

# Rats Show Adaptive Choice in a Metacognitive Task With High Uncertainty

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Metacognition refers to the use of one's cognitive processes to coordinate behavior. Many higher cognitive functions such as feeling-of-knowing judgment and theory of mind are thought to be metacognitive processes. Although some primate species also show this ability in the form of behavioral control, a rodent model of metacognition is required for advanced studies of this phenomenon at behavioral, molecular, and neural levels. Here we show that rats could reliably be trained in a metacognitive task. The rats were trained to remember the location of a nose-poke hole and later indicate the location via a behavioral task. Rats had options of either demonstrating their memory or switching to an easier task (escape). Four rats were used in a two-choice metacognitive task, and 3 were used in a six-choice task. In the six-choice task, rats increased the likelihood of receiving a reward by utilizing the option to escape, in exchange for a decrease in the amount of reward received per correct trial. Furthermore, rats escaped more in sample-omitted trials than in standard trials. Results are consistent with the hypothesis that rats have metacognition, and could be utilized as a benchmark for further metacognition studies in rats. However, rats in the two-choice task did not use the escape response adaptively. These results were consistent with those seen in capuchin monkeys. Similarity between rodents and primates in task switching should expand the possibility of comparative studies of metacognition.

**Keywords:** rats, metacognition, uncertainty, delayed matching to place task, task chance level

Metacognition is defined as “knowledge and cognition about cognitive phenomena” (Flavell, 1979) or, operationally, as the “evaluation and control of one's cognitive processes” (Shimamura, 2000). Many higher cognitive functions such as feeling-of-knowing, judgment of learning, and theory of mind are thought to be metacognitive manifestations (Efklides, 2008). Therefore, metacognition was thought to be a human-specific ability (Metcalfe & Shimamura, 1994). To challenge this notion, metacognition has been studied in dolphins, pigeons, rats, monkeys, and apes (Smith, Couchman, & Beran, 2014).

The most common way in which animal metacognition is tested is through a discriminative approach (Basile & Hampton, 2014). This paradigm should meet the following requirements (Basile & Hampton, 2014; Fujita, 2010; Hampton, 2009; Smith, Shields, & Washburn, 2003; Tanaka & Funahashi, 2007). First, the perceptual or cognitive tasks should be evaluated using indices such as

accuracy and reaction time. These tasks should be sufficiently difficult, and within-individual variations in performance should be observed. Second, an alternative option to those made as part of the primary discrimination should be available. This alternative choice option should enable the subject to decline the current trial and instead either skip the current trial for the next randomly assigned trial, switch to an easier trial, use a hint, or change the betting ratio (this decline option is also referred to as the uncertainty response or escape response). Third, the use of an alternative option should either decrease the maximum reward amount, or require an additional cost.

In a paradigm that follows the three requirements listed above, if an animal has metacognition and can regulate its behavior based on memory or perceptual confidence, that animal should only use the alternative decline option in low confidence trials. Similarly, when comparing two conditions in which an alternative option is available or not, accuracy of trials in which the alternative was not used should be significantly higher when animals chose not to use the alternative than when the option was not available to them. However, it is possible that animals can exhibit an adaptive decline response without metacognition. For example, animals might learn to associate using an alternative option with a particular stimulus during training. Therefore, animals should be tested as to whether they can generalize adaptive use of a decline response rapidly to a stimulus or task has not been used in training (Hampton, 2009). There is still controversy regarding the validation criteria for whether adaptive use of a decline response can be interpreted as metacognition (Jozefowicz, Staddon, & Cerutti, 2009; Le Pelley, 2012; Smith et al., 2014; Smith, Zakrzewski, & Church, 2016). However, adaptive use of a decline response and its generalization

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to untrained stimuli or tasks are reported repeatedly in great apes and rhesus macaques (Call, 2010; Hampton, 2001; Kornell, Son, & Terrace, 2007) and validation methods have been characterized (Basile, Schroeder, Brown, Templer, & Hampton, 2015; Smith, Coutinho, Church, & Beran, 2013).

Although several metacognitive studies in rats have also been reported, the results are not consistent with regard to whether an adaptive decline response was observed (Foote & Crystal, 2007, 2012; Roberts, McMillan, Musolino, & Cole, 2012; Smith & Schull, 1989, as mentioned in Smith et al., 2003). In most studies, rats did not exhibit an adaptive decline response (Foote & Crystal, 2012; Roberts et al., 2012; Smith & Schull, 1989). However, three of the eight rats in Foote and Crystal (2007) exhibited adaptive trial decline in a psychophysical discrimination task. One issue, however, is that the authors did not test whether these rats could generalize to other stimuli or tasks. At present, therefore, results are not sufficient to conclude the existence of an adaptive decline response in a metacognitive task in rats. It has been reported previously that rats can change their behavior adaptively according to an increase in information (Kirk, McMillan, & Roberts, 2014). Therefore, it should be possible to demonstrate that rats behave adaptively in a metacognitive task if an appropriate experimental design is used.

Two particular points should be considered as to why consistent results could not be obtained in rat studies. First, there is a possibility that high demand of cognitive load in the task prevented the emergence of positive results in metacognitive research (Iwasaki, Watanabe, & Fujita, 2013). In the task in Foote and Crystal (2007, 2012), information about the length of a sample sound and a standard sound were necessary to respond correctly. Therefore, it is possible that the cognitive load of these tasks was too heavy and prevented the use of an adaptive decline response. Moreover, there is the possibility that the perceptual discrimination required in these previous studies, such as sound length or color discrimination, did not demonstrate high ecological validity for the rats. This may also raise the cognitive load of the tasks used in previous studies. Second, all responses in the previous metacognitive tasks using rats comprised only two choices. This means that the chance level of the task was 50%. In metacognitive studies in capuchin monkeys, it has been reported that when the chance level was 50% (2 choices), capuchins did not show use of an adaptive decline response due to uncertainty (i.e., avoiding the current trial) in a psychological discrimination task. However, when the chance level was lower (16.7%; 6 choices), they did use an adaptive decline response (Beran, Perdue, Church, & Smith, 2016; Beran, Perdue, & Smith, 2014). Moreover, Kirk et al. (2014) reported in rats that information-seeking responses were more difficult to extinguish if in a radial maze than in a T maze. Therefore, use of an adaptive decline response should be more likely to occur when the number of alternative stimuli increases and the chance level of the task decreases.

