Function and mechanisms of primate inhibition

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ABSTRACT
Inhibition in primates has proposed to relate two different factors: their social organization and their cognitive abilities according to primate phylogeny, which leads to two hypotheses. The fission-fusion hypothesis states that primates with a higher degree of fission-fusion will have a higher level of inhibition control. The phylogeny hypothesis states that according to phylogeny, primates with a higher level of cognitive skills will show a higher degree of inhibition control. The level of inhibitory abilities in primates is tested in a variety of procedures. Delay choice tasks, in which subjects have to choose between a small, immediate reward and a large, delayed reward. Reverse-reward contingency tasks, in which subjects have to reach for the smaller reward to obtain the larger reward. The third procedure is delay maintenance tasks, in which a reward grows over time or a small reward can be exchanged for a larger reward and subjects have to choose when to act. Additional and modified procedures of these three task are conducted for further exploration of inhibition control. The aim of the tasks could relate to the social function of inhibition, where assessing a situation before acting could be advantageous. It is unclear which hypothesis can be confirmed, because the results from the different procedures show contradicting patterns. However, it seems the hypotheses do not exclude one another, but are coherent with different aspects of temporal inhibition.

INTRODUCTION
Primates have a large variety of social systems, for example groups which are stable in size and composition and groups in which size and composition differs throughout time, which are called fission-fusion societies. This type of social organization in primates has been proposed to relate to inhibition: species with fission fusion societies will show a higher level of inhibition that species living in permanent groups (Amici et al. 2008). It is also presumed that cognitive abilities according to phylogeny are coherent with inhibition: species with a higher level of cognitive skills will show a higher level of inhibition control (Aureli et al. 2008).

Inhibition is the suppression of an impulse, thereby showing self-control. Inhibition can have relations to reciprocal altruism, were individuals have to cope with a loss of some sort and accept a delay before getting something in return, by showing a degree of self-control (Dufour et al. 2007; Ramseyer et al. 2006). It is interestingly to know whether primates differ in their ability to inhibit impulses, if this relates to their social organization or to their cognitive abilities and how this applies to the social function of inhibition. Therefore, my research question is: Does the pattern in inhibitive abilities fit the social organization of primates or does it relate to phylogenetically determined differences in intelligence?

In this thesis, I will describe the social function of inhibition and address the different hypotheses that are given in the literature regarding inhibition. Then I will discuss the research that has been conducted to examine the aspects of inhibition. After that I will evaluate the used methods to try to establish a comparison between the results. That will lead to an overview of the abilities of primates in inhibition tasks. I will discuss critical points and will establish a conclusion. I will also explore how this relates to the social function of inhibition.

Two hypotheses are proposed in regarding to the inhibitory abilities of primates.

Social function of inhibition
The first hypothesis concerns the social organization of primates. In certain social situations, assessing a situation before acting and thereby showing inhibition control

can be advantageous. Inhibition can be of value in aggressive encounters, in which careful consideration about the appropriate response could be key to a successful outcome. These aggressive encounters can occur in various contexts, in relation to mates, food resources, social rank and territorial conflicts. In the process of finding a mate, inhibition can be favorable, depending on the social status of the male and female. For example, if a lower-ranking male tries to court a higher-raking female, the male will most likely have competition of higher-raking males, which can result in fighting. Therefore, the lower-ranking male has to weigh the costs of his action and decide if the outcome would be beneficial. Waiting to get access to food until higher-ranked individuals are finished is also an example in which showing inhibition control can be advantageous. In order to achieve or maintain a higher social rank, it can be beneficial to inhibit certain impulses. To act immediately or wait for a more suitable moment can make the difference. The same is true in territorial conflicts, where members of different social groups defend their territory. Thus, inhibition can be favorable in different contexts and can even be a means for survival.

Primates life in groups, which can be of stable composition, but can also be less stable, in which subgroups of variable composition separate from their own group to merge with another. When this happens frequently, individuals show a high level of fission-fusion. In this situation, individuals have to deal with changing social partners and must remember information about these social partners, even if they are absent. In this regard, individuals may possess enhanced skills to inhibit responses if this is more favorable in certain situations, depending on the social partners present (Aureli et al. 2008). Thus, individuals may have a higher ability to inhibit impulses due to their behavioral flexibility necessary in fission-fusion societies (Amici et al. 2008). Therefore, the fission-fusion hypothesis states that primates with a higher degree of fission-fusion have a higher ability to show inhibition. For all the primates species that have been researched for inhibitory capabilities (Figure 1) this implies that chimpanzees, bonobos, orangutans and spider monkeys have a high degree of inhibitory control, because they have a high degree of fission fusion (Campbell et al 2006; Smuts et al. 1987). Orangutans are the least social species of the species with high levels of fission-fusion and experience lower levels of competition. Therefore, they may show even higher levels of inhibition control, because they can afford to be more patient (Shumaker et al. 2001). For gorillas, capuchin monkeys, macaques, lemurs, squirrel monkeys, tamarins and marmosets it implies having a lower degree of inhibitory control, because they have a lower degree of fission fusion (Boinski 1999; Campbell et al 2006; Ferrari & Digby 1996; Savage et al. 1996; Sussman 2003).

Inhibition and cognitive abilities of a clade

The second hypothesis concerns the cognitive abilities of primates. Individuals with high levels of fission-fusion have to cope with changing social environments and hence have to be able to reestablish relationships with previous group members and have to frequently form new alliances, establish dominance status and uncover relationships among individuals (Barrett et al. 2003). These abilities may require cognitive skills, such as memory for temporal and spatial information and inferential and analogical skills (Aureli et al. 2008). So the degree of cognitive abilities could be an important factor in fission-fusion societies and thus could be a measure for the ability to inhibit impulses. The cognitive abilities of a number of primates species were examined in Reader et al. 2011. The investigated species were derived from three different clades: prosimians, monkeys and great apes. To measure the level of cognitive skills, five aspects were researched, namely extractive foraging, innovation, social learning, tactical deception and tool use. They found that great apes outperformed monkeys and prosimians and therefore posses the highest level of cognitive abilities. Monkeys scored better than prosimians, although the difference was not significant. According to their findings, the level of cognitive abilities is coherent with primate phylogeny. Therefore, the phylogeny hypothesis states that according to phylogeny, primates with a higher level of cognitive skills will show a higher level of inhibition control. The expectation is that great apes would show the highest levels of inhibition, then monkeys and last prosimians.

