (see below for each task specific analysis). The random factor of individual identity remained in all models to account for repeated measures of individuals.

As in chapter 3, we used linear mixed models and general linear models from the same packages with the same parameters (see 1.3.3). We also applied backward reduction to analyse the contribution of each variable on the models (see 1.3.3 for more details).

## 4.4 Inhibition of a distraction: Distraction task

### 4.4.1 Design

We use the same Distraction task validated in chapter 2 and used in chapter 3 (see chapter 2.5 for a complete description of the task). Stimulus of different valences (object, neutral or threatening conspecific faces) were presented at the same time as a target.

With this task, we wanted to see how macaques with different degrees of social tolerance managed their emotional response to distractors while doing a task. We

hypothesised that the more tolerant species will be better at controlling their emotional response to a distractor than the less tolerant species. Particularly, we predicted that the least tolerant species will have the strongest emotional response with a longer response latency toward the threatening stimulus compared to the other subjects (Bethell et al., 2012; Landman et al., 2014; Joly et al. 2017).

#### 4.4.2 Analysis

As in the previous chapters, for the analysis of the Distraction task, we computed a *Distraction control score*, representing the difference between the mean response latency in “Control” trials for each individual (baseline) minus the response latency in one trial with pictures. A higher score would indicate better control of a distraction, as the subject’s reaction to the stimuli interfered less with the goal of the task. As before, we applied the following transformation (as advised in Field et al. 2012; Tabachnick et al. 2007):

$$\text{normalised } \textit{Distraction control score} = \sqrt{(\max(\textit{Distraction control score} + 1)) - \textit{Distraction control score}}$$

We computed LMMs (function ‘lme’ from the R package ‘nlme’ v3.1-144, Pinheiro et al., 2019) with normalised Distraction control score as the outcome, demographic (tolerance, sex, age and institution for the low tolerant species) and experimental factors (trial, session and type of picture) as explanatory variables. Type of picture was nested within the individual identity. We used the function ‘contrasts’ (from the package ‘stats’ v.3.6.2, R Core Team, 2019; Chambers & Hastie, 1992) to look at the difference between “Control” trials and trials with pictures in general, to look at the difference between a picture of an object and a face and between a neutral and a threatening face. We also used the post-hoc test Tukey’s Honest Significant Difference test (Tukey HSD test, function ‘glht’,

package 'multcomp', version 1.4-18, Hothorn, 2008), to analyse the difference between species with different degree of tolerance and between each type of pictures.

As described before, we recorded the number of times each subject withheld any response (freezing behaviour), reaching the time limit (35s), while still focusing their attention on the screen (Bethell et al., 2019a). We also used GLMMs with a Poisson distribution and the same explanatory variables as before to look at the effect of these factors (tolerance, sex, age, institution for the low tolerant species and type of picture) on the number of responses withheld.

Finally, we also looked at the number of facial expressions displayed by the subjects from the different species toward each type of trials ('bared teeth', 'open mouth teeth', 'teeth chattering', 'lip smacking'). We used zero-inflated regression models (function 'zeronfl' from the package 'pscl', version 1.5.5, Jackman, 2020) via maximum likelihood to analyse the effect of social tolerance or the type of picture on the number of facial expressions displayed by the subjects. We compared the model obtained to a null model without the predictor using a chi-squared test on the difference of log likelihoods (function 'pchisq' from the package 'stats', version 3.6.2, R Core Team, 2019). We then completed the analysis with a Tukey post Hoc test to analyse the effect of each category.

#### 4.4.3 Results

There was no effect of the institution for the species of the lowest tolerance grade for this Distraction task ( $\chi^2_1 = 0.292$ ,  $N = 28$ ,  $P = 0.589$ ). Therefore, we pooled all the macaques of the lowest grade together.

**Distraction control score**All sessions together

We first started to analyse all sessions together, for all types of trials. We found a significant main effect of the tolerance degree on the normalised Distraction control score ( $\chi^2_2 = 15.481$ ,  $N = 66$ ,  $P < 0.001$ ). When looking at the LMM results (Table 4.1), we found that the species with medium tolerance had significantly higher scores (results are not normalised here,  $M = 350.21$  ms,  $S.D. = 5983.53$ ) than species with lower tolerance ( $M = 514.91$  ms,  $S.D. = 5609.27$ , see Table 4.1). The effect was barely significant for the difference between medium and high tolerant species ( $M = 122.08$  ms,  $S.D. = 4324.94$ ).

Predictors		Estimate	Std. Error	t value	Pr(> t )
<b>(Intercept)</b>		95.019	2.157	44.042	0.000
<b>age</b>		-0.012	0.132	-0.103	0.9127
<b>sex</b>	female vs male	0.502	1.360	0.369	0.669
<b>tolerance</b>	low vs high	2.608	1.709	1.497	0.091
	high vs medium	3.349	1.736	-1.929	0.049*
	low vs medium	5.922	1.560	-3.797	0.000***
<b>type of picture</b>	control vs picture	0.553	0.164	3.382	0.001**
	object vs face	0.877	0.2777	3.162	0.002**
	threat vs neutral	-1.194	0.482	-2.475	0.013*
<b>trial</b>		-0.075	0.030	-2.506	0.012*
<b>session</b>		-2.780	0.331	-8.405	0.000***

Table 4.1. Results of the LMM for the normalised Distraction control score (Distraction task) when all the sessions were taken together. Explanatory variables were individual characteristics (sex, age and tolerance), experimental determinants (type of picture, trial and session). All full models included the type of picture nested in the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, t-value and p-value are represented. 6822 observations were analysed. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

When running the Tukey Post Hoc test (Table 4.2), we found the same difference between medium and low tolerant species, but we did not find the difference between medium and high tolerant species so this difference was not considered as truly significant.

<b>Tolerance degree</b>	<b>Estimates</b>	<b>Std. Error</b>	<b>Z value</b>	<b>Pr (&gt; z )</b>
low - high	2.605	1.516	-1.718	0.198
high - medium	3.317	1.653	2.007	0.110
low - medium	5.922	1.560	-3.797	0.000***

Table 4.2. Results of the Tukey HSD test comparing the normalised Distraction control for each tolerance degree (low, medium and high tolerant species), all sessions together. \*\*\*  $p < 0.001$

When all sessions were taken together, the type of pictures presented during a trial also had a main significant effect on the Distraction control trial ( $\chi^2_3 = 27.203$ ,  $N = 66$ ,  $P < 0.001$ ).

When looking at the LMM result (Table 4.1.), the Distraction control score for the trials with pictures (results are not normalised here,  $M = -106.1$  ms,  $S.D. = 5609.77$ ) were lower than Distraction control scores of “Control” trials ( $M = 42.79$  ms,  $S.D. = 5083.78$ ).

Distraction control scores of trials with pictures of an object ( $M = 256.34$  ms,  $S.D. = 5183.16$ ) were higher than the Distraction control score of trials with pictures of a face ( $M = -289.80$  ms,  $S.D. = 5806.33$ ).

Finally, Distraction control scores of trials with a threatening stimulus ( $M = -539.18$  ms,  $S.D. = 6057.79$ ) were lower than Distraction controls of trials with neutral stimulus ( $M = -44.93$  ms,  $S.D. = 5536.69$ ).

When looking at results of the Tukey HSD test (Table 4.3), we can see that the “Threatening” stimulus has the most distracting effect with a lower Distraction control score than “Control” and “Object” trials. Threatening stimuli tended to be more distracting than neutral ones but the difference was not statistically significant.

Type of picture	Estimates	Std. Error	z value	Pr (> z )
Control - Neutral	-1.895	0.858	-2.210	0.120
Object - Neutral	-1.438	0.959	-1.498	0.437
Threat - Neutral	2.388	0.965	2.475	0.063 .
Object - Control	0.457	0.855	0.535	0.950
Threat - Control	4.284	0.863	4.965	<0.001 ***
Threat - Object	3.826	0.965	3.967	<0.001 ***

Table 4.3. Results of the Tukey HSD test comparing the normalised Distraction control score all sessions together, for each type of picture: Control (no picture presented), Neutral (a picture of a neutral conspecific face presented), Threat (a picture of the face of a threatening conspecific is presented), Object (a picture of an object). \*\*\*  $p < 0.001$

There were also significant main effects of the trial ( $\chi^2_1 = 6.27$ ,  $N = 66$ ,  $P < 0.05$ ) and the session ( $\chi^2_1 = 70.33$ ,  $N = 66$ ,  $P < 0.0001$ ) on the Distraction control score when all the session were taken together. As the trials and sessions increased the Distraction control score was higher as the subjects were getting habituated and less distracted by the stimuli.

The factors age and sex a had no effect on the Distraction control score.

### Session 1

With repeated exposure to the same picture, the monkeys were quickly getting habituated, so we chose to analyse the Distraction control score for the first session to capture their initial emotional reaction.

Predictors		Estimate	Std. Error	t value	Pr(> t )
<b>(Intercept)</b>		96.243	3.352	28.708	0.000
<b>age</b>		0.044	0.237	0.187	0.853
<b>sex</b>	male vs female	-0.909	2.352	-0.386	0.701
<b>tolerance</b>	low vs high	7.535	2.847	-2.647	0.010*
	high vs medium	0.282	3.133	-0.09	0.929
	low vs medium	7.817	2.923	-2.675	0.009**
<b>type of picture</b>	control vs picture	1.245	0.301	4.136	<0.000** *
	object vs face	1.332	0.494	2.694	0.0071**
	threat vs neutral	-2.314	0.865	-2.675	0.008**
<b>trial</b>		-0.021	0.056	-0.375	0.708

Table 4.4. Results of the LMM for the normalised Distraction control score (Distraction task) for session 1. Explanatory variables were individual characteristics (sex, age and tolerance), experimental determinants (type of picture and trial). All full models included the type of picture nested in the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, t-value and p-value are represented. 2102 observations were analysed. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

As before there was a significant main effect of the tolerance degree on the normalised Distraction control score ( $\chi^2_2 = 9.857$ ,  $N = 66$ ,  $P < 0.01$ ). The least tolerant species had the lower Distraction control score (given not normalised here,  $M = -1279.12$  ms,  $S.D. = 6396.71$ ), compared to the medium tolerant species ( $M = -235.24$  ms,  $S.D. = 6814.77$ ) and the highest tolerant species ( $M = 293.29$  ms,  $S.D. = 4133.27$ , see Table 4.4. and Figure 4.1.). When looking at the Tukey Post Hoc test (Table 4.5.), we found the same difference with the low tolerant species being different from the medium tolerant species and the high tolerant species.

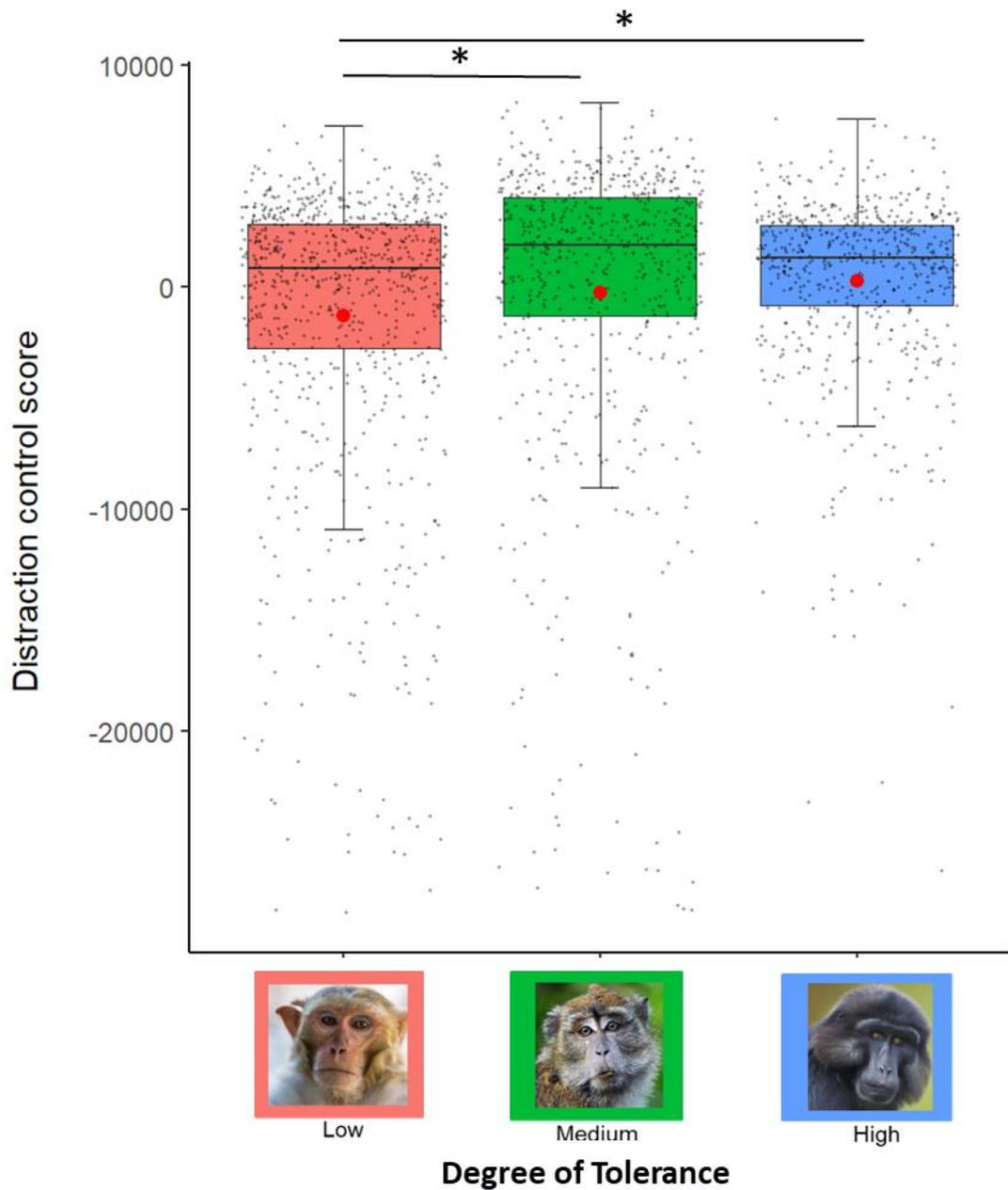


Figure 4.1. Distraction control score (not normalised) between species with low, medium and high tolerance, for session 1 of the Distraction task. Lower tolerant species had a lower Distraction control score than medium and high tolerant species. The red dot represents the mean. Horizontal lines represent the 25th, 50th and 75th percentile and error bars are represented. Black dots represent each data point \*  $p < 0.05$  (from the analysis of the models).

Tolerance degree	Estimates	Std. Error	Z value	Pr (> z )
low - high	7.535	2.487	-2.47	0.022*
high - medium	0.282	3.133	0.090	0.996
low - medium	7.817	2.923	-23.675	0.021*

Table 4.5. Results of the Tukey HSD test comparing the normalised Distraction control score for each tolerance degree (low, medium and high tolerant species), for session 1. \*  $p < 0.05$

When looking at session 1, the type of pictures presented during a trial also had a main significant effect on the Distraction control score ( $\chi^2_2 = 30.506$ ,  $N = 66$ ,  $P < 0.001$ ). When looking at the LMM result (Table 4.4.), the Distraction control score for the trials with pictures (results are not normalised here,  $M = -69.51$  ms,  $S.D. = 5602.427$ ) were lower than Distraction control scores of “Control” trials ( $M = 151.24$  ms,  $S.D. = 5206.49$ ). Distraction control scores of trials with picture of objects ( $M = -217.1$  ms,  $S.D. = 5485.02$ ) were higher than Distraction control score of trials with pictures of a face ( $M = -827.8$  ms,  $S.D. = 6363.585$ ). Finally, Distraction control scores of trials with a threatening stimulus ( $M = -1653.67$ ,  $S.D. = 7213.77$ ) were lower than Distraction control scores of trials with neutral stimulus ( $M = -655.47$  ms,  $S.D. = 6252.41$ ). When looking at results of the Tukey HSD test (Table 4.6.), we can see that the “Threatening” stimulus has the most distracting effect with a lower Distraction control score than “Control”, “Object” and “Neutral” trials. “Neutral” trials also had a lower Distraction control score than “Control” trials. The other explanatory factors (age, sex and trial) did not have a significant effect on the Distraction control score.

Type of picture	Estimates	Std. Error	z value	Pr (> z )
Control - Neutral	-3.995	1.552	-2.573	0.049*
Object - Neutral	-1.678	1.706	-0.984	0.758
Threat - Neutral	4.615	1.731	2.667	0.038*
Object - Control	2.317	1.553	1.492	0.441
Threat - Control	8.61	1.579	5.452	<0.001***
Threat - Object	6.293	0.729	3.64	0.002**

Table 4.6. Results of the Tukey HSD test comparing the normalised Distraction control score for session 1, for each type of picture: Control (no picture presented), Neutral (a picture of a neutral conspecific face presented), Threat (a picture of the face of a threatening conspecific is presented), Object (a picture of an object). \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

**Response withheld**

When looking at the number of responses withheld, there was a significant main effect of the tolerance degree, ( $\chi^2_3 = 25.759$ ,  $N = 66$ ,  $P < 0.001$ , Figure 4.3.).

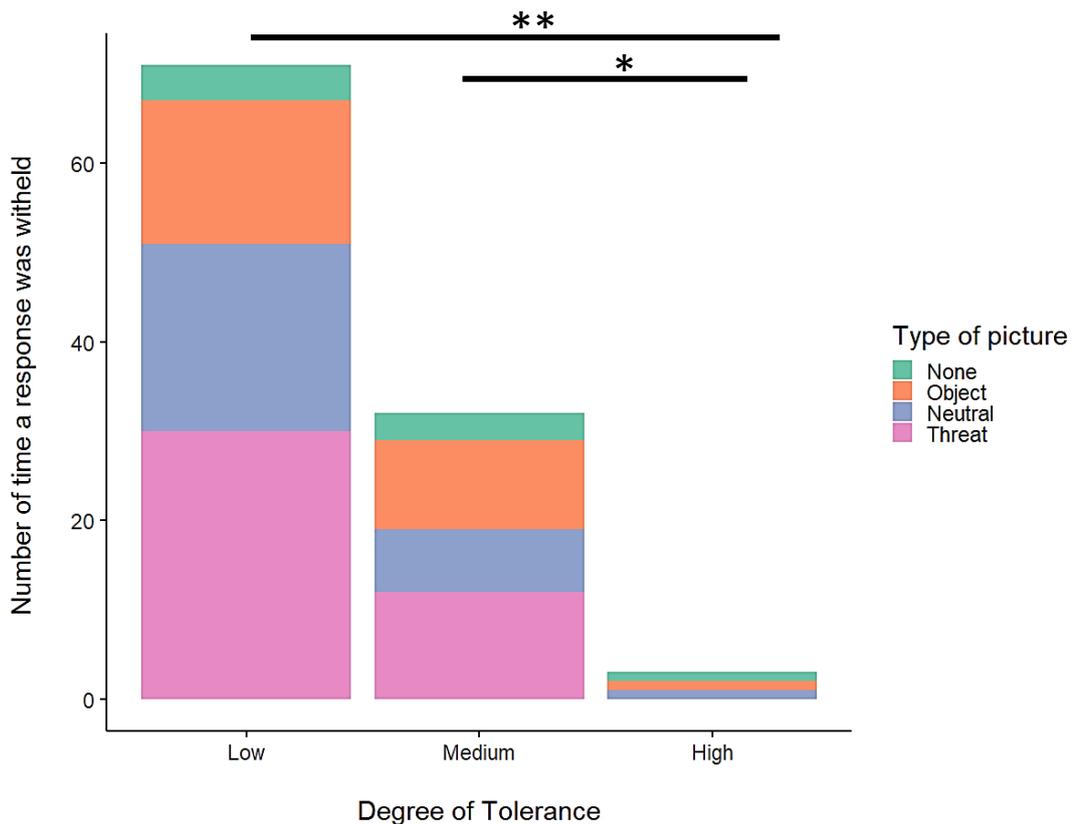


Figure 4.2. Number of times a response was withheld for each tolerance degree (low, medium or high tolerant species) and the type of picture (None: no picture, Object: picture of an object, Neutral picture of a neutral conspecific's face and Threat picture of a threatening conspecific's face). High tolerant species withheld their response less than low and medium tolerant species. \*  $p < 0.05$

The species with medium tolerance (response withheld 80 times) and low tolerance (116 times) withheld more their response than high tolerant species (68 times, see Table 4.7.).

Predictors		Estimate	Std. Error	z value	Pr(> z )
<b>(Intercept)</b>		-1.799	0.598	-3.009	0.003
<b>age</b>		0.029	0.043	0.685	0.493
<b>sex</b>	male vs female	0.131	0.442	0.296	0.768
<b>tolerance</b>	low vs high	2.282	0.698	-3.272	0.001**
	medium vs high	1.798	0.742	2.422	0.015*
	medium vs low	-0.485	0.512	-0.947	0.344
<b>Type of picture</b>	control vs picture	0.347	0.092	3.768	0.000***
	object vs face	0.086	0.076	1.131	0.258
	threat vs neutral	-0.185	0.121	-1.533	0.125

Table 4.7. Results of the GLMM for the number of responses withheld (Distraction task) in all sessions. Explanatory variables were age, sex, tolerance and type of picture. All full models included the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, t-value and p-value are represented. 264 observations were analysed. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$

When running the Tukey Post Hoc test (Table 4.8.), we found the same difference between high and low tolerant species. For the high tolerant species the experience with pictures did not have a main significant effect on the number of times the response was withheld ( $\chi^2_1 = 2.146$ ,  $N = 18$ ,  $P = 0.143$ ).

