



ELSEVIER

Comparative metacognition

Herbert S Terrace¹ and Lisa K Son²

Metacognition is knowledge about knowledge, often expressed as confidence judgments about what we know. Most of the literature on metacognition in humans is based on subjects' verbal reports. Investigators of animal cognition have recently described nonverbal methods for investigating metacognition in animals. In one, subjects are given the option to escape from difficult trials. In another, subjects are trained to place bets about the accuracy of their most recent response. To rule out noncognitive interpretations of purported evidence of metacognition in animals, one must ensure that escape responses do not increase the overall density of reinforcement and that they do not occur in the presence of the stimuli on which the subject was trained. The nonverbal techniques used to investigate metacognition in animals make possible two interesting lines of research: investigating the contribution of language and explicit instruction in establishing metacognition, and the investigation of the neural substrates of metacognition.

Addresses

¹ Columbia University and the New York State Psychiatric Institute, United States

² Barnard College, United States

Corresponding author: Terrace, Herbert S (terrace@columbia.edu) and Son, Lisa K (lson@barnard.edu)

Current Opinion in Neurobiology 2009, 19:67–74

This review comes from a themed issue on
Cognitive neuroscience
Edited by Michael Platt and Elizabeth Spelke

0959-4388/\$ – see front matter
Published by Elsevier Ltd.

DOI 10.1016/j.conb.2009.06.004

“*Know thyself*”, attributed to the Delphic oracle, Socrates and Solon.

It can be safely said that the Delphi oracle did not have animals in mind when she uttered her famous dictum about self-knowledge. That possibility was not even considered until the latter part of the 20th century, when evidence began to accrue that animals have minds. The evidence came from experiments in which behavior could not be explained by reference to stimulus–response associations between observable events because the behavior in question occurred in the *absence* of the stimulus to which the subject was trained to respond [1]. Accordingly, the control of those behaviors was attributed to a *representation* of the training stimulus

and the animal's mind was considered to be the repository of such representations [2].^a

Metacognition is arguably the most complex form of cognition studied in animals because it requires the animal to form a representation about a representation (as opposed to a single representation, as in other examples of animal cognition) [4,5]. But the complexity of metacognition in animals is miniscule when compared to the complexity of human metacognition as observed in experiments on thinking, learning, and problem solving [6,7].

Experiments on metacognition in animals raise a slew of intriguing questions. How similar is metacognition in animals, which cannot be based on verbal knowledge, to human metacognition? Is language necessary for human metacognition? Are the neural mechanisms that give rise to human and animal cognition analogous? At present, the answers to these questions are sketchy at best. At worst, they are inchoate in the sense that comparisons of models of human and animal metacognition suffer from the acute absence of relevant data.

The most direct point of comparison between studies of human and animal metacognition is at the level of prospective and retrospective metacognition. Retrospective metacognition occurs when people make confidence judgments about their knowledge of prior events; prospective metacognition, judgments about future events, for example, confidence in one's performance on an upcoming test. In a typical experiment on prospective metacognition, subjects are asked to engage in some cognitive task, say, memorizing a list of paired-associates. They are then asked to rate their confidence about responding accurately on a test on which they would have to recall which cues were paired with which associates. Once the test is administered, a correlation between subjects' accuracy on the test and their pretest confidence is used as a measure of subject's metacognitive knowledge [8]. Similarly, to assess retrospective metacognition, subjects would be asked to make judgments about their confidence in the accuracy of their responses *after* taking a test.

Although people are fairly good at judging the accuracy of their own knowledge, there has been a consistent tendency to be overconfident [9–11]. Such faulty metacognition was an important instigator of a surge of

^a This is the same argument that initiated the so-called cognitive revolution [3].

