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The Old School, Brewhouse Hill, Wheathampstead,
Hertfordshire AL4 8AN, UK

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*Emotional consequences when chimpanzees (*Pan troglodytes*) face challenges: individual differences in self-directed behaviours during cognitive tasks*

Y Yamanashi and T Matsuzawa*

The Section of Language and Intelligence, Primate Research Institute, Kyoto University, 41-2 Kanrin, Inuyama City, Aichi, Japan
* Contact for correspondence and requests for reprints: yamanash@pri.kyoto-u.ac.jp

Abstract

Self-directed behaviours (SDBs) are said to be indicative of negative emotions. The present study focused on chimpanzees' SDBs during cognitive experiments in order to investigate how each chimpanzee reacted to his or her errors and to changes in task difficulty. We recorded and analysed the behaviour of six chimpanzees during cognitive experiments at the Primate Research Institute, Kyoto University, in Japan. We compared the rate of SDBs after correct trials versus incorrect trials, and in easy tasks versus difficult tasks. Our results suggest that the chimpanzees' reactions to making an error and the degree of difficulty of the task varied depending on the individual. Three out of the six chimpanzees exhibited higher rates of SDBs after incorrect trials than after correct trials, and in difficult tasks than in easy tasks whilst the other three did not. This finding suggests that chimpanzees may differ in the degree to which they exhibit internal conflict and we should carefully assess subjective evaluations of task situations; taking these differences into consideration when conducting experimental research in chimpanzees.

Keywords: *animal welfare, chimpanzee, cognitive task, individual difference, reaction to error, self-directed behaviours*

Introduction

Cognitive experiments on chimpanzees (*Pan troglodytes*) are performed in many research institutions and zoos across the world. Chimpanzees at the Primate Research Institute (Kyoto University, Japan) have participated in cognitive experiments since 1978 (Matsuzawa 2003). Although these experiments provide them with a good opportunity to exert their cognitive abilities (Meehan & Mench 2007), no study to-date has explored both the degree of stress that chimpanzees might experience when participating in such experiments and individual differences in response patterns.

Over the last few decades, several studies have explored the association between self-directed behaviours and negative emotions (for a review, see Maestripieri *et al* 1992). Studies have shown that SDBs are useful behavioural measures of internal conflict. Kutsukake (2003) reported that the rate of male chimpanzees' SDBs was positively correlated with social rank and that female chimpanzees' SDBs were higher when more than one conspecific was in close proximity. Baker and Aureli (1997) showed that chimpanzees living in a social group exhibit higher rates of SDBs after hearing the vocalisation of a neighbouring group. An ethopharmacological study also revealed a link between SDBs and emotion: an anxiolytic drug decreased the rate of SDBs, whereas an anxiogenic drug increased the rate (Schino *et al* 1996). In this study, we recorded the SDBs exhibited by individual chimpanzees during cognitive experiments in order to assess each chimpanzee's emotional state after the chimpanzee made an error or when the task difficulty was changed. Previous studies showed that chimpanzees exhibit a higher rate of SDBs after negative feedback, such as the sound of a buzzer, and no reward than after positive feedback, such as the sound of a chime, and a reward (Itakura 1993), and at difficult compared to easy tasks (Leavens *et al* 2001, 2004). Two out of these three studies were case studies of a single subject. In the multiple subject study, little attention was paid to individual differences, although there appeared to be differences among individual subjects. Analysing individual differences in emotional states during cognitive experiments with chimpanzees is important, especially with regards to animal welfare. Our aim here was to investigate how individual chimpanzees react to stimuli during daily cognitive experiments and investigate the possible influence of ability and genetic lineage on explaining individual variation.

Materials and methods

Participants

This study was conducted on six chimpanzees (three mothers and three offspring) at the Primate Research

Table 1 Profile of each chimpanzee.

Name	Sex	Age	Mother	Origin
Ai	F	30	Unknown	Africa
Chloe	F	26	Unknown	France
Pan	F	23	Puchi (PRI)	PRI
Ayumu	M	7	Ai	PRI
Cleo	F	7	Chloe	PRI
Pal	F	7	Pan	PRI

Figure 1

Pal rough-scratches her left side with her right hand after making an error.

