Working memory of action: a comparative study of ability to selecting response based on previous action in New World monkeys (*Saimiri sciureus* and *Callithrix jacchus*)

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Abstract

Working memory of the outcome of one’s own action is important for organizing and learning appropriate behaviors in a given condition. To examine whether non-human primates with different neocortical sizes show different abilities regarding working memory for action, the performance of squirrel monkeys (*Saimiri sciureus*) and common marmosets (*Callithrix jacchus*) in a kind of delayed-response task was compared. In this task, subjects were required to select a response based on short-term memory of the outcome of their own prior action, which requires working memory of action. These monkeys have a similar phylogenetic status (i.e. Ceboidea), but the size of the neocortex relative to the rest of the brain (relative size of the neocortex) is quite different. We found that both two species could attend to and remember their own actions and could select a response based on that memory. However, the performance level was higher for squirrel monkeys than for marmosets. These results suggest that non-human primates with differentially developed neocortices have different abilities regarding working memory of action.

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1. Introduction

Animals with higher cognitive abilities are able to act appropriately not only with regard to sensory information but also to the behavioral context. Working memory is a brain system that is necessary for various cognitive operations (Baddeley, 1992), and its processing aspect is implicated in this flexibility in response selection (Goldman-Rakic, 1987). Like humans, non-human primates show working memory for various kinds of information, and the neocortex, particularly the prefrontal cortex, is involved in working memory processes (Funahashi et al., 1989; Wilson et al., 1993; Sawaguchi and Goldman-Rakic, 1994; Rao et al., 1997). Behavioral studies have demon
strated that different species of non-human primates show different abilities regarding visuospatial working memory, and this ability appears to depend on the size of the neocortex relative to the rest of the brain (Harlow et al., 1932; Miles, 1957). Therefore, it is likely that the size of the neocortex relative to the rest of the brain (relative size of the neocortex, RSN) may be associated with the ability regarding working memory for other information. However, systematic studies on this point have been limited, particularly with regard to working memory for one’s own action.

In the present study, we focused on working memory of the outcome of one’s own action. This cognitive function is important for organizing and learning appropriate behaviors in a given condition, and previous studies with self-ordered tasks or serial learning tasks have demonstrated that monkeys show working memory for their own action (Passingham, 1985; Petrides, 1991, 1995; Swartz et al., 2000), and that the neocortex, particularly the prefrontal cortex, plays a major role in this process (Passingham, 1985; Petrides, 1991, 1995; Collins et al., 1998). We hypothesized that monkeys with different RSN may show different abilities regarding working memory of action. To test this hypothesis, we used two different species of New World monkeys (squirrel monkeys and common marmosets) as subjects, since these two species have quite different RSNs (Sawaguchi, 1992). We used a behavioral task in which subjects had to pay attention to their own action and were required to decide upon and perform their next response according to their memory of that information.

2. Methods

2.1. Subjects

Two adult female squirrel monkeys (*Saimiri sciureus*, ‘SQM’ A, B) and two adult female common marmosets (*Callithrix jacchus*, ‘MAM’ A, B) served as subjects. During the experimental period, their water intake was restricted, and after each experimental session they received water ad libitum for about 15 min. Throughout the experiment, the monkeys were treated according to the ‘Guidelines for the Care and Use of Laboratory Animals’ of the National Institutes of Health.

2.2. Apparatus

We used a modified version of the Wisconsin general test apparatus (WGTA) (Harlow, 1949). The apparatus was a box (50 × 50 × 50 cm$^3$) with a window (14 cm high and 10 cm wide). An opaque acrylic plate was attached to the window, which enabled us to shut the window quickly by sliding it. A tray (20 cm wide × 12 cm high × 9 cm long), on which there were two spots (2 cm diameter) for placing a food reward, was located in front of the test apparatus. Green round plastic caps (3 cm in diameter, 0.5 cm tall) were used to cover the rewards, and a stopwatch was used to measure the duration of the delay period and the intertrial interval.

