

## Enhanced recognition of emotional stimuli in the chimpanzee (*Pan troglodytes*)

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**Abstract** Humans often have a better memory of emotional events than neutral events. From the comparative–cognitive perspective, we explored the enhancement of recognition memory by emotion in chimpanzees (*Pan troglodytes*) using a serial probe recognition task. In this task, we sequentially presented a list of pictures to subjects and then tested their recognition of specific pictures from within the list. We selected pictures of aggressive chimpanzees as emotional stimuli and less tensed, relaxed chimpanzees as neutral stimuli. In Experiment 1, we gave four-item lists to two young chimpanzees; one showed significantly greater recognition of pictures depicting aggressive chimpanzees than neutral ones. In Experiment 2, this chimpanzee was further tested using a recognition task with eight-item lists. The subject again showed better recognition of emotional stimuli than neutral. Furthermore, the presence of an emotional stimulus in the list also facilitated recognition of the neutral item immediately following it. Overall, although only one of the two chimpanzees showed enhanced recognition memory by emotional stimuli, this is the first demonstration of such a response in the chimpanzee. The findings are discussed in comparison with those of human studies.

**Keywords** Aggressive behaviour · Chimpanzee · Emotional memory · Serial probe recognition

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### Introduction

Emotion interacts with and influences other domains of cognition. In humans, the cognitive domain in which the influence of emotion is best understood is memory (Dolan 2002). Studies have shown that emotionally arousing events are more likely to be recollected than neutral events (e.g., Christianson 1992b). Recent findings from neuroimaging, neuropsychological, drug, and neural stimulation studies indicate that emotional stimuli engage specific cognitive and neural mechanisms that enhance memory (Cahill et al. 1994; Cahill and McGaugh 1998; Hamann 2001). From an evolutionary perspective, such “emotional memory” is likely to have both immediate and future relevance to survival and reproductive success (Hamann 2001) because emotional arousal signals important occasions such as fights among conspecifics, encounters with predators, finding favourite foods, and mating. Therefore, certain characteristics of emotional information could be perceived and retained in a way common to humans and non-human animals. As a candidate for a common mechanism, Zajonc (1980) proposed that affective reactions to stimuli are the first reactions that influence cognitive processes such as recognition memory and feature discrimination. Similarly, in an extensive review of emotional memory, Christianson (1992a) suggested that emotion-eliciting stimuli undergo some preferential processing mediated by factors related to early perceptual processing and late conceptual processing. Comparative studies of non-human primates may be useful for exploring the phylogenetic origins of the link between memory and emotion. A number of studies have shown that primates store detailed memories that contribute to survival or reproductive success (e.g., Menzel 1973; Dittrich 1994). However, few studies have taken a direct approach to the interaction of emotion and memory in primates. Thus, we

examined such an interaction in the chimpanzees, the closest relatives of humans.

Extensive studies of animal memory have revealed that basic features of animal memory are similar to those of human memory (Kendrick et al. 1986), although comparing memories between different species is somewhat difficult. Buchanan et al. (1981) trained a chimpanzee in a multiple-item recognition task and obtained similar list-memory performance to that seen in humans. Sands and Wright (1980) tested memory in a rhesus macaque using a serial probe recognition task. A list of pictures was presented to the macaque, and after a short delay, two probe items were presented. One of the items was from the list just presented, while the other was not. The serial position curve obtained from the macaque was similar to that for a human participant. The serial probe recognition task is often used in animal memory studies (dolphins, Thompson and Herman 1977; pigeons and macaques, Wright et al. 1985). In the present study, we used this type of task to test chimpanzees' recognition memory of emotionally arousing pictures from lists.

In human studies, the injury or death of a character or a crime in the story is often used for the emotional stimuli (Christianson 1992a). For chimpanzees, foods, mating, and aggressive behaviors of conspecifics are thought to be emotional scenes. In an experimental setting, non-linguistic methods can be designed using picture stimuli. For example, some studies have reported physiological changes in chimpanzees viewing the pictures that have emotional contents (Parr and Hopkins 2000; Parr 2001). In addition, Parr (2001) demonstrated that the chimpanzee participants used still pictures of chimpanzee facial expressions to categorize emotional video scenes according to their positive and negative valance (e.g., matching a hypodermic needle to the bared-teeth display), suggesting their emotional awareness. In the present study, we used still pictures of chimpanzee aggressive behaviors for emotional stimuli (see “Methods” of Experiment 1 for details).

