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Spontaneous behavior of a rhesus monkey (*Macaca mulatta*) during memory tests suggests memory awareness

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Abstract

Humans can predict with some accuracy whether or not they know the correct answer to a question before responding. In some cases the capacity to make such predictions depends on memory awareness, the ability to introspectively discriminate between knowing and not knowing. In this unplanned retrospective analysis of video taped behavior we asked whether a rhesus monkey's apparent frustration predicted his accuracy in a matching-to-sample task on a trial-by-trial basis. The monkey was likely to aggressively strike the computer touchscreen when committing errors, whereas he generally touched the screen more gently when selecting the correct stimulus. This difference in behavior, which occurred before the monkey received feedback on the accuracy of his choice, suggests that he knew whether or not he remembered the correct response.

Keywords: Metacognition; Metamemory; Declarative; Explicit; Introspection; Memory awareness

1. Introduction

It can be frustrating not to know the answer. Consider traveling partners raising their voices in the car while failing to navigate efficiently, or a caller heaving an exasperated sigh because she just forgot the number she intended to dial. While the travelers or the caller would go about their business calmly if they thought they were on the right track or knew the number, the realization that they do not know what they need to know leads to an overt display of frustration.

It is conscious access to memory that gives humans the ability to introspectively discriminate between knowing and not knowing, a type of metacognition or "thinking about thinking". In contrast to conscious memories, unconscious memories are, by definition, those which we cannot directly know whether or not we possess (Schacter, 1992; Tulving and Schacter, 1990). In this paper, we refer to the ability to discriminate between knowing and not knowing as *memory awareness*. While the exasperated sighing of the caller in our previous example suggests memory awareness in this case, human memory awareness is more typically inferred from verbal reports. Humans can report: "I remember", "I know", or "I forget", reflecting the state of their knowledge. While some nonverbal behavior, like sighing, might suggest memory awareness under specific circumstances, verbal reports are the most frequently used basis on which inferences about memory awareness are made. The lack of such verbal reports makes memory awareness much more difficult to detect in nonhumans than in humans (Shettleworth, 1998, pp. 6–10; Tulving and Markowitsch, 1994).

Recently several authors have argued that nonverbal indices of memory awareness may be adequate under specific conditions. These authors have reported evidence for memory awareness in apes and monkeys (Call and Carpenter, 2001; Hampton, 2001; Hampton et al., 2004; Smith et al., 1998), and have tested for memory awareness in pigeons (Inman and Shettleworth, 1999). The common logic of these studies requires collection of two types of behavioral measure from subjects, a primary measure of accuracy and a secondary measure that reflects the subject's putative assessment of his memory (Hampton, 2005; Smith et al., 2003; Weiskrantz, 2001). When the two measures correlate it suggests that the secondary measure does indeed represent a subjective assessment by the subject of his memory. For

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example, subjects were observed to either avoid tests when they did not know the correct response (Hampton, 2001; Smith et al., 1998) or collect more information before making a choice (Call and Carpenter, 2001; Hampton et al., 2004). Critical to evaluating these findings is the argument that lack of information does not directly cause subjects to avoid a test or collect more information, but rather the subjects' own recognition that they lack information controls this response. Thus, while a relationship between the primary measure of accuracy and the secondary measure of the animal's assessment of its own knowledge is required to infer memory awareness, the two measures must also be shown to be distinct.

A general function of memory awareness that could account for the evolution of this capacity might be that it allows an organism to adaptively avoid situations that require knowledge the individual lacks, while permitting approach to such situations when the required knowledge is available. Thus, memory awareness would presumably help animals to avoid adverse outcomes. In the laboratory setting the adaptiveness of memory awareness is evident when subjects avoid memory tests when they have forgotten material presented during the study phase of the trial, but take the test when the relevant memory is available (Hampton, 2001; Inman and Shettleworth, 1999; Smith et al., 1998). A human parallel to these situations is our ability to determine whether or not we know a phone number before dialing. If we know the number, and we are aware of that knowledge, we proceed with dialing. If we cannot bring the number to awareness, we take the time to look up the number before calling.