2.3. Behavioral procedures

The behavioral task we adopted was a kind of delayed-response task based on the result of self-choice. During an intertrial interval (> 20 s), the window was closed. In this phase, a piece of apple (~ 0.5 g), which we used as a food reward throughout the experimental session, was set on one of the two reward spots, which were then covered by the plastic caps. The location of the reward was chosen randomly. The window was then opened and the monkey chose the right or left location voluntarily (choice period). If it chose the location with the reward, it could obtain the apple (‘win’). Regardless of whether or not the monkey obtained the food reward, the choice period was followed by a delay period (1–8 s). During this delay period, the acrylic plate prevented the monkey from obtaining any visual information outside the apparatus and we again set the reward on the spot where the reward had been set in the choice period. After the delay period, the opaque plate was removed and the monkey reached to one of the two locations to get the reward (response period). To obtain the food
Fig. 1. Percentage of ‘shift’ responses for ‘win’ and ‘lose’ choice trials for each delay period. (A) Individual data shown separately. (B) Group data pooled according to species.
reward, it had to respond based on the results of its previous action (i.e. directed response and its outcome) in the choice period: a ‘win’ choice required a ‘stay’ response, whereas a ‘lose’ choice required a ‘shift’ response. We classified the performance in each trial into one of the four possible combinations of choice (‘win’ or ‘lose’) and response (‘stay’ or ‘shift’): ‘win–stay’, ‘win–shift’, ‘lose–stay’, ‘lose–shift’. Here, we focused on the performance in ‘lose–shift’, since this requires a flexible ability to shift the direction of the response according to the outcome of one’s previous action (i.e. working memory of one’s own action).

The duration of the delay period was initially 1 s. After the subjects performed 200 trials, the duration was increased to 2 s. After 200 2-s delay trials, the duration was increased to 4 s. Finally, the duration was extended to 8 s. Hence, all four subjects performed at least 200 trials with each delay duration, although MAM A performed 280 1-s and 2-s delay trials and MAM B performed 280 1-s delay trials for confirmation because of their lower performance levels even in these short-delay trials.

3. Results

Each squirrel monkey (SQM A, B) performed a total of 800 trials while the marmosets performed 960 (MAM A) or 880 trials (MAM B), and the performance data were analyzed. We compared the ratio of ‘win–shift’ trials to the total number of ‘win’-choice trials (percent ‘win–shift’) with that of ‘lose–shift’ to the total number of ‘lose’-choice trials (percent ‘lose–shift’) in each species. Since the response strategy is the same in both ‘win–shift’ and ‘lose–shift’ trials (i.e. shift response), a significantly higher ratio of ‘lose–shift’ would reflect flexibility to shift the direction of choice according to the outcome of one’s previous choice: working memory of one’s own action. Individual data for these comparisons are shown in Fig. 1A. All four subjects showed a similar tendency for these comparisons; the percentage of ‘shift’ responses was higher when the choice was ‘lose’ than when it was ‘win’ in short-delay trials (i.e. 1 and 2 s), although the squirrel monkeys showed a more distinct difference between ‘win–shift’ and ‘lose–shift’.

Since the results for the two monkeys in each species were similar, we pooled the data according to species (Fig. 1B) and compared the percentage of ‘lose–shift’ with that of ‘win–shift’ statistically. For squirrel monkeys, the percentage of ‘lose–shift’ was significantly higher than that of ‘win–shift’ when the delay period was 1 or 2 s ($\chi^2 = 45.61$, $P < 0.05$ for 1 s; $\chi^2 = 67.86$, $P < 0.05$ for 2 s). For marmosets, the difference between ‘lose–shift’ and ‘win–shift’ was also significant when the delay period was 1 or 2 s ($\chi^2 = 11.18$, $P < 0.05$ for 1 s; $\chi^2 = 5.02$, $P < 0.05$ for 2 s). In addition, for squirrel monkeys, but not for marmosets, there was a considerable difference between ‘win–shift’ and ‘lose–shift’ in 4-s delay trials ($\chi^2 = 3.78$, $P < 0.10$).