We conducted two experiments. In the first, we initially trained chimpanzees on a simple delayed matching task and then shifted to a task with four-item lists using non-chimpanzee stimuli to observe the basic characteristics of list memory in chimpanzees. After these pretraining phases, we ran test sessions in which we presented lists containing neutral and emotional pictures and those containing only neutral pictures. If emotional contents enhance chimpanzee memory, it is predicted that emotional pictures would be better recognized than control pictures. In humans, emotional items (or events) can affect other temporally proximate items or events. However, no studies to date have examined these effects on non-human primates. To examine the effects of emotional items on adjacent neutral items, we additionally tested one of the two chimpanzee participants using eight-item lists in Experiment 2.

## Experiment 1

### Methods

#### Participants

Two young chimpanzees (*Pan troglodytes*; Pal and Cleo, both female) participated in Experiment 1. Both were 6 years old at the onset of the experiment. They had experience taking part in various types of testing for cognitive development (Tanaka et al. 2003; Tomonaga et al. 2003, 2004; Matsuzawa et al. 2006; Tomonaga 2007) including computer-controlled perceptual–cognitive tasks (Tanaka et al. 2003; Tanaka 2007a, b). They had also been trained on matching-to-sample tasks but had never experienced experimental tasks in which emotional responses were rewarded. Both had been reared by their own biological mothers from birth and lived in a social group of 14 individuals in an environmentally enriched outdoor compound and an attached indoor residence. No special food or water deprivation was conducted during the study period. Care and use of the chimpanzees adhered to the 2002 version of the Guideline for Care and Use of Laboratory Primates by the Primate Research Institute, Kyoto University. The experimental protocol was approved by the Animal Welfare and Care Committee of the institute.

#### Apparatus

The experimental sessions were conducted in an experimental booth ( $1.6_mW \times 1.8_mD \times 2.1_mH$ ). Two sets of 15-inch LCD monitors with touch-sensitive screens ( $1,028 \times 768$  pixels, 32 bit color, Touch panel systems, U2-BA; Attic, TP-153U) were installed on different sides of the booth. Touch to the stimulus on the screen was defined as a response. A universal feeder (Biomedica, BUF-310) delivered pieces of food (apples or raisins) into a food tray below the monitor. All the equipments were controlled by a personal computer running a program written in Microsoft Visual Basic 6.0.

#### Stimuli

We prepared 200 full-color still pictures of fish, reptiles, birds, and sea mammals ( $10.0 \times 5.6$  cm on the screen; see Fig. 1) for the initial training phases (referred to as “non-chimpanzee stimuli”). For the test stimuli, we prepared still color pictures of wild chimpanzees ( $10.0 \times 6.6$  cm) from video recorded in Bossou, Guinea, West Africa, for research purposes (Biro et al. 2003). We used Adobe Photoshop 6.0 to prepare the images.

Pictures of chimpanzees were categorized into two types based on their behaviors. The “Aggressive” (A) category

**Fig. 1** Examples of aggressive and neutral stimuli used in the test sessions. Chimpanzee photographs courtesy of Tetsuro Matsuzawa



contained images of aggressive behaviors performed by chimpanzee(s), while the “Neutral” (N) category contained images of less tensed behavior (see Fig. 1). Aggressive behaviors were defined as attack, defence, and threat (Goodall 1986). Previous studies have reported that chimpanzees responded emotionally to pictures of chimpanzee aggressive behaviors (Parr and Hopkins 2000; Parr 2001). We prepared 76 pictures for each category. From among these pictures, we selected the best 40 within each category based on the rating scores of subjective emotional value and picture quality, as judged independently by three researchers with extensive experience observing chimpanzees.