Institute, Kyoto University, in Japan (Matsuzawa *et al* 2006). Details of chimpanzees' age and sex and relationship are provided in Table 1. These chimpanzees live in an outdoor enclosure with other conspecifics. The outdoor enclosure is separated into two compartments; one is a 700 m^2 outdoor compound with 15-m high climbing frames, a small stream and numerous trees, and the other is a 250 m^2 outdoor compound with climbing frames and two small streams (Ochiai & Matsuzawa 1997). The group is comprised of 13 chimpanzees (three males and ten females) aged from 7 to 42 years. The 13 chimpanzees were divided into two groups which used the two compartments alternately. Care and use of the chimpanzees complies with this institute's *Guide for the Care and Use of Laboratory Primates, Second Edition* (2002). The chimpanzees were fed seasonal fruits and vegetables, and monkey pellets three times a day. The cognitive experiments were carried out six days a week from Monday to Saturday.

Data collection

Observations were made from August to November 2007. The behaviour of individual chimpanzees was recorded whenever they participated in cognitive experiments. At least 12 days were randomly selected for the video data analysis. We used split-half test for checking the consistency within individuals (Martin & Bateson 2007). The total number of observed trials differed between individuals and is listed in Table 2. Two types of cognitive task were used. The first was the Numerical Sequence Task whereby a chimpanzee chooses numerals in ascending order. When a chimpanzee touches the first numeral, the remaining numerals disappear. (Kawai & Matsuzawa 2000; Inoue & Matsuzawa 2007). In the second, the Masking Task, chimpanzees have to memorise numerals in a split-second, thereby making it a harder task for the chimpanzees. The number of numerals that appeared on the screen differed between individuals and trials depending on the chimpanzee's level of ability on the task. For example, in the Numerical Sequence Task, Ai was presented with up to 10 numerals (0 to 9), whereas the other five chimpanzees were presented with only up to 9 numerals (1 to 9). Correct responses were immediately followed by a chime and pieces of apple were delivered as a positive reinforcer. When a chimpanzee made an incorrect response, a buzzer sounded and each trial was separated by a three-second time-out. We analysed the chimpanzees' SDBs during the interval between the end of one trial (onset of chime or buzzer) and the start of the next trial. We recorded three categories of SDBs (Scratch, Nose-gesture, Other SDBs) using the 1–0 sampling method (Martin & Bateson 2007). Scratch signifies 'moving the nails over the skin of some part of the body while bending the fingers' (Plooij 1984; Figure 1). Nose-gesture refers to 'rubbing the nose with moving the back of the hand once from one side to the other' (Plooij 1984; Figure 2). Although Nose-gesture is not frequently used and mentioned in the previous literature, all individuals performed this behaviour and some of them performed it more than any other SDBs. We deemed it necessary therefore to separate this behaviour from other SDBs. There are many other types of SDBs such as 'Slap the mouth' and 'Fumble with clitoris' (Nishida *et al* 1999), but not all of the individuals performed these behaviours. Hence, SDBs other than Scratch and Nose-gesture were classed as 'Other SDBs'. The term 'SDBs' includes all three categories of SDBs (ie, behaviours that include the individual touching their body with another body part). In addition to these three categories, we recorded simple presence or absence of any SDBs. Baker and Aureli (1996) reported that Rough self scratching is a more reliable indicator of anxiety than Gentle self scratching. However, three out of six chimpanzees in the present study seldom exhibited Rough self scratching during cognitive experiments. Therefore, we used a single category 'Scratch' rather than using two categories.

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Table 2 Task performance of each chimpanzee and total number of observed trials.

				Number of observed trials	
		Numerical			Numerical
	Sequence Task	Masking Task	*P*-value	Sequence Task	Masking Task
Ai	82.9 (± 5.69)	73.1 (± 5.75)	< 0.01**	728	1,068
Chloe	63.3 (± 6.56)	67.8 (± 7.64)	0.11	850	850
Pan	89.6 (± 4.25)	65.4 (± 5.34)	< 0.001**	950	950
Ayumu	92.6 (± 4.05)	84.7 (± 4.85)	< 0.001**	1,150	900
Cleo	72.4 (± 5.41)	48.8 (± 6.27)	< 0.001**	800	800
Pal	90.3 (± 3.69)	63.6 (± 5.72)	< 0.001**	750	750
Mean (± SD)				871 (± 158)	886 (± 113)

The performance of the five chimpanzees decreased when the task was changed from the Numerical Sequence Task to the Masking Task (paired *t*-test, $P < 0.01$). Only Chloe's performance did not change between the tasks (paired *t*-test, ns). ** $P < 0.01$.