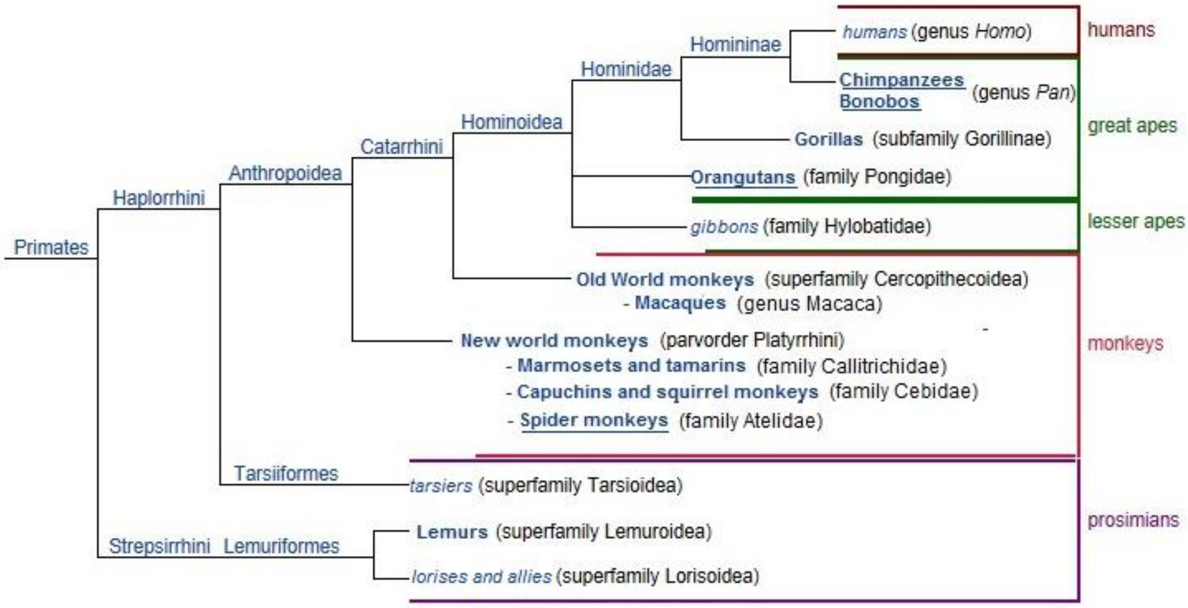

Figure 1. Phylogenetic classification of primates (Cartmill & Smith 2011), non-investigated species are shown in italics, investigated species are shown in bold and species with a high degree of fission-fusion are underlined.

DESCRIPTION OF INHIBITION RESEARCH

Inhibition can be considered as delaying action for obtaining some sort of benefit later on. This is researched in experimental tasks, which have a non-social character and in which food is used to examine inhibition. The experiments that are done with regarding to inhibition are often called delay of gratification tasks. Within that field of tasks, a number of different procedures are carried out. I am going to discuss four of them: namely delay choice tasks, reverse-reward contingency tasks, delay maintenance tasks and tasks in which abstract representation of food rewards is used. Then I will discuss two other procedures that are not fitting in the other categories, in which they looked at the spatial aspect and at the motor aspect of inhibition. Per procedure, I will give the specifics of the experimental set-up, name the variations within those set-ups and look how this variation will affect the results. Variation in the number of subjects that is used will affect the reliability of the results, while variation in number of sessions, trials within those sessions and amount of food rewards will affect the comparability between the results. I will compare the results and examine which hypothesis can be confirmed.

The social organization is given for each species, if they live in groups of stable composition or if they live in unstable groups with a high level of fission-fusion. The rank of performance, in which 1 is the best performance and 10 is the worst, is established when species of different clades have participated in the task and when species with a different social organization have participated. If the same species is researched in multiple studies within a task, the average of the results will be calculated. This is done by multiplying the number of subjects with the outcome of the task for each study, adding those values and dividing this with the total number of subjects of the same species that are researched. These rankings will be used to compare results within a task and later on to compare the results of the different tasks. When more than two studies are conducted in the same task, the studies are labeled (A, B, C, etc.) to be able to discuss the variations and results in a clear manner.

Task 1: Delay choice tasks

In these tasks, subjects have to choose between food that is directly available or food that becomes available after a delay. These tasks can occur in two conditions: quantitative tasks and qualitative tasks. In qualitative tasks, subjects have to choose between a immediate, smaller amount of food or a delayed, larger amount of food. In qualitative tasks, subjects have to choose between immediate, less-preferred food or delayed, more-preferred food. During this tasks, subjects cannot alter their first decision. The subjects are tested in a number of trials that end when the indifference point is reached, which is when the mean delay to the larger reward in the last five sessions differed by less than 10% from the mean delay to the larger reward in the previous five sessions (Addessi et al. 2011). Thus, the indifference point is the point of delay at which subjects equally value the smaller, immediate reward and the larger, delayed reward (Stevens et al. 2005b).

Table 2. Delay choice task. Study label, reference number of the study, social organization (G = stable group, FF = fision-fussion), number of subjects and sessions*, qualitative or quantitative task, ratio smaller/larger reward, indifference point (s) and performance rank for each species. N/A means that the specifics are not present in the experiment.

	Study	Social org.	Species	Number of subjects	Number of sessions	Qualitative of Quantitative task	Ratio smaller/ larger reward	Indifference point (s)	Rank
			Prosimians						
A	42	G	Lemur**	5	22-56 (14)	Quantitative	2/6	17±8	8
			New world monkeys						
B	44	G	Common Marmoset	5	15-32 (14)	Quantitative	2/6	7.9±0.6	10
	44	G	Cotton-top Tamarin	6	15-32 (14)	Quantitative	2/6	14.4±1.5	9
C	2	G	Capuchin monkey	16	15-30 (14)	Quantitative	2/6	81.1±7.7	6
D	3		Capuchin monkey	27	N/A (14)	Quantitative	1/3	22±3	
E	16		Capuchin monkey	8	10-20 (2) 8-24 (2)	Quantitative Qualitative	1/4	8.75 15	
D	3	FF	Spider monkey	18	N/A (14)	Quantitative	1/3	76±8	2
			Old world monkeys						
D	3	G	Long-tailed macaque	12	N/A (14)	Quantitative	1/3	24±4	7
			Great apes						
D	3	FF	Orangutan	10	N/A (14)	Quantitative	1/3	50±9	4
	3	G	Gorilla	7	N/A (14)	Quantitative	1/3	44±11	5
	3	FF	Chimpanzee	8	N/A (14)	Quantitative	1/3	124±11	1
F	37	FF	Chimpanzee	5	N/A (14)	Quantitative	2/6	122.6±15.9	
G	13	FF	Chimpanzee	3	8 (6)	Qualitative		210±30	
D	3	FF	Bonobo	4	N/A (14)	Quantitative	1/3	74±9	3
F	37	FF	Bonobo	5	N/A (14)	Quantitative	2/6	74.4±8.5	

* The number of trials of which one session consisted is indicated between parentheses
** The species examined were black lemur, black-and-white ruffed lemur and red-ruffed lemur

The specifics of the experimental procedures differ among the research that has been done (Table 2). A small number of subjects is used in a number of studies (A, B, D, F, G). The number of sessions conducted for each species is variable and not always indicated. One session consist of a number of trials, in which the delay is held constant. The number and condition of trials within a session is also variable per research. Trials can occur in two forms, namely forced choice trials, in which just one reward is available for familiarization with the experimental conditions, and free choice trials, in which the subject can make a choice between the smaller, immediate reward and the larger, delayed reward. The dispersion and number of the two forms of trials per session differs across the research that has been done. In study A, B, C, D and F, the total number of trials in a session is 14. Four of them are forced choice trials and 10 are free choice trials. In study E, 10 forced choice trials were completed before starting with the experiments. Sessions consisted only of 2 trials, this could be due to the fact that they conducted a number of small experiments, because they had another goal in their study compared to the other research, as described later on. In study G, the total number of trials in a session is 6, with 2 forced choice trials and 4 free choice trials. For most studies, the ratio between the smaller and larger reward in quantitative tasks is 2/6, while in study D the ratio is 1/3 and in study E this is 1/4.