#### *Procedure*

Both participants came to the experimental booth with their mothers but were trained separately with different monitors in the booth. Almost no interaction occurred between them during the task. Each trial began with the presentation of a warning stimulus at a random position on the screen. When the chimpanzee touched the stimulus, the first item of the list was presented as a sample stimulus for 1 s before being masked with a gray square. Touching the mask was followed by the presentation of the next item with a 0.4-s delay at a position different from the previous item. After all the sample items were thus presented, probe items were displayed after a 1.2-s delay. One of the probe items was chosen from the pictures in the list (correct item) while the other was not part of the list (incorrect item). Incorrect items were selected in a pseudorandom order from among the unused pictures in the given trial. Response to the

correct item was rewarded with a piece of apple and a chime, while an incorrect response was not rewarded and was followed by a buzzer sound.

The training phase began with a simple matching task (i.e., single-item lists). When accuracy in two consecutive sessions exceeded 80%, we introduced two-item lists to the participants. Sample items were thus added successively until the list length reached four items. Each training session consisted of 36 trials, and the chimpanzees were given two to three sessions daily. The training pictures were presented in a session-based trial-unique manner; that is, the same picture was never presented more than once within the same session. The order of test pictures in each sample list was changed after each session.

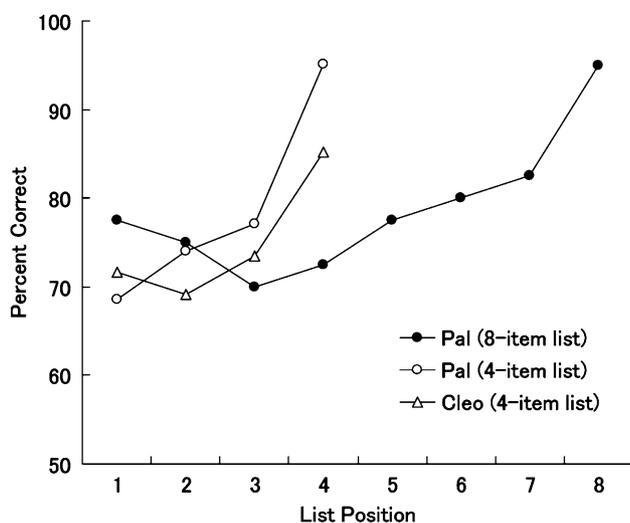
After reaching the criterion for the four-item lists, we conducted additional sessions of steady-state training with four-item lists to obtain serial position curves and then moved on to test sessions. In Experiment 1, we prepared two control conditions, N-N-N-N (all-N lists) and A-A-A-A (all-A lists), in which N (neutral) and A (aggressive) denote the category of pictures for each position of the four-item list, and four test conditions, in which one of the list items (called the test item) was in a different category from the other list items: N-A-N-N and N-N-A-N (A-with-Ns lists) and A-N-A-A and A-A-N-A (N-with-As lists). The latter two counterbalanced conditions (lists with one emotional and three neutral pictures and those with one neutral and three emotional pictures) were controls to exclude the possibility of better recognition of emotional pictures simply because they were in a different category than neutral pictures (Jitsumori et al. 1989; Strange et al.

2003). A test item appeared only in the second or third position to separate the effects of emotional items from serial position effects such as primacy or recency effects (i.e., superior performance on last and first items relative to medial list items). Thus, although all list items were used as the probe items, only the second and third list items were analyzed. The accuracy for each test item was compared to that for the control item at the same list position. Each condition was pseudorandomly presented in a session. Each test session consisted of 32 trials, and each block consisted of five sessions. Test pictures were presented so that each picture was seen once before any repetition. The order of test pictures in each sample list was changed after all the pictures were presented. Both of the probe items were in the same category to ensure that chimpanzees did not discriminate them based on category difference. Each participant was given eight session blocks (i.e., 40 sessions). We also collected the response-time data for correct trials.

## Results

### Training phase

Pal reached the criterion in 8, 8, 4, and 2 sessions and Cleo in 6, 21, 9, and 11 sessions for training phases involving list lengths of 1 through 4 items, respectively. As stated in the “Methods”, we continued training with four-item lists until both the participants had completed 18 sessions. We then calculated the mean accuracy for each list position in the 18 sessions. Figure 2 illustrates the upward curves for the first through last list items for both the participants.



