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Rhesus monkeys (*Macaca mulatta*) discriminate between knowing and not knowing and collect information as needed before acting

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Abstract Humans use memory awareness to determine whether relevant knowledge is available before acting, as when we determine whether we know a phone number before dialing. Such metacognition, or thinking about thinking, can improve selection of appropriate behavior. We investigated whether rhesus monkeys (*Macaca mulatta*) are capable of a simple form of metacognitive access to the contents of short-term memory. Monkeys chose among four opaque tubes, one of which concealed food. The tube containing the reward varied randomly from trial to trial. On half the trials the monkeys observed the experimenter baiting the tube, whereas on the remaining trials their view of the baiting was blocked. On each trial, monkeys were allowed a single chance to select the tube containing the reward. During the choice period the monkeys had the opportunity to look down the length of each tube, to determine if it contained food. When they knew the location of the reward, most monkeys chose without looking. In contrast, when ignorant, monkeys often made the effort required to look, thereby learning the location of the reward before choosing. Looking improved accuracy on trials on which monkeys had not observed the baiting. The difference in looking behavior between trials on which the monkeys knew, and trials on which they were ignorant, suggests that rhesus monkeys discriminate between knowing and not knowing. This result extends similar observations made of children and apes to a species of Old World monkey, suggesting that the underlying cognitive capacities may be widely distributed among primates.

Keywords Metacognition · Metamemory · Declarative · Introspection · Memory awareness

Introduction

In humans, stored information is sometimes accessible to conscious awareness and sometimes not. Conscious access to memory gives humans the ability to discriminate between knowing and not knowing, an ability we term memory awareness. Because memory awareness is inferred primarily on the basis of verbal reports from human subjects (e.g. “I remembered” versus “I guessed”) it has been difficult to conduct parallel studies in nonhumans. In addition, the fact that humans can accomplish a good deal of learning without awareness cautions against inferences of memory awareness in animals based on the complexity of learned behavior alone (classical conditioning: Clark and Squire 1998; priming: Tulving and Schacter 1990; Hamman and Squire 1997; skill learning: Cohen et al. 1985; Knowlton et al. 1992; Knowlton and Squire 1993). Recent investigations have pioneered ways around dependence on verbal reports (Cowey and Stoerig 1995; Smith et al. 1998; Inman and Shettleworth 1999; Call and Carpenter 2001; Hampton 2001). The success in applying these new techniques has paved the way for comparative studies that chart the distribution of memory awareness among species and that clarify the cognitive capacities underlying it in nonhuman animals (Weiskrantz 2001; Smith et al. 2003).

A critical feature of these studies is that memory awareness is inferred on the basis of the functional properties of behavior, rather than on the basis of subjective reports of phenomenal experience. That is, the studies specify what an animal with memory awareness should be able to do, not what that animal should experience subjectively. A general function of memory awareness might be to allow an organism to adaptively avoid situations that require knowledge the individual lacks, while approaching such situations when the required knowledge is available. Specifically, subjects in typical laboratory memory experiments could use memory awareness to avoid memory tests when they have forgotten material presented during the study phase of the trial, and to opt for taking the tests when they remember (Smith et al. 1998; Inman and Shettleworth 1999; Hampton 2001). A human parallel to these situa-

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Fig. 1 *Left panel* Example of looking behavior. In this case, monkey B is looking down the tubes searching for the hidden food on an unseen trial. *Right panel* Example of tube selection; in this photograph monkey B is choosing, without first looking, on a seen trial. As the monkey pulls the tube upward, the food concealed inside slides out. Selecting any one tube caused a mechanism to lock the other tubes in position. Thus, only one tube could be selected per trial. The clear screen that separates the monkey from the apparatus during the baiting procedure can be seen, captured in the picture as it was being raised

tions 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. Another example might be determining whether we know the route to take before starting a road trip in a car. If we already know the route, we proceed straightaway, but if we cannot bring the relevant knowledge to mind, we consult a map. The capacity for awareness of memories underlies the ability to adaptively choose between beginning a call or trip immediately, and collecting information before acting.

Adapting the methods of Call and Carpenter (2001), we allowed rhesus monkeys (*Macaca mulatta*) to choose from among four opaque tubes in which a piece of food could be concealed. Preceding their choice, monkeys either observed the placement of the food in one of the tubes (*seen* trials) or their view of the tubes was blocked during baiting (*unseen* trials). The tubes were arranged such that the monkeys could, with some effort, bend over and look down the length of the tubes to locate the hidden food; this behavior will be referred to as “looking” hereafter. Alternatively, they could choose a tube without first looking (Fig. 1). Monkeys with memory awareness should discriminate between knowing and not knowing the location of the food. Much as a human would resort to the phone book only if he or she did not know the phone number for a particular call, memory awareness may manifest behaviorally in monkeys through selective information seeking. Monkeys aware of the food location (*seen* trials) should choose the correct tube without looking, whereas monkeys unaware of the food location (*unseen* trials) should look for the food before choosing.