Reliability

To assess reliability in video data recording, an individual naïve to the hypotheses being tested, analysed approximately 10% of the video sessions. These sessions were selected randomly. The inter-observer reliability was high with a Cohen's κ equal to 0.85.

Data analysis

We defined the rate of SDBs as the number of intervals that involved SDBs. The number of correct and incorrect trials varied across individuals and the performance of certain chimpanzees was extremely high; some seldom made errors (see Table 2). Therefore, we pooled all interval data and then divided the data into two groups based on the trial outcome (Correct/Incorrect). The total number of intervals which chimpanzees exhibited SDBs was divided by the total number of observed trials for each group and we compared the two groups using a Chi-squared test. Scratch, Nose-gesture and Other types of SDBs were also compared between correct and incorrect trials using a Chi-squared test. The rates of SDBs on the difficult versus the easy task were compared using a paired sample *t*-test. Then, we analysed the differences in the rates of SDBs after correct versus after incorrect trials, and at easy versus difficult tasks. The average rate of SDBs after incorrect trials was divided by the average rate of SDBs after correct trials, and the proportion was then standardised. The average rate of SDBs at the more difficult task was divided by the average rate of SDBs for the easy task, and the proportion was also then standardised. We then performed a Pearson's correlation between the two standardised ratios above to test whether there was an association between them. For the data analysis, we used the statistical software SPSS 13.0 and R 2.6.1. The level of significance was set at $P < 0.05$.

Figure 2

Pan exhibits Nose-gesture before starting a trial.

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Table 3 The rate of SDBs and trial outcomes.

Name	Ai			Cleo			Pal		
Trial outcome	Correct	Incorrect	*P*-value	Correct	Incorrect	*P*-value	Correct	Incorrect	*P*-value
Scratch	0.131	0.23	< 0.001**	0.064	0.223	< 0.001**	0.0947	0.352	< 0.001**
Nose-gesture	0.0251	0.04	0.30	0.0113	0.0327	< 0.05*	0.00175	0.00577	n/a
Other SDBs	0.00331	0.0136	n/a	0.237	0.503	< 0.001**	0.019	0.18	< 0.001**
SDBs	0.16	0.267	< 0.001*	0.286	0.633	< 0.001**	0.116	0.491	< 0.001**

Name	Chloe			Pan			Ayumu		
Trial outcome	Correct	Incorrect	*P*-value	Correct	Incorrect	*P*-value	Correct	Incorrect	*P*-value
Scratch	0.202	0.194	0.725	0.0297	0.032	0.933	0.047	0.0287	0.281
Nose-gesture	0.0565	0.0616	0.688	0.0672	0.0405	0.779	0.0179	0.0182	n/a
Other SDBs	0.0169	0.0264	0.282	0.00235	0.0015	n/a	0.0107	0.0202	n/a
SDBs	0.262	0.239	0.324	0.141	0.0826	< 0.05*	0.0751	0.0671	0.59

The sensitive group of chimpanzees (top) exhibited a higher rate of SDBs after incorrect trials than after correct trials (Chi-squared test, $P < 0.05$) The other non-sensitive group of chimpanzees (bottom) did not show any difference in the rate of SDBs between the two conditions. * $P < 0.05$, ** $P < 0.01$.

Table 4 The rate of SDBs and task complexity.