Table 1

Experiment	Species	Task	Judgment
Category 1			
Smith <i>et al.</i> [19]	Monkey	Psychophysical	Concurrent ^a
Shields <i>et al.</i> [20]	Monkey	Psychophysical	Concurrent
Smith <i>et al.</i> [21]	Monkey/humans	SPR ^b	Concurrent
Inman and Shettleworth [22]	Pigeon	DMTS ^c	Concurrent
Call and Carpenter [23]	Ape/children	Hidden objects	Concurrent
Shields <i>et al.</i> [24]	Monkey	Psychophysical	Concurrent
Beran <i>et al.</i> [25]	Monkey	Psychophysical	Concurrent
Suda-King [26]	Orangutan	Spatial Memory	Concurrent
Washburn <i>et al.</i> [27]	Monkey	Psychophysical/MTS ^d	Concurrent
Sutton and Shettleworth [28]	Pigeon	MTS/DMTS	Concurrent
Basile <i>et al.</i> [29]	Monkey	Hidden objects	Concurrent
Kepecs <i>et al.</i> [30*]	Rat	Psychophysical	Concurrent
Footo and Crystal [31]	Rat	Psychophysical	Concurrent
Category 2^e			
Smith <i>et al.</i> [33]	Monkey	Psychophysical	Prospective
Category 3^f			
Hampton [34**]	Monkey	DMTS	Prospective
Category 4			
Kornell <i>et al.</i> [35**]	Monkey	SPR	Retrospective

^a Concurrent metacognition is based on judgments made in the presence of the discriminative stimuli that are presented during a particular trial. They should be distinguished from prospective metacognition, which is based on confidence to perform accurately on an upcoming test and, retrospective metacognition, which is based on confidence in the accuracy of their response on the present trial.

^b SPR = serial probe recognition (see p. 7).

^c DMTS = delayed-matching-to-sample (see p. 6).

^d MTS = matching to sample.

^e Category 2 includes experiments that claim that there was no reinforcement for escape responses, but that claim can be questioned on two grounds. These studies used subjects that were trained previously to use escape responses that were reinforced and it has been shown that metacognitive skills transfer readily to new tasks [35**].

^f Although food reward was provided in experiments in Categories 3 and 4, none of the discriminative stimuli were present during the delivery of the reward. In the absence of those stimuli, subjects could opt for large rewards if they were confident about their ability to solve a problem that they could take during an upcoming test (prospective metacognition) or about their performance on the trial that had just ended (retrospective metacognition).

research on cognitive mechanisms underlying metacognitive judgments [12]. Several theories have been proposed to investigate this question, but none are able to explain a majority of the existing data [13–15]. One explanation, known as *target retrieveability or accessibility*, is perhaps the most intuitive [16]. It postulates that people base their judgments on the number of features of the target they can access or retrieve that is the more features that are retrieved, the higher their confidence. By contrast, the *inferential* view states that people base their judgments on the basis of cue-familiarity rather than target-familiarity [17].

Metacognition in animals

Table 1 provides a summary of recently developed *non-verbal* paradigms to assess metacognition in animals. Each paradigm assumes that subjects experience varying degrees of uncertainty that is inversely related to the difficulty of the task. Because verbal reports are typically used to assess metacognitive knowledge, it has not been possible to determine the extent to which metacognition depends on language, and whether this phenomenon is uniquely human. Although we can be sure that metacognition in animals does not require verbal ability, it is unclear to what extent metacognition in animals is analogous to that

observed in humans. To see why, we have assigned recent experiments on animal metacognition shown in Table 1 into one of four categories. The main contrasts to be drawn in Table 1 are whether or not an animal's purported metacognitive judgments were made in the presence of the stimuli on which they were trained (Category 1), whether that judgment was differentially reinforced (Category 2) and whether the judgments they made were prospective (Category 3) or retrospective (Category 4).

Category 1

The earliest studies of animal uncertainty make up the largest category [18–29,30*,31]. Unfortunately, the results of these studies are ambiguous because it is possible to account for purported examples of metacognitive behavior with simpler noncognitive explanations. In Table 1, we refer to such judgments as 'concurrent' because the purported metacognitive response is made in the presence of the stimuli the subject is asked to discriminate. Consider, for example, Smith *et al.*'s influential study in which dolphins were required to discriminate the auditory frequencies of two tones by responding to one of two stimuli [18]. Whenever the tone was exactly 2100 Hz, a response to a '2100 Hz'-icon was rewarded; for lower frequencies, a response to a '<2100 Hz'-icon' was

rewarded. Any error terminated a trial without reinforcement and resulted in a time out (TO). A response to a third stimulus ended a trial with neither reward nor punishment. It also allowed the subject to start a new trial. Because easy problems were more frequent than hard problems, opting for a new trial increased the likelihood that the next trial would be easier. Accordingly, responses to the third stimulus had a direct effect on the number of rewards a subject could earn in a session.^b

Discriminating tones whose frequency was within ~100 Hz of the 2100 Hz standard was exceedingly difficult. Unsurprisingly, subjects' accuracy fell to chance in that range and the relative frequency of opting out was maximal. That relationship prompted some investigators to interpret responses to the third stimulus as a measure of uncertainty. There are, however, simpler ways to interpret responses to the third stimulus [32]. One is that it maximizes the frequency of reward during each session. Another is based on the avoidance of frustration that would result from the absence of a reward or from a TO. However, the most important problem with the experiments in Category 1 is the presence of the discriminative stimuli until the trial ended. If the value of an external stimulus can account for a response, why postulate a representation?