But even in situations where memory awareness does not permit an adaptive response as in the examples above, it may still manifest itself in behavior. Imagine driving by yourself to a location you have never visited. You thought that you had memorized the route, but now you are at an intersection and do not know which way to go. With cars behind you it is not possible to stop and avoid making a wrong turn, or to consult the map. Forced to make a decision without sufficient information, you may feel frustrated and may even hit the steering wheel or vocalize angrily. Nonhuman subjects may be in an analogous situation when they do not know the correct response on a forced-choice memory test. They have no option but to choose one of the available responses. When the correct response is known, all can go smoothly. But when the correct answer is not known, subjects might give some sign that they are aware that they do not know how to respond, perhaps with some sign of anger or frustration. Such negative emotions might reflect the anticipation of an incorrect response.

In this study, we examined video taped behavior (recorded for unrelated reasons) of one monkey participating in a matching-to-sample experiment. Serendipitously, we noted that this monkey showed two distinct response types when selecting stimuli at test—he either lightly touched the computer touchscreen monitor, or he hit it much more forcefully. Because striking the computer screen appeared to reflect frustration on the part of the monkey, we wondered whether this behavior might indicate that he knew he had forgotten the correct response and was unlikely to receive a reward.

While previous reports indicate that rhesus monkeys may indeed be capable of memory awareness (Hampton, 2001; Hampton et al., 2004; Smith et al., 1998, 2003), this study may provide additional important evidence for this capacity because the behavior we observed was entirely spontaneous. In two previous studies, monkeys were explicitly trained to avoid memory tests when they did not know the answer (Hampton, 2001; Smith et al., 1998). Because the monkeys were explicitly trained, and contingencies were in place that made it profitable to avoid tests when memory was poor, it remains a concern that the monkeys may have attended to some cue other than the state of their memory in selecting which trials to avoid. In the current study, the monkey was not explicitly trained to hit the screen aggressively on some trials but gently on others, and he could not improve his rate of reward through use of these two types of response. His behavior is unlikely to be a "clever Hans" phenomenon for these reasons. Thus, the main aim of the present study was to investigate a phenomenon that might reflect memory awareness in nonhuman primates—one that could not be attributed to unintentional training effects.

2. Materials and methods

2.1. Subject

One 6-year-old male rhesus macaque monkey (*Macaca mulatta*), weighing approximately 10 kg was the subject in this study. This monkey had participated in cognitive testing for several years (and tens of thousands of trials, with over 1000 different images) and was proficient in matching-to-sample with delays up to 32 s, as well as object discrimination, with clip art images. The monkey was housed individually and was fed daily an amount of biscuits and fruit adjusted to ensure sufficient motivation and nutrition. Water was always available in the home cage.

2.2. Testing apparatus and procedure

During each testing session, the monkey was seated in a standard primate chair that enclosed his torso and lower body, but permitted unrestricted use of his forelimbs. A delayed matching-to-sample task was used. During the sample phase of each trial an image appeared in the center of the touchscreen, which the monkey had to contact twice (FR 2) in order to advance the trial. The screen then went blank, and one of six delay intervals followed (0, 2, 4, 8, 16, or 32 s). During the choice phase four images appeared in the corners of the touchscreen and the monkey was required to select (FR2) the image that matched the sample to receive a food reward. The FR schedules were programmed such that they required two consecutive touches to the same image for completion of the FR to be registered. If the monkey touched one image a single time, and then touched a different image, the FR counter reset, registering only a single touch (to the most recently contacted image). Completion of the FR2 schedule was finally registered once two consecutive touches to a given image occurred. A large set of images was used such that each image was seen only once in each daily 48 trial session. A camera mounted on the top of the testing chamber was connected to a VCR that recorded target sessions. The camera was aimed at the touchscreen from over the monkey's shoulder such that the monkey's head, arms, hands, and the entire touchscreen were visible. Testing was performed once per day and three consecutive sessions were recorded and analyzed for the current study. A total of 125 trials were available for analysis.

The videos were edited so as to include as much of the last 4 s of each trial as possible, up to but not including the conclusion of the trial where it was evident whether the monkey responded correctly or not. The sample phase of the trial was also excluded. Thus, the clips allowed for the entire test phase of each trial to be viewed (and subsequently coded) while at the same time keeping the rater blind to whether the monkey had chosen correctly or not.

Each trial was reviewed by the second author (BMH) who coded responses as either touches or strikes. A "touch" occurred when the animal used his fingers to gently tap the selected image on the computer monitor. Such selections clearly lacked force. Conversely, a "strike" was coded when the monkey rapidly struck the image by placing the palm of his hand flat against the screen or by closing his hand as he struck the screen in a forceful manner. Because no audio signal was available, all trials were coded based on visual inspection alone. Each clip was coded in three separate sessions over a 3-day period. In order to qualify as a strike for analysis, a given response had to be coded as such in each of the three coding sessions. The remaining responses were coded as touches. Intrarater correlations for the three sessions ranged from 0.84 to 0.89. Later, these data were classified according to the accuracy of the response on each trial through co-registration of the video tape with the computer data file that was produced during original testing. The computer also recorded the latency to select an image in the choice phase and the latency to touch the sample at the beginning of each trial.