Tolerance degree	Estimates	Std. Error	Z value	Pr (> z )
low - high	2.278	0.687	3.316	0.002**
medium - high	1.840	0.23	2.546	0.028*
medium - low	-0.438	0.476	-0.918	0.623

Table 4.8. Results of the Tukey HSD test comparing the number of responses withheld for each tolerance degree (low, medium and high tolerant species) all sessions together. \*  $p < 0.05$ , \*\*  $p < 0.01$

We found a main significant effect ( $\chi^2_2 = 25.759$ ,  $N = 66$ ,  $P < 0.001$ ) on the number of responses withheld depending on the type of picture (Figure 4.2.). When looking at the GLMM result (Table 4.7.), the number of responses withheld in trials with pictures (98 times) were greater than the number of responses withheld with pictures in “Control” trials (8 times).

When looking at the Tukey HSD test (Table 4.9.), the number of times a response was withheld in “Threatening” trials (42 times), in “Neutral” trials (29 times) and in “Object” trials (27 times) was significantly higher than “Control trials”.

Type of picture	Estimates	Std. Error	z value	Pr (> z )
Control - Neutral	-1.288	0.399	-3.225	0.007**
Object - Neutral	-0.071	0.267	-0.267	0.993
Threat - Neutral	0.370	0.241	1.534	0.401
Object - Control	1.216	0.402	3.022	0.013*
Threat - Control	1.658	0.386	4.299	<0.001***
Threat - Object	0.442	0.247	1.791	0.268

Table 4.9. Results of the Tukey HSD test comparing the number of response withheld, for each type of picture: Control (no picture presented), Neutral (a picture of a neutral conspecific face presented), Threat (a picture of the face of a threatening conspecific is presented), Object (a picture of an object). \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$

**Emotional reactions**

The number of facial expressions in response to stimuli (“bared teeth”, “lip smacking”, “teeth chattering”) depended on the type of picture. Individuals of the species with the lowest tolerance reacted 18 times to the “Threatening” conspecific faces, and 6 times to the “Neutral” conspecific. The medium tolerant species reacted 4 times to “Neutral” conspecific faces and 4 times to “Threatening” conspecific faces. The highly tolerant species never reacted to pictures of conspecifics. None of the individuals reacted to “Control” trials with no pictures and “Object” trials ( see Figure 4.3. and Table 4.10).

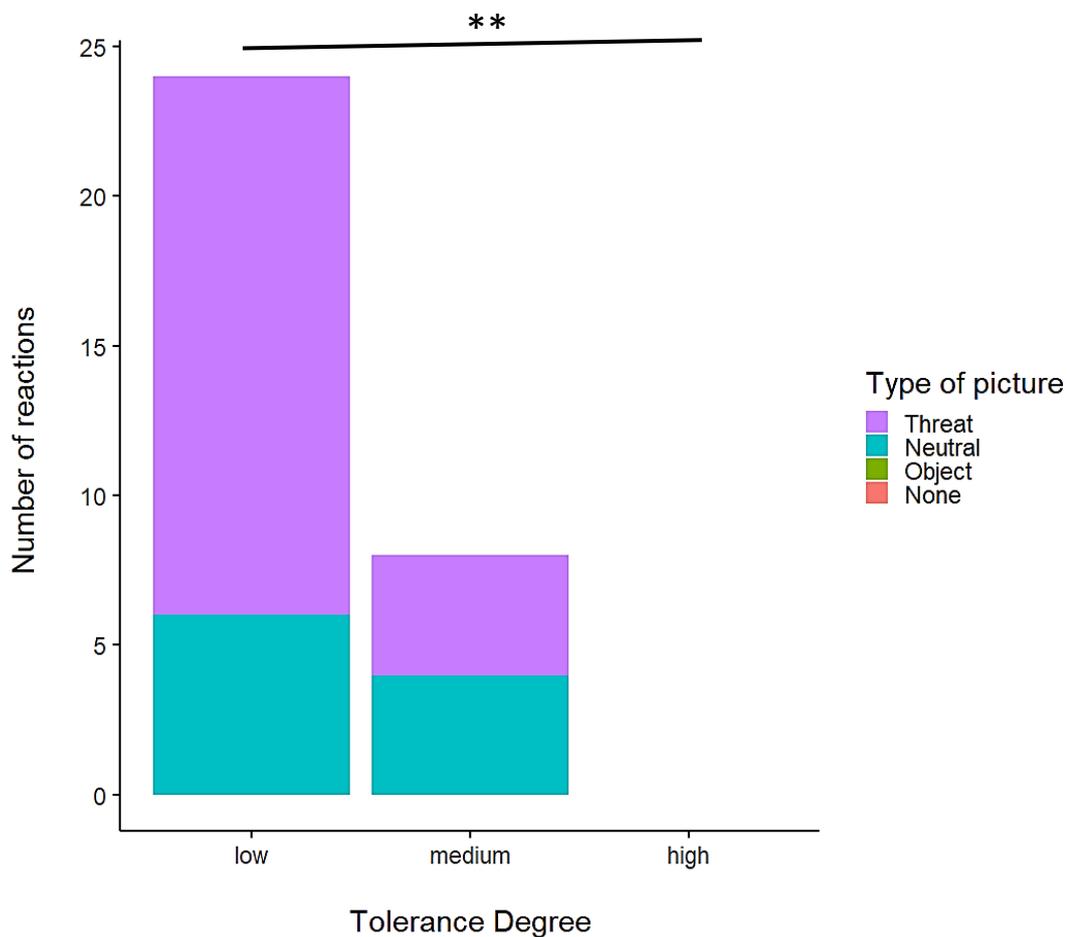


Figure 4.3. Number of emotional reactions for each species tolerance grade (low, medium or high tolerant species) and the type of picture (None: no picture, Object: picture of an object, Neutral picture of a neutral conspecific’s face and Threat picture of a threatening conspecific’s face). Low tolerant species made more emotional responses than high tolerant species. \*\*  $p < 0.01$

			Tolerance		
			Low	Medium	High
Type of pictures	Control		0	0	0
	Object		0	0	0
	Neutral		6	4	0
	Threat		18	4	0

Table 4.10. Summary of the number of emotional reactions (threats, lips smacking and teeth chattering toward the screen) for each tolerance degree (low, medium and high tolerant species) and the type of picture (control: no picture, picture of an object, picture of a neutral conspecific and picture of a threatening conspecific).

There was a main significant effect of the tolerance on the number of emotional reactions (Chi-squared test, Log likelihood  $p < 0.01$ ). When looking at each species separately we found thanks to the Tukey post-hoc test a difference between high and low tolerant species (Table 4.11.) with tolerant species displaying more emotional responses.

Tolerance degree	Estimates	Std. Error	Z value	Pr ( $> z $ )
high - low	-0.214	0.068	3.176	0.0043**
high - medium	-0.100	0.056	1.791	0.1725
low - medium	0.114	0.088	1.305	0.3923

Table 4.11. Result of the Tukey HSD test comparing the number of emotional responses for each tolerance degree (low, medium and high tolerant species) all sessions together. \*\*  $p < 0.01$

There was also a main significant effect of the type of picture on the number of emotional reactions (Chi-squared test, Log likelihood  $p < 0.001$ ). When looking at each type of picture separately (Table 4.12.), we found that the individuals made more emotional reactions toward the “Threatening” stimulus compared to “Object” trials or compared to “Control” trials.

Type of picture	Estimates	Std. Error	z value	Pr (> z )
Control - Neutral	-0.152	0.061	2.492	0.0611
Object - Neutral	-0.152	0.061	2.492	0.0611
Threat - Neutral	0.182	0.134	-1.356	0.527
Object - Control	0.000	7.03e-6	0.000	1.000
Threat - Control	0.333	0.120	-2.788	0.027*
Threat - Object	0.333	0.120	-2.788	0.027*

Table 4.12. Results of the Tukey HSD test comparing the number of emotional reaction, for each type of picture: Control (no picture presented), Neutral (a picture of a neutral conspecific face presented), Threat (a picture of the face of a threatening conspecific is presented), Object (a picture of an object). \*  $p < 0.05$

Two rhesus macaques were not willing to participate in further testing after this task.

#### 4.4.4 Discussion

In line with our hypothesis, we found a significant difference in the *inhibition of a distraction* between species with different degrees of social tolerance (see Table 4.20. for a summary of the results). In this distraction task, less tolerant species were more distracted by the pictures than intermediate and highly tolerant species. When looking at the number of withheld responses, which could be interpreted as a freezing behaviour (no response while staring at the screen), low and medium tolerant species withheld their responses more than high tolerant species. Finally when looking at the number of emotional expressions low tolerant species made more emotional expressions than high tolerant species. Medium tolerant species produced some emotional reactions but there was no significant difference with the other species. High tolerant species did not express any emotional reactions toward pictures. To summarise, low tolerant species had the worst performances in all measurements of the Distraction task. They were less able to control their emotional response to a social distractor. High tolerant species had the best performances; they controlled their emotional response in all measurements. The picture was intermediate for medium tolerant species, they were still able to control their

emotional reaction toward the distractors while performing the task, but they still demonstrated emotional reactions toward social pictures.

First, we found a significant difference in the control of a distraction while doing a task; low tolerant species were more distracted by the stimulus than medium and high tolerant species. We also found a significant difference in the emotional reaction toward pictures. Low and medium tolerant species withheld more their responses and the low tolerant species made more emotional facial expressions compared to high tolerant species. None of the individuals from the high tolerant species reacted to the pictures, even the four individuals naïve to pictures. One explanation for this increase in the emotional arousal, only found in low and medium tolerant species, could be the difference in negative valence associated with the threatening facial expression used in the experiment. It is possible that, in low and medium tolerant species, the “open mouth threat” has a stronger negative valence than in high tolerant species. Similarly, it has been demonstrated that the “silent bare teeth”, has a different meaning depending on the species considered. This facial expression is used to express submission in rhesus and long-tailed macaques (Thierry, 2017). On the contrary, in Tonkean macaques, the silent bared teeth is used to signal peaceful intentions and affiliation (Thierry et al., 1989, 2000). There is no formal sign of submission in Tonkean macaques (Thierry et al., 1989, 2000). Thus, in our study, this difference in facial expression meaning, could explain why high tolerant species did not emotionally react to the picture of conspecifics, as the meaning and valence of the facial expression displayed vary between species.

Besides, it is possible that the threshold of arousal is higher in the most tolerant species and the design we used (with only pictures) was not powerful enough to elicit an

emotional response in this species. It would be interesting to compare performances of these three species but using positive stimuli (food or positive facial expression such as lip smack). A study in Japanese macaques and chimpanzees showed that positively valenced stimuli had one of the most distracting effects (compared to neutral and threatening stimuli; Hopper et al., 2021). We could also replicate the same experiment using videos instead of pictures as animals have been shown to react strongly to videos (Fagot & Vauclair, 2000).

Another possible influencing factor which can explain species differences is recent stressful experiences. In chimpanzees (Allritz et al., 2016) or in rhesus macaques (Bethell et al., 2012, 2016; Howarth et al., 2021) recent veterinary procedures strongly influence the attentional bias of the subjects toward threatening stimuli. At the CPUS, medium tolerant species were frequently anaesthetised to collect cerebrospinal fluid and blood samples (at least once a month). Thus it could be argued that they live in a more stressful environment than high tolerant species (living in semi-captivity with less frequent veterinary interventions) and thus be more distracted by the threatening stimuli. However, we found no difference in the distraction score between high and medium tolerant species. It would be interesting to integrate recent stressful experiences in our analysis to have a more accurate understanding of the effect of stress on inhibitory control performances.

Finally, the factors age and sex had no effect on the Distraction control score which contradicts what we found when analysing each species separately (see chapter 3). It is possible that these factors influenced species' performances in opposite directions, cancelling the effect. For instance, in the *inhibition of distraction* task, males from the low

tolerant species had the poorest performances, but, in the medium tolerant species, females performed the poorest. Overall these findings, in opposite directions, could lead to an absence of effect when taking all macaque species together.

## 4.5 Inhibition of an action: Go/No-go task

### 4.5.1 Design

We used the Go/No-go task validated in chapter 2 (see chapter 2.5 for a complete description of the task). The subjects had to touch a “Go” stimulus while refraining from touching a less frequent “No-go” stimulus.

With this task, we wanted to investigate whether macaques with different degrees of social tolerance managed their impulsive action differently. We hypothesised that the more tolerant subjects will be better at controlling their impulsive action and will less frequently touch the No-go stimulus (Joly et al., 2017).

### 4.5.2 Analysis

For the second task, the Go/No-go task, to quantify the individual’s ability to inhibit its prepotent action, we recorded, as in chapter 3, the *success* in a trial when a No-Go was presented (i.e. not touching the No-go stimulus). We computed GLMMs (function ‘glmer’ from the R package ‘lme4’ v1.1-21, Bates et al., 2015) with accuracy as the outcome, demographic (tolerance, age, sex and institution for the low tolerant species) and experimental factors (trial and session) as explanatory variables. Individual identity was included as a random factor. A higher probability of success for No-go trial would indicate an individual better at inhibiting the action.

4.5.3 Results

There was no effect of the institution for the species of the lowest tolerance for this task ( $\chi^2_1 = 2.026$ ,  $N = 26$ ,  $P = 0.155$ ). Therefore, we pooled all the macaques of the lowest grade together.

All sessions together

When taking all sessions together, there was a significant main effect of the tolerance degree on the proportion of success on a No-go trial ( $\chi^2_2 = 9.683$ ,  $N = 64$ ,  $P < 0.01$ ).

When looking at the GLMM results (Table 4.13.), the species with medium tolerance had higher scores than species with lower tolerance. The effect barely reached statistical significance for the difference between medium and high tolerant species

Predictors		Estimate	Std. Error	z value	Pr(> z )
<b>(Intercept)</b>		0.168	0.297	0.567	0.571
<b>sex</b>	male vs female	-0.025	0.177	-0.142	0.887
<b>age</b>		-0.017	0.017	-0.958	0.338
	low vs high	-0.426	0.214	-1.992	0.046*
	medium vs high	0.300	0.231	1.303	0.192
<b>tolerance</b>	medium vs low	0.726	0.219	3.322	0.001**
<b>trial</b>		-0.001	0.003	-0.453	0.650
<b>session</b>		0.116	0.027	4.311	0.000***

*Table 4.13. Results of the GLMM for the probability of success in the Go/No-go task for a No-go stimulus when all the sessions were taken together. Explanatory variables were individual characteristics (sex, age and tolerance), experimental determinants (trial and session). All full models included the type of picture nested in the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, t-value and p-value are represented. 3150 observations were analysed. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .*

When looking at the Tukey Post Hoc test (Table 4.14.) we only found a difference in the probability of success on a No-go trial between the medium tolerant species and the high tolerant species. Therefore, we considered it as the only true significant difference.

Tolerance degree	Estimates	Std. Error	Z value	Pr (> z )
low - high	-0.426	0.214	1.993	0.114
medium - high	0.300	0.231	-1.303	0.393
medium - low	0.727	0.219	3.322	0.003**

Table 4.14. Results of the Tukey HSD test comparing the success on a No-go trial for each tolerance degree (low, medium and high tolerant species) all sessions together.

The explanatory factor session had also a main significant effect on the proportion of success on a No-go trial ( $\chi^2_1 = 18.672$ ,  $N = 64$ ,  $P < 0.001$ ), with better performances as the number of sessions increased. The other variables (sex and age) did not have a significant effect on the proportion of success on a No-go trial.

#### Session 5

As performances increased with the number of sessions, we looked at subjects' performances at their last session. When looking at the GLMM results (Table 4.14.), the species with medium and high tolerance had higher scores than species with lower tolerance.

Predictors		Estimate	Std. Error	z value	Pr(> z )
<b>(Intercept)</b>		0.355	0.369	0.962	0.336
<b>sex</b>	male vs female	-0.442	0.251	-1.761	0.078.
<b>age</b>		-0.005	0.024	-0.224	0.823
<b>tolerance</b>	low - high	-0.701	0.301	2.334	0.020*
	medium - high	0.189	0.326	0.579	0.563
	medium - low	0.890	0.312	2.854	0.004**
<b>trial</b>		0.003	0.008	0.403	0.687

Table 4.15. Results of the GLMM for the probability of success in the Go/No-go task for a No-go stimulus for session 5. Explanatory variables were individual characteristics (sex, age and tolerance) and trial. All full models included the type of picture nested in the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, t-value and p-value are represented. 624 observations were analysed. \*  $p < 0.05$ , \*\*  $p < 0.01$

When looking at the Tukey Post Hoc test (Table 4.16) we found only the difference between the low tolerant species and the medium tolerant species. Therefore, we considered it as the true significant difference (Figure 4.4.).

Tolerance degree	Estimates	Std. Error	Z value	Pr (> z )
low - high	-0.702	0.301	2.334	0.051.
medium - high	0.189	0.326	-0.579	0.813
medium - low	0.890	0.312	2.854	0.012*

Table 4.16. Results of the Tukey HSD test comparing the success on a No-go trial for each tolerance degree (low, medium and high tolerant species) for session 5. \*  $p < 0.05$

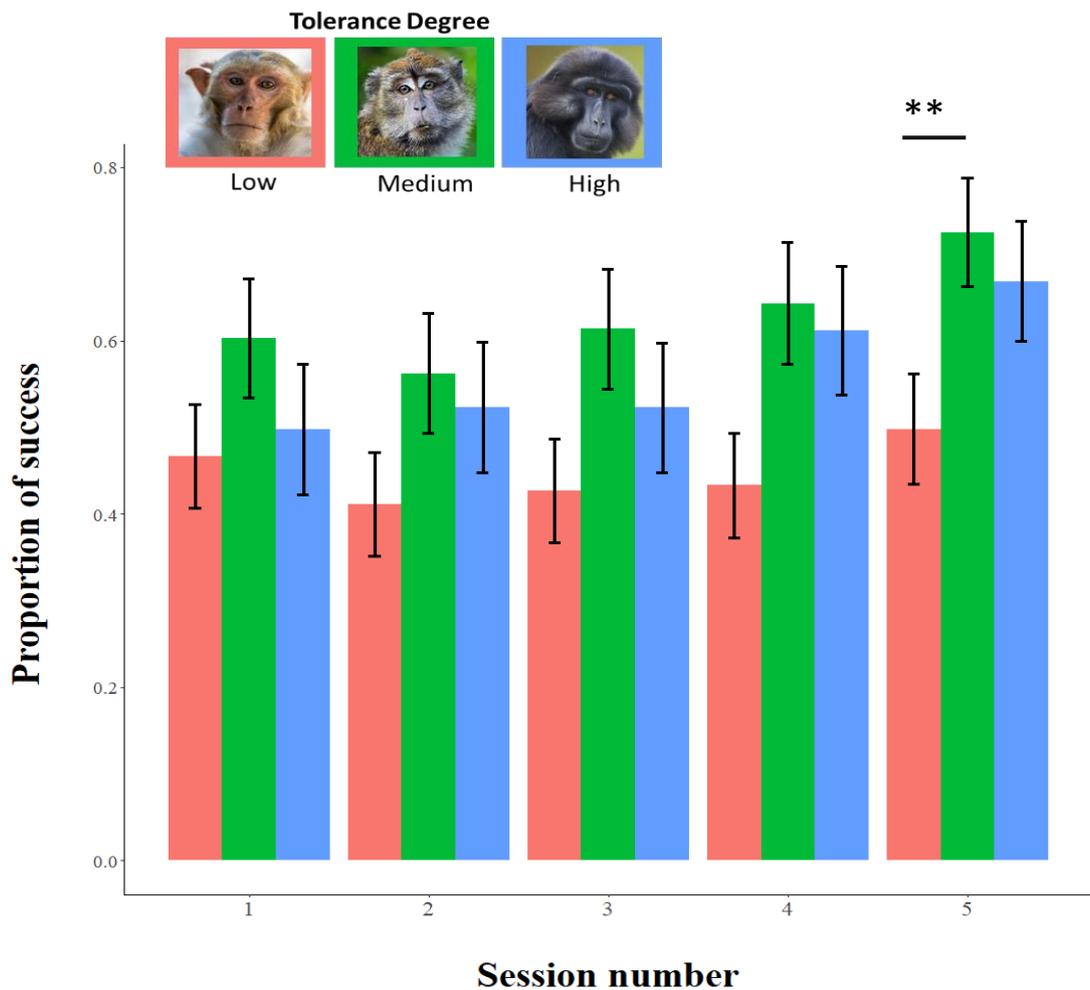


Figure 4.4. Proportion of success for each session in low, medium and high tolerant species. Error bars are represented. \*\*  $p < 0.01$  (from the analysis of the models)

#### 4.5.4 Discussion

We demonstrated that the low tolerant species had worse accuracy than the medium tolerant species. The low tolerant species had a tendency to have worse performance than the high tolerant species. In this task, only medium and high tolerant species learned through sessions and were above the chance level (see chapter 3, 3.5.3.) for the last session. Overall, in this task the low tolerant species were more impulsive than the other species (see table 4.20. for a summary of the results).

Low tolerant species have been shown to be more impulsive and emotionally reactive than medium and high tolerant species (Thierry 2010, 2017). This reactivity and impulsivity could impair low tolerant species' capability of focusing their attention in learning a new rule. For instance, in marmoset (*Callitrix jacchus*), high emotional reactivity impaired animal's attention in cognitive testing (Schubiger et al., 2015). Lowest performances in low tolerant species could be also explained by differences in cognitive abilities. For instance, Joly and colleagues (2017) found that high tolerant species outperformed low tolerant species in a socio-cognitive task (the pointing task) and in a simple task of inhibition of an action (the middle cup task). However, in this study, there was no difference in performances in physical cognition tasks (e.g. a spatial memory task). Another study demonstrated that bonnet macaques (*Macaca radiata*, a tolerant macaque species placed on grade 3 on the scale of social tolerance, Thierry, 2007), outperformed rhesus macaques on spatial short memory task and on an object-reward association task (Comrie et al., 2018). The authors suggested that there might be differences in the neural systems between different species of macaque or differences in engagement of alternate cognitive strategies during learning. These results should be interpreted with caution as

only females were tested in bonnet macaques and mostly male in rhesus macaques (24 males out of 35 individuals). This unbalanced sampling could have led to a sex bias in favour of bonnet macaques. Similarly, Hare and colleagues (2007), demonstrated that the more tolerant bonobo species (*Pan paniscus*) outperformed the more despotic chimpanzee species (*Pan troglodytes*) in a cooperative task. Another study showed that chimpanzees outperformed bonobos in tool and physical causality tasks, but bonobos outperformed chimpanzees in a theory of mind task and tasks of social causality (Hermann et al., 2010). It is possible that inhibitory control relates more to socio-cognitive abilities (e.g., as it allows individuals to behave appropriately in a social group), that would explain why high tolerant species have better inhibitory performances than lower tolerant species but only in social tasks (such as cooperative tasks and theory of mind tasks). However, in a more basic socio-cognitive task, Barbary macaques (medium degree on the scale of tolerance) and rhesus macaques did not differ in their performances (Arre et al., 2020). In this task the subjects had to take a human's visual perspective as an experimenter looked for an object at an unexpected location. It is possible that this interspecies difference only emerges in task tapping in higher socio-cognitive functions, such as inhibitory control, essential to navigate in a complex social environment. Further studies are needed to better understand the impact of social tolerance on performances in social or non-social tasks and the degree of task complexity needed to reveal an interspecies difference.