**Fig. 2** The effect of list position on recognition memory of the non-chimpanzee items for both the subjects. *Open symbols* show the results from Experiment 1, and the *filled circles* show the results from Experiment 2

### Test conditions

Overall, Pal and Cleo were, respectively, 76.8% (SEM  $\pm$  1.51) and 71.8% (SEM  $\pm$  1.65) correct in the test session blocks. For each test session block, we calculated the mean accuracy of each list position under each list condition. To test the effects of the emotional stimuli on recognition memory, we compared the mean accuracy for test items at the second and/or third positions for A-with-Ns and N-with-As lists and that for control items at the corresponding positions for all-N and all-A lists. Figure 3 shows the mean accuracy for the test and corresponding control items for each participant. As shown in these figures, one of the two chimpanzees, Pal, exhibited better recognition for emotional pictures among neutral ones than for neutral items at the corresponding list position (87.5% correct vs. 67.5% correct, paired-comparison *t*-test,  $t(7) = 4.32$ ,  $P = 0.003$ , using Bonferroni’s corrections for the two comparisons of test-control pairs; the corrected alpha level for statistical significance was set to 0.025, which corresponds to 0.05). However, recognition accuracy was not facilitated when neutral items were presented among emotional ones (78.8 vs. 74.4%,  $t(7) = 1.21$ ,  $P = 0.26$ ). In contrast to Pal, the other participant, Cleo, did not exhibit enhanced recognition neither under the all-N and N-with-As list conditions (70.0 vs. 73.7%,  $t(7) = 0.426$ ,  $P = 0.68$ ), nor under the all-A and A-with-Ns list conditions (71.8 vs. 76.2%,  $t(7) = 0.747$ ,  $P = 0.48$ ).

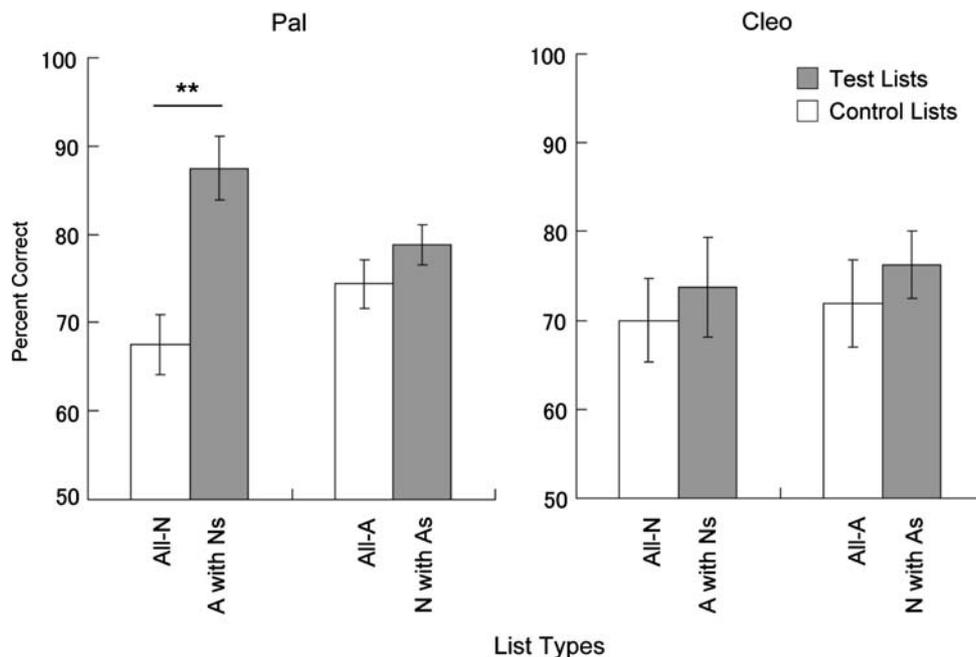
To further investigate the individual differences between the two chimpanzees, we calculated the mean response times for the last training session and the first test session for each participant. Response times did not differ between chimpanzees in the last training session [*t*-test,  $1,055 \pm 38$  (SEM) ms for Pal vs.  $1,136 \pm 56$  ms for Cleo,  $t(36) = 1.18$ ,  $P = 0.23$ ], but Pal showed significantly longer response times than Cleo for the first test session ( $2,299 \pm 192$  ms vs.  $1,499 \pm 99$  ms,  $t(32) = 3.63$ ,  $P < 0.001$  using Bonferroni’s correction for the two comparisons; the corrected alpha level was set to 0.025).