3. Results

The monkey made an error on 47% of strike trials compared to 25% of touch trials (Table 1). A χ^2 analysis of the 2 × 2 classification of responses as either strikes or touches and either correct or incorrect indicates a significant relationship between response type and trial outcome (Table 1; $\chi^2(1) = 5.47, p < .05$). Latencies were log transformed prior to statistical analysis (Kirk, 1984). Analysis of variance (Response Type × Trial Outcome) showed that the monkey was significantly slower to select an image at test when he struck compared to when he touched the screen and was significantly slower when wrong than when correct (Fig. 1; $F_{1,121} = 16.52, p < .01$; $F_{1,121} = 4.53, p < .05$). The interaction of these two factors was not significant ($F_{1,121} = 0.66$).

Table 1
Frequencies of strikes and touches classified as correct or incorrect

	Correct	Incorrect
Strike	18 (53%)	16 (47%)
Touch	68 (75%)	23 (25%)

Percentages of row totals are in parentheses.

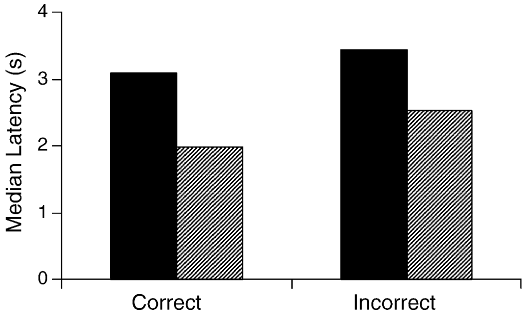

Fig. 1. Median response latencies for completing the FR2 required in selecting an image at test. Black bars represent trials on which the monkey struck the screen, striped bars represent those trials on which he touched the screen.

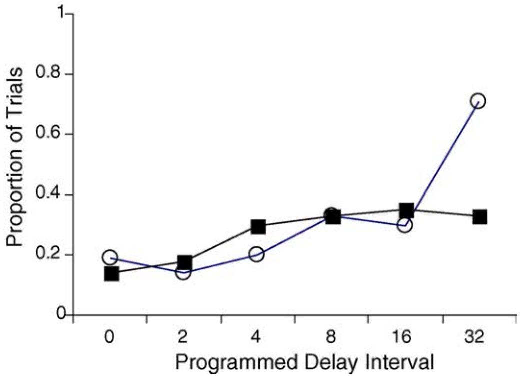

Fig. 2. Proportion of errors and strikes as a function of delay interval. Solid squares represent the proportion of strikes at each delay; open circles represent the proportion of errors at each delay.

The same analysis applied to sample latencies revealed no significant differences (Response Type: $F_{1,121} = 0.94$; Trial Outcome: $F_{1,121} = 0.60$; Interaction: $F_{1,121} = 0.45$).

Because the monkey experienced six different delays, and errors are expected to increase at longer delays, we further analyzed the trials by delay interval. Both the proportion of errors and the proportion of strikes appear to increase with delay (Fig. 2). However, analysis of the small amount of data available indicated that accuracy varied significantly with delay, but the probability of a strike did not (analysis of two way tables classifying trials by Delay and Trial Outcome, and by Delay and Response Type: Trial Outcome: $\chi^2(5) = 21.67, p < .01$; Response

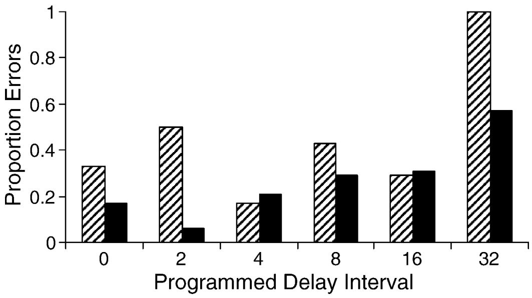

Fig. 3. Frequency of errors following strikes and touches at each delay. Striped bars indicate the proportion strike trials ending in error; solid black bars the proportion for touch trials.