Category 2

In this study, subjects were not given any feedback until as many as eight trials had elapsed [33]. Since subjects were not given immediate feedback for each response, it was claimed that metacognitive responding could not be explained by reward. However, that argument would only apply to naïve subjects that had no history of metacognitive training. Since all of the subjects used in this experiment had extensive metacognitive training in previous experiments, it is not surprising that they showed that ability when trained on a new task [35**].

Categories 3 and 4

The third and fourth categories list experiments that have provided more convincing evidence of metacognition in animals. All of them are based on a subject's memory of the stimuli to which they were required to respond. The experiment assigned to Category 3 [34**] used a delayed-matching-to-sample-paradigm (DMTS) in which the sample disappeared after the subject responded to it and it did not reappear until test. Toward the end of some trials, a subject was required to make a prospective judgment of firstly, its confidence that it would respond accurately during test (selecting the sample from various distractors) or secondly, its lack of confidence that it

remembered the sample. Subjects had been trained previously to discriminate a pair of 'high-confidence' and 'low-confidence' icons and the consequences of choosing each icon. When subjects chose to take the test by responding to the high-confidence icon, they were given an opportunity to win a highly desirable reward (an M&M), whereas a response to any of the distractors produced a TO. If the monkey chose not to take the test by choosing the 'low-confidence' icon, it was given a simple 'test' on which any response produced a less preferred banana pellet. Subjects' ability to choose the high-confidence and the low-confidence icons appropriately was a measure of prospective metacognition. The evidence supporting that ability was the high rate of responding to the high-confidence icon after making a correct response and to the low-confidence icon after making an error. Additional evidence that subjects were indeed responding metacognitively was provided by their accuracy on 'catch' trials on which taking the test was their only option. Accuracy on catch trials was reliably lower than it was on trials on which subjects could choose the test option. That difference shows that subjects could anticipate the outcome of a trial.

Category 4

The contingency for reward in the experiment listed in Category 4 was based on a subject's ability to *remember* the accuracy of its response on a particular trial [35**]. If, for example, a monkey was trained on a serial probe recognition (SPR) task,^c reward during baseline training was determined solely by the subject's ability to recognize an item that was presented during the sample. During a test for metacognition, reward was based solely on its confidence it had about the accuracy of its response on the SPR task.

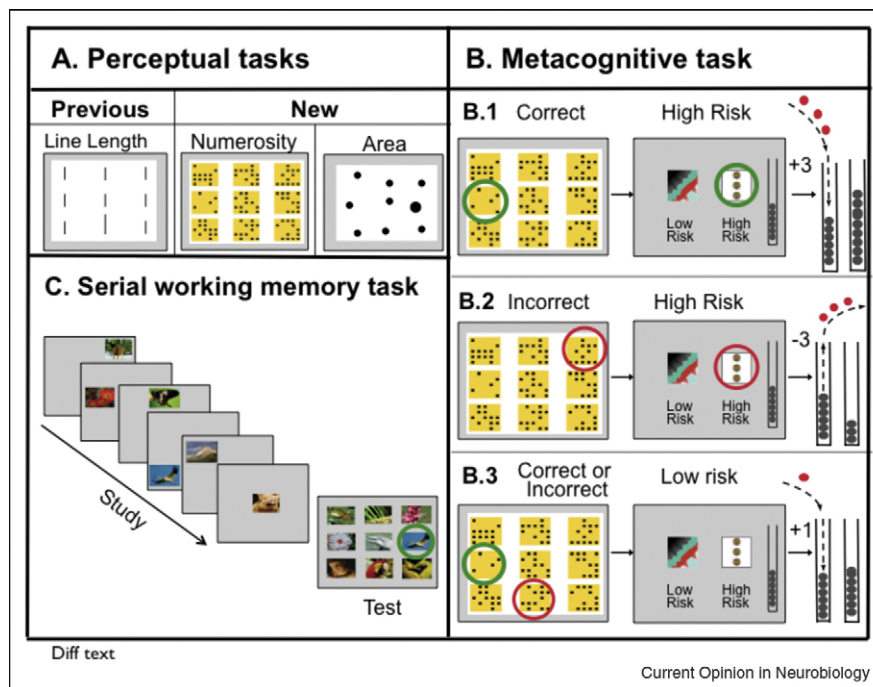
The low-confidence and the high-confidence icons were presented following a subject's response on the SPR task. As shown in Figure 1B, reward and punishment consisted of, respectively, the addition and the subtraction of tokens that were displayed in a bank on the right side of the subject's monitor. Choosing the high-risk icon following a correct response on the SPR task resulted in the addition of three tokens. Choosing the high-risk icon after an incorrect response resulted in the *removal* of three tokens. In order to maintain responses to the low-risk icon, correct and incorrect responses to that icon were each rewarded by the addition of one token; however, the subject responded.