Contrary to what we expected, high tolerant species did not have the best accuracy in this task (but only a tendency to be better than the low tolerant species). It is possible that highly tolerant species had the same inhibitory control skills as intermediate tolerant species in this task. This lack of difference could also be due to a high number of high ranked males in our sample of high tolerant species which could have decreased the

overall performance in this species. Males have been shown to be more impulsive and more perseverent (see Chapter 2.2.4.4). For instance, human studies demonstrated that women outperform men on the no-go trials, indicating greater inhibition (Sjoberg & Cole, 2018; Yuan et al., 2008). Similarly, a study in guppies also demonstrated sex differences in tasks of *inhibition of an action*, the cylinder and the tube task (Lucon-Xiccato et al., 2020a,b). It is possible that male performances (even if not significantly different from females' performances), slightly lower the overall high tolerant species' performances and thus decreasing the difference between high and low tolerant species, with only a tendency to have significantly different performances.

## 4.6 Inhibition of a cognitive set: Reversal learning task

### 4.6.1 Design

We used the same design as the Reversal learning task described in chapter 2 (see chapter 2.5 for a complete description of the task). With this task, we assessed how macaques with different degrees of social tolerance control an automatic pre-learned response to learn a new rule. As before, we used the Reversal learning task in which the subjects first learn a stimulus-reward contingency (acquisition rule). Once a pre-specified criterion is reached, this first association is reversed (reversed rule). Subjects must then inhibit a prepotent response to previously correct stimuli and shift responses to a new stimulus-reward contingency. We hypothesised that the highly tolerant species would be less distracted by the previously learnt rule and would be less likely to persevere with the pre-learned rule.

### 4.6.2 Analysis

For the Reversal learning task, individuals were required to inhibit a response that was previously successful. As in chapter 3, we looked at the number of trials to learn the

acquisition rule and the reversed rule. To compare each species, we applied a Tukey multiple comparison of means (function 'glht' from the package 'multcomp', Hothorn et al., 2008).

We also recorded the perseverative error (number of errors on the wrong stimulus when the trial was a failure, meaning the individual did not touch the correct stimulus at first). We log transformed the number of errors to better approximate a normal distribution of the residuals. We computed LMMs (function 'lme' from the R package 'nlme' v3.1-144, Pinheiro et al., 2019) with the number of trials or perseverative errors as the outcome, demographic (tolerance, age and sex) and experimental factors (trial, session and rule) as explanatory variables. Individual identity was included as a random factor.

#### 4.6.3 Results

##### ***Number of trials to learn the rules***

Here we analysed the acquisition rule and the reversed rule separately (Figure 4.5.). For the acquisition rule, there was a main significant effect on the tolerance on the number of trials to learn the rule ( $\chi^2_2 = 12.856$ ,  $N = 63$ ,  $P < 0.01$ ). From the pairwise comparison, there was a significant difference between low and high tolerant species ( $p < 0.01$ ) and between medium and low tolerant species ( $p < 0.05$ ). Low tolerant species needed more trials ( $M = 106.4$ ,  $S.D. = 94.47$ ) than medium tolerant species ( $M = 58$ ,  $S.D. = 41.5$ ) and high tolerant species ( $M = 40$ ,  $S.D. = 20.58$ ). For the reversed rule, there was no main significant effect on the tolerance on the number of trials to learn the rule ( $\chi^2_2 = 1.038$ ,  $N = 63$ ,  $P = 0.361$ ). From the Tukey's post Hoc test, we found the same absence of difference between species (Table 4.17.). Low tolerant species needed as many trials ( $M = 81.67$ ,  $S.D. = 76.2$ ) to learn

the rules as medium (M = 93.68, S.D. = 69.92) and high tolerant species (M = 117.78, S.D. = 96.5).

<b>Tolerance degree</b>	<b>Estimates</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr (&gt; z )</b>
high - low	-36.11	025.21	-1.433	0.331
high - medium	-24.09	26.59	-0.906	0.638
low - medium	12.02	24.83	0.484	0.879

*Table 4.17. Result of the Tukey HSD test comparing the number of trials to learn the reversed rule for each tolerance degree (low, medium and high tolerant species).*

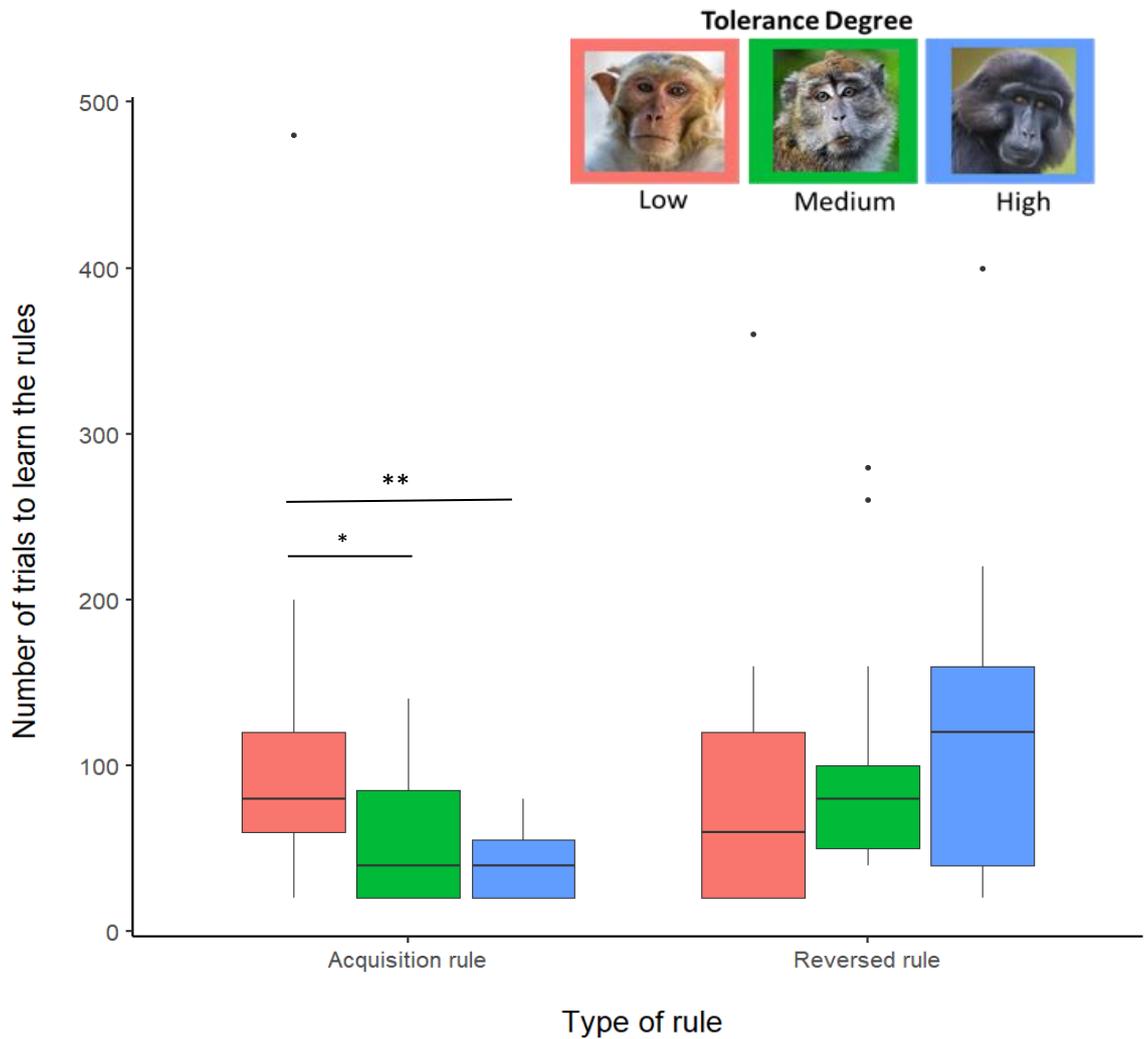


Figure 4.5. Number of trials to learn the rules (acquisition or reversed rules for each tolerance degree (low, medium and high tolerant species). Low tolerant species needed more trials to learn the acquisition rule. \*  $p < 0.05$ , \*\*  $p < 0.01$  (from the pairwise comparison).

#### Perseverative errors

We also looked at the number of errors a subject made on a trial or the number of perseverative errors (i.e. when the subject did not touch the correct stimulus at first, how many times did he keep touching the wrong stimulus before switching to the correct stimulus, Figure 4.6.). We found a main significant effect of the tolerance on the number of perseverative errors ( $\chi^2_2 = 11.149$ ,  $N = 63$ ,  $P < 0.01$ ). We also found a main significant effect of the rule on the number of perseverative errors ( $\chi^2_1 = 13.481$ ,  $N = 63$ ,  $P < 0.001$ ),

the subjects made more perseverative errors on the reversed rule (Table 4.18.). We finally found a main significant effect of the session on the number of perseverative errors ( $\chi^2_1 = 35.244$ ,  $N = 63$ ,  $P < 0.001$ ), the subjects made less perseverative errors as the number of sessions increased (Table 4.18.). When looking at the LMM result (Table 4.18.), we found that high tolerant species made less perseverative errors than medium and low tolerant species. We found similar results when looking at the Tukey's HSD test (Table 4.19.), with high tolerant species making less perseverative errors than medium and low tolerant species.

In the low tolerant species, there was a significant main effect of the institution on the number of perseverative errors, the low tolerant species from the MRC made more perseverative errors than the low tolerant species from the CPUS ( $\chi^2_1 = 12.11$ ,  $N = 25$ ,  $P < 0.001$ ). We ran the analysis again with and without the 6 remaining low tolerant species from CPUS, it did not alter the results, the low tolerant species were still making more perseverative error than the high tolerant species and there was still no difference between medium and low tolerant species. When comparing models, age and sex did not have a main significant effect on the number of perseverative errors.

Predictors		Estimate	Std. Error	t value	Pr(> t )
<b>(Intercept)</b>		1.775	0.068	26.219	0.000
<b>age</b>		-0.007	0.004	-1.487	0.142
<b>sex</b>	male vs female	0.062	0.046	1.342	0.185
<b>tolerance</b>	medium vs low	-0.036	0.057	-0.642	0.523
	high vs low	-0.200	0.056	-3.591	0.001**
	high vs medium	-0.163	0.061	2.668	0.010*
<b>rule</b>	reversed vs acquisition	0.073	0.020	3.643	0.000***
<b>session</b>		-0.033	0.006	-5.910	0.000***

Table 4.18. Results of the LMM for the number of perseverative errors (normalised) for the Reversal learning task. Explanatory variables were individual characteristics (sex, age and tolerance), experimental determinants (acquisition or reversed rule and session). All full models included the type of picture nested in the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, t-value and p-value are represented. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$

Tolerance degree	Estimates	Std. Error	Z value	Pr (> z )
medium - low	-0.037	0.057	-0.657	0.788
high - low	-0.190	0.056	-3.367	0.002**
high- medium	-0.153	0.062	-2.459	0.037*

Table 4.19. Results of the Tukey HSD test comparing the number of perseverative errors for each tolerance degree (low, medium and high tolerant species). \*  $p < 0.05$ , \*\*  $p < 0.01$

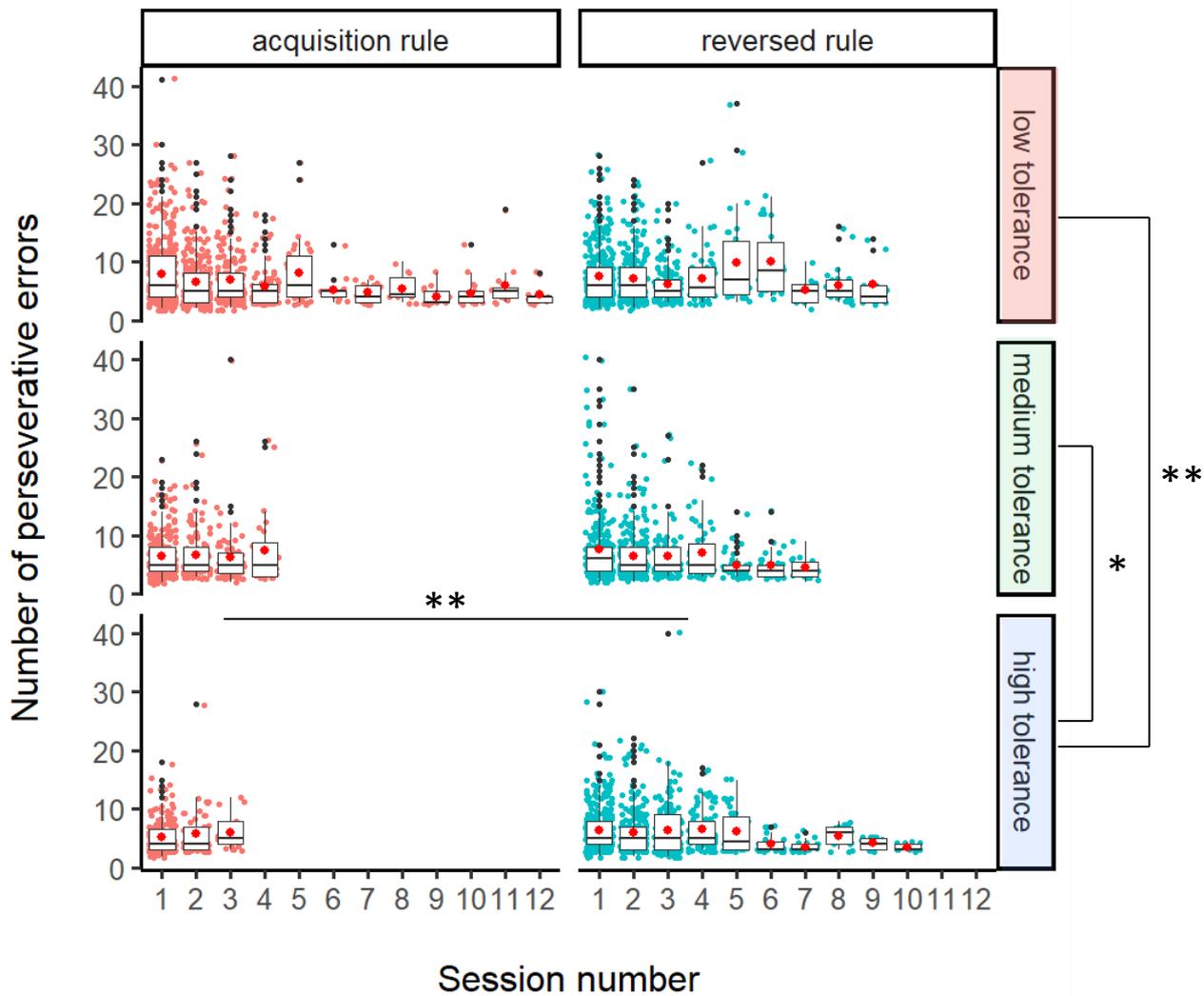


Figure 4.6. Number of perseverative errors (number of incorrect responses on the wrong stimulus) for the different sessions, the type of rule (acquisition or reversed rule) and the species tolerance degree (low, medium or high tolerance). Species with tolerance made overall less perseverative errors than species with medium and low tolerance. Only high tolerant species made more perseverative errors on the reversed rule compared to the acquisition rule. \*  $p < 0.05$ , \*\*  $p < 0.01$  (from the analysis of the models)

#### 4.6.4 Discussion

We demonstrated that the low tolerant species needed more trials to learn the acquisition rule compared to the medium and high tolerant species. All species needed the same number of trials to learn the reversed rule. Regarding the number of perseverative errors, the low and medium tolerant species were more perseverative than the high tolerant species (see Table 4.20. for a summary of the results).

This species difference in the Reversal learning task could be due to a difference in cognitive ability between species. As discussed in 3.3.4, it is possible that low tolerant species have lower socio-cognitive skills such as inhibitory control compared to high tolerant species. Supporting this, we also found that the high tolerant species was less perseverant in their mistakes than the other species. It could be due to a better flexibility in the high tolerant species compared to lower tolerant species.

The previously learnt rule only distracted medium and high tolerant species in learning a new rule (see 2.5.3), low tolerant species had similar performances in the acquisition and in the reversed rule. It is possible that only medium and high tolerant species truly comprehend and memorise the first acquisition rule which would explain why they had trouble reversing it. The low tolerant species could have learnt both rules by chance (they needed a high number of trials to learn both rules), without truly understanding it. When looking at the accuracy on trials in the low tolerant species (see chapter 2, 2.6.2), there was a difference between the rules, so it is possible that low tolerant species were still influenced by the reversed rule (worse accuracy on the reversed rule) but it is not clear if they truly understood the overall task. To test this argument we looked at the accuracy of the low tolerant species from for the MRC, for the reversed rule, at the first session, first trial, at time point 1 (the first time the subjects were tested on the reversed stimulus, see chapter 2) and we compared it to their accuracy for the same reversed rule, at the first session, first trial, at time point 2 (2 weeks after the subjects reached the criterion of success at time point 1). There was no statistical difference between their accuracy at the two time points (Student test  $t = 0.333$ ,  $df = 33.472$ ,  $p = 0.742$ ). This result could mean that even if the subjects reach the criterion of success for

the reversed rule at time point 1, they did not correctly assimilate the rule as they were also performing poorly at time point 2 (Wilcoxon test, chance level = 0.5, mean proportion = 0.64,  $p = 0.236$ ). It is also possible that they did not remember the reversed rule after 2 weeks or were still influenced by the acquisition rule. It would be interesting to also test the medium and high tolerant species in the Reversal learning rule two weeks apart to see if, contrary to the low tolerant species, the subjects correctly assimilate the reversed rule.

Furthermore, this task has been criticised for not truly measuring inhibitory control. Instead, it has been suggested that this task could be a measurement of cognitive flexibility, the ability to learn from rewards and non-rewards or the ability to estimate the likelihood that reversals can occur (Izquierdo et al., 2017). We also demonstrated in chapter 2, that subjects did not have consistent performance in the *inhibition of an action* task compared to the *inhibition of a distraction* task and the *inhibition of an action* task, showing a lack of contextual validity. It was also unclear if this task really elicited a prepotent response in the low tolerant species. Further studies comparing for instance cognitive flexibility abilities and reversal learning performances could try to disentangle the implication of each cognitive process in this task.

Low tolerant species were the only species showing impairment of performance with age. Similarly, Comrie et al., 2019, looked at cognitive ageing in rhesus macaques and bonnet macaques (*Macaca radiata*) in a battery of behavioural tasks. They found that bonnet macaques outperformed rhesus macaques in the spatial short-term memory and the object-association memory. Age impairment was significantly stronger in rhesus macaques in the object recognition memory and object-reward association memory. The authors suggested that older bonnet macaques invoked compensatory neural resources

on prefrontal cortex dependent tasks more effectively than aged rhesus macaques do. As we saw before, this study had an unbalanced distribution (only females were tested in bonnet macaques and mostly males in rhesus macaques) which could have biased these results.

This greater cognitive impairment in low tolerant species could also be due to a higher level of stress experienced in this species compared to other species (as discussed in 4.3.4.4). Similarly, authors suggest that one origin of cognitive decline could be the amount of stress experienced by a subject during his life (Veenema et al., 1996). The first evidence of the neurotoxic effect of cortisol was found in male rats (Landfield et al. 1978) as it disturbs the calcium homeostasis in brain areas that are involved in cognitive processes (Landfield et al. 1992). Prolonged exposure to high-level cortisol can lead to neuronal dysfunction or death in primates (Uno et al., 1989). These results highlight the value of cross-species comparisons as not all macaque species can be an equivalent model of cognitive ageing.

## 4.7 Summary of the findings

**Legend:**

- Significantly worst inhibitory performances compared to
- No significant difference

Inhibitory control	Task outcome		Low tolerant species	Medium tolerant species	High tolerant species
<b>Control of emotions</b> <i>Distraction task</i>	Distraction control score (first session)		<b>More</b> distracted compared to medium and high tolerant species	<b>Less</b> distracted compared to low tolerant species	<b>Less</b> distracted compared to low tolerant species
	Response withheld		<b>More</b> responses withheld compared to high tolerant species	<b>More</b> responses withheld compared to high tolerant species	<b>Less</b> responses withheld compared to low and medium tolerant species
	Emotional expression		<b>Higher</b> number of expressions compared to high tolerant species	Some expressions	<b>No</b> expressions
<b>Control of an action</b> <i>Go/No-go task</i>	Accuracy on a No-go trial (last session)		<b>Worse</b> accuracy compared to medium tolerant species, no learning	<b>Best</b> accuracy compared to low tolerant species, learning through sessions, above chance level	<b>Tendency</b> to be better than low tolerant species, learning, above chance level
<b>Control of a cognitive set</b> <i>Reversal learning task</i>	Number of trials to learn	Acquisition rule	Need <b>more</b> trials compared to medium and high tolerant species	Need <b>less</b> trials compared to low tolerant species	Need <b>less</b> trials compared to low tolerant species
		Reversed rule	Same number of trials	Same number of trials	Same number of trials
	Perseveration	Both rules	<b>More</b> perseverant compared to high tolerant species	<b>More</b> perseverant compared to high tolerant species	<b>Less</b> perseverant compared to high tolerant species

Table 4.20. Summary of the results of the 3 tasks for low, medium and high tolerant species.

