Report

Metacognition in the Rat

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Summary

The ability to reflect on one's own mental processes, termed metacognition, is a defining feature of human existence [1, 2]. Consequently, a fundamental question in comparative cognition is whether nonhuman animals have knowledge of their own cognitive states [3]. Recent evidence suggests that people and nonhuman primates [4–8] but not less "cognitively sophisticated" species [3, 9, 10] are capable of metacognition. Here, we demonstrate for the first time that rats are capable of metacognition—i.e., they know when they do not know the answer in a duration-discrimination test. Before taking the duration test, rats were given the opportunity to decline the test. On other trials, they were not given the option to decline the test. Accurate performance on the duration test yielded a large reward, whereas inaccurate performance resulted in no reward. Declining a test yielded a small but guaranteed reward. If rats possess knowledge regarding whether they know the answer to the test, they would be expected to decline most frequently on difficult tests and show lowest accuracy on difficult tests that cannot be declined [4]. Our data provide evidence for both predictions and suggest that a nonprimate has knowledge of its own cognitive state.

Results and Discussion

People are sometimes aware of their own cognitive processes. For example, a college student entering a classroom to take a test will often have some knowledge about how she will perform on the test. It is noteworthy that this knowledge (whether accurate or inaccurate) is available *before* the student actually responds to the test questions and obtains feedback about performance. We can easily assess this familiar experience (i.e., knowing that we know or do not know the answer) in humans by requesting verbal reports about our experiences. Of course, this option is not available with nonverbal species. Consequently, researchers in comparative cognition have sought to identify experimental conditions in which a human or nonhuman subject could demonstrate through its behavior knowledge of a cognitive state. Therefore, studies in metacognition test the hypothesis that animals behave functionally the same as an organism that is aware of its own cognitive state.

One approach used for studying metacognition in nonhumans [4] is giving the animal an option to decline to take a test. Presumably, an animal that knows that it does not know the answer to a test question will decline to take the test. Moreover, being forced to take a test is likely to degrade performance because forced tests include trials that would have been declined had that option been available. Although considerable evidence supports the existence of metacognition in primates, a paucity of research has been conducted with other mammalian species. Developing a rodent model of metacognition may allow for new opportunities to explore its underlying neural mechanisms. To this end, we adapted Hampton's [4] experimental design with monkeys for an experiment with rats.

Each trial consisted of three phases: study, choice, and test phases (Figure 1). In the study phase, a brief noise was presented for the subject to classify as short (2–3.62 s) or long (4.42–8 s). Stimuli with intermediate durations (e.g., 3.62 and 4.42 s) are most difficult to classify as short or long [11, 12]. By contrast, more widely spaced intervals (e.g., 2 and 8 s) are easiest to classify. In the choice phase, the rat was sometimes presented with two response options, signaled by the illumination of two nose-poke apertures. On these choice-test trials, a response in one of these apertures (referred to as a take-the-test response) led to the insertion of two response levers in the subsequent test phase; one lever was designated as the correct response after a short noise, and the other lever was designated as the correct response after a long noise. The other aperture (referred to as the decline-the-test response) led to the omission of the duration test. On other trials in the choice phase, the rat was presented with only one response option; on these forced-test trials, the rat was required to select the aperture that led to the duration test (i.e., the option to decline the test was not available), and this was followed by the duration test. In the test phase, a correct lever press with respect to the duration discrimination produced a large reward of six pellets; an incorrect lever press produced no reward. A decline response (provided that this option was, indeed, available) led to a guaranteed but smaller reward of three pellets.

The rate of declining to take the test increased as the difficulty of the discrimination increased (Figures 2A–2D; see also Figure S1 in the Supplemental Data available online). This observation was confirmed for the mean of the rats ($F[3,6] = 17.6$, $p < 0.01$, Figure 2D) and for each rat separately ($p < 0.01$, 0.05, and 0.01 for Figures 2A–2C, respectively). The horizontal axis in Figure 2 represents an index of stimulus difficulty (see Data Analysis section below for details). For example, the leftmost point in each panel corresponds to performance after the study item was 2 or 8 s, and such an item was the easiest stimulus to discriminate. By contrast, the rightmost point in each panel corresponds to the most difficult durations to discriminate (3.62 and 4.42 s).