Subjects' choices of risk icon were highly accurate. Other features of their performance provided new evidence of

^b Because responses to the third stimulus could increase the overall frequency of reward, it would be helpful if the authors of articles that use this procedure estimate how many 'extra' rewards a subject would have lost if that contingency were absent.

^c In the SPR task, a multi-image sample containing *n* items, is displayed successively. During test, the subject is presented with a single item from the sample. The subject's task was to choose in item that was included in the sample.

Figure 1



Tasks used in Experiment 1. **(A)** In Task 1 (trained before this study) subjects had to select the longest line. Task 2 was to select the item with the largest (or, for one subject, the smallest) number of items. Task 3 was to select the smallest (or, for one subject, the largest) circle. **(B)** In the metacognitive task, the high-confidence and low-confidence icons were presented immediately after the subject made its selection on the perceptual task. A response to the high-confidence icon resulted in a gain of three tokens after a correct response (B.1). Tokens were accumulated in a 'bank' located to the right of the high-confidence and low-confidence icons. There were nine tokens in the bank at the start of every trial. When 12 or more tokens accumulated in the bank, two pellets were delivered and the number of tokens reset to 9. A response to the high-confidence icon after an incorrect response resulted in the loss of three tokens (B.2). A response to the low-confidence icon always resulted in a gain of one token, whether or not the subject responded correctly (B.3). **(C)** Trial structure of the serial working memory task: six sample pictures were displayed successively, each separated by a 2-s interval. Following the last sample and a .5-s pause, the test phase of the trial began. One of the six sample photographs was selected at random. Either that stimulus or an unfamiliar stimulus was shown and the monkey had to identify it as familiar or unfamiliar. The same two confidence icons that were displayed during the perceptual tasks were presented immediately after the subject responded to the probe.

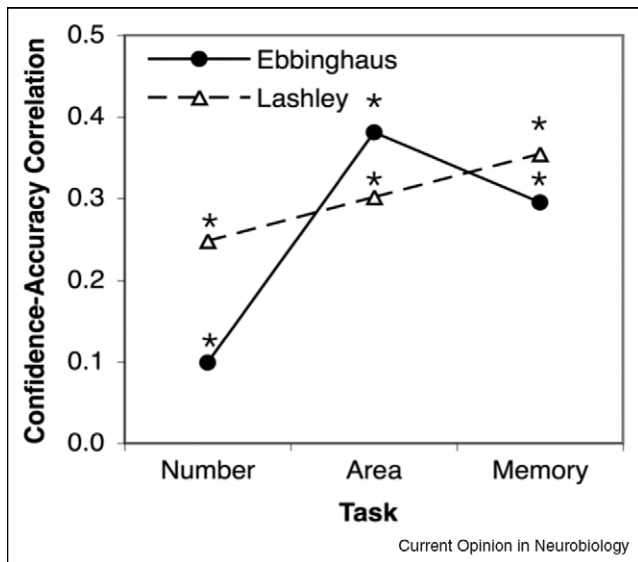
retrospective metacognition in animals. As shown in Figure 2, there was immediate and complete positive transfer from metacognitive tests that were administered following training on one task to a qualitatively different task, for example, from tasks on which subjects were trained on various types of magnitude discrimination tasks to an SPR task that was a test of short-term memory [36]. Positive transfer of metacognitive ability across qualitatively different tasks suggests that it was readily available in monkey's cognitive tool kit.