Chimpanzees, orangutans, and 2.5-year-old children were studied by Call and Carpenter (2001) and shown to pass

this test for memory awareness. All three species were more likely to look before choosing when they did not know the location of the reward than when they did. By studying rhesus monkeys, we examine whether this ability is confined to humans and apes or is more widely distributed among the primates.

Thus, there were two main aims of the present study. The first aim was to perform an additional, independent test for memory awareness in nonhuman primates. Although there is evidence for memory awareness in monkeys from two studies using recognition memory (Smith et al. 1998; Hampton 2001), evidence gathered from a variety of experimental situations would provide a more compelling case for the phenomenon. The second and more specific aim was to determine whether the findings of Call and Carpenter (2001) would extend to a species of Old World monkey, a group which is less closely related to humans than are the great apes.

Methods

Subjects

Seven male and two female adult rhesus monkeys (*M. mulatta*) were used. Five monkeys were housed individually, while the other four lived in two socially compatible pairs. Monkeys were fed a controlled diet to ensure sufficient motivation and healthy body-weight. Preferred foods were used as rewards to minimize the need for diet restriction. Water was always available in the home cage.

All monkeys had previously taken part in studies examining the neural substrates of learning and memory (Hampton and Murray 2002), and all had extensive experience with object discrimination learning and delayed matching-to-sample tasks administered in an automated apparatus. Five monkeys (F, B, R, H, L) had received bilateral removals of the perirhinal cortex and four were unoperated controls (K, C, S, G). One monkey included in the report by Hampton and Murray (2002) was not included here because it failed to complete early phases of the experiment. Because our task was similar to spatial delayed response, and because no deficit in performance was observed in spatial delayed response following lesions that involved perirhinal cortex (Murray and Mishkin 1986), we did not expect the removals to have an impact in the present study.

Apparatus

We used a specially constructed apparatus consisting of a free-standing frame and attached horizontal tray on which four tubes were

mounted. The monkey, held in a mobile transport cage, was positioned in front of the apparatus; the cage was fitted with bars on one side that allowed the monkey to reach outside the cage and to interact with the apparatus. The four tubes, 25 mm in diameter and 166 mm in length, were aligned parallel to one another, 95 mm apart center to center, on an aluminum tray. The tubes were affixed to the tray using hinges such that pulling on a given tube caused that tube to tip upward and a food reward, if present, to tumble out the end nearest the monkey (see Fig. 1). Pulling any tube triggered a latching mechanism that prevented additional choices on the same trial. The tray could be placed at one of five levels, the lowest being near the bottom of the monkeys' cage and the highest position being near the monkeys' eye level when sitting normally in the transport cage. Levels 1–5 were 3, 12, 22, 34 and 46 cm from the bottom of the cage, respectively. A short removable visual barrier (55 mm high) could be mounted on the test tray between the monkey and the tubes. Although the barrier prevented the monkeys from seeing into the tubes, it did not prevent the monkeys from viewing the tubes from above nor from manipulating them. A clear screen and an opaque screen could be raised and lowered, individually or together, between the monkey and the test tray. Unlike the small visual barrier, these large screens prevented the monkey from reaching the tubes. The clear screen allowed visual access only, whereas the opaque screen completely blocked the monkey's view of the experimenter and the test tray. Peanuts, M&Ms, Mike and Ikes, or Skittles were used as rewards, according to the monkeys' preferences. A video camera was mounted behind the apparatus, on the side opposite the monkey. The camera was linked to a monitor located to one side of the apparatus. This closed-circuit video system permitted the experimenter to score the monkeys' behavior by watching the monitor rather than by looking directly at the monkey.

Behavior scoring

On each trial the number and location of looks made into the tubes was noted, as well as whether the correct tube was selected. The experimenter watched the monkey in real time on the closed circuit television monitor, and a look was scored any time the monkey's eye was visible through the length of a tube. Sessions were not recorded on videotape. Lifting a tube even slightly caused the latching mechanism to engage, and was scored as a choice.