There are differences in the assessment of the indifference point. In most research, delay time was increased or decreased with 5-10 s or was held constant based on the subjects performance. However, study E and G conducted another approach. The aim of study E was to examine new methods that would allow subjects to understand the nature of the task more quickly, therefore the delay time was never changed. They conducted four experiments, in which the delay time was fixed at 15 s for the two qualitative experiments and 10 s for the two quantitative experiments. Their task consisted of two food items on a mechanized, revolving tray that moved the food items in reach of the subjects. The subject was allowed to choose only one food item. All of the subjects accomplished the task in the minimum number of trials or with perfect performance, indicated that the nature of the task was simple to understand. In study G, subjects first had to reach 180 s in a training phase. Then if subjects succeeded in the tasks, the delay time was increased by 60 s. The assessment of the indifference point in this experiment is less accurate than in the other experiments, because the delay time was increased by a relatively long time period of 60 s, compared to 5-10 s in the other studies. Therefore, it is more difficult to find the actual indifference point of the subjects. The reliability and comparability of the results decreases because of studies with low number of subjects, variable conditions and number of sessions and variable assessment of the indifference point.

Study E and G used qualitative tasks instead of quantitative tasks. The results of the qualitative tasks are more difficult to compare with each other, because the kind of more-preferred food differs among individuals and species. Confirmation of a hypothesis cannot be achieved, because only two species have been researched in qualitative tasks. However, chimpanzees are both examined in quantitative tasks (study D and F) and in a qualitative tasks (study G), which makes it possible to compare performance between the two different tasks. Chimpanzees perform better in the qualitative task than in the quantitative task, which could mean that the qualitative version is easier to understand for the subjects or there is interspecies variation in inhibition levels. Research in more subjects performing the qualitative task is necessary to explore which explanation can be applied.

Variation in performance of subjects within the same species can also be seen in capuchin monkeys (study C and D). The performance of the capuchin monkeys in study C is much better than the performance in study D. The lower amounts of rewards in study D compared to the amounts used in study C could be an explanation for the decreased performance. More experiments with capuchin monkeys under the same conditions are necessary to discover the actual level of inhibition the species possess. The performance of the capuchin monkeys in study E can be left out of consideration, because the set-up of the study was different, as described previously.

The results follow the fission-fusion hypothesis in which a high degree of fission-fusion means a high degree of inhibitory control. Chimpanzees, spider monkeys, bonobos and orangutans perform better than capuchin monkeys, gorillas, macaques, lemurs, tamarins and marmosets. However, the results also tend to follow the phylogeny hypothesis, because most great apes perform better than most monkeys and most monkeys perform better than the prosimians. Not all great apes perform better than monkeys: orangutans and gorillas perform worse than spider monkeys. Also, not all monkeys perform better than prosimians: marmosets and tamarins perform worse than lemurs. More similar research in a larger number of subjects is needed to strengthen a hypothesis.

Modified delay choice task
In one study (Table 3) the qualitative version of the delay choice task is conducted, only edible tools are used as immediate reward and those tools could be used to obtain a more-preferred food item. Thus, this task requires a combination of self-control and tool use. They tested 20 subjects, of which 5 were highly experienced with tool use, 5 were moderately experienced and 10 were little experienced.

Table 3. Modified delay choice task. Reference number of the study, social organization (G = stable group), experience group, number of subjects and sessions* and percentage of succeeded subjects.

Study	Social org.	Species	Experience Group	Number of subjects	Number of sessions	Succeeded subjects (%)
22	G	Capuchin monkey	High Moderate Low	5 5 10	6 (1)	95 60 20

* The number of trials of which one session consisted is indicated between parentheses

Out of table 3 can be concluded that in this task, a high level of experience in tool use relates to a high performance rate in inhibition ability. With less experience in tool use, the ability to delay gratification declines. A higher number of sessions and trials within those sessions could be conducted to further examine the reliability of the results. Conducting the same experiments in other species would show how their abilities in this task would differ from the capuchin monkeys. This task shows how the decision between eating the edible tool or using the tool could have consequences on the outcome.

Task 2: Reverse-reward contingency tasks
Subjects have the choice between a smaller or less-preferred array of food or a larger or more-preferred array of food. Thus, these tasks also occur in a quantitative and qualitative version, the same as delay choice tasks. By reaching for the smaller or less-preferred array, they receive the larger or more-preferred array and vice versa. Subjects must resist their initial impulse to choose the more appealing, larger or more-preferred array, thereby showing inhibition control. The subjects were

considered successful if they chose the smaller array for 80% of the time in at least five consecutive sessions. The results are displayed by the percentage of succeeded subjects.

Table 4. Reverse-reward contingency task. Study label, reference number of the study, social organization (G = stable group, FF = fision-fussion), number of subjects and sessions*, qualitative or quantitative task, ratio smaller/larger reward, succeeded subjects (%) and performance rank for each species. NS means the species was not successful in the task.

	Study	Social org.	Species	Number of subjects	Number of sessions	Qualitative or quantitative task	Ratio smaller/ larger reward	Succeeded subjects (%)	Rank
			Prosimians						
A	27	G	Lemur**	10	20 (10)	Quantitative	1/4	0	3
B	28		Brown lemur	5	75 (20)	Quantitative	1/4	20	
C	25		Lemur**	7 8	5 (20) 5 (20)	Quantitative Qualitative	1/4	57 88	
			New Wold monkeys						
D	29	G	Cotton-top tamarin	4	10 (10)	Quantitative	1/3	0	NS
E	31		Cotton-top tamarin	11	10 (10)	Quantitative	1/3	0	NS
F	4	G	Squirrel monkey	8	10 (20)	Quantitative	1/4	0	NS
G	1	G	Capuchin monkey	8	16 (20)	Quantitative	2/5	13	4
H	5		Capuchin monkey	7	10 (20) 10 (20)	Quantitative Qualitative	1/4	0 100	
			Old World monkeys						
I	32	G	Rhesus macaque	6	17-135 (20)	Quantitative	1/4	100	1
			Great apes						
J	15	FF	Chimpanzee	5	20 (18)	Quantitative	Various combi-nations 0-6	0	NS
K	40	FF	Orangutan	2	21 (20)	Quantitative	Various combi-nations 0-6	100	2

* The number of trials of which one session consisted is indicated between parentheses
** The species examined were black and brown lemurs

Among the research that is conducted, variation occurs in the set-ups (Table 4). The number of subjects varies across the conducted research from 2 subjects to 11 subjects. The number of sessions is variable across studies, with a minimum of 5 sessions and a maximum of 135 sessions. Most studies conducted between the 10 and 21 sessions, but study B and I differ substantially from that range with a maximum of 75 and 135 sessions that were conducted. This much larger number of sessions could be of great influence on the results. The trials within sessions are mostly 20, while in study A, D and E 10 trials were conducted within a session and in study J 18 trials were conducted. This difference in trials will probably not be of much influence on the results. The variation in sessions and trials can cause a less reliable comparison of the results. In most studies, the ratio is 1/4 or 1/3, while in some experiments the ratio is different, namely 2/5 or various combinations of ratios within one experiment. This could be of influence on the comparability of the results.