## Discussion

Both the young chimpanzees successfully mastered the serial probe recognition task and showed upward serial position curves from the first through the last items. Similar serial position curves have been reported for both non-human animals (Thompson and Herman 1977; Morimura and Matsuzawa 2001) and humans (Hines 1975).

One of the chimpanzees, Pal, exhibited significant enhancement in the recognition memory of emotional items. Because the neutral and emotional stimuli were presented with equal frequency, we can exclude training bias

**Fig. 3** Percentage of correct trials ( $\pm$ SEM) for control and test lists. A picture of aggressive chimpanzee behaviours, N picture of less tensed, relaxed chimpanzee behaviours.  $**P < 0.01$



for each category. Pal only showed enhanced recognition when the emotional items were embedded among neutral items in the list, but not vice versa. This asymmetry avoids the simple category–contrast account that predicts the symmetrical effect of enhanced recognition for an odd item among items from another category.

By contrast, the other participant, Cleo, showed no enhancement of recognition memory. Several possible explanations exist for these individual differences. The most plausible is that the “emotional” pictures were not sufficiently salient for Cleo, possibly because of the size and clarity of the images, the appropriateness of the scenes, or Cleo’s task-solving strategy.

Behavioral observations provided indirect but suggestive evidence for differences between the individuals. For example, we observed on several occasions that Pal exhibited emotional responses when she was shown emotional stimuli; she intensively attended to the stimulus, erected her hair, shook her body, and sometimes hit the pictures. We did not observe such emotional responses in Cleo. Pal’s mean response time for the last training session was almost the same as Cleo’s but was significantly slower for the first test session. In the first test session, Pal held her response to the probe items and attended to them longer than did Cleo. It is therefore possible that Cleo did not pay enough attention to the stimuli or to the task to figure out the contents of the stimuli. The stimuli were still pictures; thus, some concentration was probably required to discern the meanings. It is also plausible that Cleo paid attention mainly to local features, whereas Pal focused on the emotional contents in the picture.

These individual differences should be tested in future studies under different settings. In addition, greater study

control is necessary to avoid the category–contrast account because the observed enhancement might reflect the asymmetry of the visual properties of the stimulus sets, rather than their emotional contents.

Overall, although only one of the two chimpanzees showed enhanced recognition memory of emotional items, this is the first demonstration of such a response in the chimpanzee. Experiment 2 further tested Pal to replicate the results of Experiment 1 in a task with eight-item lists. By increasing the number of items, we were able to further examine how emotional items affected memory of other adjacent items.

## Experiment 2

### Methods

#### *Participant, apparatus, and stimuli*

Pal, the chimpanzee that showed enhanced recognition of emotional items in Experiment 1, participated in this experiment. The experimental setting was identical to that of the previous tests. Training stimuli were the same as those in Experiment 1. For test stimuli, we selected new set of 20 pictures in the emotional category and 60 pictures in the neutral category from the stimuli pool used in Experiment 1.

#### *Procedure*

The flow of each trial was identical to that in Experiment 1. Pal was shifted to this experiment immediately after

completing Experiment 1. As in Experiment 1, she was trained with non-chimpanzee stimuli to extend the list length. The list length was increased by one as soon as Pal showed accuracy better than 75% correct for two consecutive sessions, until eight-item lists were reached. Each training session consisted of 18–24 trials depending on the list length.

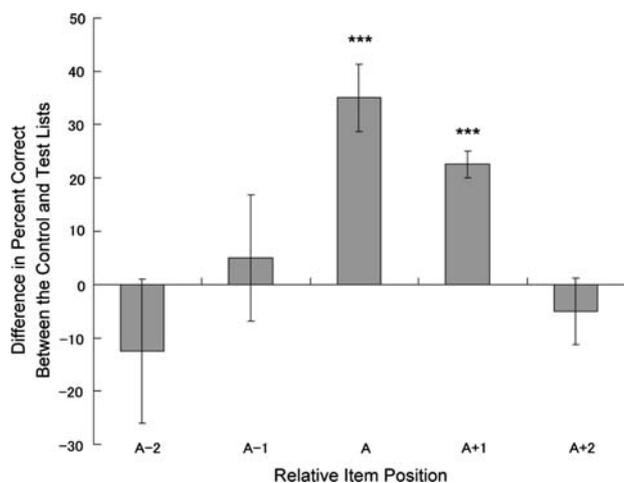
In the test condition, Pal was given 8 five-session blocks. Each session consisted of 24 trials, in which 16 trials used test stimuli and the other 8 trials used non-chimpanzee stimuli. We prepared two types of list conditions, all-N lists (N-N-N-N-N-N-N-N) as the control and A-with-Ns lists (N-N-N-A-N-N-N-N and N-N-N-N-A-N-N-N) as tests. Emotional items appeared either in the fourth or fifth position. The two types of lists appeared in equal number but were distributed randomly within a session.