Procedure

In pilot work with a monkey not included in this report, we found that familiarization with the individual components of the final task was required. For example, the monkeys needed to learn that "pulling" a tube led to the contents of the tube dropping out the end. Familiarization was conducted in three phases, followed by the main task.

Familiarization

Phase 1: selecting and pulling transparent tubes

During this phase the apparatus was fitted with clear acrylic tubes that allowed the monkeys to see the location of the food reward without having to look down the length of the tube. Monkeys were first adapted to the apparatus and trained to pull whichever tube contained a food reward. By reaching for the visible reward, most monkeys rapidly learned to pull on the tubes. When the tube was tipped at an angle, the food slid out where the monkey could collect it. In this phase the monkeys were also habituated to the raising and lowering of the opaque and transparent screens. All trials began with both screens down, i.e. with the screens separating the monkey from the tubes. The tray was positioned at level 3; in this position it was easy for the monkey to watch the food reward being placed in the tubes, and for the monkey to pull the tubes. On half of the trials the opaque screen was raised and subjects could

therefore see the experimenter place the reward in the tube through the clear screen (seen trials). On the other half of the trials the opaque screen blocked the monkeys' view of the baiting procedure (unseen trials). The order of seen and unseen trials, and the location of the food reward were randomized. The clear screen was kept in place for 2 s after the baiting (seen trials) or after the opaque screen had been raised (unseen trials). The clear screen was then raised, and the monkey was allowed to choose one tube. After a choice had been made both screens were lowered, ending the trial. In this and the following phases of familiarization monkeys were given 24 trials per daily session. Monkeys advanced to phase 2 after making 100% correct choices in a single session.

Phase 2: transition to opaque tubes

In phase 1, the monkeys could directly see which tube contained the food, and make their choices accordingly. In phase 2, opaque aluminum tubes replaced the clear tubes. Furthermore, the short visual barrier was put in place on the tray to prevent the monkeys from seeing the food reward once it had been placed in a tube. Consequently, in this second phase of familiarization, monkeys were required to attend to the baiting of the tubes in order to choose correctly. Because the tube containing the reward was opaque and, furthermore, was randomly chosen on each trial, the only way for the monkey to know the location of the reward was to watch while the experimenter placed the reward in the tube. In this phase the monkeys were allowed to see the baiting procedure on every trial, through the clear screen. Two seconds after baiting, the screen was raised and the monkey was allowed to select a single tube. Tray height was the same as in phase 1, and criterion was 21 correct responses out of 24 trials in a single session.

Phase 3: looking

Our pilot monkey did not spontaneously look down the length of the tubes. Given that our monkeys may have little or no experience with the visual affordances of tubes, this is not surprising. Accordingly, in this phase of familiarization the short visual barrier was removed, and the test tray was raised to the approximate eye level of the monkey (level 5). Placing the tubes at eye level encouraged the monkeys to look down the length of the tubes to see the reward being placed at the far end. As in phase 2 all trials in this phase were seen trials. When a monkey made at least 21 correct responses out of 24 trials in a single session, the monkey advanced to the main task.

Main task

In the main task monkeys were presented with a mixture of seen and unseen trials using the opaque tubes. These constituted "critical trials" in the sense that each monkey would now have, for the first time, the opportunity to engage in looking behavior, or not, as the situation demanded. There were 28 trials in each session. Sessions began with four refresher trials conducted exactly as in phase 3. Thus, four seen trials, with the tray holding the tubes located at eye level, began each session. For the remaining 24 trials, the height of the tray differed across sessions. Because looking behavior depended on the balance of costs (i.e. the effort of looking down the tube combined with the delay of reward) versus benefits (i.e. the greater probability of obtaining reward when the location was known versus when it was unknown), and because these differed among monkeys, a titration procedure was used to determine the appropriate tray height for each monkey. The titration procedure prevented ceiling and floor effects from masking differential looking behavior on seen and unseen trials. In the first session, the test tray was placed in the middle position (level 3), which was near the midpoint between eye level and the floor of the transport cage. Half of the trials were seen and the other half unseen, presented in pseudorandom order. As in familiarization, all trials began with both screens in the down position. On seen trials the

opaque screen was raised before baiting, whereas on unseen trials it was raised after baiting. On both trial types, the monkey could view the tubes for 2 s before the clear screen was raised. If the subject looked down the tubes on fewer than six of the 24 experimental trials, the tray was raised one position for the next session. If the subject looked down the tubes on more than 18 of these trials, the tray was lowered one position. Raising the tray made it easier to look down the tubes, whereas lowering the tray made it more effortful. Test sessions continued until each monkey completed two consecutive sessions with from 6 to 18 looks, or had completed two consecutive sessions with the tray at the lowest position. Monkeys were given 60 s to select one of the tubes on each trial; if no tube was selected, the trial was aborted and the intertrial interval was initiated.