The results (Table 4) show that most species perform badly in the quantitative version of the reverse-reward contingency task. However, when the number of sessions is high, all the macaques in study I succeeded in the task. In study B, one lemur succeeded when the number of sessions was high. Macaques (study I) appear to perform better than lemurs (study B), but macaques received more sessions than the lemurs did, so firm conclusions cannot be made. In another study (C), more lemurs succeeded in the task, only those subjects participated earlier in study A and received a training before attending in study C, which may account for their high performance. Furthermore, it appears that orangutans can be successful in quantitative reverse-reward contingency tasks (study K). This is remarkable if you compare their performance with the other great ape that has been tested on the quantitative task (study J). Chimpanzees in that study have been tested under the same conditions as orangutans, and they failed to perform on the reverse-reward task. This striking difference can be caused by differences at the individual level, which could be differences in personality, overall mental ability, or varying levels of exposure to cognitive tasks (Shumaker et al. 2001). Another explanation, as mentioned in the introduction, could be that orangutans are, in comparison to chimpanzees, are the least social and therefore may encounter less competition. Which means that orangutans can afford to be more patient, other than chimpanzees, who face much more situations in which competition is high (Shumaker et al. 2001).

Subjects are more successful in the qualitative task. In study C, most of the lemurs that were researched succeeded and in study H all of the capuchin monkeys showed a high performance. The quantitative version of the task could be more difficult to process than the qualitative version. This could be due to the incentive value of the larger array, which interferes with the ability to inhibit the initial response (Boysen et al. 1996). Because of the small number of species researched, no firm conclusions can be made. Also, the kind of more-preferred food differs among species, which makes the results of qualitative tasks less comparable. These two factors make it difficult to confirm a hypothesis.

Overall, because of the low number of successful subjects in the quantitative task and the low number of species researched in the qualitative task, no hypothesis can be confirmed. Performances can improve when a higher number of sessions is used, therefore more research is needed with a higher number of sessions. Also, more research with a higher number of subjects is necessary to reach more reliable results.

Training trials for reverse-reward contingency tasks

As mentioned earlier, training could improve performances of the subjects tested in the quantitative version of the reverse-reward contingency task. In five studies (A, C, D, E and F) training was conducted in the form of modified procedures of the reverse-reward task. One of those procedures is the large-or-none task, in which no reward followed a reach to the larger array. Study C and F also used correction trials, which consisted of time-out or leaving the tray with the smaller and larger array in sight but out of reach of the subjects. These trials were continued until the subjects choose the smaller array or completed a particular number of sessions. In the case of a time-out, the experiment took the tray with both arrays out of sight for 20 s and then the same rewards were represented. Ranking was only applied in the standard version of the reverse-reward contingency task, because this procedure is an addition to the standard reverse-reward contingency task.

Table 5. Large-or-none procedure and correction trials. Study label, reference number of the study, social organization (G = stable group), number of subjects and sessions*, ratio smaller/larger reward, percentage of succeeded subjects and performance rank for each species.

	Study	Social org.	Species	Number of subjects	Number of sessions	Ratio smaller/ larger reward	Succeeded subjects (%)	
							Large-or-none	Correction trials
			Prosimians					
A	25	G	Lemur**	8	7-11 (20)	1/4	100	
C	27		Lemur**	9	15-40 (10)	1/4	67	100
			New World monkeys					
D	29	G	Cotton-top tamarin	4	10-44 (10)	1/3	100	
E	31		Cotton-top tamarin	11	10-30 (10)	1/3	0	
F	4	G	Squirrel monkey	8	5-10 (20)	1/4;1/2	13	75

* The number of trials of which one session consisted is indicated between parentheses
** The species examined were black and brown lemurs

The specifics of the experiments differ across studies (Table 5). The majority of the studies tested between the 8 and 11 subjects, while study D used 4 subjects, leading to a less reliable outcome of that study. The number of sessions and trials within those sessions differs across studies, which could influence the comparability of the results. The ratios across studies is quite similar, which makes the results more comparable.

After conducting the large-or-none procedure (Table 5), an increase in performance of choosing the smaller array can be seen compared to the results of the standard reverse-reward contingency task (Table 4), indicating that more training could affect performance in this task. An even greater increase in performance is shown after correction trials, indicating that the use of correction trials is the best way to improve performance. However, more research is necessary to confirm this. The lemurs in study A performed better than the lemurs in study C, which can be explained by the fact that the lemurs participating in study A participated earlier in study C. Previous experience with the task could cause increased a performance level. In study E, all the tamarins failed to succeeded in the large-or-none task. It seems that the tamarins were unable to refrain from reaching to the larger array, because of the appealing nature. To examine this phenomenon, study D used a modified procedure of the large-or-none task, by giving the small reward when subjects reached for it, instead of giving the large reward. They hypothesized that tamarins would still choose the larger array, but in contrast, all tamarins chose the smaller array. Therefore, the reason underlying the failure in study E remains unclear. After conducting correction trials, lemurs (study C) performed better than squirrel monkeys (study F). However, lemurs received more sessions compared to the squirrel monkeys, which could explain why not all the squirrel monkeys succeeded in the task.

The underlying understanding of successful subjects was examined in three studies (Anderson et al. 2000; Genty et al. 2004 and Kralik 2012) by presenting them with novel combinations of food arrays. They wanted to know if the subjects simply learned to reach for the single piece of food, which was the standard representation of the smaller award, or that the subjects really learned to distinguish between the different quantities. All three species (squirrel monkeys, lemurs and macaques) succeeded when presented by novel combination of food ratios, which means the subjects really learned to discriminate between different quantities.

Overall, more training in modified procedures of the reverse-reward contingency task seem to improve performance in the species that have been tested. This success shows that the failure in the standard task is not due to just the inability to retain from reaching to the larger reward. However, it is difficult to draw a conclusion towards the fission-fusion hypothesis or the phylogeny hypothesis, because the training procedures are only conducted on three different species. Therefore, more research on a variety of species with the same methods is necessary to reach a reliable conclusion.

Task 3: Delay maintenance tasks
In these tasks, subjects have to overcome a delay period in order to receive a larger reward. These tasks can occur in two conditions, accumulation tasks and exchange tasks.

Accumulation tasks
Subjects are presented with a reward that grows as time passes, allowing them to take it at any point (thereby ending the accumulation) or wait until the growth is complete. There is a specific number of maximum food items in these tasks, which is visible for the subjects during the experiment. The percentage of succeeded subjects is based on the number of subjects that managed to reach the maximum delay time indicated. Subjects have the possibility to alter their decision these sorts of tasks.

Table 6. Delay accumulation task. Study label, reference number of the study, social organization, number of subjects and sessions*, maximum number of food items), percentage of succeeded subjects, maximum delay time (s) and performance rank per species.

	Study	Social org.	Species	Number of subjects	Number of sessions	Maximum number of food items	Succeeded subjects (%)	Maximum delay time (s)	Rank
			New World monkeys						
A	6	G	Squirrel monkey	4	10 (10)	6	25	30	5
		G	Capuchin monkey	4	4 (10)	6	0		4
B	23		Capuchin monkey	8	8 (4) 10 (2)	5 50	88 0	10	
C	34		Capuchin monkey	3	30 (2)	5	100	42	
			Old World monkeys						
C	34		Long-tailed macaque	6	30 (2)	8	100	72	3
D	20	G	Rhesus macaque	9	15 (1)	10	44	30	
E	33		Tonkean macaque	9	30 (2)	6	67	54	
			Great apes						
F	12	FF	Orangutan	1	5 (2)	20	100	180	2
		FF	Chimpanzee	4	5 (2)	20	100	180	1
G	9		Chimpanzee	4	5 (2)	15	100	150	
H	10		Chimpanzee	4	10 (1)	36	50	600-650	

* The number of trials of which one session consisted is indicated between parentheses

The experimental set-up differs across studies (Table 6). The number of subjects is low in most studies (A, C, F, G, H), which can cause less reliable results. The number of sessions and the number of trials of which those sessions consisted differs among the studies. This can lead to a less reliable comparability of the results, just as the considerable differences seen in the maximum number of food items used in each study. The assessment of the maximum delay time depends on the maximum number of food items, the time between transfer of food items and the duration of the transfer of the food items. For example, if the maximum number of food items is 36, subjects can reach a longer maximum delay time, because more time is needed to transfer the food items than when 6 food items are used. If the time between transfer of food items or duration of the transfer is longer, subjects also have the opportunity to reach a longer maximum delay time. More research under the same conditions for each species is necessary to more accurately assess maximum delay times.