## 4.8 General discussion

To summarise, we demonstrated, as expected, the best control of a distraction and emotions in the high tolerant species and the worst control of distraction and emotions in low tolerant species. The picture was intermediate in the medium tolerant species with a good *inhibition of a distraction* but displaying an emotional reaction toward pictures. In the *inhibition of an action*, we found that the medium tolerance species was the least impulsive species and the low tolerant species the most impulsive. The high tolerant species had only a tendency to be more accurate than the low tolerant species but had comparable performance than medium tolerant species regarding the learning of the task. Lastly when looking at *inhibition of a cognitive set*, the medium and high tolerant species had better learning skills compared to the low tolerant species and they were more distracted by the pre-learned rule. High tolerant species were the least perseverant compared to the other species. Overall, the low tolerant species had the worst inhibitory control performances in all three tasks; this species was the most impulsive and emotive. Medium tolerant species had the best performances in the *inhibition of an action* but intermediate performances in the *inhibition of a distraction* and of *a cognitive set*. Medium tolerant species had an intermediate level of emotivity and a good control of its impulsivity. High tolerant species had the best performances in the *inhibition of a distraction* and of *a cognitive set* but there was no clear difference to the other species in the *inhibition of an action* task. High tolerant species were less emotive and had a good control of their impulsivity.

#### Social tolerance and inhibitory control

Overall, when comparing the highest tolerant species and the lowest tolerant species we can say that our hypothesis that species characterised by higher tolerance would have better inhibitory control skills is confirmed (when considering that the high tolerant species had better performances in the *inhibition of an action task* than the low tolerant species). Developing in a more tolerant social group, socially more complex (Rebout et al., 2021), may be associated with better inhibitory control skills, corroborating the social intelligence hypothesis. These results confirm our previous findings from a basic task of inhibitory control whereby the more tolerant macaques outperformed less tolerant ones (Joly et al., 2017).

This relationship between social tolerance and cognitive skills was also demonstrated in social and physical cognitive tasks. In the social domain, several studies demonstrate that social tolerance is associated with better socio-cognitive performances. For instance in the pointing cup task, which involved cooperating with a human experimenter, more tolerant macaque species outperformed the less tolerant ones (Joly et al., 2017). In another cooperative task (simultaneously lifting a heavy stone), high tolerant species (Tonkean macaques) performed better than low tolerant species (rhesus macaques; Petit et al., 1992). Similar findings were found in non-human primates when taking “co-feeding” (to allow close proximity of others while feeding) as a measurement of social tolerance (DeTroy et al., 2021a). For instance, bonobos, considered a more tolerant species (measured by cofeeding), were better in a cooperative task than the less tolerant chimpanzees (Hare et al., 2007). More generally in the Primate Cognition Task Battery, bonobos were more skilled in social tasks (theory of mind task or social causality task) than chimpanzees (Herrmann et al., 2010).

The relationship between social tolerance and physical cognition is less clear. For instance, Harrison et al., 2021, demonstrated that a more tolerant group of chimpanzees (measure by co-feeding and socio positive interactions) had better flexibility skills in tasks of foraging (subjects needed to use different types of tools depending on the context) compared to a less tolerant group. Contrarily, in another study, chimpanzees, considered as a low tolerant species, had better performances in the use of tools and the understanding of physical causality than bonobos, a more tolerant species (Herrmann et al., 2010). Similarly, in another primate research, bonobos had poorer performances in physical tasks (i.e. spatial and causality tasks) compared to chimpanzees (Herrmann et al., 2010). More research is needed to better understand the influence of social tolerance on problem solving skills.

Interestingly, a recent review argues that social tolerance at the scale of a group structure (as Thierry, 2000, 2007 defined it) should be differentiated to dyadic tolerant behaviours (e.g. co-feeding; DeTroy et al., 2021b). In this sense, a study demonstrated a strong contrast between social tolerance measured at the group level and social tolerance measured by co-feeding behaviour (Amici et al., 2020). The researchers showed, using four macaque species (*Macaca fuscata*, *M. fascicularis*, *M. sylvanus*, *M. maura*) that social tolerance over food was higher in more despotic species than in less despotic species. This result seems counter intuitive when following the phylogenetic model established by Thierry, 2007; according to this theory high tolerant species are supposed to have more relaxed relationships. The authors explained their results by citing the potential influence of specific socio-ecological factors (i.e. the long-tailed macaque groups were used to humans and partially food-provisioned) which could have explained their higher tolerance over food. In our sample of macaques, it would be interesting to test food tolerance to see

if it correlates with the degree of social tolerance that species have been assigned to (by Thierry et al., 2007).

In our study, we did not find a linear correlation between social tolerance and inhibitory control skills as the picture was less clear for the species with intermediate degree of social tolerance. Medium tolerant species had, overall, good control of their impulses compared to low tolerant species and high tolerant species (for only one measurement of the *inhibition of action*). However this medium tolerant species was still comparably emotive and perseverant than low tolerant species. It is possible that fitting species with intermediate levels of social tolerance in the four-grade scale might not be as straightforward. Thierry (2000) himself calls for caution as classifying species along a discrete and bipolar scale is inevitably reducing, particularly for species with intermediate level of tolerance. The author states that each species should be represented as a cluster of points (representing each population studied) along a continuous scale. In addition, the phylogenetic model of macaque social tolerance is based on a series of studies focused on female behaviours (Balasumarian et al., 2012; Thierry et al., 2008; Thierry, 2007). As we demonstrated in this thesis, male and female macaques can drastically differ in their behaviours, it is thus possible that a new phylogenetic model based only on males' behaviours, could lead to unexpected findings.

Conversely to Thierry's model, authors suggested that social tolerance can also take root in another systematic variation model: the socio-ecological model of female relationships (Isbell & Young, 2002; Sterck et al., 1997; van Schaik, 1989). There is a consensus that social organisation patterns in behaviours in primates are linked to the environment in which they have evolved (DeTroy et al., 2021b; Isbell & Young, 2002; Sterck

et al., 1997). According to this model female relationships can be explained by a combination of variables such as predator vulnerability, food distribution, population density and inter and intra group competition. In this model, relationships varied along two dimensions: egalitarian to despotic and individualistic to nepotic (DeTroy et al., 2021b; Isbell & Young, 2002; Sterck et al., 1997; van Schaik, 1989). Later social tolerance was added as a third dimension (DeTroy et al., 2021b; Sterck et al., 1997) and characterised a situation in which a dominant individual concedes their priority to mating opportunities or food resources to subordinates. Contrary to the phylogenetic model, in the socio ecological model, tolerance is placed on a dimension separated from despotism. Here social tolerance requires a certain level of despotism with a clear dominance hierarchy (DeTroy et al., 2021b), as dominant individuals need to rely on the support of subordinates. According to this model, a dominant individual in a group with no clear hierarchy no longer needs to tolerate subordinates for coalition and collaboration. Despotism here is not considered to decrease tolerance. The authors suggest that the socio-ecological model can be represented as an inverted U-shape: “both a lack of dominance hierarchy (i.e. egalitarianism) and high levels of despotism prohibits social tolerance, while an intermediate level of despotism, combine with the reliance of dominant individuals on coalitionary support foster social tolerance” (DeTroy, 2021b; Sterck et al., 1997). It could be possible that our lack of clear relationship between social tolerance and inhibitory control skills could be due to the characterization of social tolerance. According to the socio ecological model, the medium tolerant species could be, in fact, more tolerant than the species with the higher degree of social tolerance (given by Thierry’s classification). More studies are needed to clarify the definition and measurement of social tolerance but also to better understand the relationship between social complexity and the evolution of socio

cognitive skills. One approach to reinforce our findings could be to compare inhibitory control skills in species with intermediate degree of social tolerance (e.g. Barbary macaques, grade 3 on Thierry's classification) to the performances of our sample of macaque species.

#### *Social vs ecological intelligence hypothesis*

In this thesis, we chose to follow the path of the 'social intelligence hypothesis'. However, in the literature, there are still heated debates between the supporters of the social model versus the defenders of the ecological model when looking at the selective forces that favour the evolution of cognition (Amici et al., 2008; MacLean et al., 2014). According to the 'ecological intelligence hypothesis' (Milton, 1981), larger brain size evolved to allow species to adjust their behaviour adaptively in response to foraging challenges.

We could also have wanted to interpret our results through the lens of the 'ecological intelligence hypothesis'. Species studied in this thesis have different living conditions in the wild, such as predation risk. Long-tailed macaques are likely to be the most vulnerable to predators, indeed they are smaller than the other two species, primarily arboreal, they live along rivers and in forest margins occupied by numerous predators (Crockett & Wilson, 1980; Fooden, 2006). This type of habitat could have selected them to be reactive and cautious to their environment (thus being more emotive as in our results). The larger-bodied Tonkean macaques, given their quiet behaviour and smaller group size (Crockett & Wilson, 1980), may be less likely to attract predators (they also have less predators). This small risk of predation would select quieter and less reactive behaviours (thus being less emotive and impulsive as in our results). Rhesus macaques favour open habitats where they are likely to encounter numerous smaller predators

(Fooden, 2006), and thus may benefit from being highly reactive and defending themselves by aggressive confrontation (thus being more impulsive and reactive as in our results). Species' inhibitory control (which could be associated with aggressivity, reactivity and impulsivity) might be adaptive to the predation risk (Dingemanse & Reale, 2005; Réale et al., 2007).

In comparative studies authors often confront environmental factors and another marker of social complexity, the group size, but the results are contradictory (for review see Kappeler, 2019). For instance, in a meta-analysis, brain size was associated with ecological variables (home range size, diet and activity period) but not the size of the social group (Powell et al., 2017). Similarly, brain size seems to be linked to diet, rather than multiple measures of sociality such as group size; specifically, frugivores exhibit larger brains than folivores (DeCasien et al., 2017). Regarding inhibitory control, a large comparative study, using the A-not-B and the Cylinder task to 567 individuals from 36 species, found a positive association between inhibitory control performances and the dietary diversity, particularly in non-human primates, independently of the size of the social group (Maclean et al., 2014). Pheasants with poor performance on variants of the Detour task and in the Cylinder task, also displayed a wider dietary breadth (van Horik et al., 2018b). In addition, Maclean et al., 2013, using the Cylinder task with 6 species of primates did not find an effect of the group size on their performances. On the other hand, it has been demonstrated with the Cylinder task in spotted hyenas, that developing in a larger group generates better inhibitory control skills (Ulrich-Johnson & Holekamp, 2020). This result was also found in Australian magpies with the Cylinder task and the Reversal learning task (Ashton et al., 2018). It could be argued that social group size is not an

accurate proxy for social complexity. However, measuring social complexity is rather difficult (Bergam & Beehner, 2015) as it is a volatile parameter which changes with the stability of the group, the relationships with others or the sex, the age and the rank of the individuals (Massen et al., 2010). By taking a finer proxy parameter reflecting the social landscape, such as we did with social tolerance degree, we may better predict the selective pressure acting on social cognition.

Frequently splitting and merging in subgroups of variable composition (fission-fusion dynamics) has also been proposed as one aspect of social complexity influencing inhibitory control (Amici et al., 2008; Aureli et al., 2008). A primate comparative study presented 5 tasks putatively measuring inhibitory control (the A-not B task, a variant of the detour reaching tasks, a middle cup task and a measure of self-control) to 7 species of non-human primates (Amici et al., 2008). The authors found an association between performances on these tasks and the social structure of these species. Species living in more dynamic and fluid social environments (fission–fusion societies) outperformed those having more cohesive group structures. The authors concluded primates living in more complex social groups often require inhibition of inappropriate prepotent responses in a dynamic social environment, and this partly explains why they performed better in Detour tasks. In another study in 6 species of non-human primates, with tasks of social inhibition and behavioural flexibility, Amici and colleagues (2018) demonstrated inter-species differences which reflected differences in fission-fusion dynamics. It would be interesting to replicate these results by comparing inhibitory control skills, thanks to our battery of tasks, in species differing in fission fusion dynamics. In addition, it is assumed that macaques are all cohesive societies but there might be differences in their fusion-fission

dynamic. For instance, within-group competition may result in different patterns of group fission with variation between species (Thierry, 2004). It would be interesting to investigate further the relation between macaque fission fusion dynamics and inhibitory control.

#### Difference in impulsivity, reactivity and emotivity in macaque species

Beyond differences in inhibitory control skills, it seems, when looking at our results, that differences in pattern of behaviours emerge between species. Rhesus macaques could be considered as more impulsive, perseverant, reactive and emotive than the other species of macaques. Long-tailed macaques could be considered as emotive and reactive, perseverant but not as impulsive as rhesus macaques. Finally, Tonkean could be considered as less reactive, emotive, perseverant or impulsive than the other species of macaques. In the literature, several authors have described differences in temperament between macaque species for more than 50 years. For instance, Davis and colleagues (1968), found that rhesus macaques were considerably more vigilant, neophobic and easily aroused than pigtailed (*Macaca nemestrina*) or stumptails macaques (*M. arctoides*), both high tolerant species. Similarly, Caine and colleagues (1981), found that rhesus macaques showed much more vigilant behaviour than bonnet macaque (*M. radiata*), another high tolerant species. It is possible that this high degree of reactivity associated with high impulsivity could be associated with aggressive behaviours. For instance, researchers described rhesus macaques as being more aggressive and hostile than other species (significantly more than long-tailed and pigtailed macaques; Clarke and Mason, 1988; Sussman et al. 2013). In captive social groups, rhesus macaques engage in more frequent and more severe intergroup aggression than other macaques (Bernstein et al., 1983;

Thierry, 1985; Ruehlmann et al., 1988; Thierry, 2000). For instance, rhesus macaques' hourly rates of aggression are about twice that of pigtail macaques (Bernstein et al., 1983) and they received more than twice as many wounds as pigtailed macaques (Ruehlmann et al., 1988). To summarise, an impairment in inhibitory control abilities could make low tolerant species more reactive and impulsive compared to other species and thus more aggressive toward others.

On the other hand, researchers have described long-tailed macaques as being shy, more cautious and fearful than lion-tailed macaques, and bonnets macaques, both high tolerant species (Clarke & Lindburg, 1993; Sussman et al. 2013). Both long-tailed and pigtailed macaques show comparatively less social aggression and more friendly behaviours toward humans (Bernstein et al., 1983; Thierry, 2000; Maestriperi, 2005; Thierry, 2006). It seems that long-tailed macaques are an emotive species but still less aggressive than rhesus macaques. Intermediate level of inhibitory control (good cognitive and action control but still not as good as high tolerant species at controlling their emotions) could be linked to medium tolerant species' fearful but still friendly temperament.

Finally, researchers described high tolerant species such as the Tonkean macaques as being less aggressive, not easily aroused and impulsive and as having a more friendly temperament compared to lower tolerant species (Thierry, 2000, 2007). Good inhibitory control skills could be linked to high tolerant species temperament associated with a good control of emotions, a good control of action and cognitive set. Differences in raising conditions and in field study methodologies might relate to differences in species

temperament. However, the directions of these differences are consistent in most of these comparative studies and fit with our findings in this study.

#### Difference in the serotonergic system

We have demonstrated that species with different tolerance degrees have different abilities in inhibitory control which could be associated with a disparity in their temperament. But the mechanisms underlying these species differences remain unclear. In the literature, several authors described a link between the serotonergic system and differences in impulsivity, aggressivity and emotional reactivity (Weinberg-Wolf & Chang, 2019). For instance, a neurochemical study looked at the functional allelic variation in the transcriptional control region of the serotonin pathway (serotonergic transporter and monoamine oxidase A genes) in different macaque species (Wendland et al., 2006). Both these genes have been associated with anxiety- and aggression-related behaviour in humans and, more recently, in non-human primates (Caspi et al., 2003; Munafò et al., 2003; Sen et al., 2004; Roseblum et al., 2002 ; Wendland et al., 2006). Interestingly, a team of researchers found that tolerant species (stump-tailed, Barbary, and Tibetan macaques) were monomorphic for both the serotonin transporter genes, with the exception of Tonkean macaques displaying two alleles for one of the gene (the monoamine oxidase A gene; Wendland et al., 2006). On the contrary, more intolerant macaques (pigtailed, long tailed, and rhesus macaques) appear to be polymorphic for these genes (as humans do). Moreover, the most intolerant species (rhesus macaques) displayed the largest number of alleles at both loci, and it is the only species that possesses the S allele of the serotonin transporter. It could be possible that interspecies genetic variability could

be partly responsible for the difference in inhibitory control performances (Wendland et al., 2006).

Furthermore, in captive rhesus macaques researchers demonstrated a link between stressful early rearing experience and serotonergic transporter gene expression (Champoux et al., 2002; Kinnally et al., 2010). This association between environment and gene expression influenced attentional and affective capabilities, aggressivity and stress response (Barr et al., 2004; Newman et al., 2005; Weinberg-Wolf & Chang). More particularly, central serotonin is implicated in several species in regulating maladaptive aggression (Weiberg-Wolf & Chang, 2019). Low central serotonin level has been linked to only one sub-type of aggression: impulsive aggression (unprovoked or unproductive) as it will not help an individual to secure dominance status or maintain access to resources (Higley & Linnoila, 1997). Interestingly a modulation of the central serotonin function impacts impulsivity, perseverative behaviours and cognitive biases (Mendelsohn et al., 2009; Merens et al., 2007; Riedel et al., 2002; Weiberg-Wolf & Chang, 2019). For instance, increasing the central serotonin system seems to decrease negative attentional biases and a depletion may heightened aversive valence of emotional stimuli (Harmer et al., 2004, 2006). Similarly, authors demonstrated that long-tailed macaques with reduced serotonergic activity had increased aggressive responses to a threatening slide picturing humans (Kyes et al., 1995). The strength of this modulation is dependent on the prior experience of the individuals such as parental deprivation (Higley & Linnoila, 1997; Weiberg-Wolf & Chang, 2019).

Most importantly, several authors clearly established an association between the serotonergic system and inhibitory control (for review see Pattij & Schoffelmeer, 2015;

Robbins and Crockett, 2010). For instance, depletion in the serotonergic system was associated with a lack of inhibitory control in rats in humans using the Go/No-go task, the Stop signal task, the Stroop task, the Reversal learning task and the 5CSRTT task (Nomura et al., 2016; Pattij & Schoffeleers, 2015; Robbins & Crockett, 2010). Researchers also replicated these findings in rhesus macaques using the reversal-learning task (Vallender et al., 2018).

Furthermore, authors demonstrated biological correlates between the serotonin system activity and differences in aggressivity and stress responsiveness in different species of macaques. For instance, higher aggressivity was associated with lower serotonergic activity in rhesus macaques compared to pigtailed macaques (Westergaard et al., 1999). Interestingly, it has been suggested that the diversity in serotonergic function may be linked to social styles across species. Low rates of serotonin are responsible for a pattern of behaviours as reported in rhesus macaques (impulsivity, aggressivity, easily aroused, bias to threat stimuli). According to the authors, species with more despotic dominance hierarchies have greater diversity in social threat and would have developed more variations in genes related to serotonergic function (Weiberg-Wolf & Chang, 2019).

To summarise, whereas serotonin clearly modulates inhibitory control processes, the exact mechanisms remain unclear. Differences in the serotonergic system, either genetic and/or in environmental factors, can explain differences in temperament between species which could also be linked to differences in inhibitory control. Overall, a decrease in the serotonin system associated with a stressful rearing experience activity is related in low tolerant species with high aggressivity and poor inhibitory control performances.

Social instability in social interactions linked to cortisol level

Another mechanism underpinning differences in inhibitory control between species could be the cortisol system associated with group instability. First, we know that species with different degrees of social tolerance vary in their group stability (Thierry 2000, 2007) and degree of uncertainty (Rebout et al., 2021). Researchers have described low tolerant species as having a strict and rigid dominance hierarchy which is more stable than in other species (Thierry, 2000, 2007) with more predictable social interactions (Rebout et al., 2021). In these social groups, female members of the same family hold similar dominance positions and support kin against lower-ranking families. This results in a dominance hierarchy that remains relatively stable often for the entire life of an adult individual (Thierry, 2000, 2007; Walter et al., 1987). In medium tolerant species, kinship is also important in social interaction but the level of aggression is less important (Thierry 2000, 2007). In high tolerant species, kinship is not an important factor as rank varies by body weight. Frequent altercation, and counter aggression are frequent, which lead to a high uncertainty in the social interactions (Rebout et al., 2021; Thierry 2000, 2007). Social life in these species of macaques results in long-term differences between individuals in levels of psychosocial stress (Higham et al., 2013).

Similarly, a recent study (Sadoughli et al., 2021) demonstrated a difference in cortisol level (marker of chronic stress) in medium tolerant species (long-tailed macaques) and in high tolerant species (Tonkean macaques). Both groups were living in the same semi free-ranging condition (the group of Tonkean was the same as the large group we studied in our study). Surprisingly, hair cortisol concentrations were significantly higher in the more relaxed Tonkean macaques than in the despotic long-tailed macaques (with no

difference between males and females). The authors suggested that this difference could be due to a difference in uncertainty in the social interactions. Authors suggest that in high tolerant species, male-male competition, frequent alpha turnover, and frequent low-grade agonistic interactions may lead to a social structure with low levels of predictability. Furthermore, a tolerant organisation may fail to buffer socially induced stress because of the lack of predictable long-lasting bonds. Social instability makes it difficult to know whether and from whom an attack will come, or help will come. Interestingly, a recent study demonstrated a higher degree of social uncertainty in Tonkean macaques compared to rhesus macaques (Rebout et al., 2021). However, unpredictability in the hierarchy is among the strongest social stressors in primates and it can lead to a rise in cortisol concentrations across species (Bergman et al., 2005; Preis et al., 2019; Wooddell et al., 2016).