Type: $\chi^2(5) = 4.16$). We also compared the proportion of errors that occurred following strikes and touches across the six delays (Fig. 3). A one-tailed paired *t*-test comparing the proportion of errors made during strike and touch trials across the six delays was significant ($t_5 = 2.16$, $p < .05$).

4. Discussion

We serendipitously observed that a monkey either touched or struck the computer touchscreen during the test phase of matching-to-sample trials. Blind coding of video segments edited to exclude all but the response phase of these trials showed that the monkey was more likely to choose correctly on trials on which he gently contacted the touchscreen than he was on trials on which he struck the screen with more force. This difference suggests that the monkey knew in advance when he was likely to choose incorrectly, and the anticipated failure to receive a reward caused him to respond aggressively. We suggest that this result is consistent with the monkey making metacognitive judgments about his own memory states, an ability that depends on memory awareness.

The conclusion that the monkey was attending to his memory state in deciding whether to strike or touch the screen requires that the monkey's behavior was not controlled by an external event that might signal poor performance independently of internal memory assessment. In the current case the delay interval offers one possible such external event—the monkey may have been frustrated following long delay intervals because he had learned that long intervals were less frequently associated with reward than short intervals. Because accuracy was poorer at long delays, frustrated responses (striking) and poor performance might correlate. Indeed, inspection of Fig. 2 suggests that both errors and strikes increase with delay interval (although only the increase in errors is statistically significant). However, the analysis depicted in Fig. 3 shows that across the six delays the monkey was generally more likely to make an error following a strike than following a touch. The poorer performance on strike trials than on touch trials at different delays indicates that the delay interval does not drive the correlation between response type and accuracy.

Metacognition is characterized as requiring two levels of representation, an object level consisting of the target memory or information and a meta level consisting of an evaluation or monitoring of the object level (Nelson, 1996). The existence of the second, meta level representation is what distinguishes *meta*cognition from cognition. In considering this distinction, note that if the monkey's behavior had been controlled directly by the object level representation (i.e., the strength of his memory of the sample), he might be expected to respond gently or tentatively when he did not know the answer. That is, vacillation might be expected in the absence of a strong response tendency. Here the opposite was observed—the monkey responded most strongly when he did not know the correct answer. The stronger response on error trials supports the argument that these responses resulted from the monkey knowing that he did not know the answer (a meta level representation). Thus, his strike responses were likely a secondary (metacognitive), rather than a primary, effect of not knowing the answer—he knew he did not know and that was frustrating.

The latency data (Fig. 1) are consistent with the analysis above. The monkey was slower in selecting a stimulus at test on trials where he struck the screen, and on incorrect trials. These differences in latency may reflect a search of memory conducted just prior to selecting an image at test. On trials in which a memory is located, the search is terminated and the monkey rapidly makes his choice. On trials on which he forgot the sample, the search continues for some time without a memory being located. Eventually the search of memory is terminated and the monkey guesses (Briggs and Blaha, 1969; for review see Van Zandt and Townsend, 1993). Thus, the occurrence of longer latencies on strike trials is consistent with the argument that the monkey was unable to retrieve a memory of the sample on these trials. Furthermore, the longer latencies on strike trials rule out the possibility that these responses were inaccurate because they were impulsive. Impulsive responses would have shorter than normal latencies.

In the present study, the monkey was more accurate than expected by chance after strikes, although less accurate than following touches. If striking the screen occurred only when the monkey thought he did not know the correct response, and his ability to judge his knowledge were perfect, then it would be expected that he would perform at chance (25%) on these trials. Instead the monkey scored 53% correct on strike trials. Whether this above chance performance is due to error in our categorization of strikes and touches, inaccuracy in the monkey's metacognition, or was caused by residual implicit memory not accessible to metacognition is a question to be addressed by future work.

4.1. Alternative explanations

When ascribing "higher" cognitive function to nonhuman species there is always a concern that the data are overinterpreted and that conclusions are the result of uncritical anthropomorphism. It is therefore appropriate to consider "simpler" explanations of the behavior we observed here. One possible alternative explanation for our results is that we have the order of causality reversed. Perhaps when the monkey strikes the screen he is inaccurate in directing the strike and often contacts an image other than the one intended. Thus, frustration (caused by some non obvious variable) may cause errors, rather than anticipated failure causing frustration as we propose. The locations to which the monkey could respond at test were well separated, occupying the four corners of a 14 in. monitor. Furthermore, strikes to the screen were very well concentrated on a single image; they were not poorly directed swipes that contacted large areas of the screen. Finally, because completion of the FR required two consecutive touches to the same image, inaccurate strikes are unlikely to account for the larger number of errors on strike trials. More difficult to rule out is the possibility that whatever causes the monkey to strike the screen also interferes with his ability to remember the correct response (delay was discussed in this context above). In this case a single (unidentified) cause has two consequences, making the monkey strike the screen, and interfering with memory. Ruling out this possibility would require a direct experimental manipulation of memory, such as the use of no-sample trials on which the monkey would be expected to act as if he had forgotten (Hampton, 2001). With the current results we cannot therefore rule out this possibility.