To examine the difference in the ability to select a response based on the outcome of one’s own action (i.e. working memory of action), we compared the percentage of ‘shift’ responses in ‘lose’-choice trials between the two species. Fig. 2 shows the data for each delay period by species. A two-factor ANOVA (species × delay duration) revealed that there was a significant main effect for species ($F(1, 8) = 10.19$, $P < 0.05$), indicating that the percentage of ‘lose–shift’ was significantly higher for squirrel monkeys than for the marmosets. There was also a significant main effect

![Fig. 2. Comparison of the percentage of ‘shift’ responses in ‘lose’ choice trials in the two species.](image-url)
for delay duration \((F(3, 8) = 13.79, P < 0.01)\). According to a post hoc test by Tukey’s method, the percentage in 1-s delay trials differed from that in 2-s and 4-s delay trials, and the difference between 2-s and 4-s trials was also significant \((P < 0.05, \text{in each case})\). The two-way interaction was not significant \((F(3, 8) = 1.82, P > 0.05)\). To investigate the difference in the percent of lose–shift between two species with each delay duration, we performed \(\chi^2\)-tests separately for each delay duration. The percentage of ‘lose–shift’ was significantly higher for squirrel monkeys than for marmosets when the delay duration was relatively short (i.e. for 1-s, 2-s and 4-s delay trials, \(\chi^2 = 4.61, P < 0.05; \chi^2 = 40.58, P < 0.05; \chi^2 = 32.87, P < 0.05\), respectively). In 8-s delay trials, this percentage was almost 20% for both species.

4. Discussion

4.1. General

The neocortex, particularly the prefrontal cortex, appears to play a critical role in making appropriate decisions in a given condition. For example, prefrontal patients are unable to shift their attention to the appropriate visual category in the Wisconsin card sort test (Milner, 1963), which requires the subject to select an appropriate behavior depending on the context. To examine the relationship between the ability to select an appropriate response depending on the previous action and neocortical development from the perspective of comparative psychology, the performances of squirrel monkeys (S. sciureus) and common marmosets (C. jacchus) were compared in a kind of delayed-response task. The results of this experiment suggest that these two species have different abilities regarding the selection of an appropriate response based on one’s own action: working memory of action.

4.2. Subjects and behavioral task

We used squirrel monkeys and common marmosets as subjects. Although, these two species are similar in terms of phylogenetic status (i.e. Ceboidea), the RSN in squirrel monkeys is much greater than that in marmosets. RSN indicates the degree of neocortical development (Sawaguchi, 1992), and brain evolution appears to be related to selective adaptation (Barton and Harvey, 2000; de Winter and Oxnard, 2001). Thus, a comparison of behavioral performance in these two species should be important, although natural selection regarding particular behavioral capacities would have caused not only size changes but also mosaic changes in the brain (Barton and Harvey, 2000). Furthermore, previous studies using a WGTA similar to our test apparatus showed that both squirrel monkeys (French, 1959) and marmosets (Miles, 1957) could perform delayed-response tasks that require visuospatial working memory. Therefore, it is reasonable to use these subjects to examine whether a cognitive function such as working memory is associated with the size of the neocortex relative to the rest of the brain.