Moreover the mating strategies are different between high and low tolerant species. Long-tailed and rhesus macaques are seasonal breeders and use opportunistic breeding, as multiple females can be ovulating at the same time (Thierry, 2007). Whereas Tonkean macaques need to adopt a mate guarding strategy as the breeding is spread all year-round (Thierry, 2007). In more tolerant species there is a skew toward high-ranking males, which can lead to high-risk tactics for rank acquisition in males; males must aggressively challenge top-ranking males and defeat them to gain access to females. This mating pattern could also be at the source of a higher stress level in male Tonkean macaques. It would be interesting to compare cortisol levels in rhesus macaques living in similar conditions. According to these authors as the hierarchy is more predictable and more stable in rhesus macaques, they should have a counterintuitively lower-level of cortisol, marker of a lower chronic stress. Interestingly these results were similar to a study

in rhesus monkeys comparing a group with a steep and despotic hierarchy and a group with a more relaxed hierarchy. Researchers found that low ranking individuals, living in a less steep hierarchy, had higher cortisol levels than high-ranking individuals. In the despotic group, there was no difference between individuals (Qin et al., 2013).

However, in the previous study (Sadoughli et al., 2021), Tonkean macaques had cortisol levels slightly above the normal range. This group could have been particularly unstable, as it was composed of a high number of high-ranked males, which cannot disperse (six males before the first higher ranked females). So these results should be considered carefully as this large group is likely not an exact reflection of natural conditions. Currently, studies on long-term cortisol concentrations are heavily skewed toward species with strict hierarchies (Davenport et al., 2006; Dettmer et al., 2014; Feng et al., 2016; Linden et al., 2019; Wooddell et al., 2016) and little is known about the distribution of cortisol concentrations in more egalitarian social systems (Marty et al., 2017). Further studies are needed to establish a clearer link between cortisol level, group stability and social tolerance.

On the other hand, human studies demonstrated a link between stress, cortisol level and difference in inhibitory control (Bradlet & Linda, 2007; Richard et al., 1992; Roelofs et al., 2007; Zhang et al., 2019). For instance, a study indicates that an individual's emotional state plays a crucial role in mediating their social attention. For example, anxious participants demonstrated a threat-related attentional biases (for review see Bar-Haim et al., 2006). In studies with chimpanzees (Allrizz et al., 2015), or rhesus macaques (Bethell et al., 2012), the subjects were more distracted by negatively valenced stimuli if they had received a recent veterinary procedure. Similarly, high levels of trait anxiety led to an impairment in the Reversal learning task in long-tailed macaques (Toxopeus et al.,

2005). One study in squirrel monkeys (*Saimiri sciureus*) demonstrated that subjects treated with cortisol simulating a prolonged stress response had impairment in inhibitory control performance (an *inhibition of an action* task with a transparent box; Lyons et al., 2000). To summarise, disparities in stress level (due to inconsistent stressful experiences such as group instability) could lead to differences in inhibitory control abilities in species with different degrees of social tolerance. The association between inhibitory control, social tolerance, and stress level remains unclear and more studies are needed to better understand the underlying mechanisms.

#### Inhibitory control and problem-solving skills

We have previously seen that inhibitory control skills are crucial in navigating a complex social environment. But, in the day-to-day life, inhibitory control seems also important to solve various physical tasks. In the literature, the relationship between this ability and problem-solving skills has been demonstrated in humans (Diamond, 1990) and in animals (Müller et al., 2016; Vlamings et al., 2010; Hauser et al., 2002). For instance, a study in cottontop tamarins (*Saguinus oedipus*), showed that inhibitory control skills were positively correlated with discrimination learning performances (i.e. choosing a piece of a cloth to access a reward; Hauser et al., 2002). Dogs' inhibitory control skills were also positively associated with the subjects' performances in a size consistency task (Müller et al., 2016). However, in the same study, dog's inhibitory control performances were negatively correlated with an on-off task (the subjects needed to pull a wooden board only if the reward was on it). Contradictory results were also found in hyenas, as inhibitory control skills (measured by a cylinder task) did not predict performance in a problem-solving task (using a multi-access box; Johnson-Ulrich, 2018). More research is needed to better understand the implication of inhibitory control in problem solving skills.

#### Limitations and future directions

Our study suffers from several limitations common in primate studies (for review see ManyPrimates et al., 2019a). First, the tested subjects did not have the same experience with cognitive experiment. The large group of high tolerant access had *ad libitum* access to touch screen modules with cognitive experiments (e.g. delay match-to-sample task) which could explain their good performances in our battery of tasks. However, the medium tolerant species, which did not have any experience of any type of cognitive testing, were better than high tolerant species in the Go/No-go task. Furthermore, four high tolerant species never worked with pictures before and showed no difference in performances compared to the group that previously worked with neutral conspecific faces. Thirteen of the low tolerant species from the MRC already took part in an experiment in which they had to look at pictures, but they were still highly reactive to pictures of conspecifics. Thus, previous experience could not totally account for the differences in inhibitory control we found.

Similarly, the high tolerant species were housed in semi-captivity with large enclosures. Differences in captive conditions could explain differences in cognitive abilities as a more enriched environment could help the individuals to develop better cognitive capacities (Davenport et al., 1973; Gallup et al., 1971; Schubiger et al., 2020). For instance, shelter dogs displayed poorer performances in the A-not-B task than pet dogs (Fagnani et al., 2016). According to the authors, shelter dogs might live in an impoverished environment with less interaction with humans which would decrease their chances to learn to inhibit certain behaviours. However, high tolerant species were still at the same level of performance than medium tolerant species for the Go/No-go and the Reversal learning task, so the environment did not lead to a difference in cognitive abilities.

Finally, there was only two groups of the high tolerant species whereas low and medium tolerant species were from several family groups in which there was a bias toward high ranking-individuals even if we could test low-ranking individuals in each species (7 low tolerant species, 9 in high tolerant species and 13 in the high tolerant species). The bias causing interaction between sex and rank was controlled for by analysing only the effect of the rank in one sex. Furthermore the ages were not distributed exactly in the same manner in the three species with, for instance we had a lack of young individuals in the medium tolerant species. This age limitation is common in primates' study so it would be interesting to use collaborating projects such as ManyPrimates et al. 2019b, to have access to a more important diversity of individuals in each species.

One factor we did not control for was the potential difference in brain size or structure between macaque species. In the animal cognitive literature it has been hypothesised that brain size predicts cognitive abilities (Horschler et al., 2019; Maclean et al., Reader & Laland, 2002, 2014) even if this hypothesis remains highly controversial (Barrett, Henzi & Rendall, 2007; Powell et al., 2017). In the inhibitory control literature, it has been demonstrated that larger-brained dog breeds had better performances, in a task of *inhibition of an action* (Horschler et al., 2019). Similarly, in a large interspecies comparison, researchers found a positive correlation between inhibitory control performances and absolute brain volume for primates' species (Maclean et al., 2014). However this relationship between inhibitory control and absolute brain size was challenged when several *Corvus* species (corvids) parallel great apes' inhibitory control performances, in the A-not-B task (Jelbert et al., 2016) and the Cylinder task (Kabadayi et al., 2016). It would be interesting to compare the brain structure and relative brain size of

the different species we used in our studies to see if differences in inhibitory control could be linked to brain differences.

### Conclusion

To conclude, we have demonstrated the content validity and repeatability of our battery of tasks. Then, in different species of macaques we looked at individual variations and potential confounding factors we needed to control for to study inhibitory control. Finally, we compared inhibitory performances in close species of macaques considering social tolerance as an evolutive factor. The next step would be to use our battery of inhibitory control tasks to compare performances in more distant species to establish the tasks external validity, i.e. if they measure the same cognitive abilities in different species (Schubiger et al., 2020). Such evaluated test batteries will then hopefully provide a solid base to further our understanding of the evolution of inhibitory control.

## Chapter 5: General Discussion

### 5.1 Overview

The overarching focus of this thesis was to develop a framework to study the main components of inhibitory control in non-human primates. First, we validated a battery of inhibitory control tasks in a species of macaque. This task battery gave us a first insight into the multifaceted structure of inhibitory control. Once this battery of tasks was validated, we used it to assess individual differences in inhibitory control across three closely related macaque species (*Macaca mulatta*, *M. fascicularis* and *M. tonkeana*). Interestingly, we replicated the common effect of sex and age on individuals' inhibitory performances, however these effects depended on the species and the task considered. These findings highlighted again the non-unitary structure of inhibitory control. In general, females had better inhibitory control performances than males except in long-tailed macaques. Older individuals had impaired cognitive performances only in rhesus macaques. Surprisingly even closely-related macaque species were not equivalent models to study individual differences in inhibitory control. Depending on the species of macaques considered, researchers studying inhibitory control should be careful to choose a balanced sample of subjects to avoid biases (sex and age biases). Once inhibitory control performances were examined at the scale of the species, we broadened our approach to an interspecies scale. We evaluated social tolerance as a factor influencing inhibitory control skills in three species of macaques with different degrees of social tolerance. We demonstrated that, rhesus macaques, the less tolerant species had the worst performances in all domains of inhibitory control. Tonkean macaques, the most tolerant species, had the best performances in all components of inhibitory control except in the inhibition of action in

which there was no difference with long-tailed macaques, the species with the intermediate level of social tolerance. This intermediate species performed well in the *inhibition of an action* and *a cognitive set* but poorly in the *inhibition of a distraction*. In summary, our results clearly indicate that the least tolerant species, living in a despotic environment with less diverse interactions, has developed poorer inhibitory control skills compared to other species of macaques. However, the picture is mixed for the species with intermediate tolerance degree, indicating that inhibitory control performances might not be predicted in a linear manner according to different degrees of social tolerance. Rhesus macaques, compared to the other species, seem to stand out as a highly impulsive, reactive, and emotive species which could have an important impact on the welfare management of this particular species in captivity. Overall, our results give more insight into the influence of social style on the evolution of cognition.

## 5.2 Main findings and implications

### 5.2.1 Inhibitory control, a complex structure

Firstly, this thesis demonstrates, as many studies before (Bray et al., 2014; Brucks et al., 2017; Duckworth & Kern, 2011; Fagnani et al., 2016; Friedman & Miyake, 2004; Marshall-Pescini et al., 2015; Nigg, 2017, Vernouillet et al., 2018), that inhibitory control is not of a unitary structure but could be considered as a suite of intricate functions. From the second chapter, we demonstrate that the *inhibition of a distraction* and the *inhibition of an action* share a common underlying inhibitory ability. However, between the *inhibition of a cognitive set* and the other functions, no clear pattern emerges that would support the notion of a common cognitive ability (as demonstrated in Friedman & Miyake, 2004). Inhibitory control could then be divided in sub-components, with on the one hand, a

cognitively low demanding process involving the inhibition of a prepotent, stimulus driven response and on the other hand a more controlled, deliberate inhibition of a mental state. Thus, authors should be careful when making evolutionary assumptions based on animal performances measured by tasks tapping on different components of inhibitory control. For example, Maclean and colleagues (2014), drew an evolutionary conclusion on the evolution of inhibitory control by comparing multiple species using the A-not-B tasks (an *inhibition of a cognitive set task*) and the Cylinder task (an *inhibition of action task*). However, it is possible that these two tasks are not measuring the same underlying ability in the species considered. A better understanding of the structure of inhibitory control is particularly crucial as impairments in inhibitory control have been associated with several psychopathologies. For instance, in children suffering from ADHD, it is still unclear if it is inhibitory control as a general ability which is impaired or only some independent components (Gaultney, 1999; Nigg 2001). Consistent with this last view, there is some evidence that individuals with ADHD are impaired on tasks measuring *action inhibition*, whereas it remains unclear if these patients are also impaired in *cognitive inhibition* tasks (Gaultney et al., 1999; Nigg, 2001).

From the third chapter, we found that individual characteristics (age and sex) influence the different components of inhibitory control inconsistently in three species of closely related macaques. Similarly dog studies have demonstrated an inconsistency in the effect of different demographic factors (e.g., age) on various inhibitory control tasks (Bray et al., 2014; Vernouillet et al., 2018). However, in some animal studies only one sex is represented when studying inhibitory control. For instance, several studies testing the distracting effect of pictorial stimuli only tested male rhesus macaques (Bethell et al. 2012,

2016; Lacreuse et al., 2013 King et al., 2012). Here, we have demonstrated that males of this species were more reactive than females which could bias the result toward a higher emotivity. Besides, in chapter 3, we demonstrated that only aged rhesus macaques had impairment in their cognitive abilities. Similarly, a study demonstrated that aged rhesus macaques had a higher cognitive impairment compared to bonnet macaques (Comrie et al., 2019). However, due to similar ageing phenotypes and cortical organisation between non-human primates and humans, different species of macaques are commonly used as equivalent models to explore cognitive ageing (Comrie et al., 2019). These findings can have a major impact in the choice of non-human primate model in biological research.

Finally, in the fourth chapter, we have demonstrated, depending on the task, important inhibitory control differences between closely related macaque species. Or most of what we know on cognition of non-human primates and inference about its evolution comes from studies on rhesus macaques, an overrepresented species in science. Rhesus macaques might not be the best representative of the cognition of all the macaques and even less of other primates (ManyPrimates et al., 2019a). Thus, we need additional cross-species studies to have a better understanding of the strengths and weaknesses of each animal model with respect to specific cognitive functions and influencing factors.

### 5.2.2 A stepwise approach to study cognitive abilities in animals

Overall, this thesis highlights the need to adopt a stepwise approach when measuring any cognitive ability in animals (see Figure 5.1; Schubiger et al., 2020). First, by developing a reliable and valid battery of tasks in one species that truly measured the tested ability (Shaw & Schmelz, 2017; Völter et al., 2018; Völter et al., 2018). Then, to use this battery of

tasks, in the same species, to gather precious information about inter individual variations (Boogert et al., 2018, Shaw and Schmelz, 2017; Thornton & Lukas, 2012; Völter et al. 2018). This second step allows us to assess potentially influencing factors such as individual (e.g., sex or age) or environmental factors (e.g., rearing conditions) that need to be controlled for as far as possible (Schubiger et al., 2020). Then, the next step would be to compare performances of the previously studied species to its closest evolutionary relatives based on social or environmental characteristics (Boogert et al., 2018, Shaw and Schmelz, 2017; Thornton & Lukas, 2012; Völter et al. 2018). As this study demonstrated, researchers need to carefully consider that a task valid in one species is not necessarily valid in another species, even a close evolutionary relative. Finally this cognitive ability could be compared between more distant species to better understand the evolution of cognitive abilities in animals and particularly in humans.

### 5.2.3 Other conditions to study the evolution of inhibitory control

After individual variations, heritability is the second condition for evolution to act upon inhibitory control (Thornton & Lukas, 2012; Thornton & Wilson, 2015). Heritability estimates provide a measure of the relative contribution of genetic and environmental factors in generating phenotypic variation (Croston et al., 2015). More specifically, it measures the part of the total variability of inhibitory control caused by genetic differences among the animals. In humans, inhibitory control is reported to be highly heritable. For instance, researchers reported that the inhibition of a dominant response is highly heritable ( $h^2 = 0.99$ ; Friedman et al., 2008). Another study reported a moderate heritability ( $h^2 = 0.27-0.50$ ), in more than 900 families tested in a modified Go/No-go task (Schachar et al., 2011). In animals, we know little about the heritability of inhibitory control performances. Bethell and colleagues (2019b), in a study of 67 female rhesus macaques,

reported a low heritability of attention to social threat ( $h^2 = 0.10$ ). In another study, Langley and colleagues (2020), using 450 pheasants, over 4 generations, demonstrated a low to moderate heritability for inhibitory control ( $h^2 = 0.17$ ). Valid and reliable battery of inhibitory control tasks could thus help to better understand heritability of inhibitory control by looking at performances over generations.

Finally, the third condition to natural selection is that the possession of this trait confers a fitness benefit, i.e., a competitive advantage in access to mating opportunities or resources (Thornton and Lukas, 2012). Given the advantages of efficient inhibitory capacities, allowing flexibility in hazardous situations (Estep et al., 1988; Lindsay et al. 1976), we can be tempted to propose that inhibitory control skills are associated with greater success and chance of survival. However, in animal research, findings are contradictory. On one hand, performance on a battery of cognitive tasks (among them the Detour reaching task and the Reversal learning task) seem to be associated with a greater female reproductive success in wild Australian magpies (*Gymnorhina tibicen*; Ashton et al., 2018). Similarly, performance of male song sparrows (*Melospiza melodia*) in an inhibitory control task (e.g. a detour reaching task and a reversal task) was correlated with song repertoire size, a trait predictive of reproductive success in this species (Boogert et al., 2011). Detour reaching performance was also influenced by robins' body condition (*Petroica longipes*; Shaw, 2017). On the other hand, pheasants' performances in the reversal learning task were negatively related with survival when released into the wild (Madden et al., 2018). Newly developed battery of inhibitory control tasks could help to better understand the relationship between inhibitory control performances and markers of fitness (e.g. reproductive success or survival).

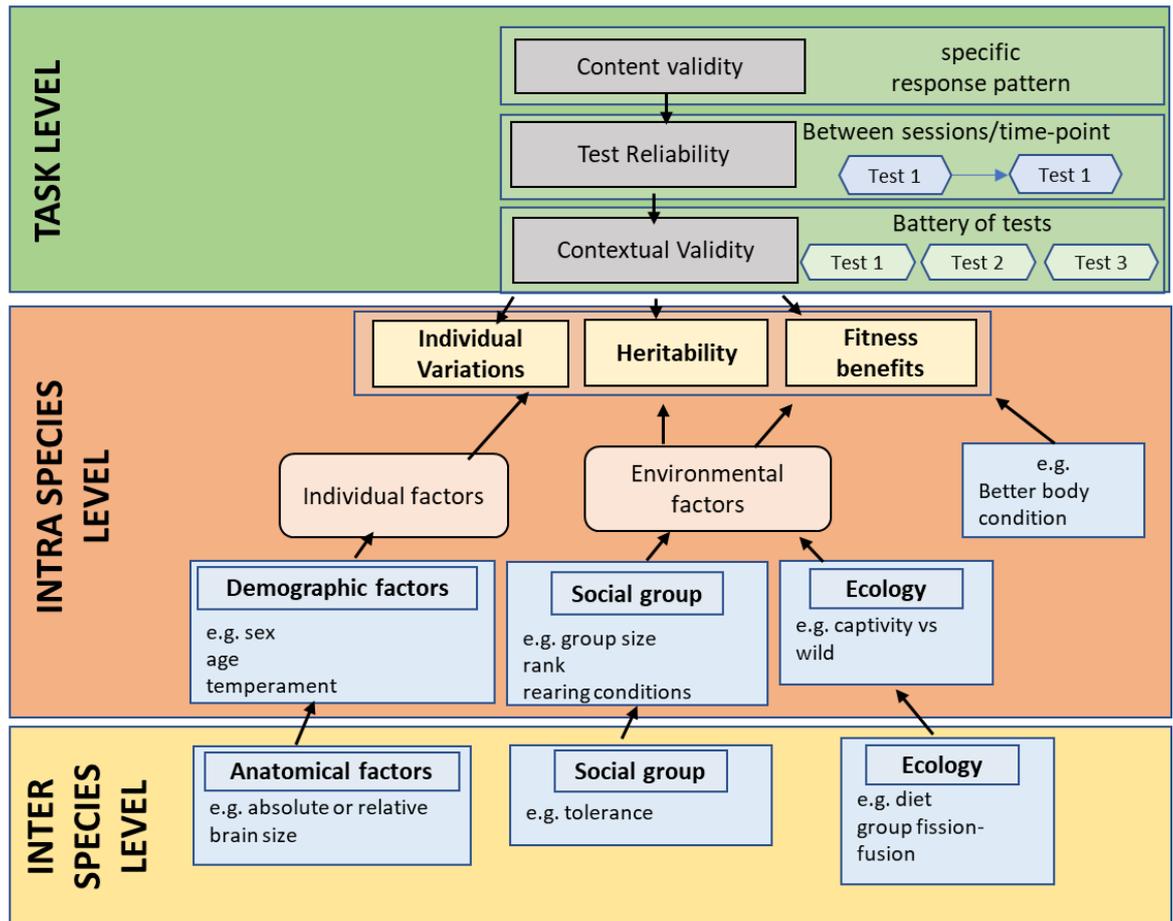


Figure 5.1. A framework to study inhibitory control and its evolution. We develop a three steps approach which starts by the validation of a battery of task (checking for content validity, test reliability and contextual validity). Then, using this task battery researchers could study intra and inter species differences to better understand the evolution of inhibitory control.

#### 5.2.4 A comparative approach in primates

Thus, interspecies comparative studies seem to be a mandatory step to better understand the evolution of inhibitory control in primates. In this thesis, the small sample size and the limited variations in age, rank and sex might have prevent us from finding stronger effects. In primate cognition research, an insufficiently diverse and large sample is an important and common limiting factor. Historically, primate cognition research has been conducted by a small number of independent teams of researchers on small populations of a few captive species. A review conducted in 2019 (ManyPrimates, 2019a) demonstrated that across 574 primate cognitive studies less than 15% of primate species were represented

and the median sample size was of only 7 individuals per study. To tackle this issue, [ManyPrimates](#) has developed a large-scale collaborative framework to develop primate comparative studies. ManyPrimates aims to offer an Open science infrastructure to pool together resources and datasets across research sites. For instance, a first pilot study, using a simple short memory task, rallied together 11 research centres, and tested more than 12 species of non-human primates (ManyPrimates et al., 2019b). More ManyPrimates projects are about to be conducted such as a study on self-control with a delay of gratification tasks. Interestingly, in the literature, one orangutan (*Pongo pygmaeus*) and four chimpanzees were able to wait for a more valuable reward for 3 min (Beran 2002), whereas rhesus macaques tested in a comparable task waited no longer than 30 sec (Evans and Beran 2007). Long-tailed macaques waited between 30 sec and 1 min (Pelé et al., 2010), and Tonkean macaques waited between 38 and 72 sec (Pelé et al., 2011). We should be cautious when interpreting these results as experimental methods can vary across studies. Using the dataset from the ManyPrimates project, with the standardised protocol of self-control, we could look at the performances of the same macaque species we tested. As in our study, it would be interesting to see if rhesus macaques are also more impulsive in this higher form of inhibitory control than the rest of macaque's species.