Data analysis

Sessions were counted whether or not the monkey completed all trials in the session. In the early phases of familiarization, we found that the two female monkeys, S and L, would not complete full sessions. Therefore, they were both given sessions of half the length of those given to the other monkeys. For consistency, pairs of consecutive sessions given to monkeys S and L were combined and scored as one session. On the main task, the dependent measure was the number of times a monkey looked down the length of the tubes on seen and unseen trials during the last two sessions; the first four (seen) trials of each session were not included in the analysis. Analysis of proportions was preceded by arcsine transformation (Kirk 1982).

Results

Familiarization

Phase 1: selecting and pulling transparent tubes.

All monkeys learned to pull the clear tube that contained a food reward on each trial, taking an average of 10.0 sessions to meet criterion (Table 1). As expected, monkeys never looked down the length of the tubes during this phase, presumably because they could easily see the food reward through the sides of the clear tubes.

Phase 2: transition to opaque tubes

During this phase, the short visual barrier prevented monkeys from looking down the length of the tubes. Thus, to choose accurately, monkeys were required to attend to the

baiting of the tubes, and to retain information about the location of the baited tube for a few seconds. Monkeys required an average of 24.9 sessions to meet criterion (Table 1).

Phase 3: looking

Most monkeys generalized to the new tray position and thus met criterion within a few sessions (mean=1.7, Table 1).

Main task

Looking as a function of trial type

An average of 4.9 sessions was required to achieve a tray height at which the number of looks made by each monkey fell within the targeted range, or the monkey had completed two sessions with the tray at the lowest position (Table 1). All monkeys looked down the tubes on at least some seen and some unseen trials (Fig. 2). Seven of the nine monkeys looked significantly more often on unseen trials than on seen trials. In contrast, none of the monkeys looked significantly more often on seen than on unseen trials (Fig. 2; chi-square value for each monkey is shown in Table 2). The two monkeys (F and G) for which trial type did not affect looking showed different patterns of behavior. Monkey F looked on every trial but one seen trial, even at the lowest tray position. Monkey G looked much less often overall than did the other monkeys.

With the exception of monkey K, the monkeys chose a tube on nearly every trial (Table 2). In the final two sessions, monkey K failed to choose a tube on 16 trials, a large percentage of the trials he was given. Fifteen of the 16 aborted trials were unseen trials. Nonetheless, of the nine unseen trials on which he made a choice, all were preceded by looking in the tubes. Aborted trials for the other monkeys were rare, but also tended to occur on unseen trials rather than on seen trials.

Accuracy and looking

To maximize the data available for this analysis, data from all sessions of the main task were used. Monkeys chose

Table 1 Sessions to criterion and final tray height. Scores include sessions comprising the criterion run. Numerals indicate the number of sessions to criterion for each phase of familiarization (phases 1–3) and for the main task, or the tray level during the final sessions of the main task. Sessions were counted whether or not all trials were completed. Tray levels varied from 1 to 5, with 1 being near the bottom of the monkeys' cage, and 5 being near the

monkeys' eye level (see text for detailed description). *Capital letters* identify the nine rhesus monkeys studied. Due to experimenter error, monkey R received his first session of the main task with the tray at level 1, and did not make a single look. He then met criterion on the subsequent two sessions completed with the tray at level 3

Stage of training	K	C	S	G	F	B	R	H	L	Mean
Phase 1	31	3	15	8	5	4	4	7	13	10.0
Phase 2	34	13	49	14	18	9	3	27	57	24.9
Phase 3	2	2	2	2	1	1	1	1	3	1.7
Main task	4	6	2	7	6	4	3	6	5	4.8
Tray level	4	2	3	5	1	2	3	1	2	2.6