Another type of evidence was derived from an analysis of the contribution of reaction time (RT) to metacognitive judgments. In experiments on human metacognition, RTs are typically shorter for correct than for incorrect responses [37]. A similar difference was observed in the case of monkeys, that is, a negative correlation between RTs during test and the accuracy of their choice of risk icon. Although there is no simple method to control for the influence of RT duration on confidence judgments, it is possible to partial out that factor. The resulting values

were significantly greater than zero. It follows that the duration of RTs on correct and incorrect trials could not be the sole determinant of subjects' metacognitive performance.

Like RTs, other peripheral or external cues may influence metacognition, for example, item difficulty. Figure 3 presents the percentage of trials on which a 'high-confidence' bet was made at each level of difficulty (top two panels) and the SPR task (bottom two panels). Level of difficulty was measured by the size difference between the target and distractors on a circle-size test and by serial position on the memory test. As can be seen, subjects could have used difficulty as a cue for making their metacognitive judgments, for example, 'choose high risk when the difference between target and distractors is sufficiently large'. However, the differences in level of difficulty cannot explain the risk selections on the SPR task because the relative frequency of accurate high-confidence bets was essentially the same at virtually every serial position. In other words, monkeys assessed the

Figure 2



ϕ -Correlations. The value of ϕ was calculated for the block of 10 days of training on the numerical and physical area perceptual tasks and for the serial working memory task. Each value is significantly greater than zero ($P < .05$).

accuracy of their own responses, while ignoring obvious external cues like serial position.

Monkeys can not only make reliable judgments about the accuracy of their responses on various tasks, but they can also request hints when they do not know the correct response [35••]. In one experiment, subjects were trained to learn four novel four-item sequences composed of arbitrary photographs. Subjects were given the opportunity to ask for 'hints' as to the next response in the sequence. The hint was four blinking lines that appeared around the item to which the subject should next respond. Without hints, they would have to learn each sequence by trial and error. If the subject completed a trial correctly without requesting any hints, its reward was a highly desirable M&M. If the subject requested one or more hints during the course of completing a trial correctly, its reward was a less enticing banana pellet. Subjects could obtain as many as four hints on each trial, one for each list item. The crucial finding was that hint seeking was inversely related to accuracy on each of the four novel lists on which they were trained.

Neurological bases of metacognition

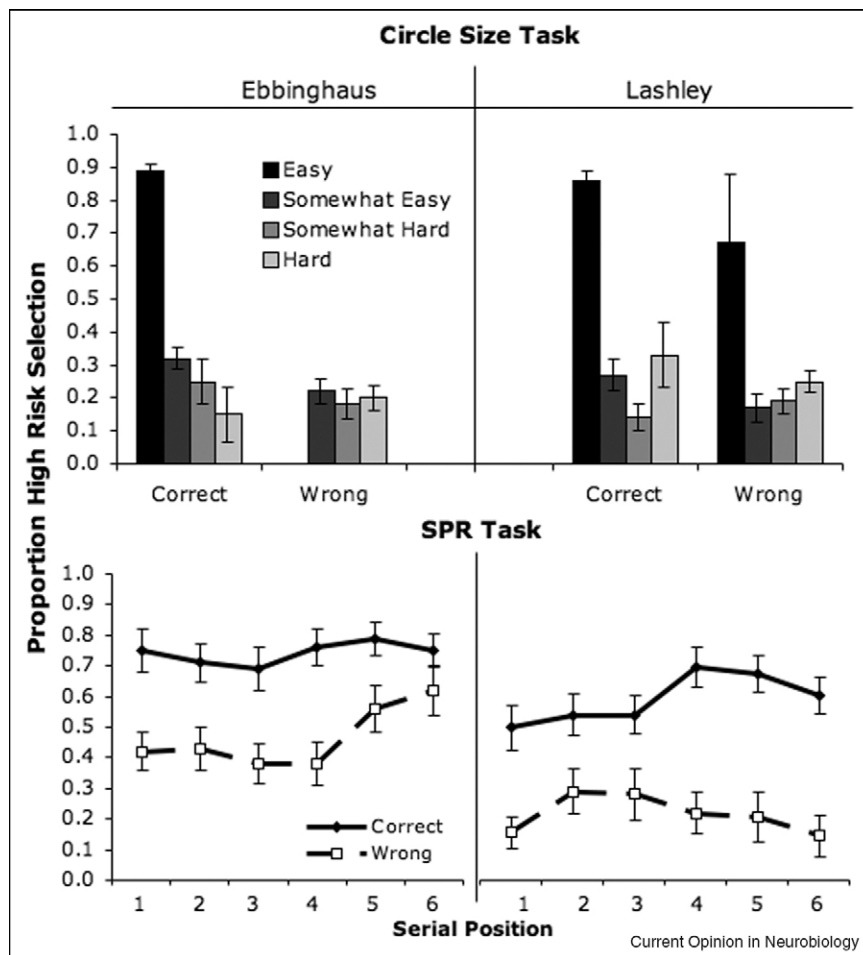
Research on human patients provides clear evidence that metacognition is mediated by the frontal and the prefrontal cortex [38]. Imaging studies of normal human subjects confirmed these clinical observations [39,40]. For obvious reasons, research on the neurological bases of metacognition in animals has only recently begun. In an innovative experiment, Kepecs *et al.* [30•], reported