The behavioral task we adopted was a modified version of the delayed-response task to examine working memory of one’s own action. Delayed-response tasks have been frequently used to examine visuospatial working memory. In the conventional delayed-response task, the subject must remember during a delay period where the bait was placed at cue presentation, and, hence, the cue constitutes visuospatial information. In the present study, we used the outcome of one’s own action as a cue, which is appropriate for examining working memory of one’s own action. Behavioral studies with a classical delayed-response task have suggested that subjects, especially New World species, use the strategy of postural orientation to the location of the reward throughout the delay period (French, 1959; Miles, 1957). According to our careful visual inspection, however, our subjects did not seem to use this strategy during performance of the present task; i.e. they behaved similarly during the delay period regardless of their selection (left or right, or lose or win) in the choice period. Furthermore, the percentage of ‘lose–shift’ was lower in trials with longer delays, suggesting that the monkeys selected their response according to memory rather than body orientation. Therefore, it is unlikely
that the subjects used the strategy of postural orientation.

4.3. Working memory of action

Since the percentage of a ‘shift’ response was significantly higher when the choice was ‘lose’ than when it was ‘win’ for both species (Fig. 1), both squirrel monkeys and marmosets appear to be able to attend to their own action and to retain and manipulate that information to obtain a reward. Squirrel monkeys, however, showed better performance than marmosets for ‘lose’-trials with 1-s, 2-s and 4-s delay periods; the percentage of ‘lose–shift’ trials for squirrel monkeys was significantly greater than that for marmosets (Fig. 2). In our experimental paradigm, working memory of one’s own action is particularly required for shifting the direction when the choice is ‘lose’ (i.e. lose–shift performance). Since squirrel monkeys have much greater RSN values than marmosets (Sawaguchi, 1992), these results suggest that working memory of action depends on the size of the neocortex relative to the rest of the brain.

However, there are alternative explanations for the present findings. For example, the difference in performance between the two species might reflect different strategies. Indeed, at least two different strategies can be used in the present task; a shift paradigm and a stay paradigm. Overman et al. (1983) showed that squirrel monkeys perform better in the non-matching-to-sample task (i.e. shift paradigm) than in the matching-to-sample task (i.e. stay paradigm), while MacDonald et al. (1994) reported that marmosets prefer the win–stay strategy to the win–shift strategy. In the present study, the lower percentage of lose–shift trials for marmosets might indicate that marmosets used a stay paradigm when the choice was ‘lose’. However, the percentage of lose–shift trials declined as the duration of the delay increased for both squirrel monkeys and marmosets, suggesting that they performed the task using their memory. Therefore, we do not believe that the difference in performance between the two species is due to different strategies.

As another possible explanation for the difference in performance between the two species, the present findings may be due to a difference in social structure and feeding ecology rather than a difference in RSN, since it has been suggested that differences in performance in several memory tasks can be explained by a difference in feeding ecology rather than by different phylogenetic niches (Platt et al., 1996). Indeed, there are some differences in social and feeding ecology between the two species used in this study. For example, squirrel monkeys are frugivores that seem to specialize on large fruit trees throughout the year, whereas common marmosets are primarily frugivorous and insectivorous, and rely on exudates primarily at the end of the wet season when fruits are scarce (Fleagle, 1988). However, this explanation is not inconsistent with our account that the species differences in task performance are attributable to different RSNs, since diet/foraging is closely related to the relative size of the brain (Clutton-Brock and Harvey, 1980) as well as RSN in primates (Sawaguchi, 1992). Therefore, the ability regarding working memory of action might depend on differences in both ecological factors and RSN. To clarify this problem, further studies are required with other species that are similar regarding either RSN or feeding behavior.

Thus, the ability of working memory of action in non-human primates appears to be associated with the degree of neocortical development. This conclusion may be consistent with previous studies on visuospatial working memory (Harlow et al., 1932; Miles, 1957), since the level of performance in visuospatial delayed-response tasks appears to be related to RSN. Indeed, in our preliminary study, squirrel monkeys were better at a visuospatial delayed-response task than marmosets. The ability of working memory should be associated with neocortical development regardless of modality/context. However, it is unknown whether the neocortex encompasses multiple working memory systems for different modalities of information or a single working memory system for various kinds of information. To address this problem, further studies are required using various approaches, including comparative psychology and neuroscience.
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