Most of our present understanding of animal cognition originates from research conducted on captive animals bred in laboratories or sanctuaries zoos. On one hand, experiments conducted with captive animals can help to control for intrinsic and extrinsic factors that can influence animal behaviour (e.g. test context, developmental factors, experience). On the other hand, the sample tested might be only representative of one group of individuals from one population in one specific context and can hardly be extrapolated to wild animals. It would be interesting to adapt our battery of tasks to a wild

population of macaques. Indeed, compared with captive animals, free-living populations have radically different developmental trajectories and potentially important differences in inhibitory control (Boogert et al., 2018). Recent studies made a remarkable effort to adapt inhibitory control tasks to the wild. For instance, a Reversal learning task was successfully adapted to test wild vervet monkeys (*Chlorocebus pygerythrus*; et al., 2020) or semi-captive Barbary macaques (Rathke & Fischer, 2020). Inhibitory control skills were investigated in more than 60 wild spotted hyenas using a Cylinder task (Johnson-Ulrich & Holekamp, 2020). Inhibitory control skills were also assessed in wild Australian magpies (56 adults and 21 juveniles) using one single Detour task (Ashton et al., 2018). A field-based approach offers a valuable complement to laboratory-based studies as it enables to determine whether cognitive abilities found in captive subjects are generalizable to wild animals (see Cauchoix et al, 2017). These results suggest that it would be possible to study inhibitory control abilities of wild animals directly in their natural environment in much the same way that we study captive animals.

## 5.3 Implication for animal welfare

### 5.3.1 Implications for primate welfare

In research, rhesus macaques are historically and still are the most used species of non-human primates, notably because of its close genetic relationship with humans (93% of average sequence identity; Cauvin et al., 2015; Camus et al., 2014; ManyPrimates et al., 2019a). Despite the 3R recommendations (reduction, refinement, replacement; NC3Rs, 2017), the number of macaques used in research is increasing. This trend has been exacerbated after the historic shortage of macaque subjects due to Covid-19 (Subbaraman, 2020). National organisations have since made massive investments in non-

human primate breeding. For instance the National Institutes of Health (NIH) has invested about US\$29 million over the past two years in refurbishing housing and building non-human primate enclosures (Subbaraman, 2020).

In this thesis we demonstrated that rhesus macaques had strikingly poorer inhibitory control skills compared to other closely related macaque species. However, several studies demonstrated that deficits in inhibition of distraction (attention bias toward a threatening stimulus) can be an indicator of poor animal wellbeing (Paul et al., 2005; Bethell et al., 2012; Crump et al., 2018). Authors have suggested that deficits in inhibitory control can lead to a higher level of chronic stress associated with high cortisol and low serotonin levels (Weinberg-Wolf & Chang, 2019; Wendland et al., 2006). We also demonstrated that only rhesus macaques showed impairment of cognitive abilities while ageing. We have seen in chapter 4 (see 4.3.6.4), that this greater age impairment could be linked to the neurotoxicity of high cortisol levels (Landfield et al. 1978; Veenema et al., 1996).

In the literature, high levels of cortisol and low level of serotonin (associated as we have seen in 4.5. with poor inhibitory control skills) have been correlated with neuronal dysfunction, reduced reproductive success, infant losses and patterns of high maternal abandon in female rhesus macaques (Cleveland et al. 2004). Low levels of serotonin in male rhesus macaques have been associated with frequent wounding and heightened mortality rates (Cleveland et al., 2004; Higley & Linnoila, 1996; Uno et al., 1989; Weinberg-Wolf & Chang, 2019). In wild animal populations, elevated cortisol concentration was associated with reduced survival (Campos et al., 2021), while in humans and captive animals it was associated with an increased risk of various diseases (e.g. Hostinar et al.,

2014). Another study demonstrated that rhesus macaques may be more vulnerable to develop a despair-like state compared to long-tailed macaques which made them a more suitable model of depressive disorders (Camus et al., 2014).

Despite the potentially dramatic consequences of poor inhibitory control on rhesus macaques' health and wellbeing, the "European directive on the protection of animals used for scientific purposes" makes no distinctions between macaque species for training, capture, restrain and housing conditions (Mitchell et al., 2021). Appropriate rearing conditions seem particularly crucial in rhesus macaques. For instance, the rearing environment drastically buffers the rhesus macaque infant from the potentially negative effect of serotonin deficits (Westergaard et al., 1999). Thus the captive and management conditions of the different species of macaques should not be equivalent. It is possible that, in rhesus macaques, the stress of experimental or medical manipulations has a more harmful effect on their health and wellbeing than other species. Particular care should then be developed to keep rhesus macaques' stress level as low as possible; they should, for instance, be housed in a quieter and more predictive environment, with few stressful manipulations. In rhesus macaques these specific housing conditions could improve the ease of management of social groups and the ability to train individuals for voluntary cooperation with scientific procedures.

Another solution would be to train the inhibitory control skills of the most reactive individuals to reduce their emotivity and their aggressivity. In humans, it has been demonstrated that inhibitory performances can be improved with training (Rueda et al., 2005). For instance, a study suggests that Go/No-go training paradigms can influence health behaviour (Allom et al., 2016). In this direction, in canines, researchers have found

evidence that training can increase problem-solving ability (Marshall-Pescini et al., 2008). Besides, assistance dogs trained to have low-arousal showed the most inhibition in a Detour task compared to control dogs without training (Bray et al., 2015).

Besides, several studies have demonstrated that the welfare of captive primates can be improved using cognitive testing in a zoo environment (for review see Meehan & Mench, 2007). In captive animals, implementing touchscreen computers in an enclosure offers new enrichment possibilities and simultaneously allows researchers to test cognitive abilities of non-human animals (Schmitt, 2019). For instance, macaques using a touch screen regularly have been observed to be less aggressive toward other individuals (Whitehouse et al., 2013). We could consider the implementation of touch screen modules with inhibitory control tasks in captive macaques to improve animal's welfare in captivity.

In situations in which the previous improvements could not be implemented, we could also envisage increasing the level of serotonin in the most anxious individuals. For instance in veterinary medicine, anxious and reactive animals are commonly treated with tryptophan supplementation (a precursor of serotonin) or Fluoxetine (also known as Prozac, an inhibitor of the recapture of serotonin). In human and animal patients such daily supplementation has been associated with improvements in inhibitory control skills (Robbins & Crockett, 2010). For instance, oral administration of tryptophan led to an improvement in the Stroop task, the Go/No-go task and the Reversal learning task in humans (Ilieva et al., 2005). These supplementations also significantly alleviate ADHD and depression symptoms (Robbins & Crockett, 2010). In veterinary practice, the use of Fluoxetine or tryptophan is commonly prescribed to treat deficits in 'impulse control', anxiety, aggressivity and compulsive behaviour in cats, dogs, horses and farm animals

(Kaur et al., 2016). We could consider adding these types of supplement in the diet of macaques suffering from their lack of inhibitory control.

### 5.3.1 Implication for the welfare of other species

All around the world, similar inhibitory control deficits have been commonly described in our closest companion, the domesticated dog. For instance, a Japanese study demonstrated that in 2,000 dogs tested 86 % of them had behavioural problems related to impulsivity and anxiety (Yamada et al., 2019). A recent study testing over 13,700 pet dogs in Finland found that 75% of them had anxiety and compulsivity related behavioural issues (Salonen et al., 2020). Besides, it has been demonstrated that behavioural problems such as deficit in inhibitory control increase the likelihood of aggression, relinquishment, and euthanasia (Salman et al. 2000). As in primates, training a dog's inhibitory control could also provide a simple intervention to avoid such dramatic outcomes (Olsen, 2018). As inhibitory control has been demonstrated to be heritable (see 5.2.3), strict breed legislations and restrictions would greatly benefit from improved knowledge on dog's inhibitory control (Salman et al. 2000). Breeding policies including selecting the Sire and the Dam with good inhibitory control skills could also help to improve dog's global welfare. With over 470 million pet dogs worldwide (Bedford, 2020), this inhibitory deficits can affect millions of animals and represents a major welfare issue which should be seriously considered (Salonen et al., 2020).

## 5.4 Conclusion

The findings of this thesis provide a new framework to study inhibitory control in animals. Firstly, assessing the content validity, the temporal and contextual repeatability of a battery of tasks can help to better understand the structure of any cognitive ability. The battery of tasks we developed gave us precious information about the multifaceted structure of inhibitory control. Secondly, by adopting an intra and interspecies approach, we demonstrate that not all primate models are equivalent, even closely-related species. This finding can have major implications in the choice of animal models, e.g. in biomedical research. Finally, we demonstrated that closely-related macaque species present striking differences in inhibitory control. These non-human primate species do not manage their emotions and impulsive actions consistently which can have a considerable impact on their welfare management. By adopting a four-step perspective to study inhibitory control, i.e. at the task level, the individual level, the species level, and the interspecies level, we highlight the importance of using valid tasks before making evolutionary assumptions on any cognitive ability.

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**Appendix 1. List of the articles used in the literature review**

List of the literature (79 articles in total) used in this review with the domain of inhibitory control tested, the task, the animal classes, the authors, and the name of the species. We chose articles containing at least one task of inhibitory control (from one domain of inhibitory control: inhibition of action, of a cognitive set, of a distraction or social inhibition), in at least one non-human animal species.

	Task	Classes	Reference	Species
<b>ACTION INHIBITION</b>	Cylinder task		Bray et al., 2014	dog ( <i>Canis familiaris</i> )
			Fagnani et al. 2016	
			Maclean et al. 2014	
			Marshall-Pescini et al., 2015	
			Vernouillet et al., 2018	
			Maclean et al., 2017	
			Bobrowicz & Osvath, 2018	cat ( <i>Felis catus</i> )
			Langbein, 2018	goat ( <i>Capra aegagrus hircus</i> )
			Maclean et al., 2014	coyote ( <i>Canis latrans</i> )
			Maclean et al., 2014	fox squirrel ( <i>Scurius niger</i> )
			Maclean et al., 2014	Mongolian gerbil ( <i>Meriones unguiculatus</i> )
		Mammals	Maclean et al., 2014	aye aye ( <i>Daubentonia madagascariensis</i> )
				black lemur ( <i>Eulemur macaco</i> )
				bonobo ( <i>Pan paniscus</i> )
				brown lemur ( <i>Eulemur fulvus</i> )
				capuchin monkey ( <i>Cebus apella</i> ),
				chimpanzee ( <i>Pan troglodytes</i> )
				Coquerel's sifaka ( <i>Propithecus coquereli</i> )
				golden monkey ( <i>Rhinopithecus roxellana</i> )
				golden-headed lion tamarin ( <i>Leontopithecus chrysomelas</i> )
				gorilla ( <i>Gorilla gorilla</i> )
				hamadryas baboon ( <i>Papio hamadryas</i> )
				marmoset ( <i>Callithrix jacchus</i> )
				mongoose lemur ( <i>Eulemur mongoz</i> )
				olive baboon ( <i>Papio Anubis</i> )
				orangutan ( <i>Pongo pygmaeus</i> )
				red bellied lemur ( <i>Eulemur rubriventer</i> )
				rhesus macaque ( <i>Macaca mulatta</i> )
				ring-tailed lemur ( <i>Lemur catta</i> )
ruffed lemur ( <i>Varecia variegata</i> )				
squirrel monkey ( <i>Saimiri sciureus</i> )				
Rudolph & Fichtel, 2017	red-shanked douc langurs ( <i>Pygathrix nemaeus</i> )			

<b>ACTION INHIBITION</b>	<b>Cylinder task</b>			<i>grey-shanked douc langurs (Pygathrix cinerea)</i>	
			Marshall-Pescini et al., 2015	<i>grey wolves (Canis lupus)</i>	
			Maclean et al., 2014		
			Johnson-Ulrich et al., 2018		
			Johnson-Ulrich & Holekamp 2020	<i>spotted hyenas (Crocuta crocuta)</i>	
		<b>Birds</b>	Maclean et al., 2014		<i>Eurasian jay (Garrulus glandarius)</i>
					<i>orange-winged amazon (Amazona amazonica)</i>
					<i>song sparrow (Melospiza melodia)</i>
					<i>swamp sparrow (Melospiza georgiana)</i>
					<i>western scrub jay (Aphelocoma californica)</i>
			Kabadayi et al., 2016		<i>white carnea pigeon (Columba livia)</i>
					<i>zebra finch (Taeniopygia guttata)</i>
					<i>raven (Corvus corax)</i>
			Kabadayi et al., 2017 (Sept)		<i>New Caledonian crow (Corvus moneduloides)</i>
					<i>jackdaw (Corvus monedula)</i>
		<i>blue-headed macaws (Primolius couloni)</i>			
		<i>blue-throated macaws (Ara glaucogularis)</i>			
		<i>great green macaws (Ara ambiguus)</i>			
		<i>African grey parrots (Psittacus erithacus)</i>			
	Kabadayi et al., 2017 (Nov)	<i>ravens (Corvus corax)</i>			
	van Horik et al., 2018 (March)				
	vanHorik et al., 2018 (June)	<i>pheasant (Phasianus colchicus)</i>			
	van Horik et al. 2019				
	Isaksson et al., 2018	<i>great tit (Parus major)</i>			
	Boogert et al., 2011	<i>song sparrow (Melospiza melodia)</i>			
	<b>Reptiles</b>	Szabo, Hofer & Whiting, 2020		<i>tree skinks (Egernia striolata)</i>	
				<i>gidgee skinks (Egernia stokesii)</i>	
			<i>eastern blue-tongue skinks (Tiliqua s. scincoides)</i>		
			<i>sleepy lizards (Tiliqua r. asper)</i>		
			<i>eastern water skinks (Eulamprus quoyii)</i>		
<b>Modified cylinder</b>	<b>Mammals</b>	Brucks et al., 2017 (transparent box)	<i>dog (Canis familiaris)</i>		
		Bobrowicz & Osvath, 2018 (box)	<i>cat (Felis catus)</i>		
		Damerius et al. 2017 (transparent box)	<i>Bornean orangutans (Pongo pygmaeus)</i>		
			<i>Sumatran rangutans (Pongo abelii)</i>		
			<i>brown capuchin (Cebus apella)</i>		

<b>ACTION INHIBITION</b>		Amici et al., 2008 (plexiglas hole)	<i>long-tailed macaque (Macaca fascicularis)</i>	
			<i>gorilla (Gorilla gorilla)</i>	
			<i>orangutan (Pongo pygmaeus)</i>	
			<i>spider monkey (Ateles geoffroyi)</i>	
			<i>chimpanzee (Pan troglodytes)</i>	
			<i>bonobo (Pan paniscus)</i>	
		Vlamings et al., 2010 (swing door)	<i>gorilla (Gorilla gorilla)</i>	
			<i>orangutan (Pongo pygmaeus)</i>	
			<i>bonobo (Pan paniscus)</i>	
		Amici et al., 2008 (swing door)	<i>chimpanzee (Pan troglodytes)</i>	
			<i>brown capuchin (Cebus apella)</i>	
			<i>long-tailed macaque (Macaca fascicularis)</i>	
	<i>gorilla (Gorilla gorilla)</i>			
	<i>orangutan (Pongo pygmaeus)</i>			
	Forss et al., 2016 (transparent box)	<i>spider monkey (Ateles geoffroyi)</i>		
		<i>chimpanzee (Pan troglodytes)</i>		
	<b>fishes</b>	Lucon-Xiccato et al., 2020 (transparent tube)	<i>bonobo (Pan paniscus)</i>	
			<i>guppy (Poecilia reticulata)</i>	
	<b>Detour task</b>	<b>Fishes</b>	Brandão et al., 2019 (modified detour U shaped)	<i>guppy (Poecilia reticulata)</i>
			Gatto et al., 2018 (C barrier with group as reward)	<i>guppy (Poecilia reticulata)</i>
Santacà et al., 2019 (transparent barrier)			<i>guppy (Poecilia reticulata)</i>	
			<i>zebrafish (Danio rerio)</i>	
			<i>red-tailed splitfin fish (Xenotoca eiseni)</i>	
			<i>Sarasins minnows (Oryzias sarasinorum)</i>	
<b>Mammals</b>		Bobrowicz & Osvath, 2018	<i>cat (Felis catus)</i>	
		Juszczak & Miller, 2016	<i>mouse (Mus musculus)</i>	
		Smith & Litchfield 2010 (galvanized fencing)	<i>dingo (Canis dingo)</i>	
		Marshall-Pescini et al., 2015 (v fence wire mesh)	<i>dog (Canis familiaris)</i>	
		Pongrácz et al., 2001 (V shape mesh fence)		
		Vernouillet et al., 2018 (V fence)		
		Maclean et al., 2017		
		Marshall-Pescini et al., 2015 (v fence wire mesh)	<i>grey wolves (Canis lupus)</i>	
<b>Birds</b>		Langley et al., 2020 (transparent barrier)	<i>pheasant (Phasianus colchicus)</i>	

<b>ACTION INHIBITION</b>			van Horik 2018 (March) (transparent barrier)	
			van Horik 2019 (transparent barrier)	
			Kabadayi et al., 2017 (Nov) (mesh barrier)	<i>raven (Corvus corax)</i>
		<b>Insects</b>	Cross & Jackson 2016 (detour on platforms)	<i>jumping spider (salticidae)</i>
	<b>Middle cup task</b>	<b>Mammals</b>	Brucks et al., 2017	<i>dog (canis familiaris)</i>
			Amici et al., 2008	<i>spider monkey (Ateles geoffroyi)</i>
				<i>brown capuchin (Cebus apella)</i>
				<i>long-tailed macaques (Macaca fascicularis)</i>
				<i>gorilla (Gorilla gorilla)</i>
				<i>orangutan (Pongo pygmaeu)</i>
				<i>chimpanzee (Pan troglodytes)</i>
			<i>bonobo (Pan paniscus)</i>	
			Schmitt et al., 2012	<i>long-tailed macaque (Macaca fascicularis)</i>
				<i>olive baboon (Papio anubis)</i>
			Herrmann et al., 2007	<i>chimpanzee (Pan troglodytes)</i>
				<i>orangutan (Pongo pygmaeu)</i>
		<i>human (homo sapiens)</i>		
	Joly et al., 2017	<i>long-tailed macaque (Macaca fascicularis),</i>		
		<i>rhesus macaque (macaca mulatta)</i>		
		<i>barbary macaque (macaca sylvanus)</i>		
		<i>tonkean (macaca tonkeana)</i>		
	<b>Go/No-go task</b>	<b>Mammals</b>	Tremblay & Schultz, 2000	<i>long-tailed macaque (macaca fascicularis)</i>
			Loyant et al., unpublished	<i>rhesus macaque (Macaca mulatta)</i>
Morita et al., 2004			<i>Japanese macaque (Macaca fuscata)</i>	
Cook et al., 2016;			<i>dog (canis familiaris)</i>	
Dolzani et al., 2014			<i>rat (Rattus norvegicus)</i>	
Cole et al., 2020				
<b>Birds</b>	Campos et al., 2011	<i>pigeon (Columba livia)</i>		
<b>Stop task</b>	<b>Mammals</b>		<i>human (homo sapiens)</i>	
		Middlebrooks & Schall 2014	<i>rhesus macaque (Macaca mulatta)</i>	
Liu et al., 2009				
<b>5CSRTT task</b>		Fletcher et al., 2008	<i>rat (Rattus norvegicus)</i>	
<b>A-not-B</b>	<b>Mammals</b>	Amici et al., 2008	<i>spider monkey (Ateles geoffroyi)</i>	
			<i>brown capuchin (Cebus apella)</i>	
			<i>long-tailed macaques (Macaca fascicularis)</i>	
			<i>gorilla (Gorilla gorilla)</i>	
			<i>orangutan (Pongo pygmaeu)</i>	
	<i>chimpanzee (Pan troglodytes)</i>			

<b>COGNITIVE SET INHIBITION</b>	<b>A-not-B</b>		<i>bonobo (Pan paniscus)</i>
		Bray et al., 2014	<i>dog (Canis familiaris)</i>
		Cook et al. 2016	
		Fagnani et al. 2016	
		Maclean et al. 2014	
		Vernouillet et al. 2018	
		Maclean et al., 2014	<i>coyote (Canis latrans)</i>
		Maclean et al., 2014	<i>fox squirrel (Scurius niger)</i>
		Maclean et al., 2014	<i>Mongolian gerbil (Meriones unguiculatus)</i>
		Maclean et al., 2014	<i>black lemur (Eulemur macaco)</i>
			<i>bonobo (Pan paniscus)</i>
			<i>capuchin monkey (Cebus apella),</i>
			<i>chimpanzee (Pan troglodytes)</i>
			<i>Coquerel's sifaka (Propithecus coquereli)</i>
	<i>golden monkey (Rhinopithecus roxellana)</i>		
	<i>gorilla (Gorilla gorilla)</i>		
	<i>hamadryas baboon (Papio hamadryas)</i>		
	<i>long-tailed macaque (Macaca fascicularis)</i>		
	<i>marmoset (Callithrix jacchus)</i>		
	<i>mongoose lemur (Eulemur mongoz)</i>		
	<i>olive baboon (Papio Anubis)</i>		
	<i>orangutan (Pongo pygmaeus)</i>		
	<i>ring-tailed lemur (Lemur catta)</i>		
	<i>ruffed lemur (Varecia variegata)</i>		
	<i>spider monkey (Ateles geoffroyi)</i>		
	<i>squirrel monkey (Saimiri sciureus)</i>		
	<i>stump-tailed macaque (Macaca arctoides)</i>		
<i>Asian elephant (Elephas maximus)</i>			
<b>Birds</b>	Maclean et al., 2014;	<i>Eurasian jay (Garrulus glandarius)</i>	
		<i>orange-winged amazon (Amazona amazonica)</i>	
		<i>western scrub jay (Aphelocoma californica)</i>	
		<i>white carnea pigeon (Columba livia)</i>	
	Jelbert et al., 2016	<i>New Caledonian crow (Corvus moneduloides)</i>	
<b>Reversal learning</b>	<b>Mammals</b>	Tapp et al., 2003	<i>dog (Canis familiaris)</i>
		Brucks et al., 2017	
		Chow et al., 2017	<i>grey squirrel (Sciurus carolinensis)</i>
		Schoenbaum et al., 2002	<i>rat (Rattus norvegicus)</i>
		Baragli et al. 2011	<i>horse (equus caballus)</i>
		Hauser et al., 2002	<i>cotton-top tamarins (Aguinus oedipus)</i>
		Kumpan et al., 2020	<i>vervet monkey (Chlorocebus pygerythrus)</i>