The results show that chimpanzees (study F, G, H) and orangutans (study F) performed best in the delay maintenance task. Furthermore, the order of performance is macaques (study C, D, E), capuchin monkeys (study A, B, C) and squirrel monkeys (study A). Thus, the great apes outperformed the Old World monkeys and the New World monkeys, while the Old World monkeys outperformed the New World monkeys. The results follow the pattern of the phylogeny hypothesis, in which a high level of cognitive skills means possessing a high level of inhibition control. However, the fission-fusion hypothesis can also be applied, because the species with a high level of fission-fusion, chimpanzees and orangutans, showed the highest level of inhibition. To provide more support for the fission-fusion hypothesis, gorillas and spider monkeys should also be examined in the delay maintenance task. The performance of these two species could provide a more distinct conclusion. Thus, there seems to be support for both hypotheses, although the support for the phylogeny hypothesis is more convincing.

Modification of accumulation task

In order to further investigate capabilities of the subjects, study A, D, G and H modified their previous experiment (Table 6) by changing the specifics of the set-up (Table 7). In study A, still 6 food items were used, but the food items varied in size. The food was transferred from smallest to largest, thereby creating a larger reward when time progressed compared to the standard procedure, where the food items were of equal size. The modifications helped more subjects to reach the maximum delay time in this task (Table 7), thus performing better than in the standard task (Table 6), indicating that a larger reward could improve performance. Study D adjusted the standard procedure by inserting a more-preferred food item at the beginning (1), middle (2) or end (3) of the trial, while the rest of the food items were less-preferred. The results (Table 7) show that adding a more preferred food item at the end of the task improved the performance of one subject compared to the standard task (Table 6), while adding a more preferred food item in the beginning of the task caused less subjects to succeed (Table 7), compared to the standard task (Table 6). Adding a more preferred food item in the middle of the task showed no effect. In study G, the maximum number of food items was increased and the transfer time between food items was decreased (1). In another series of sessions, they also varied the transfer time between food items according to the performance of the subject (2). If a subject succeeded in waiting for all food items to have been transferred the transfer time increased with 1 s. The results (Table 7) show that subjects could achieve a longer maximum delay time than in the standard task (Table 6). Study H added a component of working for the accumulation of rewards to the

experiment. Subjects had to perform a computer task which led to the delivery of food items (1). In another condition the subjects could perform the computer task, but this had no connection to the delivery of food items (2). Working for the delivery of food items did not have much effect (Table 7), and the performance did not improve compared to the condition with no computer task present (Table 6).
In study I, the standard maintenance task was conducted, only the subjects had the opportunity to distract themselves with toys, which could be of help to achieve higher levels of self-control. The results (Table 7) shows that performances are affected by the possibility of distraction, because the maximum delay time is higher compared to the performances of chimpanzees in study G and H.

Because these modified experiments are an addition to the standard delay maintenance task, ranking of the performance of each species is not calculated. However, it appears chimpanzees (study G, H, I) are the best performing species and that macaques, squirrel monkeys and capuchin monkeys have equal levels of performance. This points to the phylogeny hypothesis, but is also consistent with the fission-fusion hypothesis. However, confirmation is difficult, because the pattern of the results is not clear enough. The various modifications made in each study make it difficult to compare the results. Also, research in more different species is necessary to be able to confirm a hypothesis.

Table 7. Modified delay maintenance task. Study label, reference number of the study, social organization (G = stable group, FF = fission-fusion), number of subjects and sessions*, maximum number of food items, percentage of succeeded subjects and maximum delay time (s) per species. The number in column M represents the number of the modified condition as mentioned in the text above.

	Study	Social org.	Species	Number of subjects	M	Number of sessions	Maximum number of food items	Succeeded subjects (%)	Maximum delay time (s)
			New World monkeys						
A	6	G	Capuchin monkey	4		10 (10)	6	50	30
		G	Squirrel monkey	4		10 (10)	6	50	30
			Old World monkeys						
D	20	G	Rhesus Macaque	9	1 2 3	5 (1) 5 (1) 5 (1)	10	22 44 56	30
			Great apes						
G	9	FF	Chimpanzee	4 4	1 2	10 (2) 20 (2)	36	75 50	180 442-612
H	10		Chimpanzee	4	1 2	10 (1) 10 (1)	36	50 50	490-540 580-690
I	21		Chimpanzee	4		10 (1)	36	25	1080

* The number of trials of which one session consisted is indicated between parentheses

Exchange tasks
Exchange tasks can occur in two conditions. One condition (1) consists of keeping a smaller reward for a increasing period of time before returning it and receive a larger reward (study A, B, C, D). In this condition, the delay time is increased when subjects reach certain time criteria, thereby assessing the maximum time the subjects can inhibit their impulse to eat the reward they already posses. In the other condition (2), subjects return the smaller reward before the onset of the waiting period (study A and

C). After returning, the smaller reward was placed next to the larger reward, in front but out of reach of the subject. Here, the delay time is increased when subjects reach certain time criteria, thereby assessing the maximum time the subjects can wait for the larger reward after returning the smaller reward. The performance rank is only based on the performance in condition 1, because the capuchin monkeys in study B and the chimpanzees in study D are not tested in condition 2.

Table 8. Delay maintenance task with exchange procedure. Study label, reference number of the study, social organization (G = stable group, FF = fission-fusion), number of subjects and sessions*, size of food item, percentage of succeeded subjects, maximum delay time (s) and performance rank for each species. The number in column C represents the number of the experimental condition as mentioned in the text above.

	Study	Social org.	Species	Number of subjects	C	Number of sessions	Size of food item	Succeeded subjects (%)	Maximum delay time (s)	Rank
			New World monkeys							
A	34	G	Capuchin monkey	9	1 2	4(12) 4 (12)	2, 4, 8 40 40	11 11 33	80 320 1280	3
B	35		Capuchin monkey	6	1	4 (12)	2, 4, 8 40	33 17	20 40	
			Old World monkeys							
C	33	G	Tonkean macaque	9	1 2	4 (12) 4 (12)	2, 4, 8 40 40	22 22 11	160 640 2560	2
A	34		Long-tailed macaque	10	1 2	4 (12) 4 (12)	2, 4, 8 40 40	20 10 40	160 320 2560	
			Great apes							
D	19	FF	Chimpanzee	5	1	4 (12)	2, 4, 8 40	60 80	240 480	1

* The number of trials of which one session consisted is indicated between parentheses

The number of subjects is quite low in study D, compared to the number of subjects that were tested in the other studies (Table 8). Because most studies (A, B, C) tested 6 or more subjects, the results should be reliable. The number of sessions, the trials within them and the size of the food items are the same throughout the experiments (Table 8), which would lead to a reliable comparison of the results.