Therefore, we hypothesize that stronger evidence of metacognitive monitoring would emerge in rats if they are given tasks that minimize cognitive load and decrease the likelihood of a correct outcome through chance-level response. The present experiments were conducted with the goal of improving upon the experimental design of past experiments. In our two-choice test, the task was changed from a two-choice perceptual task as used in Foote and Crystal (2007, 2012) to a two-choice place memory task in order

to decrease the cognitive load. Subjects were only required to maintain place information regarding the nose poke hole location. Place memory is utilized in rats for foraging strategy (Olton, Walker, Gage, & Johnson, 1977), and the nose-poking behavior is regarded as an index of exploration (Nowak et al., 2000). Thus, an association between the memory of the nose poke location and a food reward should have some relevance to the rats' biological preparedness (Seligman, 1970). Before matching stimuli are presented, rats have the option to "escape" the current trial and switch from the continuing memory task to an easier nonmemory task, accompanied by a decrement in reward. In the six-choice task, we increased the choices from two to six in order to decrease the chance level of the task. Moreover, we introduced sample-omitted trials (Hampton, 2001) that were not a part of the original training in the two-choice and six-choice tests. In sample-omitted trials, the nose poke location to be remembered was not presented in memorizing phase. If low memory confidence does cause escape, then we predict that rats should escape these trials more than in standard trials. This prediction is supported by a report in rhesus monkeys in which they exhibited more frequent escape from sample-omitted trials than in standard trials (Hampton, 2001).

## Method

### Subjects

In total, seven adult male Long-Evans rats were used. All rats were more than 10 weeks old at the start of training. During the experimental period, the rats were food deprived and were, on average, approximately 80% of their free-feeding weight. Four rats were used in the two-choice test, and the two-choice test with sample-omitted trials (R11, R14, R15, and R16). Three rats were used in the six-choice test (R7, R8, and R9). Subsequently, R7 and R9 were used in a six-choice test with sample-omitted trials. R8 died of natural causes after the six-choice test, and for this reason was not included in the six-choice test with sample-omitted trials. All experiments were performed in accordance with the guidelines of the Animal Experiment Committee at the University of Tokyo (Permission number 22–5).

All rats were housed in a controlled environment (room temperature:  $23 \pm 2^\circ\text{C}$ ; light–dark cycle: 12 hr; 55% humidity) in single Plexiglas cages ( $24 \times 38 \times 20$  cm). R7, R8, R9 and R11 had been used in a previous behavioral and vocalization recording experiment (Yuki & Okanoya, 2014a). R9 and R11 had also been used in a previous behavioral experiment using a concurrent chain schedule (Yuki & Okanoya, 2014b). R7 and R8 had already experienced a six-choice delayed matching to position (DMTP) metacognitive task in a pilot study. Both rats exhibited escape responses and tended to show behavior patterns consistent with the hypothesis that they use metacognition in these tasks. However, none of the rats previously experienced the metacognitive task with sample-omitted trials.

### Apparatus

All experiments were conducted in two operant chambers (ENV-NPW-9L, Med Associates, Georgia, VT), each placed in a soundproof box (Muromachi Kikai, Tokyo, Japan). On one side of the operant chamber, nine nose poke holes ( $2.5 \text{ cm} \times 2.5 \text{ cm} \times 2.2$

cm) were placed in a horizontal row. The nose poke holes were illuminated from the inside with a yellow LED light. On the other side (across from the nose poke holes), two retractable levers were placed on the left and right of the pellet receptacle (Figure 1). The left and right retractable levers were used to detect whether rats chose to go to the test or to switch to an easier task (escape). The allocation of the levers for test or escape options was counterbalanced between individuals. Because the retractable levers are behind the rats when facing the nose poke holes, they must turn around in order to press the lever.

### Metacognitive Task

In this study, a DMTP task with an escape option was used as the metacognitive task. There were three types of trials: forced tests, forced escapes, and choice trials.

Choice trials progressed as described below. In the memorization phase, one of the nose poke holes (with the exception of the ones at either end or in the center) was lit to indicate it as a sample position. The receptacle light was also lit in sample memorizing phase. Once the rats poked their nose into the lit hole, the light was turned off. Then, prior to the matching phase, rats turned around to the other side of operant box to choose whether to go onto the test or escape the task by pressing one of the two retractable levers. If rats chose to go to the test, two or six nose poke holes were lit in the matching phase. If rats chose to escape, only the correct hole (same as the sample position) was lit. If rats chose to go to the test and correctly responded, the receptacle light was immediately turned off, and the rats received four pellets. Then, after a 5-s intertrial interval (ITI), the next trial began. If rats chose to go to the test and incorrectly responded, the receptacle light remained lit for 13 s and then a 1-s ITI was inserted. Rats received a 9-s time-out as punishment. On the contrary, if rats escaped and responded correctly, the receptacle light was immediately turned off and rats received three pellets. If rats escaped and responded

incorrectly, the receptacle light remained lit for 5 s and then a 1-s ITI was inserted. Rats received 1-s time-out as punishment.