## Results and discussion

Pal was given five, two, two, and five sessions to reach the criterion for training with list lengths of five, six, seven, and eight, respectively. To obtain serial position curves, we used the non-chimpanzee stimuli presented in the test sessions. We calculated the mean accuracy for each list position of the non-chimpanzee stimuli. There was an upward curve from the first through the last list items (Fig. 2), as in Experiment 1.

Overall, Pal was 72.7% (SEM  $\pm$  2.07) correct in the test session blocks. For each test session block, we calculated the mean accuracy of each list position under each list condition. Because emotional items appeared either at the fourth or fifth position in A-with-Ns lists, the comparison of A-with-Ns and All-N lists was based on relative list positions: A-with-Ns list items at A-2, A-1, A, A + 1, and A + 2 positions were compared with all-N list items at the corresponding positions (A: emotional items; A-2, A-1: 2 items, 1 item before emotional items, respectively; A + 1, A + 2: 1 item, 2 items after emotional items, respectively). Pal's correct responses for A-with-Ns list items at A-2 through A + 2 positions were 52.5, 70, 92.5, 85 and 65% (SEM = 10.52, 8.23, 9.58, 4.53, and 3.77, respectively), and her correct responses for All-N list items at corresponding positions were 65, 65, 57.5, 62.5 and 70% (SEM = 9.95, 8.45, 3.65, 5.0 and 5.0, respectively).

To visualize the comparison simply, we calculated the differences in accuracy between A-with-Ns condition and All-N condition; from the correct responses of A-with-Ns list items at A-2 through A + 2 positions, All-N list items at corresponding positions are subtracted. Figure 4 shows the results, with the vertical axis indicating the difference in accuracy (percent correct) between emotional and neutral items, and the horizontal axis showing the relative list



**Fig. 4** Differences in accuracy between test and control lists as a function of relative list position. Positive scores illustrate better recognition for emotional items, whereas negative scores indicate better recognition for neutral items. Error bars show the standard error of the mean (SEM). \*\*\* $P < 0.001$

position. Pal exhibited better accuracy for emotional items and the neutral item immediately following an emotional item in the test lists than for neutral items at the corresponding position in the control lists (Fig. 4).

Two-way (list position [5]  $\times$  list condition [2]) repeated-measures analysis of variance verified these results. Pal showed better performance on test trials than on control trials [73 vs. 64%,  $F(1,7) = 5.72$ ,  $P = 0.048$ ,  $\eta_p^2 = 0.45$ ]; the interaction was also significant [ $F(4, 28) = 4.53$ ,  $P = 0.006$ ,  $\eta_p^2 = 0.90$ ]. Post hoc analyses of simple effects revealed significant differences in accuracy at position A [ $F(1,7) = 31.18$ ,  $P = 0.001$ ,  $\eta_p^2 = 0.81$ ] and A + 1 [ $F(1, 7) = 81.0$ ,  $P < 0.001$ ,  $\eta_p^2 = 0.92$ ].

As in the four-item list condition of Experiment 1, Pal again showed enhanced recognition memory of emotional items. In addition, her performance on the recognition of items immediately following the emotional item was improved. We have two possible explanations for this effect. First, Pal could have been more motivated to inspect the emotional items and, as a consequence, paid more attention to the subsequent items than to the controls. Focused attention to both emotional items and subsequent items could have led to their enhanced recognition. It should be noted that the emotional stimuli were pictures of chimpanzee aggressive behaviors, which tend to induce strong and sustained orienting responses in chimpanzees. Daily observations clearly show that aggressive behaviors in chimpanzees capture conspecifics' focused attention. While the first explanation refers to an encoding process, the second explanation refers to a post-encoding process, "consolidation" by which new memories become more permanent and resistant to loss. Studies have pointed out that a pattern