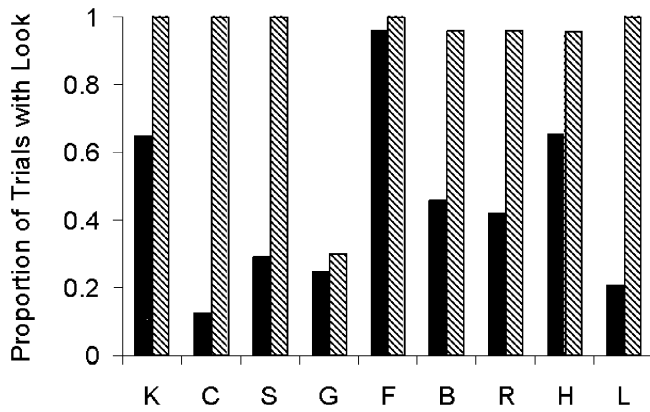


Fig. 2 The proportion of looks made by each of the nine monkeys on seen (solid black bars) and unseen (cross-hatched bars) trials. These proportions result from dividing the number of looks by the number of completed trials in the seen and unseen conditions for each monkey. Seven of the nine monkeys were significantly more likely to look on unseen trials than on seen trials. Capital letters identify the nine rhesus monkeys studied

accurately, but not perfectly, on seen trials (Table 2). On unseen trials monkeys were significantly more accurate when they looked through the tubes before choosing (84%) than on trials on which they failed to look (22%; Table 2; $t_7=11.26$, $P<0.01$; monkey S was excluded because she looked on every unseen trial, precluding an estimation of accuracy on trials without a look). Performance on unseen trials without looks did not differ from chance ($t_7=0.951$; monkey S excluded). On seen and unseen trials combined, monkeys chose accurately on 97% of the trials on which they looked down the tube containing the reward (Table 2).

Looks on seen trials

On seen trials where monkeys looked through the tubes even though they should have known the location of

the reward, the first look was most often made to the baited tube (Table 2; $t_8=6.44$, $P<0.01$; mean=0.65; chance=0.25).

Errors

There were a small number of seen and unseen trials on which monkeys looked in at least one tube, but then chose incorrectly. Six of the nine monkeys made at least five such errors (mean=7.17; range 5–10), permitting analysis. On 80% of these error trials the monkeys failed to look in the tube containing the reward before selecting a tube, looking instead in at least one tube other than the rewarded tube.

Aborted trials

As indicated earlier, if no tube was selected within 60 s, the trial was aborted. With the exception of monkey K, monkeys selected a tube on nearly all trials. Nonetheless, to ensure that exclusion of these aborted trials from the analysis did not bias our findings, each analysis described in the results was also conducted with the aborted trials included. The monkeys never looked on these aborted trials and made no selection; however, for this analysis, we scored the tube “choice” as an error. Inclusion of the aborted trials did not alter the statistical results with the exception that with aborted trials included monkey K did not look more often on unseen than on seen trials. Because the majority of the trials on which this monkey failed to select a tube were unseen trials, excluding these trials may have biased the results in favor of looks being more frequent on unseen trials. Accordingly, the results from this monkey should perhaps be given less weight than those from the remaining monkeys.

Table 2 Strategic use of looking. Capital letters indicate the individual rhesus monkeys studied. Chi square values in the first two rows are from analysis of contingency tables classifying the number of trials with and without a look into seen and unseen conditions. Aborted trials are those trials on which the monkey never selected a tube. The next row reports the probability that the monkeys first look was down the tube containing the bait, if they looked at all, on seen trials. Accuracy on seen trials averages all

seen trials on which the monkey made a choice, whether it looked or not. Accuracy on unseen trials displays accuracy as a function of whether or not the monkey had looked down any tubes before making a choice. The dash indicates that there were no unseen trials without a look for that monkey. Accuracy after seeing reward is the probability that monkeys chose correctly after they had looked down the tube containing the reward on either trial type

Monkey		K	C	S	G	F	B	R	H	L	Mean
Differential looking chi square, $df=1$		4.17	37.33	25.52	0.14	1.02	14.52	16.39	6.77	31.45	
Chi square probability		0.04	0.00	0.00	0.71	0.31	0.00	0.00	0.01	0.00	
Aborted trials	Seen trials	1	0	0	0	0	0	0	1	0	0.22
	Unseen trials	15	0	1	4	0	0	0	1	0	2.3
1st look to reward on seen trials		0.69	0.82	0.57	0.90	0.49	0.33	0.80	0.59	0.63	0.65
Accuracy on seen trials		0.96	0.99	0.96	0.96	0.86	0.98	0.86	0.93	0.87	0.93
Accuracy on unseen trials	Without look	0.25	0.09	–	0.11	0.20	0.17	0.31	0.27	0.38	0.22
	Following look	0.80	0.87	1.00	0.53	0.94	0.88	0.87	0.76	0.87	0.84
Accuracy after seeing reward		1.00	0.99	1.00	0.89	1.00	0.94	0.96	0.98	0.96	0.97

Perirhinal cortex removal

As expected, we found no evidence that perirhinal cortex lesions affected performance on this task. Three of four intact monkeys and four of five monkeys with perirhinal cortex removals showed significant differential looking behavior. As indicated earlier, monkeys with lesions including perirhinal cortex are unimpaired in spatial delayed response (Murray and Mishkin 1986), a task which is similar to seen trials in the present study, with the exception that food was hidden under a gray plaque rather than in tubes.