evidence that the orbitofrontal cortex (OFC) mediates metacognition in rats during the performance of an olfactory discrimination. The discriminative stimuli in that experiment were two compounds. When the odor contained more of compound A than B, it was rewarded for inserting its head into port 1; more of B than A, into port 2. Once that rat entered one of the side ports, the consequence of its response (food reward for correct responses or a TO following an error) was delayed for a brief interval whose duration ranged from .3 to 1 s. During the anticipation interval, the rate of firing of single neurons in the orbitofrontal cortex (OFC) was higher on difficult than on easy trials, with some cells showing the opposite pattern.

It was also shown that, during the delay interval, the firing rates of single cells to the same mixture of odors differed on trials on which subjects responded correctly and incorrectly. That difference is of interest because those cells fired differentially *before* the outcome of a trial. That disparity was interpreted as a more direct measure of subjects' confidence about the outcome of a trial because it occurred before reward or punishment was administered. It does not follow, however, that any of the *behavioral* manifestations of metacognition can be explained by the variations in the rate of firing of a single cell or by the difference in the rate of firing in anticipation of correct and incorrect outcomes on a particular trial.

A variation of the paradigm on which the rats were originally trained addressed that problem by obtaining behavioral measures of the subjects' uncertainty, similar to those obtained from experiments in Category 1 of Table 1. Instead of simply waiting for the outcome of a trial, subjects were free to terminate it by withdrawing from port 1 or 2. They could start a new trial by entering a third port that was equidistant from ports 1 and 2. Subjects' behavior matched that observed in similar experiments in which subjects were allowed to abort a trial and to start a new trial immediately. Because the rate at which subjects opted to start a new trial varied with the difficulty of the discrimination on a particular trial, Kepecs *et al.* concluded that 'a key function of OFC is to generate reward predictions based on stimulus-reward associations...and that OFC neurons signal outcome prediction.' However, like the other experiments listed in Category 1, the results of Kepecs *et al.*'s experiments are ambiguous because the same results could have been obtained if the subjects followed the simpler strategy of maximizing reinforcement or if they responded to the small difference between the discriminative stimuli as a cue for making an escape response. It would therefore be of interest to replicate the Kepecs *et al.* experiment using a paradigm in which subjects expressed their confidence about the outcome of a particular trial *after* the odors were removed from the cones, and in which responses to the purported indicators of confidence did not influence the rate of reward.

Figure 3



The proportion of trials on which two monkeys selected 'high risk', for varying levels of difficulty on the circle-size task (top two panels) and the SPR task (bottom two panels). On the circle-size task, the monkeys had to choose either the smallest or largest circle (depending on monkey) from an array of nine circles. Difficulty was determined by the difference in size from the target and the distractors (which were all the same size). On the SPR task, monkeys had to judge whether a probe stimulus that was presented after a sample containing six successively presented items was included in the sample or not (familiarity task). Difficulty was determined by the serial position of the target.

Explicit and implicit metacognition in humans

Given that a nonverbal task such as the betting paradigm provides evidence that animals are able to express uncertainty, it may be possible to pursue other interesting questions about metacognition in animals that parallel those that have been investigated with human subjects. One important issue is, what is the relationship between *explicit knowledge* and metacognition [41,42]? While some would agree that explicit knowledge improves metacognitive accuracy [43], others would even argue that 'to make conscious a metacognitive process, is interfering with the task at hand.' ([44], p. 70).