Accuracy declined as the difficulty of the discrimination increased, but this decline was greater when the rats were forced to take the test compared to trials on
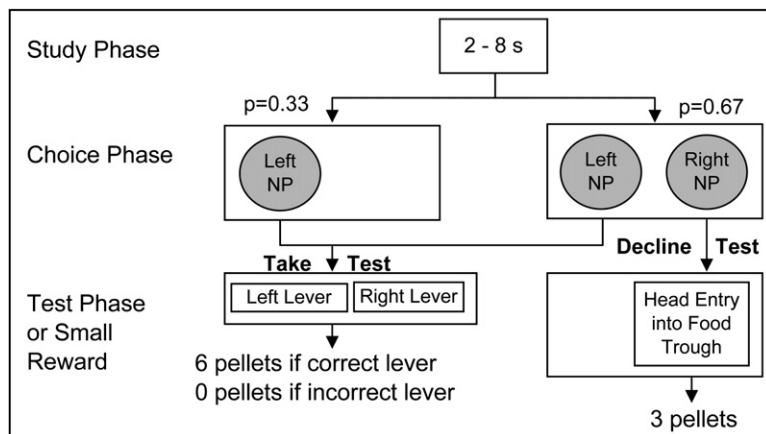
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Figure 1. Schematic Representation of Experimental Design Showing Trial Sequence in Study, Choice, and Test Phases

After presentation of a white noise (2–8 s; study phase), a choice phase provided an opportunity for taking or declining a duration test; declining the test produced a guaranteed but smaller reward than was earned if the test was selected and answered correctly (test phase). To the extent that a rat is uncertain about how to classify the interval, it will (1) decline to take the test and (2) show lower accuracy when forced to take the test relative to trials on which it chose to take the test. The gray shading indicates an illuminated nosepoke (NP) aperture.

which the rats chose to take the test (Figures 2E–2H). This observation was confirmed by an interaction of trial type and stimulus difficulty for the mean of the rats (F[3,6] = 20.3, p < 0.01, Figure 2H) and for each rat separately (p < 0.05, 0.01, and 0.05 for Figures 2E–2G, respectively). No difference between choice- and
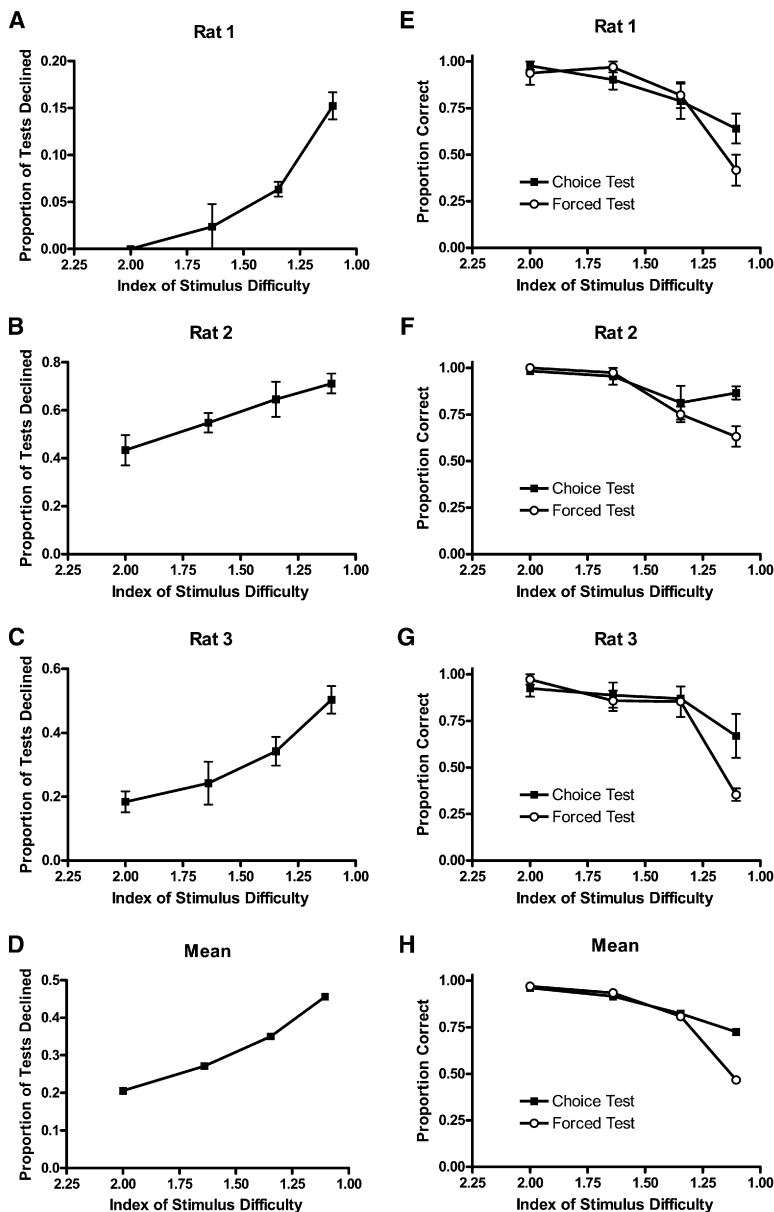