In forced test or forced escape trials, only one of the two retractable levers was presented. This forced rats to either go to the test or escape the task. Chosen and forced trials were the same except for the availability of choice. In chosen trials, the rats could either choose to take the test or they could escape, whereas in forced trials the rats were either forced to take the test or forced to escape.

### Training

First, rats were habituated to the operant box and feeder. Next, stepwise training was carried out to form the sequence of responses to sample stimuli, then to the lever, and lastly, to the sample again. All training continued until 60 min had passed or 60 trials were completed. In order to encourage equal learning for all sample stimuli, if the rats responded incorrectly in response to a certain sample position, the same sample position was used in the next trial until they responded correctly. These repeated trials were termed correction trials. During the forced two-lever training phase, the two levers were not presented simultaneously. Training for the two-choice DMTP forced test (only the test lever was presented) was continued until the accuracy of forced test trials was greater than or equal to 80% for three consecutive sessions when the retention interval was 0 s. On passing this criterion, half of the trials were switched to forced escape by presenting the other retractable lever. In this phase, forced escape trials were used as correction trials. If the rats responded incorrectly, a forced escape trial with the same sample position was inserted into the next trial until rats responded correctly for both forced test/escape trials. Training for R11, R14, R15, and R16 in the forced two-lever training of the two-choice DMTP was continued until the accuracy of the forced test trials was greater than or equal to 80% for three consecutive sessions when the retention interval was 1 s.

Training for R7, R8, and R9 in the forced two-lever training of the six-choice DMTP was continued until the accuracy of the forced test trials was greater than or equal to 70% for two (R7, R8), or three (R9) consecutive sessions when the retention interval was 0 s (R7, R8) or 1 s (R9).

### Two-Choice Test

The choice trials in the two-choice test (Figure 2) began once rats gave one nose poke to the start cue (the center nose poke hole was lit). Then, during the sample-memorizing phase, a sample stimulus was presented. The sample position was randomly and equally allocated to six possible holes. An internal light in a nose poke hole was turned on when it was selected to be the sample stimulus. One or five (randomly determined) repeated nose pokes turned off the sample stimulus. If the rats responded to other nose poke holes during this phase, the trial returned to the start cue. However, this was not considered an incorrect response. After a 1-s delay, the task choice phase began. Both levers were presented at the same time, and one lever press retracted both of the levers. In matching phase of two-choice test, the original sample nose poke hole and one additional nose poke hole (which were placed opposite and equidistant from the center cue) were lit.

If the rats responded incorrectly during the experiment, a correction trial was inserted. A correction trial was the same as a

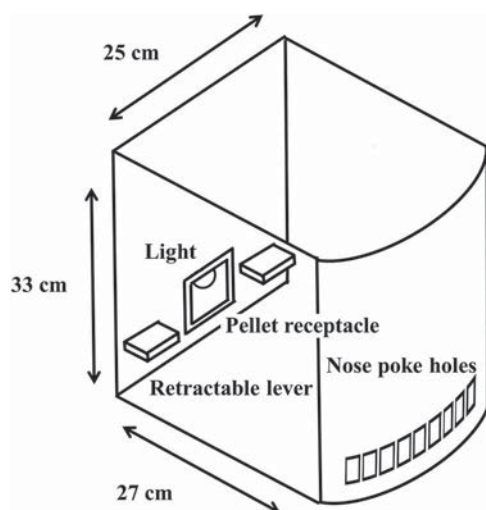


Figure 1. The operant chamber and apparatus. On one side of the operant chamber, two retractable levers were placed to the left and right of the pellet receptacle. Across from the levers, nine nose poke holes were placed in a horizontal row.

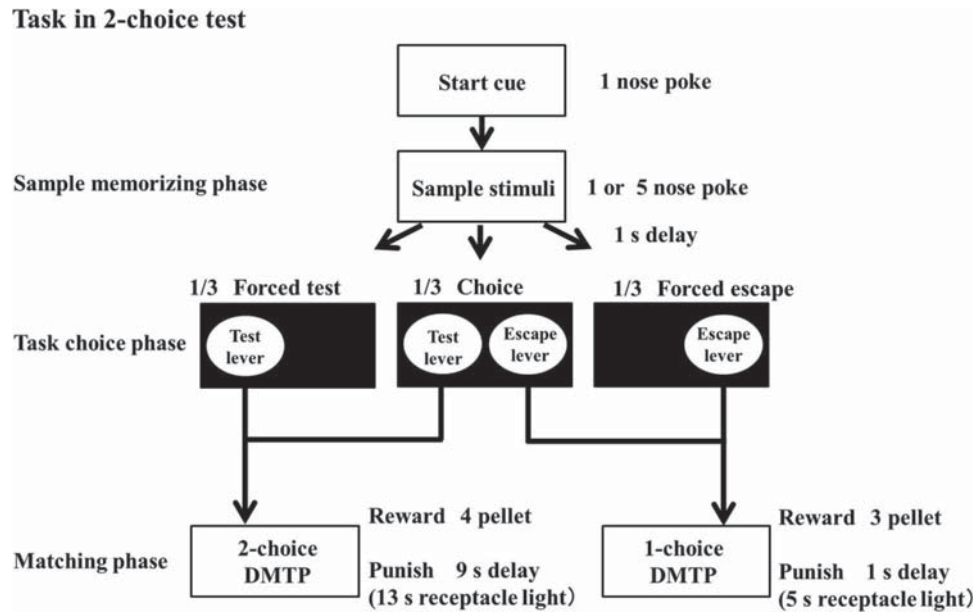


Figure 2. Schematic representation of the task in the two-choice test. If the rats responded with the test lever, a two-choice DMTP task proceeded. Otherwise, they could escape to the one-choice DMTP task by pressing the escape lever. In the six-choice task, the matching phase was a six-choice DMTP task if the rats responded by pressing the test lever. In the two-choice/six-choice test with sample-omitted trials, about 10% of all trials were randomly switched to sample-omitted trials. (NP = nose poke; DMTP = delayed matching to position).

forced escape trial except that a reward of one pellet was given for a correct response. Correction trials were not independent trials; rather, they were added to trials in which the first response was incorrect. Therefore, correction trials were not counted as part of the test session. Rats were required to poke their nose into only the lit hole during forced escape and correction trials. So it was possible for them to incorrectly respond in a forced escape or correction trial, thus necessitating a subsequent correction trial. (For example, in the two-choice and six-choice tests, rats incorrectly responded in about 5.6% of forced escape trials on average, and in about 6.9% of the subsequent correction trials.)