While verbal subjective reports may prove valid in a typical laboratory setting, their ecological validity might be much stronger if actual bets were made and carried out as they would be in the real world. A recent study of

young children, ages 5–6, used the nonverbal betting paradigm, in conjunction with an SPR task, because firstly, it was expected to be easier to comprehend than the typical 10-point rating scale of confidence; secondly, it might increase the ecological validity of metacognitive judgments; and thirdly, it would provide a comparison between the performance of humans and monkeys on the same metacognitive task [45]. In one condition, no verbal instructions were given about how to bet, which is the method used with monkeys. In another, the children were given *explicit* instructions on how to bet. Results showed that both groups learned to bet appropriately that is the correlations between accuracy on the SPR test and the size of a bet were positive, although, as expected, higher for the explicit group. More importantly, when given a transfer test on which subjects were asked to respond to multiple choice vocabulary questions, children trained by

the explicit condition performed better than children trained by the implicit 'monkey' condition (although both groups exhibited positive correlations). These results suggest that, while metacognitive processes may not require explicit awareness, declaring what you know during training is beneficial.

Conclusion

Metacognition has developed as an important field of inquiry in both human and animal cognition, but much more research is needed in each instance to provide a basis for direct comparison. In the case of humans, there are enough data to test specific models of metacognition [46,47], but none is available in the case of animal metacognition. It is also important to investigate experiments on the development of metacognition in young children to determine the extent to which metacognition requires language. In the case of animals, there is firm evidence that monkeys can make both prospective and retrospective confidence judgments about their performance on various recognition tasks, in the absence of language, but much more research is needed to define the relevant parameters. Two obvious advantages of studying metacognition in animals are that it makes it possible to study nonverbal metacognition and to investigate the neurological underpinnings of such judgments. However, before that can happen, agreement is needed as to what constitutes a valid marker of animal metacognition. Specifically, noncognitive factors have to be eliminated from purported demonstrations of metacognition in animals. Another problem when comparing animal with human metacognition is that monkeys have had far less training than human subjects at the start of an experiment. Other experiments that could clarify possible differences in the metacognitive abilities of animals and humans should address firstly, the extent to which a monkey could tolerate intervals between the response on a cognitive task beyond 1 s, the current upper limit and secondly, a monkey's ability to make finer distinctions of its confidence, than 'confident' and 'not confident' when making metacognitive judgments.^d The extent to which an animal can maintain or recall its metacognitive knowledge and make fine distinctions between different levels of confidence should help clarify its relationship to human metacognition.

Acknowledgements

We would like to acknowledge support for preparing this article from a grant from NIMH: R01 MH081153-01A1 and a grant from the DOE, Institute for Education Sciences.