perceived under high arousal shows stronger permanent memory, as the gradual process of consolidation proceeds (e.g., Kleinsmith and Kaplan 1963; Hamann 2001). Pal's performance decreased gradually from the emotional items to the subsequent neutral items. This could be explained by a decreasing arousal level. However, as a shortcoming of this explanation, the effect of arousal on consolidation is thought to work slowly over time (Kleinsmith and Kaplan 1963; Cahill and McGaugh 1998), while the recognition memory was tested immediately after presenting sample items in this study. We compare the findings with those of human studies in the general discussion that follows.

## General discussion

We examined the emotional memory in chimpanzee subjects using a serial probe recognition task. A list of pictures that depicted aggressive and less tensed, relaxed chimpanzees was presented sequentially, followed by testing for the recognition memory of pictures contained within the list. We observed enhanced recognition of emotional stimuli in one of the subjects (Experiments 1 and 2) and also of neutral items immediately following emotional items in the same subject (Experiment 2).

It is worth comparing these results with the phenomena and mechanisms of emotional memory in human studies, irrespective of some differences in the experimental settings. Many studies have demonstrated that emotional events/stimuli tend to be well remembered (Kleinsmith and Kaplan 1963; Heuer and Reisberg 1990; Christianson 1992b). In contrast, conflicting phenomena also exist. Clinical observations have found that patients sometimes repress unpleasant memories by keeping them out of their awareness (Goodman et al. 2003). In addition, several laboratory studies have shown that the details of emotionally arousing events/stimuli are remembered poorly (Loftus and Burns 1982; Strange et al. 2003). A deteriorated memory of events that occurred prior to an emotional event is called emotion-induced retrograde amnesia. Overall, despite extensive research on emotional memory, human studies have shown mixed results (see Christianson 1992a for a review).

The chimpanzee generally showed enhanced recognition memory of the stimuli, and not deteriorated recognition. How can we interpret these results with the mixed reports for humans? One explanation is that our stimuli evoked the types of arousal associated with orienting responses that enhanced the recognition memory of the stimuli. Orienting responses are typical behaviors of chimpanzees when viewing aggressive behavior of conspecifics. In humans, similar results and interpretations were made by Heuer and Reisberg (1990), who pointed out that the different types of

arousal might lead to different results. If a type of arousal is too painful, it might prevent the recollection of the stimuli/events and deteriorate the memory of them. Also, some types of arousal such as flight might narrow the attention to the stimuli/events and deteriorate the memorization of their details.

Although we have demonstrated enhanced recognition memory of emotional stimuli in the chimpanzee, it is too early to conclude that chimpanzee emotional memory is similar to that of humans. Further experimentation is needed to confirm and expand on our findings.

First, the number of participants should be increased to confirm the robustness of our findings. Second, to exclude category–contrast effects from the emotional enhancement of memory, new stimulus sets should be introduced for controls. For example, simpler stimuli such as chimpanzee facial expressions may weaken the asymmetric visual properties of the stimulus sets and highlight the differences in emotional content. Third, to explain the observed individual differences, the stimulus sets must be improved from the perspective of image quality and emotional saliency. For example, more realistic stimuli such as movie clips might cause more individuals to show enhanced recognition of emotional stimuli. In addition, to expand this finding of a serial probe recognition task to other types of tasks, different procedures should be introduced. For example, using a preferential looking paradigm, we predict that looking time will show an interaction between familiarity and the emotional content of the stimulus sets.

We used images of aggressive behavior as emotional stimuli. It may be worth doing the same experiment using other types of emotionally arousing images such as those of pant-hoot or play activities or of foods. In addition, we examined the short-term retention of emotional stimuli. The effect of long-term retention on memory has not yet been examined. Furthermore, in terms of age differences, in humans, older adults have been found to have less enhanced memory than younger adults, especially for negative emotional stimuli/events (Charles et al. 2003). This is thought to be because of enhanced emotion regulation in older adults. Our chimpanzee participants were 6 years old at the onset of the experiments. It would be valuable to examine the effect of age on emotional memory in terms of emotion regulation in chimpanzees.

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