In the two-choice test sessions, the proportion of each trial type (forced tests, forced escapes, and choice trials) was set at one third. For R11, R14, and R15, only sessions in which 90 trials were completed within 60 min were used for analysis. For R16, sessions in which 60 trials were completed within 60 min were used for analysis because this animal rarely finished 90 trials. On average, 22 sessions satisfied this criterion (R11: 21 sessions; R14: 23 sessions; R15 and R16: 22 sessions).

### Two-Choice Test With Sample-Omitted Trials

Sample-omitted trials had almost the same structure as a standard choice trial. However, after the response to the start cue, the sample stimulus was not presented and the delay started immediately. The amount of reward and punishment was the same as in the standard choice trial. If the rats chose to continue the test, they were forced to respond without a cue. Therefore, it was predicted that rats would escape more in sample-omitted trials than in standard choice trials if they rely on confidence of memory recall for the sample location in the task choice. This increase in escape

should be another index of metacognitive ability in rats. Exhibiting both an increase in accuracy of the chosen test trials and an increase in escape during sample-omitted trials should strongly suggest the existence of metacognitive ability of rats as discussed in introduction. It is possible that the absence of a sample-place memory fosters an escape response in sample-omitted trials more than in standard sample-presented trials, even when the chance levels are the same.

In the two-choice test with sample-omitted trials, the proportion of each trial type was set at 25% for forced test and escape trials, and 50% for choice trials. Moreover, about 10% of all trials were randomly switched to sample-omitted trials. Only sessions in which 60 trials were completed within 60 min were used for analysis. There were 22 sessions for each individual that satisfied this criterion. The first seven sessions were used to account for the possibility that animals may have quickly adapted to the sample-omitted trials.

### Six-Choice Test

Following the reports by Beran et al. (2014, 2016) and Kirk et al. (2014), we reduced the chance level by changing the task from a two-choice DMTP to a six-choice DMTP. The task in the six-choice test was nearly the same as in the two-choice test with the exception of the matching phase. The choice trials in the six-choice test also began with one nose poke in response to the start cue. The sample stimulus was also allotted to one of six possible holes. One, three, or five (randomly determined) repeated nose pokes turned off the sample stimulus. If the rats responded to other nose poke holes, the trial returned to the start cue (R9), or the nose poke count was reset and rats had to start again (R7, R8).

After a 1-s (R8, R9) or 3-s (R7) delay, the task choice phase began. One lever press retracted both of the levers. If rats chose to go to the test, all six of the nose poke holes were lit in matching phase. If they chose to escape, only the correct hole (same as the sample position) was lit in the matching phase.

In the six-choice test sessions, the proportion of each trial type (forced tests, forced escapes, and choice trials) was set at one third. Only sessions in which 90 trials were completed within 60 min were used for analysis. On average, 29.3 sessions satisfied this criterion (R7: 29 sessions; R8: 29 sessions; R9: 30 sessions).

### Six-Choice Test With Sample-Omitted Trials

As in the two-choice test with sample-omitted trials, we added the sample-omitted trials to eliminate the influence of task-specific cues, such as a specific sample location. The six-choice test with sample-omitted trials is the same as the six-choice test, except that sample-omitted trials were added. The amount of reward and punishment was the same as in the standard six-choice trial.

In the six-choice test with sample-omitted trials sessions, the proportion of each trial type (forced tests, forced escapes, and choice trials) was set at one third. Moreover, about 10% of all trials were randomly switched to sample-omitted trials. Only sessions in which 90 trials were completed within 60 min were used for analysis. There were 27 (R7) and 30 (R9) sessions that satisfied this criterion. For R7, there was no receptacle light for the first 15 sessions of the sample-omitted trials, but the light was functional in the last 12 sessions. To determine if there was an effect of using the receptacle light, the difference between the escape ratio in the sample-omitted trials for the 10 sessions before the light was functional and the 10 sessions after the light was functional was assessed using Welch's test. Since the difference was not significant,  $t(14) = 0.37, p > .05$ , analysis was carried out with the pooled data.

### Statistical Analysis

We used  $t$  tests and an analysis of variance (ANOVA) to statistically analyze data. This was done using the analysis tools in Microsoft Excel and R.3.1.2 (R Development Core Team, 2014). Effect sizes for  $t$  tests are presented as Cohen's  $d$ .

## Results

The difference in accuracy (probability of correct response) of the forced test trials between the two-choice test and the six-choice test was compared using Welch's  $t$  test. Accuracy of the forced test trial was significantly higher in the two-choice test than in the six-choice test (Welch's  $t$  test;  $t(5) = 3.78, p < .05, d = 2.75$ ; Figure 3).