The present findings are from a single monkey very experienced in cognitive testing. We did not observe other (similarly experienced) monkeys making such obvious apparently frustrated responses with any frequency. Of course it may be the case that more subtle behaviors could be indicative of test-related frustration in other monkeys, or that electrophysiological measures could be applied to a similar analysis. In any case, some caution should be applied in interpreting these results from a single monkey. Nonetheless, we believe that the performance of a single subject can be sufficient to demonstrate a capacity in a given species, even though a single subject is insufficient to make accurate quantitative generalizations about the species as a whole.

4.2. Comparative significance

The results of the present study, in addition to other work, suggest that memory awareness and metacognition are present in at least some Old World monkeys. In a serial probe recognition paradigm, two rhesus macaques selectively “bailed out” of trials involving middle list items, for which memory is relatively poor (Smith et al., 1998). Two different macaque monkeys performed more accurately on matching-to-sample trials they chose to take, relative to trials they were forced to take (Hampton, 2001), indicating that they chose to take the test when memory was relatively strong. Furthermore, the monkeys studied by Hampton (2001) avoided tests in two situations in which they had no recent memory of a sample, namely, on catch trials that began without a sample, and on trials with long delays. Finally, rhesus monkeys were shown to collect information selectively on trials on which they did not know the correction response (Hampton et al., 2004). The present results, taken together with findings from these earlier reports, thus provide converging evidence from four substantially different behavioral paradigms indicating the presence of memory awareness in macaque monkeys.

The presence of memory awareness in both apes (Call and Carpenter, 2001) and Old World monkeys (Hampton, 2001; Hampton et al., 2004; Smith et al., 1998) suggests that this cognitive capacity may have first evolved in a common ancestor of apes and Old World monkeys (Riley and Langley, 1993). While there are not strong a priori grounds for presuming that memory awareness is limited to primates, the strength of the evidence from primates contrasts with the weaker evidence for memory awareness in pigeons (*Columba livia*; Inman and Shettleworth, 1999; Sole et al., 2003; Sutton and Shettleworth, unpublished data). But there is still insufficient evidence to substantiate a categorical difference between species. More studies of memory awareness in non-primate species are needed to address this question adequately.

Finally, it should be noted that memory awareness is one circumscribed kind of self-awareness. Several investigators (Parker, 1998; Purdy and Domjan, 1998; Smith et al., 2003) have suggested that the most useful approach to the study of awareness would be an incremental one, focusing on the identification of specific, elemental capacities that either reflect awareness or serve as precursors of awareness. We agree with this approach, and therefore do not argue that memory awareness equates with the broader notion of self-awareness. Memory awareness is specific to the ability to introspectively discriminate between knowing and not knowing. In both human developmental and comparative studies of nonhumans, it has been common to use the “mirror test” to infer self-awareness broadly. A mark or sticker is placed on the subject’s face without their knowledge. If subjects touch the mark as a result of seeing it on their face in the mirror, they pass the test. While there is disagreement about what exactly the mirror test indicates about self-awareness (de Waal et al., 2005; Gallup, 1994; Heyes, 1994) it is still striking that no monkeys pass the test in its strongest form, while all great apes with the possible exception of gorillas (*Gorilla gorilla*) do pass the test (Gallup, 1994; Shillito et al., 1999). Nonetheless, we would encourage as much restraint in generalizing broadly about self-awareness from performance in the mirror test as in generalizing from tests of memory awareness.

Through comparative studies of fragments of the broader capacity of self-awareness it may ultimately be possible to chart the evolution of memory awareness, and other aspects of metacognition (Smith et al., 2003; Weiskrantz, 2001). Decomposing self-awareness into component processes such as memory awareness may show that some aspects of self-awareness have a more substantial role in nonhuman behavior than we have realized, and may force reconsideration of the significance of the concept of “self-awareness” in our understanding of human cognition.

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