			Tsuchida et al., 2002	<i>japanese macaque (Macaca fuscata)</i>
			Loyant et al., unpublished	<i>rhesus macaque (Macaca mulatta)</i>
			Porter et al., 2011	
			Forss et al., 2016	<i>orangutan (Pongo abelii and pygmaeus)</i>
		<b>Birds</b>	O’Hara et al., 2015	<i>Kea (Nestor notabilis)</i>
			Cauchoix et al., 2017	<i>great tits (Parus major)</i>
			Madden et al., 2018	<i>pheasants (Phasianus colchicus)</i>
			van Horik et al., 2018(June)	
			Ashton et al., 2017	<i>Australian magpies (Gymnorhina tibicen)</i>
			Bond et al., 2007	<i>pinyon jay (Gymnorhinus cyanocephalus)</i>
				<i>Clark’s nutcracker (Nucifraga columbiana)</i>
				<i>western scrub jay (Aphelocoma californica)</i>
		Boogert et al., 2011	<i>song parrow (Melospiza melodia)</i>	
		<b>Reptiles</b>	Bridgeman & Tattersal, 2019	<i>red-footed tortoise (Chelonoidis carbonaria)</i>
		<b>Fishes</b>	López et al., 2000	<i>goldfish (Carassius auratus)</i>
			Lucon-Xiccato & Bisazza 2014	<i>guppy (Poecilia reticulata)</i>
		<b>Insects</b>	Komischke et al., 2002	<i>honeybee (Apis mellifera)</i>
			Chandra et al., 2010	
<b>DISTRACTION INHIBITION</b>	<b>Stroop task</b>	<b>Mammals</b>	Beran, Washburn & Rumbaugh, 2007	<i>chimpanzee (Pan troglodytes)</i>
			Allritz et al., 2016	
		Hopper et al., 2021	<i>chimpanzee (Pan troglodytes), Japanese macaque (Macaca fuscata), gorilla (Gorilla gorilla)</i>	
	<b>Attention distraction</b>	<b>Mammals</b>	Shibasaki & Kawai, 2009	<i>japanese macaque (Macaca fuscata)</i>
			Bethell et al., 2012, 2016	<i>rhesus macaque (Macaca mulatta)</i>
			King et al., 2012	
			Landman et al., 2014	
			Lacreuse et al., 2013	
			Loyant et al., unpublished	
	Boggiani et al., 2018	<i>tufted capuchin (Sapajus apella)</i>		
	<b>Inhibition when social partner</b>	<b>Mammals</b>	Reddy et al., 2015	<i>Ring-tailed lemurs (Lemur catta)</i>
				<i>Ruffed lemurs (Varecia variegata)</i>
<i>Coquerel’s sifaka (Propithecus coquereli)</i>				
<i>Black lemurs (Eulemur macaco)</i>				
<i>mongoose lemurs (Eulemur mongoz)</i>				
Huguet et al., 2014			<i>Guinea baboon (Papio papio)</i>	
Amici et al., 2018			<i>chimpanzee (Pan troglodytes), bonobo (Pan paniscus)</i>	
			<i>orangutan (Pongo abelii)</i>	
			<i>gorilla (Gorilla gorilla)</i>	
			<i>spider monkey (Ateles geoffroyi)</i>	

Appendices

			capuchins monkey ( <i>Cebus apella</i> )
			spider monkey ( <i>Ateles geoffroyi</i> )
		Amici et al., 2009	brown capuchin ( <i>Cebus apella</i> )
			long-tailed macaque ( <i>Macaca fascicularis</i> )
		Bray et al. 2014	
		Horschler et al., 2019	dog ( <i>canis familiaris</i> )

**Appendix 2. Animal accuracy in the common tasks of inhibitory control**

Accuracy (% of correct for the total number of trials, if given for the first session of trials) for different tasks of inhibitory control (cylinder task, A-not-B task, detour task, middle cup task, Plexiglas hole and swing door) for different classes and species of animal. Mean, standard Deviation (S.D.), the number of papers used in which the accuracy of the task was available (N) and the Standard Error of Measurement (S.E.M.).

Accuracy	Cylinder Task				A-no-B Task				Detour Task			
	Mean	S.D.	N	S.E.M	Mean	S.D.	N	S.E.M	Mean	S.D.	N	S.E.M.
All animal classes	61.35	24.19	42	3.73	60.69	32.55	37	5.35	62.32	24.41	9	8.14
Canines	75.43	12.21	12	3.52	63.60	27.75	5	12.41	75.30	10.72	3	6.19
Mammals (excluding primates and canines)	71.66	11.49	4	5.74	10.83	10.10	3	5.83	80.28	23.76	5	10.63
Primates (excluding Great Apes)	53.61	21.49	18	5.06	60.92	26.24	17	6.36				
Great Apes	97.13	2.83	4	1.42	95.21	6.98	8	2.47				
Birds	63.51	24.53	8	8.67	24.48	20.26	4	10.13				
Fishes	53.00	1.00	1	1.00					46.22	17.94	8	6.34
Reptiles	34.60	7.73	5	3.46								

Accuracy	Middle cup Task				Plexiglas Hole				Swing Door		
	Mean	S.D.	N	S.E.M.	Mean	S.D.	N	S.E.M.	Mean	S.D.	S.E.M.
All animal classes	44.67	26.38	11	7.95	65.65	36.88	6	15.06	17.99	21.66	5.79
Canines											
Mammals											
Primates	36.49	23.82	7	9.00	37.53	31.46	3	18.16	0.00	0.00	0.00
Great Apes	59.00	27.49	4	13.75	93.77	6.25	3	3.61	22.90	22.06	6.65
Birds											
Fishes											
Reptiles											

**Appendix 3. Sample size statistics from the literature review**

Mean, Median, Standard Deviation (S.D.), Number of tasks (N) in which the sample size of the class of animal or species was recorded. If available, we used the sample size used in the analysis for the subjects which completed the study.

	Mean	Median	S.D.	N
All animal classes & species	53.71	11	476.65	216
Dogs	368.59	30	1483.91	22
Primates (excluding Great Ape)	10.95	10	5.77	78
Great Apes	12.15	7.50	17.29	40
Birds (Excluding Corvids and Parrots)	60.00	37	76.37	19
Mammals (excluding primates & Dogs)	16.95	11	13.28	18
Corvids and Parrots	8.78	8	4.02	18
Insects and reptiles	25.33	13	24.88	9
Fishes	30	16	26.98148	9

**Appendix 4. Ethics approval and Research Ethics Review Checklist**

This study was approved by the Animal Welfare and Ethical Review Body of the University of Portsmouth, AWERB no. 4015B and by the MRC-CFM’s Animal Welfare and Ethical Review Body, ARWEB no. CFM2019E002 and was part of the Macaque Cognition Project. All research was carried out in accordance with ethical guidelines for work with non-human primates (NC3Rs 2006). Animal Welfare and Ethical Review Body of the Centre of Primatology of the University of Strasbourg – SILABE approved the study. All research was carried out in accordance with ethical guidelines for work with non-human primates (NC3Rs 2017).

# FORM UPR16

## Research Ethics Review Checklist



**Please include this completed form as an appendix to your thesis (see the Research Degrees Operational Handbook for more information)**

<b>Postgraduate Research Student (PGRS) Information</b>		<b>Student ID:</b>	UP 907495	
<b>PGRS Name:</b>	Louise Loyant			
<b>Department:</b>	Psychology	<b>First Supervisor:</b>	Dr Marine Joly	
<b>Start Date:</b> (or progression date for Prof Doc students)	01/10/2018			
<b>Study Mode and Route:</b>	Part-time <input type="checkbox"/>	MPhil <input type="checkbox"/>	MD <input type="checkbox"/>	
	Full-time <input checked="" type="checkbox"/>	PhD <input checked="" type="checkbox"/>	Professional Doctorate <input type="checkbox"/>	

<b>Title of Thesis:</b>	Inhibitory control in macaque species: validation of a task battery, individual differences in performance and effect of social tolerance
<b>Thesis Word Count:</b> (excluding ancillary data)	62,498 words

If you are unsure about any of the following, please contact the local representative on your Faculty Ethics Committee for advice. Please note that it is your responsibility to follow the University's Ethics Policy and any relevant University, academic or professional guidelines in the conduct of your study

Although the Ethics Committee may have given your study a favourable opinion, the final responsibility for the ethical conduct of this work lies with the researcher(s).

**UKRIO Finished Research Checklist:**  
(If you would like to know more about the checklist, please see your Faculty or Departmental Ethics Committee rep or see the online version of the full checklist at: <http://www.ukrio.org/what-we-do/code-of-practice-for-research/>)

a) Have all of your research and findings been reported accurately, honestly and within a reasonable time frame?	YES <input checked="" type="checkbox"/> NO <input type="checkbox"/>
b) Have all contributions to knowledge been acknowledged?	YES <input checked="" type="checkbox"/> NO <input type="checkbox"/>
c) Have you complied with all agreements relating to intellectual property, publication and authorship?	YES <input checked="" type="checkbox"/> NO <input type="checkbox"/>
d) Has your research data been retained in a secure and accessible form and will it remain so for the required duration?	YES <input checked="" type="checkbox"/> NO <input type="checkbox"/>
e) Does your research comply with all legal, ethical, and contractual requirements?	YES <input checked="" type="checkbox"/> NO <input type="checkbox"/>

**Candidate Statement:**

Appendices

I have considered the ethical dimensions of the above named research project, and have successfully obtained the necessary ethical approval(s)		
<b>Ethical review number(s) from Faculty Ethics Committee (or from NRES/SCREC):</b>		AWERB no. 4015B
If you have <i>not</i> submitted your work for ethical review, and/or you have answered 'No' to one or more of questions a) to e), please explain below why this is so:		
<b>Signed (PGRS):</b>		<b>Date:</b> 15.03.2022

16 March 2022



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To Whom It May Concern:

Confirmation of ethical approval by the AWERB: Louise Loyant

I am happy to confirm that the work carried out by Louise was approved by the AWERB in 2020 via an amendment to the approval originally granted in 2018 (4015B) to Dr Marine Joly.

Yours sincerely,

M J Guille PhD FHEA FSB  
Professor of Developmental Genetics  
Chair, AWERB.

## **Appendix 5. Training phases**

### ***Training phase 1***

As none of the macaques had experience with touchscreen experiments prior to the beginning of the data collection, all the macaques had to complete two training phases. The first training phase used a rectangular transparent Plexiglas sheet (42 x 30 cm) with a plastic red square target (10 x 12 cm) moved by hand. Monkeys were progressively rewarded for approaching the Plexiglas sheet, touching the target as it moved. This phase was judged as complete if the macaques followed the target 20 times in a row. Two females did not complete this training stage as they gave birth during the training period, two males could not reach the success criterion.

### ***Training phase 2***

After completion of the first training phase, the touchscreen was introduced. The aim of training phase 2 was to be trained to touch a target on the screen.

### **Stimuli**

The target was a red (RGB 255, 0, 0) rectangle of a maximum of 1200 x 1000 pixels (ca. 32 x 26 cm) and was gradually reduced to 360 x 500 pixels (ca. 10 x 13 cm).

### **Procedure**

When the program was launched, the experimenter entered the name of the individual, the number of trials per session, the size of the target and the time limit to complete the task. Every session was initiated by the subject touching a red cross located in the centre of the screen, starting the time recording. Then, the target was displayed in the middle of a white background (RGB 255, 255, 255). For the first 30 trials a picture of peanuts was displayed inside the target to motivate the macaques to touch it. Once the subject touched the target, a high-pitched chime (composed of 3 sound frequencies: 800, 1300 and 2000 Hz) was played, the timer was stopped, and the reward was given. After an inter-trial of 2000 ms, with only the white background displayed, the next trial was presented. Based on a pilot study (N = 4 subjects), we set up a maximum response time of 35s.

If the subject left the testing area or was not focusing attention on the screen the session was aborted. If the target was not touched within the time limit (35 s), the timer was paused, a red cross appeared in the centre of the screen until the session was resumed by touching it. The size of the target was gradually reduced to 360 x 500 pixels (ca. 10 x 13 cm).

Once the macaques performed successfully 20 times in a row with the target in the centre of the screen, the target was displayed randomly at the far left or right of the screen. This phase was judged as complete if the macaque followed the target 20 trials in a row. If the subject stayed inactive for more than 5 min the session was stopped and continued the next testing day, if the subject did not participate for three testing days in a row the subject was excluded from the task. The training phase 2 was completed by 21 subjects (12 males, 9 females) who therefore progressed to the experimental phase. Five subjects abandoned this training phase as they stayed at distance from the screen or gave birth in the meantime.

### ***Training phase 3***

Subjects

## Appendices

The 21 subjects who progressed from the training phase 2 participated in this last training phase. This resulted in a sample of 9 females and 12 males (age ranging from 3 to 17 years old, mean age in years  $M \pm SD = 8.85 \pm 4.38$ ,  $N = 21$ ).

### Procedure

After the initiation of the session a red rectangle target (360 x 500 pixels, c.a. 10 x 13 cm) was randomly displayed at the left or right of the screen. The subjects had a time limit of 15s to complete the task (i.e. touch the red rectangle). Three sessions of 20 trials were repeated at time point 1 and time point 2 (average days between the time points  $M \pm SD = 14.38 \pm 5.30$ ,  $N = 21$ ; depending on the availability of the subjects).

## Appendix 6. Rank calculation at the MRC

### Calculated ranks by David's Scores:

Ranks obtained from David's Scores (DS) were calculated in 2016. They were also based on agonistic interactions recorded ad libitum. Agonistic behaviours included threats (e.g. open mouth threat), displacements (i.e. a macaque approaches another who departs immediately), chases, and physical conflict (e.g. bite, slaps). These calculated ranks were regularly monitored and updated during observations and training sessions by caretakers. After a regression analysis all calculated ranks were found significant.

Total Number of conflicts: 734

Number of conflicts: [48-136]

Number of observations: [4-14]

### Observed ranks:

To confirm the calculated ranks at the time our experiments were conducted we coded agonistic behaviour with a focus on the studied subject. A blind observer recorded agonistic interactions (winner/loser) between a focal individual and other members of the group during the training and test sessions. Agonistic behaviours included threats (e.g. open mouth threat), displacements (i.e. a macaque approaches another who departs immediately), chases, and physical conflict (e.g. bite, slaps). If the male never lost, he was considered as high ranked. If the female never lost against other females, she was considered as high ranked (H), otherwise she was considered low ranked (L).

Females	loser (suppl/threat)	winner (suppl/threat)	No observations	Sex	Observed rank	Rank from DS
Ylang	18	30	26	F	L	L
Adele	32	13	23	F	L	L
Rach	0	21	32	F	H	H
Ybbi	0	8	18	F	H	H
Blossom	0	33	27	F	H	H
Tes	1	7	12	F	L	L
Aqua	4	5	10	F	L	L
Saphy	0	8	7	F	H	H
Talula	0	34	27	F	H	H

Males	loser (suppl/threat)	winner (suppl/threat)	No observations	Se x	Observed rank	Rank from DS
Yew	0	6	22	M	H	H
Yorkie	0	34	39	M	H	H
Yosser	0	3	40	M	H	H
Zazy	0	2	36	M	H	H
Sol	0	81	19	M	H	H
Vincent	0	16	26	M	H	H
Abbott	0	14	28	M	H	H
Sequel	0	14	22	M	H	H
Nodon	0	41	31	M	H	H
Star	0	23	29	M	H	H
Plum	0	31	18	M	H	H
Yeti	5	0	15	M	L	L

**Appendix 7. Results of LMMs for the log transformation of the response latency in the Distraction task /chapter 2**

Confounding factors were divided in individual (sex, age, rank and experience with picture) and experimental determinants (session and time point). All full models included the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, t-value and p-value are represented. The variables in bold stimulus, age, trial and time point had a significant effect on the models. 4094 data points were analysed.

<i>log(response latency) on a trial</i>				
Predictor	Estimate	Std. Error	t-value	p-value
(Intercept)	8.223	0.213	38.526	0.000
Stimulus picture	0.112	0.035	3.189	<b>0.001</b>
Picture Object vs face	0.018	0.025	0.753	0.452
Picture Threat vs neutral	-0.058	0.043	-1.350	0.177
Sex male	0.120	0.150	0.801	0.436
Age	0.043	0.018	2.296	<b>0.035</b>
Rank low vs high	0.196	0.154	1.273	0.220
Experience picture	-0.084	0.097	-0.862	0.388
Trial	0.000	0.002	0.069	0.944
Session	-0.035	0.017	-2.20	<b>0.027</b>
Time point	-0.534	0.032	-16.877	<b>0.000</b>

**Appendix 8. Results of GLMMs for the success in the Go/No-go task /chapter 2**

Confounding factors were divided in individual (sex, age and rank) and experimental determinants (session and time point). All full models included the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, z-value and p-value are represented. The type of stimulus (Go or No-go) and session had a significant effect on the models. 7783 data points were analysed.

<i>Success on a trial</i>	Estimate	Std. Error	z-value	p-value
(Intercept)	6.824	0.671	11.072	0.000
Stimulus No-Go	-7.098	0.413	-17.196	<b>0.000</b>
Sex female	-0.300	0.200	-1.5000	0.134
Age	-0.004	0.037	-0.111	0.911
Rank low vs high	0.023	0.364	0.065	0.948
Trial	0.001	0.004	0.173	0.862
Session	0.081	0.033	2,456	<b>0.014</b>
Time point	0.091	0.093	0.972	0.331

**Appendix 9. Results of LMMs for the log transformation of the response latency in the Go/No-go task /chapter 2**

Confounding factors were divided in individual (sex, age and rank) and experimental determinants (session and time point). All full models included the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, t-value and p-value are represented. Only the variable in bold stimulus had a significant effect on the models. 7783 data points were analysed.

*log(response latency) on a trial*

Predictor	Estimate	Std. Error	t-value	p-value
(Intercept)	7.638	0.160	47.800	0.000
Stimulus No-Go	0.509	0.020	24.969	<b>0.000</b>
Sex female	-0.041	0.042	-0.967	0.334
Age	0.006	0.012	0.555	0.579
Rank low vs high	0.115	0.116	0.999	0.331
Trial	-0.001	0.001	-0.969	0.332
Session	0.010	0.006	1.640	0.101
Time point	0.001	0.018	0.068	0.946

**Appendix 10. Results of GLMMs for the success in the Reversal learning task /chapter 2**

Confounding factors were divided in individual (sex, age and rank) and experimental determinants (session and time point). All full models included the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, z-value and p-value are represented. The variables in bold rule, trial and session had a significant effect on the models. 6686 data points were analysed.

**Success on a trial**

Predictor	Estimate	Std. Error	z value	p-value
(Intercept)	0.797	0.272	2.885	0.004
Ruverse rule	-0.099	0.069	-1.437	0.150
Sex female	-0.185	0.157	-1.183	0.237
Age	-0.025	0.016	-1.607	0.108
Rank low vs high	-0.025	0.149	-0.170	0.897
Trial	0.005	0.002	2.047	<b>0.041</b>
Session	0.056	0.017	3.377	<b>0.001</b>
Time point	-0.088	0.072	-1.233	0.218

**Appendix 11. Results of LMMs for the Distraction control score (the Distraction task) /chapter 2**

Confounding factors were divided in individual (sex, age, rank and experience with picture) and experimental determinants (session and time point). All full models included the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, t-value and p-value are represented. Only the variables in bold sex, session and time point had a significant effect on the models. 346 data points were analysed.

**Distraction control score**

Predictor	Estimate	Std. Error	t-value	p-value
(Intercept)	-185.419	683.239	-0.271	0.786
Sex male	-1368.504	631.269	-2.172	<b>0.045</b>
Age	-102.284	103.125	-0.986	0.334
Rank low vs high	-1211.880	619.867	-1.955	0.068
Experience with pictures	317.939	856.463	0.371	0.715
Trial	6.374	9.807	0.649	0.517
Session	455.514	124.249	3.666	<b>0.0003</b>
Time point	2019.521	205.8753	9.815	<b>0.000</b>
Type picture Object	-117.94	245.685	-0.484	0.628
Type picture Threat	66.953	249.686	0.266	0.790

**Appendix 12. Results of LMMs for the Action Control Score (Go/No-go) /chapter 2**

Confounding factors were divided in individual (sex, age and rank) and experimental determinants (session and time point). All full models included the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, t-value and p-value are represented. None of the variables had a significant effect on the models. 120 data points were analysed.

*Action control score*

<b>Predictor</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t-value</b>	<b>p-value</b>
(Intercept)	47.742	13.653	3.497	0.001
Sex male	-10.487	9.604	-1.092	0.292
Age	0.744	1.061	0.701	0.494
Rank low vs high	-3.680	9.857	-0.373	0.714
Session	4.631	2.851	1.646	0.103
Time point	3.062	4.370	0.631	0.523

**Appendix 13. Results of LMMs for the Rule Control Score (Reversal learning task) /chapter 2**

Confounding factors were divided in individual (sex, age, rank) and experimental determinants (session and time point). The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), t-value and p-value are represented. None of the variables had a significant effect on the model. 38 data points were analysed.

*Rule control score*

<b>Predictor</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t-value</b>	<b>p-value</b>
(Intercept)	40.211	68.579	0.586	0.566
Sex male	-109.509	65.719	-1.666	0.118
Age	6.471	8.011	0.808	0.4323
Rank low vs high	-18.676	72.299	-0.258	0.799
Time point	-2.001	13.721	-0.146	0.887

**Appendix 14. Summary contextual unadjusted repeatability /chapter 2**

Contextual unadjusted repeatability estimates of the scores of executive function and inhibitory control. Distraction control score (Distraction task), Action control score (Go/No-go) and Rule control score (Reversal Learning) are represented

✓ indicates that the individual’s performances are significantly repeatable between tasks.