### Two-Choice Test

The difference in accuracy between forced test trials and chosen test trials (choice trials in which rats chose to go to the test) was compared using paired  $t$  tests. If rats are able to use escape options adaptively in a metacognitive task, the accuracy in chosen test trials should be significantly higher than in forced test trials. However, no significant difference in the accuracy was observed between the two types of trials in any of the four individuals (R11:

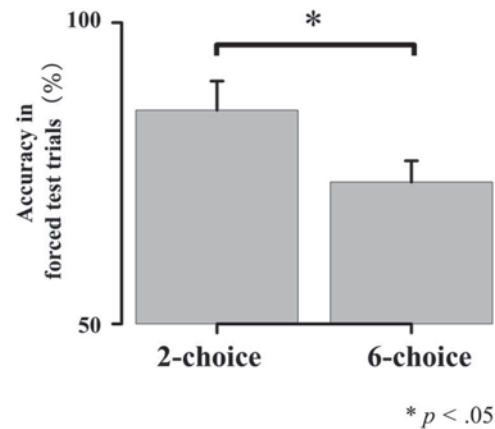


Figure 3. Difference in the accuracy of forced test trials between the two-choice test and the six-choice test was assessed by Welch's  $t$  test. Error bars represent standard deviation.

$t(20) = -0.99, p > .05, d = -0.27$ ; R14:  $t(22) = 0.71, p > .05, d = 0.23$ ; R15:  $t(21) = -1.07, p > .05, d = -0.29$ ; R16:  $t(21) = 1.14, p > .05, d = 0.33$ ; Figure 4a). The results of the two-choice test did not support the hypothesis that rats have metacognitive ability. These results are consistent with most of the previous metacognitive studies in rats (Foote & Crystal, 2007, 2012; Roberts et al., 2012; Smith & Schull, 1989). In the two-choice test, the rats chose escape, on average, in about 16.8% of the choice condition trials. Given the results of Roberts et al. (2012), where rats did not exhibit information-seeking behavior when a T maze was used, this two-choice test did succeed in producing an escape response, but failed to increase the accuracy of the chosen test trials compared with the forced test trials.

### Two-Choice Test With Sample-Omitted Trials

The escape response was measured using the escape ratio, which is the number of chosen escapes in the choice trials divided by the total number of choice trials. Paired  $t$  tests were used to compare the difference in the escape ratio between the standard choice trials and sample-omitted trials in the first seven sessions. If rats use memory confidence in the task choice, they should escape more in the sample-omitted trials than in the standard choice trials. In the first seven sessions, two of the four rats exhibited a significantly higher escape ratio in the sample-omitted trials than in the standard choice trials (R11:  $t(6) = -5.52, p < .01, d = -2.14$ ; R14:  $t(6) = 1.94, p > .05, d = -0.50$ ; R15:  $t(6) = -2.44, p > .05, d = -1.40$ ; R16:  $t(6) = -2.57, p < .05, d = -1.63$ ; Figure 4b). When examining all 22 sessions, three of the four rats exhibited a significantly higher escape ratio in the sample-omitted trials than in the standard trials (R11:  $t(21) = -8.48, p < .001, d = -2.42$ ; R14:  $t(21) = -3.37, p < .01, d = -0.88$ ; R15:  $t(21) = -2.30, p < .05, d = -0.64$ ; R16:  $t(21) = -2.01, p > .05, d = -0.68$ ).

### Six-Choice Test

The difference in accuracy between forced test trials and chosen test trials was compared using paired  $t$  tests. All three rats exhibited significantly higher accuracy in chosen test trials than in forced test trials (R7:  $t(28) = -2.90, p < .01, d = -0.81$ ; R8:

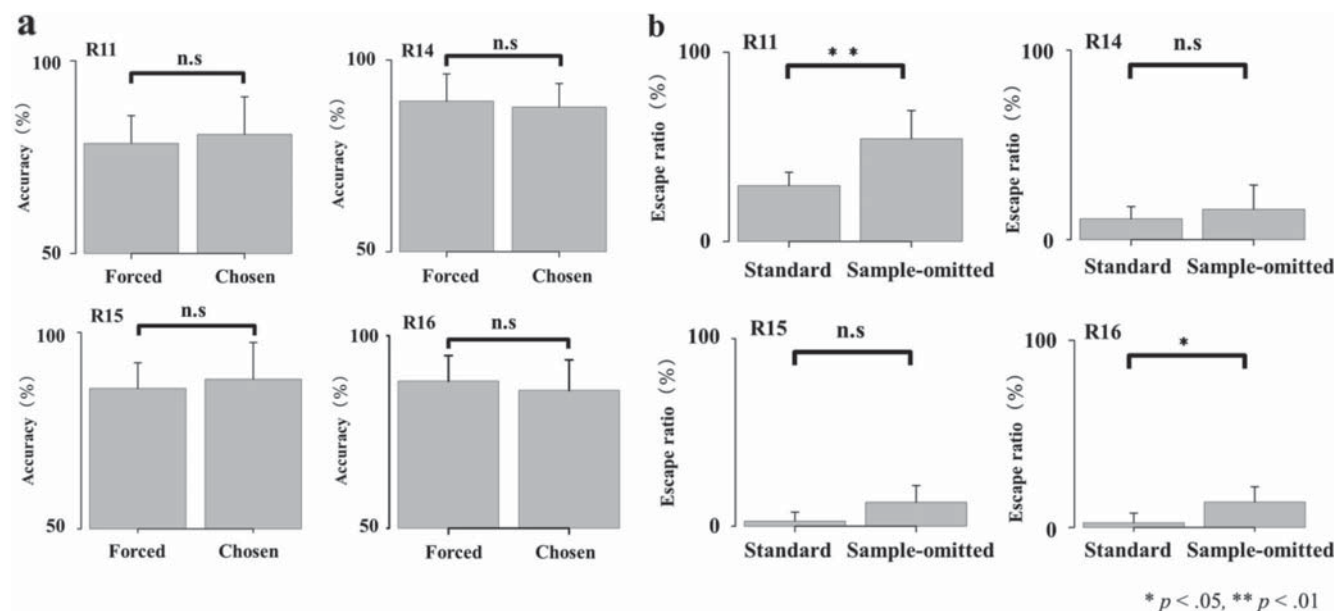


Figure 4. (a) Difference in accuracy between forced and chosen test trials in the two-choice test. For each individual, accuracy was averaged across sessions and compared by a paired  $t$  test. (b) Difference in the escape ratio between standard and sample-omitted choice trials in the first seven sessions of the two-choice test with sample-omitted trials. Error bars represent standard deviation.