Figure 2. Rats Decline Difficult Tests and Show Degraded Accuracy When They Cannot Decline the Difficult Test

(A–D) Difficult tests (defined as stimulus durations near the subjective middle of the shortest and longest durations) were declined more frequently than easy tests (defined as stimulus durations near the shortest and longest durations).

(E–H) The decline in accuracy as a function of stimulus difficulty was more pronounced when tests could not be declined (forced test) compared to tests that could have been declined (choice test).

The x-axes are plotted in reversed order. Error bars represent SEM.

forced-test accuracy is expected for easy discriminations because there is little room for improvement. However, for the most difficult discrimination (rightmost data in Figures 2E–2H; 3.62 and 4.42 s stimuli), each rat showed higher accuracy on trials in which it had chosen to take the test.

The present experiment suggests that rats know when they do not know the answer to a duration-discrimination test. The duration discrimination involved classifying brief noises as short or long. Consequently, durations near the middle of the range are more difficult to classify. The rats were more likely to decline these difficult tests, as would be expected if the rats knew that they did not know the correct duration-discrimination response. Moreover, when we compared accuracy on the duration test, the rats were more accurate when they had chosen to take the duration test compared to trials in which they were forced to take the test. This pattern is predicted by the metacognition hypothesis because forced-test performance includes trials that would have been declined had the option to do so been available. Knowledge about temporal information may play a central role in the organization of behavior [13], and consequently, detailed knowledge about when events occur [14–20] may have contributed to our experimental evidence for metacognition.

An important feature of the design of this study is that we evaluated accuracy on trials in which the rats were forced to take the test. Moreover, the rats initiated these forced tests in the same manner as they initiated choice tests (i.e., with a nose-poke response). These factors limit the ability of alternative hypotheses to explain our data. For example, the forced duration tests are unlikely to have been unexpected and thereby unlikely to have disrupted accuracy. If forced choices had been surprising, we would expect longer latencies to respond in forced tests relative to choice tests. However, there was no evidence for a difference in the latency to respond with either a nose-poke ($t[2] = 1.1$, $p > 0.05$; mean ± SEM: 0.61 ± 0.19 s and 0.80 ± 0.12 s for choice and forced tests, respectively) or lever-press response ($t[2] = 0.4$, $p > 0.05$; mean ± SEM: 2.70 ± 0.47 s and 2.65 ± 0.28 s for choice and forced tests, respectively). Consequently, the accuracy difference on forced and choice tests was not likely to be due to performance disruption from unexpected forced tests.