Name	Ai			Cleo			Pal		
Task	1	2	*P*-value	1	2	*P*-value	1	2	*P*-value
Scratch	0.13	0.173	< 0.05*	0.0886	0.131	0.12	0.104	0.219	< 0.01**
Nose-gesture	0.0233	0.0328	0.106	0.0086	0.0171	0.111	0.0013	0.0027	0.582
Other SDBs	0.0079	0.0057	0.612	0.229	0.329	< 0.01**	0.028	0.132	< 0.0001**
SDBs	0.162	0.212	< 0.05*	0.349	0.473	< 0.01**	0.125	0.309	< 0.0001**

Name	Chloe			Pan			Ayumu		
Task	1	2	*P*-value	1	2	*P*-value	1	2	*P*-value
Scratch	0.211	0.186	0.17	0.0344	0.0267	0.474	0.0533	0.0378	0.19
Nose-gesture	0.0447	0.0471	0.791	0.114	0.112	0.861	0.0222	0.0133	0.119
Other SDBs	0.0165	0.0235	0.287	0.0044	0.0056	0.717	0.0289	0.0089	0.055
SDBs	0.265	0.24	0.284	0.132	0.137	0.799	0.101	0.0633	< 0.05*

The sensitive group of chimpanzees (top) exhibited a higher rate of SDBs during the more cognitively complex task, ie the Masking Task. The other non-sensitive chimpanzees (bottom) showed no difference in the rate of SDBs between the two tasks. Task 1 was the Numerical Sequence Task and Task 2 was the Masking Task. * $P < 0.05$, ** $P < 0.01$.

Results

Performance

Each chimpanzee's performance is summarised in Table 2. Compared with the performance on the Numerical Sequence Task, the performance on the Masking Task was lower for five of the six chimpanzees (paired *t*-test, $P < 0.01$, two-tailed).

Trial outcomes and SDBs

During the tasks, three chimpanzees (Cleo, Ai, Pal) exhibited a significantly higher rate of SDBs after incorrect trials compared with correct trials. Scratch showed the same tendency in all three individuals (ie, higher rate after incorrect trials), whereas the pattern for other SDB behaviours varied among individuals (Table 3; Chi-squared test,

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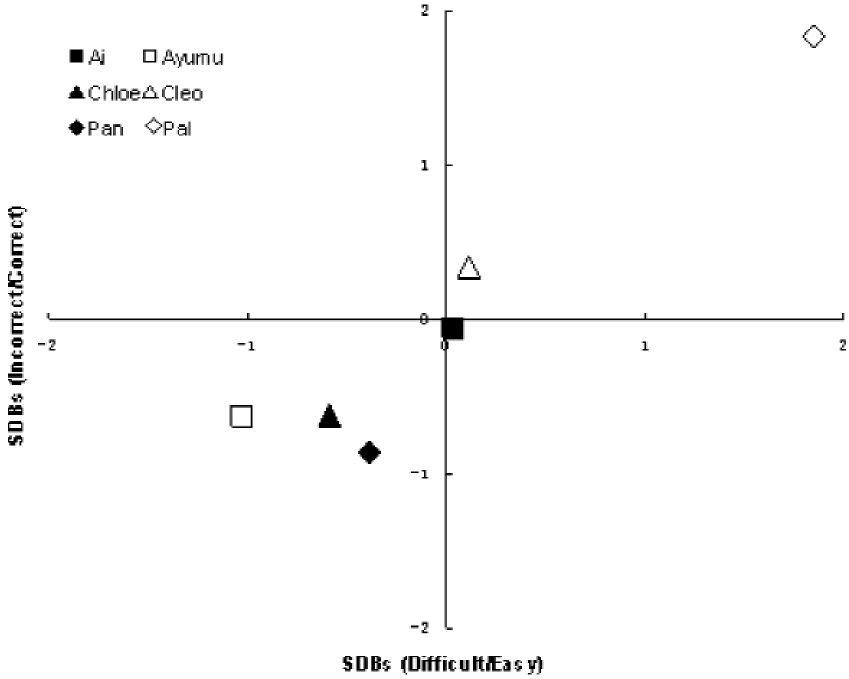
Figure 3



The relationship between individual discrepancy in SDBs between correct and incorrect trials, and the easy and the hard task. Discrepancy in SDBs of trial outcome (correct or incorrect) and of different tasks were correlated ($r = 0.956$, $P = 0.003$). The more sensitive a chimpanzee is to errors in performing the task, the more reactive he/she is to changes in task difficulty.