$t(28) = -4.01, p < .001, d = -1.12$ ; R9:  $t(29) = -4.17, p < .001, d = -0.77$ ; Figure 5a). Results indicated that rats could demonstrate adaptive escape in a metacognitive task when the cognitive load and the chance level of the task were decreased.

### Six-Choice Test With Sample-Omitted Trials

The difference in the escape ratio between the standard choice trials and sample-omitted trials in the first seven sessions was

compared using a paired  $t$  test. In the first seven sessions, both rats exhibited a significantly higher escape ratio in sample-omitted trials (R7:  $t(6) = -9.67, p < .001, d = -3.81$ ; R9:  $t(6) = -3.53, p < .05, d = -1.27$ ; Figure 5b). When examining all sessions, both rats also exhibited a significantly higher escape ratio in sample-omitted trials than in standard trials (R7:  $t(26) = -23.75, p < .001, d = -3.78$ ; R9:  $t(29) = -12.69, p < .001, d = -2.76$ ).

### Additional Analyses Across Experiments

All tasks used in this research presented the escape option before rats could provide a matching response. Therefore, rats could not use their own behavior as a cue to decide whether to use the escape. Because rats had to either choose escape or provide a matching response before the matching phase, competition between the responses required by the task and the escape also did not influence whether rats chose the escape option (Hampton, 2009). Because the retractable levers were across from the nose poke holes, rats also could not use postural mediation as a cue (Basile et al., 2015). Moreover, the sample-omitted trials in the six-choice test ruled out the possibility that rats escaped based on specific sample stimuli, because there were no sample stimuli in these test trials.

However, it is still possible that the rats learned an adaptive escape behavior using other nonmetacognitive cues as discriminative cues. For example, there is the possibility that response bias caused by a previous choice affected whether rats escaped (Marshall & Kirkpatrick, 2013; Means, Leander, & Isaacson, 1971).

To test the possibility that the previous trial affected whether rats escaped in the next trial, the escape ratio was analyzed in a one-way ANOVA for each type of previous trial (forced test/escape, and chosen test/escape), and correct or incorrect responses in the previous trial. The analysis was conducted for choice trials

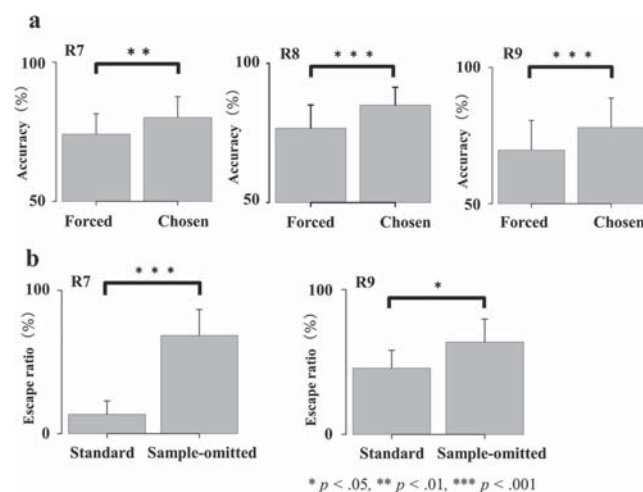


Figure 5. (a) Difference in accuracy between forced and chosen test trials in the six-choice test. For each individual, accuracy was averaged across sessions and compared by a paired  $t$  test. (b) Difference in the escape ratio between standard and sample-omitted choice trials in the first seven sessions of the six-choice test with sample-omitted trials. Error bars represent standard deviation.

in two-choice and six-choice tests, and correction trials were removed from the analysis. In general, there was no effect of the previous trial on escape behavior in the next trial. Only R16 exhibited a significantly higher escape in the two-choice test when it correctly responded rather than incorrectly responded in the previous trial ( $R16: F(1, 37) = 14.79, p < .001$ ; Figures 6 and 7).

### General Discussion

The accuracy of the forced test trials was significantly higher in the two-choice test than in the six-choice test. This result suggests that increasing the choices from two to six in order to decrease the chance level of the task affected behavior as expected. In the two-choice test, none of the rats exhibited significantly higher accuracy in the chosen test trials compared with the forced test trials. However, in the two-choice test with sample-omitted trials, two of the four rats exhibited a significantly higher escape ratio in the sample-omitted trials than in the standard choice trials, and this occurred within the first seven sessions. These results suggest that rats can adaptively escape in a high chance level task using memory confidence as a discriminative cue when there are sample-omitted trials. However, since they did not adaptively escape in the standard two-choice test, positive results in the two-choice test with sample-omitted trials were insufficient to conclude that rats can use memory confidence as a discriminative cue for escape. It is still possible that these rats just learned to escape from a novel situation, as they had never experienced sample-omitted trials previously.