Similarly, discrimination of a purely behavioral state (e.g., physical proximity to the response levers), in contrast to discrimination of a cognitive state, is unlikely to fully account for our data. Discrimination of a purely behavioral state predicts equivalent performance on forced and choice tests, and this prediction is not supported by our data (Figures 2E–2H). Although our data do not preclude the possibility that the discrimination of behavioral states contributes to the use of the decline response, such a contribution could be empirically tested in future experiments by collecting of video recordings of the rats' behavior during stimulus presentation. It is also unlikely that learning a contingency between reinforcement rate and specific stimulus durations could account for our data. First, the observed difference in accuracy between choice and forced tests is not predicted by differential reinforcement associated with specific stimulus durations. Second, for a learned contingency to contribute

to the observed increase in the decline rate, one must presuppose that rats would prefer guaranteed small rewards more than uncertain large rewards (i.e., that rats are risk averse). However, there is evidence that rats are risk prone in a situation similar to our own [21]. Ultimately, it is important to experimentally dissociate stimulus identity and difficulty by evaluation of the ability of rats to generalize the use of the decline response to a different discrimination, an ability that has recently been reported with monkeys [7, 8].

As Hampton [4] has argued, although observing putative subjective experiences that may accompany metacognition is not possible, progress in the study of evolution of the human mind and in evaluating the validity of animal models of human cognition will come from documenting objective functional features of human conscious cognition. To this end, we have documented the ability of rats to make adaptive decisions about future behavior contingent on the current availability of knowledge. Developing a rodent model of metacognition may promote new opportunities for exploring the neuroanatomical, neurochemical, neurophysiological, and molecular mechanisms of metacognition.

Experimental Procedures

Animals
Eight male Sprague-Dawley rats (Harlan, Madison, WI; 249 g, 85 days old) were individually housed in a room with a reversed light cycle (light offset at 07:00, onset at 19:00). The rats consumed 45 mg pellets (PJAI-0045, Research Diets, New Brunswick, NJ) during testing sessions and a ration of 5001-Rodent-Diet (Lab Diet, Brentwood, MO), which was adjusted so that total daily intake was 15–20 g. Water was continuously available. All procedures were approved by the institutional animal care and use committee and followed guidelines of the National Research Council Guide for the Care and Use of Laboratory Animals. Five rats rarely declined to take the duration test ($M = 97.8\%$, SEM = ±0.01%). The performance for these five rats was likely to be a result of response bias because it appeared that these rats failed to learn the experimental contingency of the nose-poke apertures. As a result, these five rats did not provide evidence for or against metacognition. The rats had participated in a pilot study, in which they received a similar training regimen to that described below, during which the reward sizes and intertrial interval were adjusted. All subjects (n = 3) that learned the experimental contingency are included in the data analysis.

Apparatus
Identical operant chambers (described in [22]), each located in a ventilated sound-attenuation cubicle, contained a recessed food trough (equipped with a photobeam used for detecting head entries) was centered between two levers on one wall of the chamber. A 45 mg pellet dispenser was positioned outside the chamber and attached to the food trough. A water bottle was placed outside of the chamber with the tube inserted across from the food trough. This wall also contained nose-poke apertures on the left and right sides of the sipper tube. Small white lights were recessed at the back of each nose-poke aperture. Each nose-poke contained a photobeam that detected the entry of the rat's snout. The chamber floor was constructed from 19 stainless steel rods. Other equipment in each chamber included a speaker, clicker, lights, and additional photobeams. Lever-press and nose-poke responses were recorded (10 ms resolution) with MED-PC software (version 4.1) on a computer in a nearby room.

Procedure
Pretraining
Rats were given one pellet per min accompanied by a click for 30 min per day on the first pretraining session. On subsequent pretraining sessions, the left lever was inserted, and each food pellet was

delivered contingent on a single lever press until ten pellets had been earned. Next, the left lever was retracted and the right lever was inserted until ten additional pellets had been earned. The lever training session continued, in this manner, until 60 min had passed or 60 pellets had been earned.

Duration-Discrimination Training

Rats were initially trained to discriminate short and long durations. A trial consisted of presentation of a white noise (70 dB) for a randomly and independently selected duration (2.00, 2.44, 2.97, 3.62, 4.42, 5.38, 6.56, and 8.00 s; equally spaced on a logarithmic scale), an insertion of two response levers, the rat's lever press, feedback, and retraction of the levers, and this was followed by an intertrial interval of 45 s. The first four durations (i.e., values less than 4 s, designated as short durations) were rewarded for pressing one lever (e.g., left), and the other four durations (values greater than 4 s, designated as long) were rewarded for pressing the other lever (e.g., right) as described elsewhere [23, 24]; the assignment of left and right levers was counterbalanced across rats prior to the start of the experiment. Each session lasted 2 hr, 5 days per week, for 35 sessions.