The results (Table 8) show that in condition 1, when the size of the food items is small, chimpanzees (study D) were able to reach the highest maximum delay time. Macaques (study A and C) reached the next highest delay time and capuchin monkeys (study A and B) reached the lowest. When food items increase in size under condition 1, macaques reached a higher maximum delay time than chimpanzees. However, only a small percentage of the total number of macaques tested were able to reach a delay time of 640 s (study C), while the other subjects reached between the 80 and 320 s (Pelé et al. 2010; Pelé et al. 2011). 80 % of the chimpanzees are able to reach a delay of 480 s (study D), which compared to macaques is a more convincing result. Overall, chimpanzees perform better than macaques and capuchin monkeys, but research in more subjects is needed to obtain more convincing results. In condition 2, macaques perform better than capuchin monkeys. In comparison to condition 1, maximum delay times are much higher, so removing of the continuous possibility to consume the food item improved performance.

The results are consistent with both hypotheses, therefore more research in a variety of species is necessary in order to confirm the phylogeny or fission-fusion hypothesis.

Task 4: Abstract representation of food rewards
In each of the three methods described above, an alternative procedure can be used in which the food rewards are replaced by abstract items or are represented by abstract means. In this way, a response bias caused by the incentive features of the food can be avoided, because the abstract representation creates psychological distancing from the food (Addessi & Rossi 2011). This procedure can lead to an increase in performance.

Abstract representation of food rewards in delay choice tasks
In two studies (A and B), qualitative delay choice tasks, in which subjects have to choose between immediate, less-preferred food or delayed, more-preferred food, have been done with abstract representation of food rewards. In study A, lexigrams were used as abstract representation and in study B lexigrams and photos of the food rewards were used instead of the actual food rewards.

Table 9. Abstract representation of the qualitative delay choice task. Study label, reference number of the study, social organization (FF = fission-fusion), number of subjects and sessions*, type of abstract item, percentage of succeeded subjects and indifference point (s) for the species.

	Study	Social org.	Species	Number of subjects	Number of sessions	Type of abstract item	Succeeded subjects (%)	Indifference point (s)
A	11	FF	Chimpanzee	3	4 (30)	Lexigram	67	160-176
B	13		Chimpanzee	3	8 (6) 8 (6)	Photo Lexigram	33 33	180 180

* The number of trials of which one session consisted is indicated between parentheses

The number of subjects is low in both studies, which can lead to less reliable results. Study A conducted fewer sessions than study B, but they conducted a much larger number of trials within those sessions, which could be of great influence on the results. However, this is not the case, because the subjects performed on a similar level in both experiments.

Comparing the performances of the chimpanzees in the abstract representation of the qualitative delay choice task (Table 9) with the performances of the chimpanzees in the standard qualitative delay choice task (Table 2, study G), shows a lower indifference point when abstract items were used. This could be due to differences in experience with photographs and lexigrams representing the food. The fact that the subjects performed better in the condition with the food items, could also suggest that in this case the incentive features of the food items did not interfere with their performance. These results could be made more reliable by testing a larger number of subjects. To be able to confirm a hypothesis, research in other species is needed to assess their abilities with the task.

Abstract representation of food rewards in reverse-reward contingency tasks
In the quantitative version of the reverse-reward contingency tasks, performances could be improved by more training, as discussed earlier. Another possibility to improve performance is to represent the food reward by other means, such as tokens (study B), rocks and Arabic numbers (study E), graphic presentation (study A) or color association (study C and D).

Table 10. Abstract representation of the reverse-reward contingency task. Study label, reference number of the study, social organization, number of subjects and sessions*, type of abstract item, ratio smaller/larger reward, percentage of succeeded subjects and performance rank per species.

	Study	Social org.	Species	Number of subjects	Number of sessions	Type of abstract item	Ratio smaller/ larger reward	Succeeded subjects (%)	Rank
			Prosimians						
A	26	G	Lemur**	4	30 (10)	Graphic presentation in the form of red spots	1/4	75	3
			New world monkeys						
B	1	G	Capuchin monkey	8	12-18 (20)	Tokens	2/5	63	5
C	31	G	Cotton-top tamarin	9	10-30 (10)	Colors	Various combi-nations of 0,1,3,6	67	4
			Great apes						
D	46	FF	Orangutan	5	30 (16)	Colors	Various combi-nations of 0, 1, 4	40	6
		G	Gorilla	5	30 (16)	Colors	Various combi-nations of 0, 1, 4	20	7
E	15	FF	Chimpanzee	5	5 (18) 6 (18)	Rocks Arabic numbers	Various combi-nations 0-6	0 100	1
D	46		Chimpanzee	4	30 (16)	Colors	Various combi-nations of 0, 1, 4	50	
		FF	Bonobo	4	30 (16)	Colors	Various combi-nations of 0, 1, 4	75	2

* The number of trials of which one session consisted is indicated between parentheses
** The species examined were black and brown lemurs

The specifics vary across the research that has been done (Table 10). In most research a low number of subjects has been used (study D and E), while in two studies (B and C) a higher number of subjects has been tested. Number of sessions, trials within those sessions and ratio of food reward differ across experiments. Type of abstract means or items is also variable across studies. So the comparability is relatively low, since most studies have few subjects and vary in conditions and number of trials and sessions.

When comparing the results of the standard reverse-reward contingency task (Table 4) with the results of the abstract representation of the standard task (Table 10), it shows that in general performances improved when abstract items were used. This means that in this case the interference of the incentive value of the food caused the subjects to perform better. In study E, it appears that rocks as abstract representation of food items does not have an effect on the performance level of the subjects. This could be due to the quantitative properties the rocks possess, which resemble the quantitative properties of food arrays. The results of study A and D show that 75% of the lemurs and 75% of the bonobos succeeded in the task, which is an equal level of performance. However, bonobos received more trials per session, which makes their level of performance more reliable. Because of that, their performance was ranked as second best in the task. The results (Table 10) show that chimpanzees, bonobos and lemurs perform best in this task, then tamarins, capuchin monkeys, orangutans and least gorillas. This order of performances does not follow the phylogeny or the fission-fusion hypothesis, thus research in more subjects and species under the same conditions is needed to come to a conclusion.

Abstract representation of food rewards in delay maintenance task
There is also a quantitative delay maintenance task in which abstract representation of the food rewards is used. In this study (Table 11) tokens were used to represent the food rewards.

Table 11. Abstract representation of the delay maintenance task. Reference number of the study, social organization (G = stable group), number of subjects and sessions*, type and maximum number of abstract items, percentage of succeeded subjects and maximum delay time (s). The number in the first column represents the reference number of the research.

Study	Social org.	Species	Number of subjects	Number of sessions	Type of abstract item	Maximum number of abstract items	Succeeded subjects (%)	Maximum delay time (s)
23	G	Capuchin monkey	8	8 (4) 10 (2)	Token	5 50	63 0	10

* The number of trials of which one session consisted is indicated between parentheses

Comparing the results of this task (table 11) with the results of the standard task (table 6) shows that there is no improvement in performance when abstract items are used. Because more subjects succeeded in the task with the food items, incentive value of the food items did not interfere with the subjects' performance. Research in more species is necessary to confirm this assumption.

The abstract representation of food items in the three procedures showed that performance only improved in the abstract representation of the reverse-reward contingency task. The subjects in that task showed previously poor performance on the standard reverse-reward contingency task, so interference from the incentive value of the food rewards caused an increased performance level. Subjects in the standard delay choice task and in the standard delay maintenance task already showed a good performance level and abstract representation of the food rewards did not improve performance. Therefore it seems that interference from the incentive value of the food rewards is only necessary if the subjects show a low performance level in the standard task.