In the six-choice test, all three rats exhibited significantly higher accuracy in the chosen test trials compared with the forced test

trials. Moreover, in the six-choice test with sample-omitted trials, both rats (one of the three rats died before this test) exhibited a significantly higher escape ratio in the sample-omitted trials than in the standard choice trials. These results suggest that rats can escape adaptively at least when trained in a six-choice metacognitive task. It should be noted that there is a possibility that R7 and R8 were influenced by a prior experience with a six-choice metacognitive task. However, R9, which was naïve to the task, also exhibited adaptive escape in the six-choice test. Moreover, sample-omitted trials were completely novel for R7 and R9, and both rats exhibited rapid generalization to this condition.

In almost all cases, the type or correctness of the previous trial did not bias the escape response in the next trial. Only R16 exhibited a significant difference in escape ratio depending on whether the previous trial was correct or not. This significant difference seems to be due to the very low escape ratio (about 3.4% per session, on average; see Figure 6). As such, this should not be attributed to a response bias in R16. Thus, it appears that escape in the two-choice and six-choice tests is not due to the type or correctness of previous trial. These results weaken the possibility that the escape response in the present study was only regulated by nonmetacognitive discriminative cues. Likewise, they strengthen the possibility that the responses were also regulated by metacognitive discriminative cues. At the minimum, results in the six-choice metacognitive task are consistent with the hypothesis that rats have metacognitive ability, and the use of several nonmetacognitive cues have been ruled out. However, our paradigm cannot completely rule out the possibility that escape responses are also influenced by nonmetacognitive cues. For example, a direct

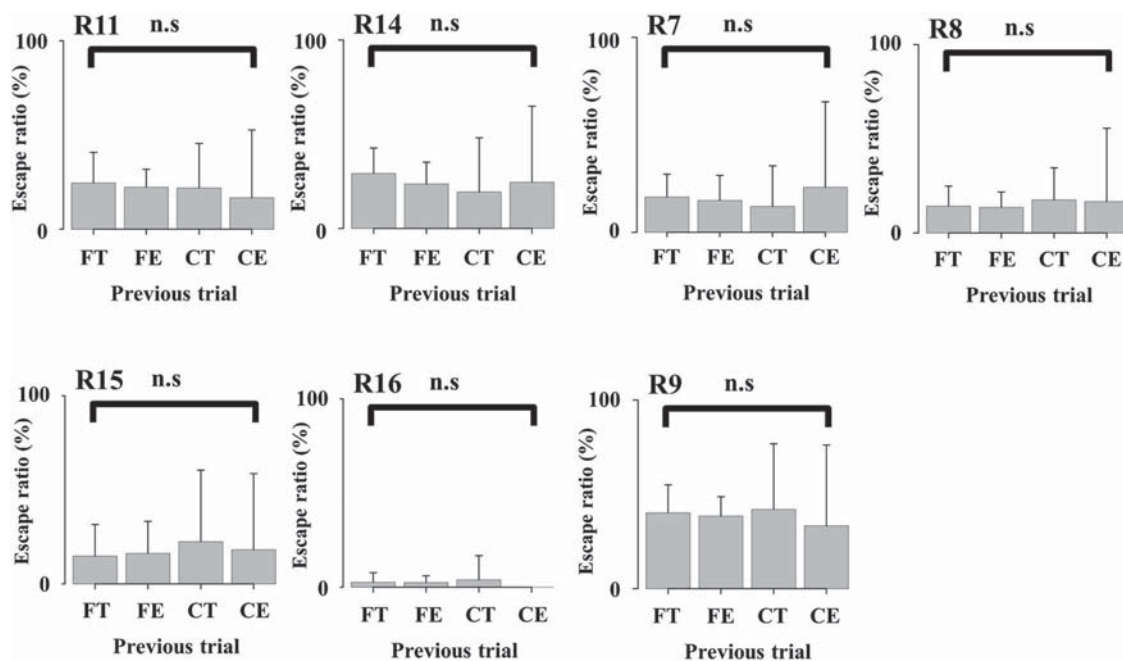


Figure 6. Difference in the escape ratio among the different types of previous trials (FT = forced test; FE = forced escape, CT = chosen test; CE = chosen escape). Error bars represent standard deviation. The analysis was conducted for choice trials in the two-choice and six-choice tests, and the data was divided according to the type of previous trial for each individual. Correction trials were removed from the analysis.