Discussion

The primary finding of the present study is that rhesus monkeys discriminated between seen and unseen trials; seven of nine monkeys were significantly more likely to look down the length of the tubes when kept ignorant of the location of the concealed food than when they had been provided with that information beforehand. In no case was the reverse pattern found. We hypothesize that when monkeys were aware of a memory for the location of the food, they selected that tube without first looking. When they did not detect the presence of a memory (at least not at sufficient strength), they collected more information before acting. Thus, at least some rhesus monkeys demonstrated awareness for the contents of short-term memory in a way that parallels that of humans making metacognitive judgments on the basis of memory awareness.

Accuracy and looking

Monkeys were much more accurate on unseen trials when they looked for the food relative to when they failed to look before choosing. In addition, they performed no better than expected by chance on unseen trials without looks. While not surprising, these results support assumptions that underlie the present experiment. Monkeys did not know the location of the reward on unseen trials, but looking informed them, and guided their responses.

“Misbehavior”

Why would monkeys ever look down the tubes on seen trials? Such looks may simply reflect a high tolerance of the effort required for looking relative to the value of the reward. Alternatively, on some trials the monkey might have been distracted during the placement of the food in the tubes or might have forgotten the location of the reward over the brief delay between baiting and the opportunity to choose. In these cases, the decision to look might reflect the weak state of the monkey's memory. It is of interest that when the monkeys did look on seen trials, they most often looked first in the tube containing the reward.

The monkeys must therefore have “known,” in some sense, where the reward was located on these trials. Whether the decision to look despite knowing was due to a conservative decision process, a weak memory awareness corresponding to weak memory, or to monkeys having an implicit memory of which they were unaware, is a question for future work to address.

Monkeys occasionally made mistakes, even after looking. On the majority of these trials the monkeys failed to look in the tube with the reward. In contrast, when monkeys did look in the tube with the reward, the subsequent choice was nearly always correct. It seems likely that on many of the error trials the monkeys mistakenly thought they saw the reward, stopped looking, and chose the tube where they thought they had seen the reward.

Alternative explanations

Although our monkeys acted in a way that parallels the behavior of a human using metacognition, the significance of these findings depends on the mechanism underlying the behavior of the monkeys. We argue that memory awareness – the ability to discriminate knowing from not knowing – underlies the ability to gather information selectively when necessary. There are at least two alternative accounts, however, for our results: (1) discrimination based on stimuli other than the presence of memory per se, and (2) direct competition between behavioral responses.

Discrimination based on nonmnemonic stimuli

Monkeys may have based the decision to look on publicly observable external stimuli, rather than on discrimination among memory states. Learning such a discrimination would presumably require a substantial number of differentially rewarded presentations of stimuli that would come to elicit the behavior of looking on unseen trials, but not on seen trials. Given that the phases of familiarization were specifically designed so that no such differential training could occur, it is unlikely that such a discrimination could account for the present results. In phase 1, monkeys never looked down the tubes because the sides of the tubes were clear. In phase 2, the short visual barrier prevented looking. Because the behavior of looking never occurred during these first two phases, it could not be reinforced. Phase 3 was intended to ensure that the monkeys had experience looking down the tubes and seeing the reward. Again there is no opportunity for differential reinforcement of looking on seen and unseen trials because all trials were seen trials. Furthermore, the monkeys' first and only choice on these trials was nearly always accurate, and thus rewarded. Only in the main task, when seen and unseen trials were intermixed, was differential reinforcement possible. Thus, before beginning the main task, looking had been associated with reward only on the seen trials of phase 3. If association with reinforcement governed the probability of looking, then looks should be more fre-

quent on seen than on unseen trials. This pattern was observed in only 2 of the total of 44 test sessions given to the monkeys in the main task (Monkey K: 1 of 4 sessions; monkey G: 1 of 7 sessions).

There is an additional argument against a nonmnemonic explanation for the differential looking behavior we observed. Seven of the nine monkeys looked on more than 18 trials in some sessions of the main task, and therefore experienced lowering of the test tray. Thus, if monkeys were learning a discrimination during the main task, it was that they did not need to look on seen trials, rather than that they did need to look on unseen trials. Extinction of looking on seen trials would be expected to proceed slowly, if at all, because looking was nearly always associated with reward on both types of trials. It is more likely that monkeys initially had a low threshold for looking (looking even when memory was strong, because looking was easy), but as the effort required to look increased as the test tray was lowered, they became more selective in the choice of when to bother looking.