Nose-Poke Pretraining

Rats were trained for three daily sessions to break the photobeam in the nose-poke apertures. At the beginning of each session, the left nose-poke light was illuminated and the rat was required to break the photobeam in the left nose-poke aperture to earn a reward. After the rat had broken the left nose-poke photobeam, the light in the left nose poke aperture was turned off and a pellet and a click were delivered. This process continued for ten pellets on the left nose-poke aperture and was followed by a switch to the right nose-poke aperture for the next ten pellets. The nose-poke trials continued, in this manner, until 60 min had elapsed or 60 pellets had been earned.

Testing

A noise was presented, as described above in Duration-Discrimination Training. In the choice phase, two nose-poke apertures were illuminated in two-thirds of the trials (see Figure 1, right). Breaking the photobeam inside one of the nose-poke apertures (designated as the take-the-test nose-poke response) caused the lights to be extinguished, the levers to be inserted, and a duration test to be initiated as described above. Breaking the photobeam inside the other nose-poke aperture (designated as the decline-the-test nose-poke response) caused the lights to be extinguished but did not produce insertion of the levers. Instead, the rat was required to break a photobeam inside the food trough to obtain food and terminate the trial. The assignment of left and right nose-poke apertures to take and decline responses was counterbalanced across rats before the experiment began. In the remaining one-third of trials, only the take-the-test nose-poke aperture was illuminated (see Figure 1, left); a response in the illuminated nose-poke aperture was required for insertion of the levers and initiation of a duration test, as described above. By contrast, a response in the other (i.e., dark) nose-poke aperture did not advance the rat to the next phase of the trial. Choice and forced tests were randomly intermixed throughout the session. The reward size was six or zero pellets after a correct or incorrect duration-discrimination lever press, respectively. If the rat declined the duration test, the reward size was three pellets. The intertrial interval was 8 min, and each session lasted 9 hr, for 22–26 sessions (1546 trials, on average). The long intertrial interval may have reduced confusion between individual trials and enhanced the salience of the auditory stimulus.

Data Analysis

Stimulus durations were equally spaced on a logarithmic scale for ensuring that pairs of durations were equated for difficulty. When rats are trained to discriminate 2 and 8 s, the point of subjective equality (i.e., the stimulus duration at which the probability of judging the stimulus as short or long are equal) occurs at 4 s [11, 12], which is the geometric mean of 2 and 8 s (i.e., the midpoint on a logarithmic scale). Note that the absolute difference between two and four and between four and eight are equal on a logarithmic scale; therefore, a point of subjective equality at 4 s means that 2 and 8 s are equated for stimulus difficulty [11, 12]. Similarly, the second and seventh stimuli (2.44 and 6.56 s) are equally spaced on a log scale with respect to 4 s, as are the third and sixth (2.97 and 5.38 s) stimuli and the fourth and fifth (3.62 and 4.42 s) stimuli. Consequently, we pooled the data within identical levels of stimulus

difficulty to obtain four levels of stimulus difficulty. The index of stimulus difficulty (horizontal axes in Figure 2) was calculated as the absolute log distance of each stimulus duration from the geometric mean of 4 s, expressed in seconds. For example, the most difficult stimuli to discriminate are closely spaced (3.62 and 4.42 s) near the geometric mean (rightmost data in Figure 2; index of stimulus difficulty = 1.1), whereas the easiest stimuli to discriminate are widely spaced (2 and 8 s; leftmost data in Figure 2; index of stimulus difficulty = 2.0).

A median latency for each rat was calculated between duration-stimulus termination and the nose-poke response and between nose-poke and lever-press responses for choice- and forced-test trials.

Terminal performance (487 trials, on average) was analyzed with repeated measures analyses of variance. A value of $p < 0.05$ was considered significant.

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