\*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$

Contextual R for the scores	Distraction control	Action control	Rule control
<b>Distraction control</b>	1	-	-
<b>Action control</b>	✓ 0.166 ( $p = 2.69e-05$ )***	1	-
<b>Rule control</b>	✓ 0.212 ( $p = 9.46e-04$ ) ***	✓ 0.138 ( $p = 0.012$ )*	1

**Appendix 15. Results of LMMs for the Distraction task (Distraction control scores) and the Go/No-go task (Action Control Score) /chapter 2**

Confounding factors were divided in individual (sex, age and rank) and experimental determinants (session and time point). The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable t-value and p-value are represented. The variables in bold session and time point had a significant effect on the models. 237 data points were analysed.

Predictor	Estimate	Std. Error	t-value	p-value
(Intercept)	-0.241	0.226	-1.065	0.282
Task Go/No-go	0.012	0.096	0.128	0.898
Sex male	-0.381	0.162	-2.338	0.032
Age	0.007	0.020	0.320	0.752
Rank low vs high	0.051	0.156	0.330	0.741
Session	0.126	0.058	2.160	<b>0.032</b>
Time point	0.268	0.096	2.809	<b>0.006</b>

**Appendix 16. Results of LMMs for the Go/No-go (Action control scores) and the Reversal learning task (Rule Control Score) /chapter 2**

Confounding factors were divided in individual (sex, age and rank) and experimental determinants (session and time point). All full models included the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable t-value and p-value are represented. Only the variable in bold sex had a significant effect on the model (when comparing with the full model). 158 data points were analysed.

<b>Predictor</b>	<b>Estimate</b>	<b>Std.Error</b>	<b>t-value</b>	<b>p-value</b>
(Intercept)	-0.325	0.367	-0.890	0.375
Task Reversal learning	0.183	0.219	0.838	0.404
Sex male	-0.528	0.218	-2.494	<b>0.023</b>
Age	0.030	0.025	1.230	0.221
Rank low vs high	-0.108	0.226	-0.447	0.656
Session	0.163	0.112	1.457	0.148
Time point	0.122	0.162	0.751	0.454

**Appendix 17. Results of LMMs for the Distraction task (Distraction control scores) and the Reversal learning task (Rule Control Score) /chapter 2**

Confounding factors were divided in individual (sex, age and rank) and experimental determinants (session and time point). All full models included the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, t-value and p-value are represented. The variable in bold had a significant effect on the models. 155 data points were analysed.

<b>Predictor</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t-value</b>	<b>p-value</b>
(Intercept)	-0.325	0.365	-0.890	0.375
Task Reversal learning	0.173	0.217	0.792	0.425
Sex male	-0.416	0.133	-3.140	<b>0.023</b>
Age	0.006	0.016	0.396	0.206
Rank low vs high	-0.108	0.224	-0.478	0.633
Session	0.166	0.11	1.430	0.128
Time point	0.1209	0.165	0.759	0.448

**Appendix 18. Rank calculation at the CPUS**

Rank of the subjects were also based on agonistic interactions recorded ad libidum. Agonistic behaviours included threats (e.g. open mouth threat), displacements (i.e. a macaque approaches another who departs immediately), chases, and physical conflict (e.g. bite, slaps). Here is presented the number of observations per group, the range of interactions, the group size, the coefficient of linearity and associated P value, the coefficient of steepness and associated P value and the proportion of dyads with no interactions. We considered high ranking individuals the two subjects at the top of the hierarchy at the time of the testing (e.g. the top-ranking male and the top-ranking female in mixed groups).

	Rhesus CPUS			Long-tailed								Tonkean
	Sesame	Attila	Kasparov	Zorro	Drumble	Oda	Berlioz	Calimero	Maske doro	Pilsner	Camus	Wallace
Number of observations	146	150	148	344	42	347	233	189	146	175	257	199
Range of interactions	92 to 101	20 to 107	84 to 125	92 to 157	42 to 42	35 to 185	19 to 135	15 to 155	15 to 73	3 to 71	98 to 157	39 to 130
Group size	3	4	3	6	2	6	7	5	7	11	4	5
Linearity	1	0.5	0.5	1	1	1	0.84	0.75	0.95	0.54	1	1
Significance test for linearity	P = 0.77	P = 0.51	P = 0.49	P = 0.02	P = 1	P = 0.01	P = 0.008	P = 0.297	P = 0.001	P = 0.006	P = 0.37	P = 0.13
Steepness	0.98	0.65	0.66	0.94	0.97	0.9	0.62	0.75	0.66	0.37	0.97	0.68
Significance test for steepness	P = 0.001	P = 0.001	P = 0.001	P = 0.001	P = 0.04	P = 0.001	P = 0.001	P = 0.001	P = 0.001	P = 0.001	P = 0.001	P = 0.004
Proportion of dyads with no interactions	0	0.2	0.2	0	0	0	0.14	0.1	0.095	0.33	0	0

**Appendix 19. Results of the Tukey’s HSD post-hoc for the comparison of the Distraction score between each types of pictures in rhesus macaques /chapter 3**

a. Male rhesus macaques, session 1

Estimate Std. Error z value Pr(>|z|)

None - Neutral == 0 -18.119 4.696 -3.859 <0.001 \*\*\*

Object - Neutral == 0 -5.701 4.998 -1.141 0.6636

Threat - Neutral == 0 4.363 5.144 0.848 0.8310

Object - None == 0 12.418 4.608 2.695 0.0352 \*

Threat - None == 0 22.483 4.742 4.741 <0.001 \*\*\*

Threat - Object == 0 10.064 5.062 1.988 0.1920

b. Female rhesus macaques

Estimate Std. Error z value Pr(>|z|)

None - Neutral == 0 -1.0477 3.5088 -0.299 0.991

Object - Neutral == 0 -2.9614 3.8156 -0.776 0.865

Threat - Neutral == 0 0.1849 3.8613 0.048 1.000

Object - None == 0 -1.9136 3.4633 -0.553 0.946

Threat - None == 0 1.2326 3.5489 0.347 0.986

Threat - Object == 0 3.1462 3.8425 0.819 0.845

**Appendix 20. Results of the LMM for the normalised Distraction control score (Distraction task) in long-tailed macaques for session 1 /chapter 3**

Explanatory variables were the experimental determinants (type of picture and trial). All full models included the type of picture nested in the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, t-value and p-value are represented. 661 observations were analysed.

\* p < 0.05

Predictors	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	95.181	11.727	8.117	0.000
type of picture control vs picture	0.662	0.640	1.035	0.307
object vs face	2.448	1.045	2.344	0.02*
threat vs neutral	-4.022	1.796	-2.239	0.02*
trial	-0.104	0.114	-0.911	0.363

**Appendix 21. Results of the Tukey’s HSD post-hoc for the comparison of the Distraction score between each types of pictures in long-tailed macaques (a. Males, b. Females) /chapter 3**

*a. Male long-tailed macaques*

	Estimate	Std. Error	z value	Pr(> z )
None - Neutral == 0	0.763	4.957	0.154	0.999
Object - Neutral == 0	-6.052	5.504	-1.100	0.689
Threat - Neutral == 0	4.650	5.567	0.835	0.837
Object - None == 0	-6.815	5.026	-1.356	0.526
Threat - None == 0	3.887	5.085	0.764	0.870

*b. Female long-tailed macaques*

	Estimate	Std. Error	z value	Pr(> z )
None - Neutral == 0	-1.889	4.601	-0.411	0.976
Object - Neutral == 0	-0.794	4.995	-0.159	0.998
Threat - Neutral == 0	11.016	4.998	2.204	0.122
Object - None == 0	1.097	4.7315	0.231	0.996
Threat - None == 0	12.905	4.736	2.725	0.032 *
Threat - Object == 0	11.810	5.121	2.306	0.096

**Appendix 22. Results of the Tukey’s HSD post-hoc for the comparison of the Distraction score between each type of pictures in Tonkean macaques (a. Females, b. Males) /chapter 3**

*a. Female Tonkean macaques*

	Estimate	Std. Error	z value	Pr(> z )
None - Neutral == 0	-1.0477	3.5088	-0.299	0.991
Object - Neutral == 0	-2.9614	3.8156	-0.776	0.865
Threat - Neutral == 0	0.1849	3.8613	0.048	1.000
Object - None == 0	-1.9136	3.4633	-0.553	0.946
Threat - None == 0	1.2326	3.5489	0.347	0.986
Threat - Object == 0	3.1462	3.8425	0.819	0.845

*b. Male Tonkean macaques*

	Estimate	Std. Error	z value	Pr(> z )
None - Neutral == 0	1.1340	2.4197	0.469	0.9658
Object - Neutral == 0	1.4383	2.6445	0.544	0.9480
Threat - Neutral == 0	7.4626	2.6883	2.776	0.0279 *
Object - None == 0	0.3043	2.4344	0.125	0.9993
Threat - None == 0	6.3286	2.4698	2.562	0.0507 .
Threat - Object == 0	6.0243	2.6884	2.241	0.1122

**Appendix 23. Results of the GLMM for the normalised Distraction control score (Distraction task) /chapter 3**

All full models included the type of picture nested in the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, z-value and p-value are represented.

\* p < 0.05

Predictors	Rhesus macaques				Long-tailed macaques				Tonkean macaques				
	Estimate	Std. Error	z value	Pr(> t )	Estimate	Std. Error	z value	Pr(> t )	Estimate	Std. Error	z value	Pr(> t )	
(Intercept)	-1.866	0.734	-2.542	0.011	-3.433	1.956	-1.755	0.079	-1.325	1156.214	-0.001	0.999	
age	-0.013	0.054	-0.235	0.814	0.119	0.135	0.886	0.376	-0.014	0.068	-0.207	0.836	
sex male vs female	0.851	0.641	1.328	0.184	0.073	0.761	0.096	0.923	-20.908	1001.310	-0.021	0.983	
type of picture	control vs neutral	0.398	0.220	1.808	0.071	-0.012	0.336	-0.036	0.971	-0.063	1156.215	0.000	1.000
	control vs object	0.134	0.236	0.565	0.572	0.345	0.302	1.141	0.254	0.000	1.414	0.000	1.000
	control vs threat	0.728	0.205	3.558	0.000	0.527	0.288	1.830	0.067	0.202	1.418	0.142	0.887

## Appendix 24. Digitrack technique

The Digitrack is a technique aiming at recording the subject's focus of attention. Subjects can explore a picture by moving their digit over a touch screen to unblur the region of interest. The apparatus used in the digitrack study is presented (b). An example of heatmap obtained with 9 tonkean macaques subjects at the CPUS (37 trials in total), the subjects focused their attention on the face of the macaque.

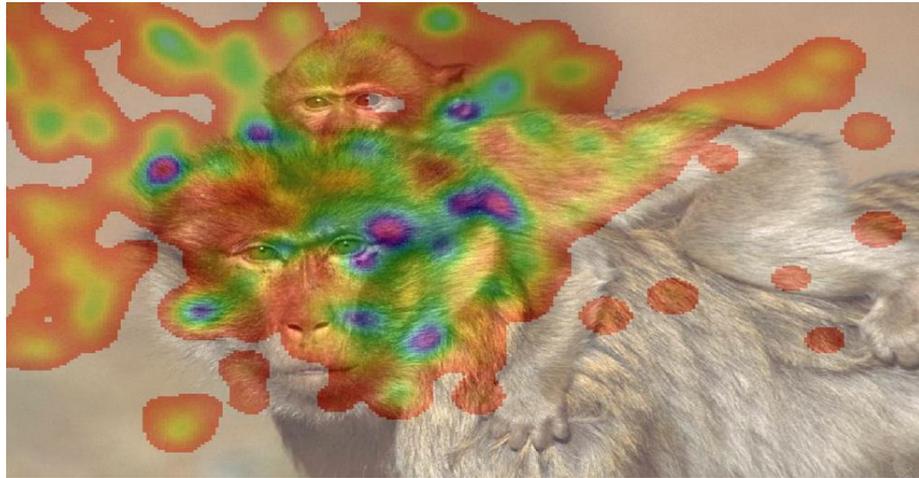
a.



b.



c.



**Appendix 25. Summary of the findings for the content validity of the tasks in the different species.**

Task	Prepotent response	rhesus macaques	long-tailed macaques	Tonkean macaques
<b>Distraction task</b>	Distractive effect of the stimuli on the response latency	likelihood-ratio test, $\chi^2$ (1, N = 21) = 16.486 , p < 0.001	likelihood-ratio test, $\chi^2$ (1, N = 21) = 66.943 , p < 0.01	likelihood-ratio test, $\chi^2$ (1, N = 21) = 2.724 , p = 0.436
<b>Go/No-go task</b>	Lower response latency in No-go trials	likelihood-ratio test, $\chi^2$ (1, N = 20) = 1878, p < 0.001	likelihood-ratio test, $\chi^2$ (1, N = 20) = 973.59, p < 0.001	likelihood-ratio test, $\chi^2$ (1, N = 18) = 1150.7 , p < 0.001
<b>Reversal learning task</b>	Better accuracy in the acquisition rule compared to the reversed rule	likelihood-ratio test, $\chi^2$ (1, N = 20) = 5.10 , p = 0.02	likelihood-ratio test, $\chi^2$ (1, N = 19) = 18.023 , p < 0.01	likelihood-ratio test, $\chi^2$ (1, N = 18) = 7.971 , p < 0.00

**Appendix 26. Results of the LMMs for the Distraction task in rhesus, long-tailed and Tonkean macaques /chapter 3**

Here the response latency is analysed. All full models included the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, t-value and p-value are represented.

<b>Rhesus macaques</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
(Intercept)	7.709	0.141	54.768	0.000
age	0.031	0.012	2.550	0.016
Sex (male)	0.205	0.128	1.600	0.122
trial	-0.001	0.002	-0.430	0.667
session	-0.055	0.022	-2.485	0.013
Location (CPUS)	-0.219	0.158	-1.391	0.175
Type picture Object	0.158	0.057	2.768	0.006
Type picture Neutral	0.181	0.057	3.147	0.002
Type picture Threat	0.185	0.058	3.223	0.001

	<b>Long-tailed macaques</b>				<b>Tonkean macaques</b>			
	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
(Intercept)	8.040	0.309	26.033	0.000	7.860	0.253	31.058	0.000
age	0.037	0.023	1.606	0.124	0.019	0.014	1.303	0.209
Sex (male)	0.059	0.135	0.435	0.668	0.120	0.165	0.726	0.477
trial	-0.003	0.002	-1.620	0.105	-0.003	0.002	-1.666	0.096
session	-0.182	0.023	-7.926	0.000	-0.049	0.021	-2.293	0.022
Type picture Object	-0.072	0.059	-1.217	0.224	0.024	0.056	0.438	0.662
Type picture Neutral	-0.032	0.059	-0.541	0.589	-0.050	0.062	-0.806	0.420
Type picture Threat	0.151	0.060	2.531	0.011	0.022	0.062	0.354	0.724

**Appendix 27. Results of the GLMMs for the Go/No-go task in rhesus, long-tailed and Tonkean macaques /chapter 3**

Here the accuracy on a trial is analysed. All full models included the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, z-value and p-value are represented.

	<i>rhesus macaques</i>				<i>long-tailed macaques</i>			
	Estimate	Std. Error	z value	Pr(> z )	Estimate	Std. Error	z value	Pr(> z )
(Intercept)	5.561	0.575	9.667	0.000	5.096	0.580	8.783	0.000
Type (NoGo)	-5.460	0.243	-22.450	0.000	-4.419	0.225	-19.611	0.000
Sex (male)	-0.463	0.482	-0.960	0.337	-0.123	0.225	-0.546	0.585
age	-0.014	0.044	-0.321	0.748	-0.022	0.038	-0.580	0.562
trial	-0.003	0.005	-0.570	0.569	-0.007	0.005	-1.238	0.216
session	0.017	0.040	0.427	0.670	0.120	0.045	2.637	0.008
Location (CPUS)	-0.245	0.609	-0.401	0.688				

	<i>Tonkean macaques</i>			
	Estimate	Std. Error	z value	Pr(> z )
(Intercept)	5.525	0.641	8.624	0.000
Type (NoGo)	-5.565	0.344	-16.193	0.000
Sex (male)	-0.216	0.351	-0.615	0.538
age	-0.024	0.030	-0.794	0.427
trial	0.009	0.006	1.537	0.124
session	0.182	0.049	3.685	0.000

**Appendix 28. Results of the GLMMs for the Reversal learning task in rhesus, long-tailed and Tonkean macaques /chapter 3**

Here the accuracy on a trial is analysed. All full models included the individual ID as a random factor. The Estimates (representing the change in the dependent variable relative to the baseline category of each predictor variable), Standard Error, z-value and p-value are represented.

	long-tailed macaques				Tonkean macaques			
	Estimate	Std. Error	z value	Pr(> z )	Estimate	Std. Error	z value	Pr(> z )
(Intercept)	1.125	0.356	3.162	0.002	1.125	0.356	3.162	0.002
Rule (reversed)	-0.339	0.080	-4.245	0.000	-0.339	0.080	-4.245	0.000
Sex (male)	0.108	0.145	0.743	0.458	0.108	0.145	0.743	0.458
age	-0.006	0.024	-0.260	0.795	-0.006	0.024	-0.260	0.795
trial	0.003	0.003	0.791	0.429	0.003	0.003	0.791	0.429
session	0.093	0.033	2.836	0.005	0.093	0.033	2.836	0.005

See chapter 2, 2.6.2. for difference in accuracy between the acquisition rule and the reversed rule in rhesus macaques.

**Appendix 29. Summary of the influencing factors of inhibitory control**

Subject and task related factors influencing inhibitory control performances. “Better” performance indicates that the influencing factor is positively influencing inhibitory control skills, “worse” performance indicates it negatively influences it.

Influencing factors		Inhibitory control performance	Task	Animal Classes	References
<b>1. Subject-related factors</b>					
<b>a) Anatomy</b>	Better body condition	better	Detour reaching task	Birds	Shaw, 2017
		worse	Cylinder task	Reptiles	Szabo, Hofer & Whiting 2020
	Absolute bigger brain size	better	Cylinder task	Primates, Canines	MacLean et al. 2014; Horschler et al. 2019; Stevens 2014
<b>b) Personality</b>	More fearful temperament	worse	Distraction task	Primates	Bethell et al., 2019
	Bolder individuals	better	Cylinder task	Fishes	Lucon-Xiccato et al., 2020b
	Higher level of anxiety	worse	Reversal learning, Detour tasks	Primates	Toxopeus et al., 2005, Kabadayi et al. 2018
		worse	Distraction task	Primates	Allritz et al., 2016; Bethell et al., 2012
	Higher curiosity level	better	Reversal learning & Cylinder tasks	Primates	Damerius et al. 2017
<b>b) Demographic factors</b>	Older individuals	worse	Reversal learning	Canines	Tapp et al., 2003
		worse	Reversal learning	Primates	Gokcekus, 2020
		worse	Reversal learning	Primates	Bonté, Kemp & Fagot, 2014
		worse	Reversal learning	Primates	Kumpan, Smeltzer & Teichroeb, 2020
		worse	Reversal learning	Primates	Tsuchida, Kubo & Kojima, 2002
		worse	Reversal learning	Rodents	Schoenbaum et al., 2002

		worse	Reversal learning	Canines	Bray et al., 2014
		worse	Reversal learning	Canines	Wallis et al., 2016
		worse	Reversal learning	Canines	Tapp et al., 2003
	Sex males compared to females	equal	Distraction task	Primates	Boggiani et al., 2018
		worse	Distraction task	Primates	Loyant et al, in publication
		better	Detour task	Fishes	Lucon-Xiccato et al. 2019
<b>c) Environment</b>	Bigger group size	better	Cylinder & Reversal learning tasks	Birds	Ashton et al., 2018
		better	Cylinder task	Canines	Johnson-Ulrich and Holekamp 2020
	More unpredictable environment	better	Detour task	Birds	van Horik et al., 2019
	Enriched environment	better	Detour task	Birds	Kabadayi et al. 2018
	Shelter vs domestic	worse	A-not-B task	Canines	Fagnani et al. 2016
	Domesticated vs wild	better	cylinder task	Canines	Marshall-Pescini et al. 2015
		worse	Detour task	Canines	Marshall-Pescini et al. 2016
	Wild vs captive	better	Detour task	Fishes	Gatto et al., 2018
	Higher social Tolerance	better	Middle cup task	Primates	Joly et al. 2017
	Lower food competition	better	Detour reaching task	Primates	Valmings et al. 2010
	Higher Fission-fusion	better	the A-not B task, Detour reaching task, a Middle cup task	Primates	Amici et al. 2008 ; Amici et al., 2018

			and a measure of self-control		
	More diverse diet	better	A-not-B task/Cylinder task	36 different species	Maclean et al., 2014
<b>2. Task-related factors</b>					
<b>a) Task modalities</b>	Larger opening apparatus	better	modified Cylinder task	Felines	Bobrowicz & Osvath, 2018
	Outward detour compared to inward detour	better	Detour task	Canines	Pongrácz et al. 2001
	Bigger size of the apparatus	better	Cylinder task	Felines	Bobrowicz & Osvath, 2018
<b>b) Salience of reward</b>	Bigger distance of the reward/barrier	worse	Detour task	Rodents	Juszczak & Miller, 2016
	Increased saliency of reward	worse	Detour task	Canines	Brucks et al., 2017
<b>c) Experience</b>	Prior experience with transparent objects	better	Detour task/Cylinder task	Birds	Kabadayi 2018; van Horik et al. 2018, 2019
	Hand tracking training	better	A-not-B task	Birds	Jelbert et al., 2016
	Training	better	Detour task/Cylinder task	Birds	van Horik et al. 2018, 2019
	Previous experience similar task	better	Detour task/Cylinder task	Birds	van Horik et al. 2018
<b>d) Presence of a conspecific</b>	Alone vs partner	better	Modified Stroop task	Primates	Huguet et al., 2014