Alternative methods

Spatial aspect of inhibition
In one experiment (Table 12), the spatial aspect of inhibition was examined in a delay choice task, instead of looking at the temporal aspect of inhibition. Subjects were presented with a small, nearby reward or a large, distant reward. There was examined if subjects were willing to inhibit their impulse to take the smaller reward and travel a longer distance to obtain the larger reward.

Table 12. Spatial delay choice task. Reference number of the study, social organization (G = stable group), number of subjects and sessions*, ratio smaller/larger reward, maximum distance (cm) and frequency of choosing large reward (%) for each species.

Study	Social org.	Species	Number of subjects	Number of sessions	Ratio smaller/ larger reward	Maximum distance (cm)	Frequency choosing large reward (%)
43	G	Cotton-top tamarin	4	14 (8)	1/3, 2/6	245	92
		Common marmoset	4	14 (8)	1/3, 2/6	245	45

* The number of trials of which one session consisted is indicated between parentheses

The 14 sessions conducted were free-choice trials. Preceding to each session was one forced-trial session, in which subjects could gain experience with the distances and the amounts of rewards. Distances were increased per session with 35 cm. After testing it appeared that difference in food magnitude had no effect on the subject performances.

Tamarins and marmosets both chose the larger reward at the farthest distance used in the experiment, but marmosets chose the larger reward less frequent at the farthest distance. As explained in Stevens et al. 2005a, the difference in performance could be due to their different dominant food sources. Tamarins primarily feed on insects, which are mobile and dispersed, thus requiring to travel larger distances. The main food source of marmosets is gum and sap, which they extract from trees. This food source is immobile and localized and requires much less traveling. Thus, the fact that tamarins chose the larger reward more frequently at the farthest distance could be because tamarins usually travel further than marmosets to obtain their food. More research in a larger number of species is necessary to discover their abilities in spatial inhibition.

Motor aspect of inhibition

Amici et al. 2008 conducted four tasks in which the motor aspect of inhibition was examined. Task 1 consisted of placing a reward three times under cup A, one of three aligned cups (A-B-C). The fourth time the reward was placed under A, but was moved, while in sight, to B. This tasks looks whether subjects can refrain from choosing the cup under which they previously found the reward, but has recently been emptied. In task 2, two rewards were placed under A and B of three aligned cups (A-B-C). This was done two times, after that two rewards were placed under A and C. The tasks tests whether subjects can refrain from choosing an empty cup that is close to a cup from which they have just retrieved a reward. In task 3, rewards were placed behind hole one or two in a Plexiglas panel for six times. The seventh time, the reward was placed between the two holes. The task examines whether subjects can refrain from reaching toward the reward through the Plexiglas and instead take a detour movement through one of the two holes. In task 4, a reward was placed on a ledge behind one of two holes covered with doors, which move forward. If the subject reach through the door in front of the reward, the reward fell off the ledge. This task tests whether subjects can refrain from reaching the reward directly and instead open the other door to grab the reward from behind. Experimental trials are the trials in which the goal of the task is examined.

Table 13. Motor aspect inhibition task. Reference number of the study, social organization (G = stable group, FF = fission-fusion, number of subjects and the mean score (%) in the four tasks* for each species.

Study	Social org.	Species	Number of subjects	Mean score (%)			
				1 (1)	2 (2)	3 (2)	4 (10)
3		**New world monkeys**					
	G	Capuchin monkey	27	79.0±9.6	34.2±9.4	78.1±7.9	0
	FF	Spider monkey	18	93.3±6.7	79.4±6.2	66.7±16.7	0
		Old world monkeys					
	G	Long-tailed macaque	12	75.0±17.9	45.8±14.4	4.2±4.2	0
		Great apes					
	FF	Orangutan	10	83.3±16.7	83.3±30.7	100.0±0	38.6±12.2
	G	Gorilla	7	100.0±0	21.4±14.9	41.7±15.4	8.3±8.3
	FF	Chimpanzee	8	100.0±0	56.3±14.8	93.8±6.3	10.0±6.6
	FF	Bonobo	4	100.0±0	75.0±14.4	87.5±12.5	0

* The number of experimental trials is indicated between parentheses

In task 1, bonobos, chimpanzees and gorillas were the best performing species, which can point to the phylogeny hypothesis. Bonobos, orangutans and spider monkeys performed best in task 2, which appears to be coherent with the fission-fusion hypothesis. Bonobos, chimpanzees and orangutans scored best in the third task, which follows the pattern of the phylogeny hypothesis. Performances were bad in task 4, but the performances that were achieved points to the phylogeny hypothesis. However, all of the subjects are tested in a small number of trials and in comparison to the other species, a lower number of bonobos, gorillas and chimpanzees has been tested. These two factors cause less reliable results and therefore drawing a reliable conclusion is difficult. More research in a larger number of trials and in a larger number of subjects is necessary to be certain which hypothesis can be confirmed.

Evaluation of used methods

In assessing inhibitory abilities in primates, three main procedures are conducted. These procedures differ in their approach. Delay choice tasks, delay maintenance tasks and reverse-reward contingency tasks differ in the level of self-control that is required to fulfill the task. In delay choice tasks, the subjects have no opportunity to modify their initial response. At the beginning of a trial, subjects have to make their choice between the small, immediate reward and the larger, delayed reward. However, in delay maintenance tasks, subjects can alter their initial response, because the smaller, immediate reward is accessible during the waiting period at all times, while refraining from taking that smaller reward leads to a larger reward at the end of the waiting period. Therefore, the delay maintenance tasks require a higher level of self-control. The reverse-reward contingency tasks also requires a high level of self-control, because the subjects have to refrain from reaching towards the larger reward. In order to receive the larger reward they have to reach for the smaller reward, which requires to overcome the incentive value of the larger reward. Whereas performance does improve when abstract representation is used in reverse-reward contingency tasks, in delay choice tasks and delay maintenance tasks, performances do not improve. Subjects already showed success in the standard version of the tasks, so it seems the use of abstract items was not necessary to improve performances. It seems that the reverse-reward contingency task was the most difficult, because additional procedures, such as large-or-none procedure, correction trials and abstract representation of the food rewards, were necessary to improve previously poor performance.

Another difference among the three procedures is by which measures the inhibitory control was assessed. In delay choice tasks, the measure used was the indifference point, which is the point of delay where subjects equally choose for the smaller, immediate reward and for the larger, delayed reward. The duration of the waiting time, in which subjects can refrain from choosing the small, immediate reward is the measure used in delay maintenance tasks. The percentage of succeeded subjects is used as a measure in reverse-reward contingency tasks. The measures taken in delay choice tasks and delay maintenance tasks are more accurate for establishing levels of temporal inhibition, because the performance is measured in time. The performance per species is more comparable in these tasks, than the percentage of succeeded subjects that is used as a measure in reverse-reward contingency tasks.

The inhibitory control of the primates is measured in food-related tasks, but it is questionable if the outcome of this task can be applied to the level of social inhibition primates posses. It is debatable if a high level of inhibition shown in the tasks means that the species posses a high level of social inhibition. More research is needed to discover the relation between the level of inhibition measured in the food-related tasks and the level of social inhibition seen in nature.