$P < 0.05$). However, the other three chimpanzees (Chloe, Pan, Ayumu), did not show any significant increase in any type of SDBs after incorrect trials (Table 3). Pan's rate of SDBs actually decreased after incorrect trials compared with after correct trials (Chi-squared test, $P < 0.05$). Based on these results, we categorised the six chimpanzees into two groups: Sensitive and Non-sensitive.

Performance and SDBs

We compared the two types of tasks which differed in their difficulty. The three chimpanzees in the Sensitive group exhibited a higher rate of SDBs at the Masking Task (the more difficult task) than in the Numerical Sequence Task (Table 4; Paired *t*-test, $P < 0.05$, two-tailed). In contrast, the Non-sensitive chimpanzees did not exhibit a higher rate of SDBs at the masking task (Table 4; paired *t*-test, $P > 0.05$, ns).

The standardised ratio

The discrepancy in the rate of SDBs after the performance of correct versus incorrect trials, and easy versus difficult tasks showed a clear positive correlation (Figure 3; Pearson's $r = 0.956$, $P = 0.003$).

Discussion

Chimpanzees may present different degrees of negative emotion during cognitive experiments. The present observations showed clear individual differences which previous studies (Itakura 1993; Leavens *et al* 2001) did not discuss. The three sensitive chimpanzees exhibited an increased rate of SDBs after incorrect trials as compared to after correct trials, whereas the other three non-sensitive chimpanzees did not. The sensitive chimpanzees also showed an increased rate of SDBs for the difficult task, whereas the other three chimpanzees did not. Furthermore, the individuals' discrepancies in the rate of SDBs for the trials' outcome (correct or incorrect) and that for the different tasks (easy or hard) were correlated. This suggests that the more sensitive a chimpanzee was to their errors when performing a task, the more sensitive they were also to the difficulty of the task.

When we consider the categories of SDBs, Scratch showed the same tendency as SDBs in the two conditions for all individuals except Cleo who showed a significant increase in Other SDBs instead of Scratch relative to task difficulty. Baker and Aureli (1997) suggested that Rough self scratching is the most reliable behavioural measure of anxiety. However, during the two cognitive tasks presented in this study, chimpanzees seldom exhibited Rough self scratching. Our results suggest that Gentle self scratch can also be used as a reliable indicator of mild stress in situations where experimenters could accurately observe the small gestures from close at hand. The rates of Other SDBs and Nose-gesture were also sensitive to the rate of errors depending on the individual. Cleo and Pal exhibited various types of SDBs during the cognitive experiments, suggesting that sensitive chimpanzees may perform an increased diversity of SDBs.

At this time, neither genetic linkage nor ability can explain individual differences noted in this study. The subjects comprised three mother and offspring pairs, but the mother of the non-sensitive juvenile and the juvenile of the non-sensitive mother were classed into the sensitive group. The performance of chimpanzees varied irrespective of their rate of SDBs. For example, Pal's and Ayumu's performance on the Numerical Sequence Task was above 90% and yet they differed in their sensitivity to error. This suggests that ability and genetic linkage might have nothing to do with this emotional difference and other aspects might affect chimpanzees' emotional states. However, given the relatively small sample size and variation in participants' age, gender and details of the tasks in this study, it is still too early to conclude anything with certainty. It is possible that these individual differences can be generalised to other situations. Such a pattern may be further studied under different task conditions with a greater number of participants. Further studies are needed to discern relevant factors affecting emotional arousability and sensitivity at the individual level.

Animal welfare implications

The fact that some chimpanzees were aroused after making an error even though the task and testing environment were familiar to them, while others were not is directly relevant to the welfare of chimpanzees used in cognitive experiments. Cognitive experiments can, it appears, be an effective enrichment tool as long as chimpanzees' stress levels are evaluated to ensure the appropriateness of the task as a welfare tool. Furthermore, this study indicates that SDBs may vary at the individual level and that not only Scratch but also other types of SDBs might be useful indicator of mild stress. Therefore, although Rough self scratching could be a good measure of anxiety, we propose that it is important to also record other types of SDBs to evaluate more accurately individual chimpanzees' emotional states.

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