Although we have argued against an associative account for the behavior of looking primarily on unseen trials, we do not argue that the behavior of attending to ones own memory states is not learned. Instead, we argue that the monkeys had acquired the ability to discriminate between knowing and not knowing before the present experiment was begun.

Competition between responses

Another mechanism that might account for the differential looking we observed is response competition. The response of reaching for a tube may compete with the response of looking for the reward. When the tendency to reach is strong, it dominates the tendency to look. When the tendency to reach is weak, looking is more likely to occur. Seeing the reward placed in a tube may so greatly strengthen the tendency to reach that looking is unlikely. The difference in the probability of looking on seen and unseen trials could therefore depend on the strength of the reaching response, which is in turn a function of whether or not the monkey has seen the reward and prepared a response. On this view, differential looking is the outcome of response competition, rather than memory monitoring per se. Nonetheless, if the decision leading to the response is driven by whether or not the monkey knows the location of the reward, and the occurrence of information seeking is contingent on the absence of such knowledge, then the distinction between “true” memory awareness and competition between responses is a subtle one. Indeed neural signals apparently reflecting competition between responses have been recorded in monkey frontal cortex (for review see Schall 2001). How such competition is resolved remains an active area of investigation, but recent work suggests that when conflicts arise, other brain regions (such as prefrontal and cingulate cortex) are recruited to monitor and resolve the conflict (e.g. Kerns et al. 2004; Matsumoto and Tanaka 2004). Thus, although

we initially proposed “response competition” as a possible alternative to memory awareness, it may instead be the case that conflicts between competing or incompatible responses trigger cognitive processes that make use of memory awareness to resolve the competition.

Comparative significance

The results of the present study suggest that humans and apes are not alone in being aware of memories. Instead, it appears that this ability is shared at a minimum by at least some Old World monkeys. A small number of other experiments support this conclusion. 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 other macaque monkeys performed more accurately on matching-to-sample trials they chose to take relative to trials they were forced to take (Hampton 2001). Like the Smith et al. (1998) monkeys, if given the chance they selectively avoided taking tests when memory was poor. 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. The present results, taken together with findings from these earlier reports, provide converging evidence from three 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 (Smith et al. 1998; Hampton 2001; the present results) suggests that this cognitive capacity may have first evolved in a common ancestor of apes and Old World monkeys (Riley and Langley 1993). Apes and monkeys last shared a common ancestor roughly 20–25 million years ago (Tomasello and Call 1997, p. 15). Should memory awareness be shown to occur in New World monkeys (capuchins or marmosets for example), or in prosimians (such as lemurs), that would suggest an earlier date for the appearance of memory awareness.

There are not strong a priori grounds for presuming that memory awareness is limited to primates. However, the strength of the evidence for memory awareness in primates contrasts with the failure to find evidence for memory awareness in pigeons (*Columba livia*; Inman and Shettleworth 1999; Sutton and Shettleworth, unpublished data) using techniques similar to those used by Hampton (2001) with monkeys. Nonetheless, currently there is insufficient evidence to substantiate a categorical difference between species, in part because the impact of variations in testing procedures have yet to be determined. One potentially significant difference is that between prospective memory judgments, which are made before the test phase of a trial, and simultaneous or retrospective memory judgments made at the time memory is being directly tested (Inman and Shettleworth 1999; Hampton 2001, 2003; Metcalfe 2003; Shettleworth and Sutton 2003). Because

prospective judgments cannot be based on any direct experience of the difficulty of a given test, nor can they be based on competition between behavioral responses like those discussed earlier, such tests arguably provide the more stringent test for memory awareness. Pigeons may show some evidence of memory awareness using retrospective judgments, but appear to be incapable of prospective judgments (Inman and Shettleworth 1999; Sutton and Shettleworth, unpublished data). In both the present study, and the work of Smith et al. (1998), monkeys employed retrospective judgments; by contrast, the monkeys studied by Hampton (2001) made prospective memory judgments.

Finally, it should be noted that memory awareness is one limited kind of self awareness. Several investigators (Parker 1998; Purdy and Domjan 1998; Smith et al. 2003) have suggested that a 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, and our experimental approach was guided by this notion. In both human developmental studies and comparative studies of nonhumans, it has been common to use the "mirror test" to infer self awareness. 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 (Gallup 1994; Heyes 1994) it is striking that no monkeys pass the test, while all great apes with the possible exception of gorillas (*Gorilla gorilla*) do pass the test (Gallup 1994; Shillito et al. 1999). The current tests for memory awareness, and the mirror test, may measure different elements in a suite of capacities collectively described as self awareness.