DISCUSSION

The comparability of the studies can be improved, but for now we assume they are comparable. The performance rank established in the delay choice task, delay maintenance task and in the reverse-reward contingency task is displayed in an overview (Table 14) to compare the patterns in the performance in each task. The order of performance in the abstract representation of food rewards in the reverse-reward contingency task is also given, because the order of performance in the reverse-reward contingency task is based on a low number of successful subjects per species. The qualitative version of tasks is left out of consideration because a low number of species was tested and because comparing between species is difficult due to the difference in kind of more-preferred food. Modified procedures such as in delay choice tasks (Evans & Westergaard 2006), in reverse-reward contingency tasks (Anderson et al. 2000; Genty et al. 2004; Genty & Roeder 2007; Kralik et al. 2002; Kralik 2005), abstract representation of food rewards in the delay choice task (Beran et al. 1999; Beran & Evans 2012) and in the delay maintenance task (Evans et al. 2012) are not taken into account because only a low number of species was tested. The modified procedures used in the delay maintenance task (Anderson et al. 2010; Beran & Evans 2006; Beran & Evans 2007a, b; Beran & Evans 2009) are not taken into account because the modified procedures differed and a low number of subjects was used, which caused less comparable and less reliable results. The alternative methods are left out of the comparison as well, because they examined other aspects of inhibition (Amici et al. 2008; Stevens et al 2005a).

There are many variable factors in the procedures that are done and a different variety of species is tested for each procedure. In delay choice tasks, a large variety of species is researched. Within this variety of species, the number of subjects differs greatly, which can therefore have influence on the results. Differences in ratio can also cause less reliable results. For a more accurate comparison, a larger and more equal number of subjects should be tested per species and the conditions of the experiment should be more similar. Compared to delay choice tasks, less species are tested in reverse-reward contingency tasks. Gorillas, bonobos, marmosets and spider monkeys have not been tested in this task. In the abstract reverse-reward task macaques, squirrel monkeys, spider monkeys and marmosets have not been tested.

Because the results of the reverse-contingency task and the abstract reverse-reward contingency task are displayed as number of succeeded subjects on the task, it is difficult to establish a performance order, especially because the number of subjects tested per species is different. Gorillas, bonobos, tamarins, spider monkeys, marmosets and lemurs have not been tested in delay maintenance tasks.

Because not all species are tested in the different procedures, it is difficult to draw a firm conclusion towards one of the two hypotheses.

Table 14. Overview of the rank of each species per procedure. NT means that the species was not tested and NS means that the species was not successful in the procedure.

	Prosimians	Lemur	**New World monkeys**	Capuchin monkey	Marmoset	Spider monkey	Squirrel monkey	Tamarin	**Old World monkeys**	Macaque	**Great apes**	Bonobo	Chimpanzee	Gorilla	Orangutan
Delay chioce task		8		6	10	2	NT	9		7		3	1	5	4
Reverse-reward task		3		4	NT	NT	NT	NS		1		NT	NS	NT	2
Abstract reverse-reward task		3		5	NT	NT	NT	4		NT		2	1	7	6
Delay maintenance task		NT		4	NT	NT	5	NT		3		NT	1	NT	2

In delay choice tasks, chimpanzees, spider monkeys, bonobos and orangutans are the best performing species, which follows the pattern of the fission-fusion hypothesis stated in Amici et al. 2008, because the four best performing species posses a high level of fission-fusion. Part of the results seems to tend to the phylogeny hypothesis, but the pattern is not clear enough to really confirm this hypothesis.

The order of performance in reverse-reward tasks is macaques, orangutans, lemurs, capuchin monkeys and squirrel monkeys, which is not in agreement with either of the two hypotheses. The pattern does not fit the fission-fusion hypothesis (Amici et al. 2008), because orangutans posses a high level of fission-fusion, but performed worse than macaques, who have a low level of fission-fusion. Other species with high levels of fission-fusion (chimpanzees, bonobos, spider monkeys) have not been tested or did not succeed in the task. Furthermore, macaques performed better than orangutans, but posses lower levels of cognitive abilities. Lemurs have the lowest level of cognitive skills, but performed better than capuchin monkeys and squirrel monkeys, therefore the phylogeny hypothesis does not apply (Aureli et al. 2008). So no conclusion can be drawn from the results.

Chimpanzees and bonobos performed best in the abstract reverse-reward task, and they have a high degree of fission-fusion, which could fit the fission-fusion hypothesis (Amici et al. 2008). However, orangutans, who also possess a high degree of fission-fusion, showed almost the lowest performance level. Orangutans and gorillas performed worst of the species tested, while lemurs, capuchin monkeys and tamarins performed better, thus the phylogeny hypothesis (Aureli et al. 2008) is also not applicable. Neither of the hypotheses can be confirmed.

In the delay maintenance task, the great apes perform best, then the old world monkeys, new world monkeys and last prosimians. This follows the pattern of the phylogeny hypothesis (Aureli et al. 2008), in which species with a higher level of cognitive abilities would show a higher level of inhibition control.

Thus, no overall conclusion can be drawn out of these four tasks. However, it seems that in delay choice tasks, when subjects have no opportunity to change their initial decision, their performance follows the fission-fusion hypothesis. In delay maintenance tasks, when subjects have the opportunity to alter their decision and have to continuously suppress their impulses, their performance follows the phylogeny hypothesis. It appears the hypotheses do not exclude one another, but may explain different aspects of temporal inhibition.

Due to all the variation that is seen across research, results become less reliable and so does the comparison and conclusion of this essay. More similar research is necessary in a larger number of subjects and the different procedures should be conducted in all species mentioned in this essay.

CONCLUSION

Primates differ in their ability to inhibit impulses. If the benefits of waiting are greater than those of acting immediately, showing inhibition control can be important. In different social situations a level of inhibition control can be advantageous and can be useful in order to survive. It is unclear if this social inhibition seen in nature can be measured by the food-related tasks that are conducted in an attempt to discover the levels of social inhibition in primates.

Two hypotheses are proposed to relate to inhibition: the fission-fusion hypothesis, in which species with a high level of fission-fusion will show higher inhibition control, and the phylogeny hypothesis, in which species with higher cognitive abilities according to phylogeny will show a higher level of inhibition control.
Overall, no hypothesis can be confirmed, because the patterns of the results of each procedure are contradicting. The results in the reverse-reward task and in the abstract reverse-reward task follow neither of the hypotheses and seems to be a very hard task to accomplish. The results of the delay choice task and the delay maintenance task show a contradicting patterns. The order of performance in the delay choice task is chimpanzees, spider monkeys, bonobos, orangutans, gorillas, capuchin monkeys, macaques, lemurs, tamarins and marmosets. This order of performance confirms the fission-fusion hypothesis which states that species with higher levels of fission-fusion will show a higher level of inhibition control (Amici et al. 2008). In delay maintenance tasks, the order of performance is chimpanzees, orangutans, macaques, capuchin monkeys and squirrel monkeys. This pattern confirms the phylogeny hypothesis which states that species with a higher level of cognitive abilities will show a higher level of inhibition (Aureli et al. 2008). However, it seems that the two hypotheses represent different aspects of temporal inhibition. If the task needs an instantaneous decision, such as in delay choice tasks, it appears the fission-fusion hypothesis is applicable. If subjects continuously have to suppress an impulse, such as in delay maintenance tasks, the phylogeny hypothesis seems to be fitting. Further research is needed to ascertain this phenomenon.

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