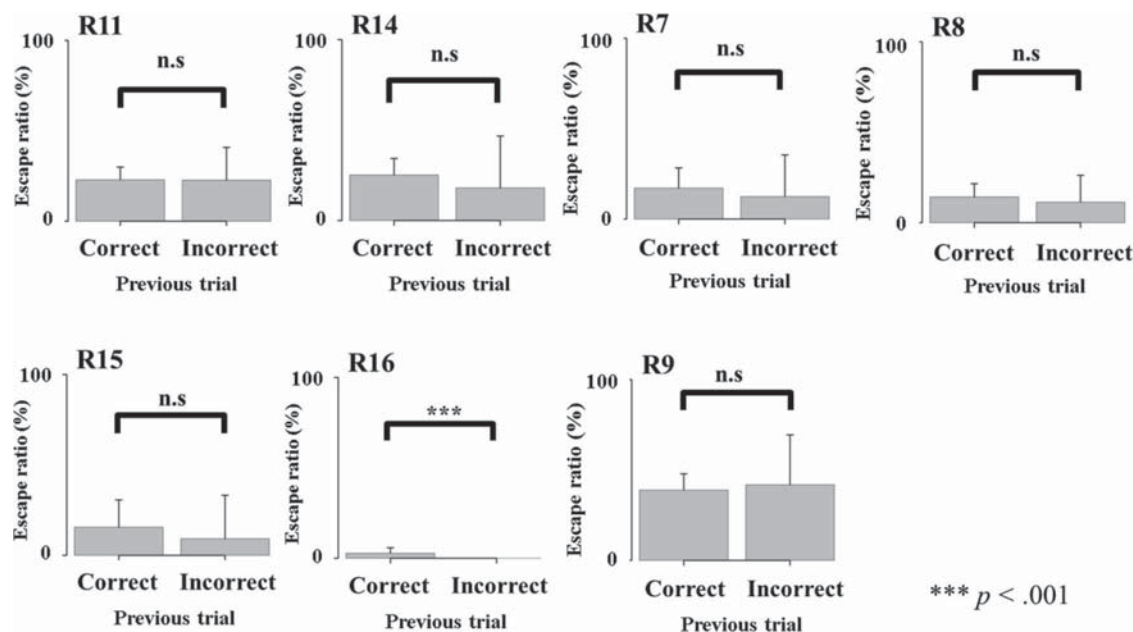


Figure 7. Difference in escape ratio between correct/incorrect responses in the previous trial. Error bars represent standard deviation. The analysis was conducted for choice trials in the two-choice and six-choice tests, and the data was divided according to the accuracy of previous trial for each individual. Correction trials were removed from the analysis.

reward for escape itself is known to promote escape independently from the metacognitive role of escape (Smith, Beran, Couchman, & Coutinho, 2008). Even if alternative, nonmetacognitive cues are partially used, this does not entirely exclude the possibility that rats can use memory confidence as a discriminative cue for escape. Therefore, while this experimental paradigm serves as a good prototype, we should continue to improve this metacognitive task so that it is more suitable for rats and will enable us to examine whether rats exhibit adaptive escape based only on metacognitive utility. Because rats are genetically and environmentally controllable, they should serve as a useful animal model to study metacognition at the molecular and neural levels.

Additionally, the difference in results between the two-choice test and the six-choice test was consistent with Beran et al. (2014, 2016), where an adaptive decline response was not observed in a two-choice psychological discrimination task in capuchin monkeys. It is thought that the capuchin monkeys did not use a decline response adaptively in this task because they have a fairly high tolerance for risk and tend to continue on to the test rather than decline the trial. The trial decline response ratio of capuchin monkeys was at times one fifth of that observed in rhesus monkeys for the same task. Kirk et al. (2014) also pointed out the possibility that information-seeking behavior in rats is proportional to the amount of information obtained by that behavior. In line with this, rats showed twice as much information-seeking behavior in a radial maze (with 8 limbs) than in a T maze.

Considering these results and those of previous studies, the reason why rats could not adaptively escape in the two-choice test may be that accuracy was too high, and rats did not feel enough uncertainty at the task choice phase to warrant using the escape option. In the training phase of the two-choice test, rats were

trained until the accuracy of the forced test trials satisfied the criterion of 80%. This criterion was reasonable for a task in which the chance level was 50%. However, the task choice itself should consume some cognitive resources. Therefore, if rats can correctly respond even in the forced test task, the utility of the escape option may have been low. On the contrary, in the six-choice test, the utility of the escape response should be higher because the accuracy of the forced test task was low and uncertainty in the task choice phase should be high. Rhesus macaques adaptively use a decline response even in a two-choice task without direct reinforcement (Beran et al., 2014; Beran, Smith, Redford, & Washburn, 2006; Smith, Beran, Redford, & Washburn, 2006). Compared with rhesus macaques, an escape response in a metacognitive task in rats may be limited, or easily affected by their psychological attributes, such as risk tolerance. One supporting result was the low escape ratios in our experiments. Even if rats never responded incorrectly in test trials, we can expect rats to press the escape in approximately three-quarters of the test trials, corresponding to the difference in the reward amount of the chosen escape trials compared with the chosen test trials. Nevertheless, the average escape ratio in the two-choice test was only 16.8%, as mentioned above. This suggests that rats subjectively perceived that the reward value for the escape lever was low. We did not have sufficient data to conclude that this was actually the case, but this discrepancy between the expected and actual escape ratio may be due to the effect of risk tolerance. However, our experiment did not directly compare performance for the two chance levels within individuals, and it is also possible that differences in prior experience between the two groups affected the results. Specifically, two of three rats (R7 and R8) in the six-choice test already experienced a six-choice metacognitive task, and one rat (R7) was

tested with the retention interval of 3 s rather than 1 s. Moreover, training was not uniform between the two groups and within the six-choice task group. Ensuring that rats continued in the experiments was our priority, even when this meant that not all rats underwent uniform training. We thought our training and test were sufficient to assess metacognitive behavior, because the reward for escape was always less than the reward for the test, and the escape trial was an easy task that did not rely on memory. However, our data has limitations in discussing individual between- and within-group differences in detail because our training was not uniform. Therefore, direct comparison within individuals, as has been conducted in capuchin monkeys (Beran et al., 2016), is needed to determine if there is a chance level effect in rats.

In order for animal metacognition research to progress, it is necessary to develop and refine nonverbal metacognition research methods. The development of animal metacognition research may contribute to clinical applications for children who have not yet reached the stage of development where they can express cognitive processes linguistically (Balcomb & Gerken, 2008), or for children with autism or developmental/linguistic delays. Expanding the target species for metacognition research enables comparative studies, and provides an opportunity to build upon the phylogeny of metacognition (Smith et al., 2008). Recently, nonmammalian animals such as pigeons (Adams & Santi, 2011; Castro & Wasserman, 2013; Iwasaki et al., 2013), crows (Goto & Watanabe, 2012), and bantams (Nakamura, Watanabe, Betsuyaku, & Fujita, 2011) were also shown to exhibit adaptive use of a decline response. When using nonprimate animals in metacognition research, it is likely that there is some limitation of the testing range, and that the design of the metacognitive task will need to be simplified. However, metacognitive study in nonprimate animals should help to reveal the most basic form of cognitive regulation, keeping the continuity with humans and primates.

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