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References

- Call J, Carpenter M (2001) Do apes and children know what they have seen? *Anim Cogn* 4:207–220
- Clark RE, Squire LR (1998) Classical conditioning and brain systems: the role of awareness. *Science* 280:77–81
- Cohen NJ, Eichenbaum H, Deacedo BS, Corkin S (1985) Different memory systems underlying acquisition of procedural and declarative knowledge. In: Olton DS, Gamzu E, Corkin S (eds) *Memory dysfunction: an integration of animal and human research from preclinical and clinical perspectives*. New York Academy of Sciences, New York, pp 54–71
- Cowey A, Stoerig P (1995) Blindsight in monkeys. *Nature* 373:247–249
- Gallup GG (1994) Self-recognition: research strategies and experimental design. In: Parker ST, Mitchell RW, Boccia ML (eds) *Self-awareness in animals and humans*. Cambridge University Press, New York, pp 35–50
- Hamman SB, Squire LR (1997) Intact perceptual memory in the absence of conscious memory. *Behav Neurosci* 111:850–854
- Hampton RR (2001) Rhesus monkeys know when they remember. *PNAS* 98:5359–5362
- Hampton RR (2003) Metacognition and explicit representation in nonhumans. *Behav Brain Sci* 26:346–347
- Hampton RR, Murray EA (2002) Learning of discriminations is impaired, but generalization to altered views is intact, in monkeys (*Macaca mulatta*) with perirhinal cortex removal. *Behav Neurosci* 116:363–377
- Heyes CM (1994) Reflections on self-recognition in primates. *Anim Behav* 47:909–919
- Inman A, Shettleworth SJ (1999) Detecting metamemory in non-verbal subjects: a test with pigeons. *J Exp Psychol Anim Behav Process* 25:389–395
- Kerns JG, Cohen JD, MacDonald AW, Cho RY, Stenger VA, Carter CS (2004) Anterior cingulate conflict monitoring and adjustments in control. *Science* 303:1023–1026
- Kirk RE (1982) *Experimental design*, 2nd edn. Wadsworth, Belmont, Calif.
- Knowlton BJ, Squire LR (1993) The learning of categories: parallel brain systems for item memory and category knowledge. *Science* 262:1747–1749
- Knowlton BJ, Ramus S, Squire LR (1992) Intact artificial grammar learning in amnesia. *Psychol Sci* 3:172–179
- Matsumoto K, Tanaka K (2004) Conflict and cognitive control. *Science* 303:969–970
- Metcalf J (2003) Drawing the line on metacognition. *Behav Brain Sci* 26:350–351
- Murray EA, Mishkin M (1986) Visual recognition in monkeys following rhinal cortical ablations combined with either amygdectomy or hippocampectomy. *J Neurosci* 6:1991–2003
- Parker A (1998) Primate cognitive neuroscience: what are the useful questions? *Behav Brain Sci* 21:128–128
- Purdy JE, Domjan M (1998) Tactics in theory of mind research. *Behav Brain Sci* 21:129–130
- Riley DA, Langley CM (1993) The logic of species comparisons. *Psychol Sci* 4:185–189
- Schall JD (2001) Neural basis of deciding, choosing and acting. *Nat Rev Neurosci* 2:33–42
- Shettleworth SJ, Sutton JE (2003) Animal metacognition? It's all in the methods. *Behav Brain Sci* 26:353–354
- Shillito DJ, Gallup GG, Beck BB (1999) Factors affecting mirror behavior in western lowland gorillas, *Gorilla gorilla*. *Anim Behav* 57:999–1004
- Smith JD, Shields WE, Washburn DA, Allendoerfer KR (1998) Memory monitoring by animals and humans. *J Exp Psychol* 127:227–250
- Smith JD, Shields WE, Washburn DA (2003) The comparative psychology of uncertainty monitoring and metacognition. *Behav Brain Sci* 26:317–339
- Tomasello M, Call J (1997) *Primate cognition*. Oxford University Press, New York, N.Y.
- Tulving E, Schacter DL (1990) Priming and human memory systems. *Science* 247:301–306
- Weiskrantz L (2001) Commentary responses and conscious awareness in humans: the implications for awareness in non-human animals. *Anim Welfare* 10:S41–46