1. Wasserman EA, Zentall TR: *Comparative Cognition: Experimental Explorations of Animal Intelligence* London: Oxford University Press; 2006.
2. Terrace HS: **Animal cognition**. In *Animal Cognition*. Edited by Roitblat HL, Bever TG, Terrace HS. Hillsdale, NJ: Erlbaum; 1984: 7-28.
3. Gardner HE: *The Mind's New Science: A History of Cognitive Revolution* NY: Basic Books; 1987.
4. Nelson TO, Narens L: **Metamemory: a theoretical framework and new findings**. In *The Psychology of Learning and Motivation*, 10:52-67. Edited by Bower GH. New York: Academic Press; 1990:
5. Metcalfe J, Shimamura AP: *Metacognition: Knowing about Knowing* Cambridge, MA: MIT Press; 1994.
6. Metcalfe J, Finn B: **Evidence that judgments of learning are causally related to study choice**. *Psychon Bull Rev* 2008, **15**:174-179.
7. Son LK, Kornell N: **Research on the allocation of study time: key studies from 1890 to the present (and beyond)**. In *A Handbook of Memory and Metamemory*. Edited by Dunlosky J, Bjork RA. Hillsdale, NJ: Psychology Press; 2008:333-351.
8. Nelson TO: **A comparison of current measures of the accuracy of feeling-of knowing predictions**. *Psychol Bull* 1984, **95**:109-133.
9. Loftus EF, Wagenaar WA: **Lawyers' predictions of success**. *Jurimetrics J* 1988, **28**:437-453.
10. Koriat A, Lichtenstein S, Fischhoff B: **Reasons for confidence**. *J Exp Psychol: Hum Learn Cogn* 1980, **6**:107-118.
11. Fischhoff B, Slovic P, Lichtenstein S: **Knowing with certainty: the appropriateness of extreme confidence**. *J Exp Psychol: Hum Percept Perform* 1977, **3**:552-564.
12. Schwartz BL: **Sources of information in metamemory: judgments of learning and feelings of knowing**. *Psychon Bull Rev* 1994, **1**:357-375.
13. Nelson TO, Narens L, Dunlosky J: **A revised methodology for research on metamemory: pre-judgment recall and monitoring (PRAM)**. *Psychol Methods* 2004, **9**:53-69.
14. Son LK, Metcalfe J: **Judgments of learning: evidence for a two-stage model**. *Mem Cognit* 2005, **33**:1116-1129.
15. Son LK, Schwartz BL: **The adaptive control of encoding and retrieval**. In *Applied Metacognition*. Edited by Schwartz BL, Perfect T. Cambridge, UK: Cambridge University Press; 2002.
16. Koriat A: **How do we know that we know? The accessibility model of the feeling of knowing**. *Psychol Rev* 1993, **100**:609-639.
17. Schwartz BL, Metcalfe J: **Cue familiarity but not target retrievability enhances feeling-of-knowing judgments**. *J Exp Psychol: Learn Mem Cogn* 1992, **18**:1074-1083.
18. Smith JD, Schull J, Strote J, McGee K, Egnor R, Erb L: **The uncertain response in the bottlenosed dolphin (*Tursiops truncatus*)**. *J Exp Psychol: Gen* 1995, **124**:391-408.
19. Smith JD, Shields WE, Schull J, Washburn DA: **The uncertain response in humans and animals**. *Cognition* 1997, **62**:75-97.
20. Shields WE, Smith JD, Washburn DA: **Uncertain responses by humans and Rhesus monkeys (*Macaca mulatta*) in a psychophysical same-different task**. *J Exp Psychol: Gen* 1997, **126**:147-164.
21. Smith JD, Shields WE, Allendoerfer KR, Washburn DA: **Memory monitoring by animals and humans**. *J Exp Psychol: Gen* 1998, **127**:227-250.

^d An experiment at the Columbia University Primate Lab [48] has shown that monkeys can reliably discriminate three levels of confidence: high-confidence, medium-confidence, and low-confidence.

22. Inman A, Shettleworth SJ: **Detecting metamemory in nonverbal subjects: a test with pigeons.** *J Exp Psychol: Anim Behav Process* 1999, **25**:389-395.
23. Call J, Carpenter M: **Do apes and children know what they have seen?** *Anim. Cogn* 2001, **3**:207-220.
24. Shields WE, Smith JD, Guttmanova K, Washburn DA: **Confidence judgments by humans and rhesus monkeys.** *J Gen Psychol* 2005, **132**:165-186.
25. Beran MJ, Smith JD, Redford JS, Washburn DA: **Rhesus macaques (*Macaca mulatta*) monitor uncertainty during numerosity judgments.** *J Exp Psychol: Anim Behav Process* 2006, **32**:111-119.
26. Suda-King C: **Do orangutans (*Pongo pygmaeus*) know when they do not remember?** *Anim Cogn* 2008, **11**:21-42.
27. Washburn DA, Smith JD, Shields WE: **Rhesus monkeys (*Macaca mulatta*) immediately generalize the uncertain response.** *J Exp Psychol: Anim Behav Process* 2006, **32**:185-189.
28. Sutton JE, Shettleworth SJ: **Memory without awareness: pigeons do not show metamemory in delayed matching-to-sample.** *J Exp Psychol: Anim Behav Process* 2008, **34**:266-282.
29. Basile BM, Hampton RR, Suomi SJ, Murray EA: **An assessment of memory awareness in tufted capuchin monkeys (*Cebus apella*).** *Anim Cogn* 2009, **12**:169-180.
30. Kepecs A, Uchida N, Zariwala HA, Mainen ZF: **Neural correlates, computation and behavioral impact of decision confidence.** *Nature* 2008, **455**:227-231.
- This article describes a series of elegant experiments that were the first to investigate the neural basis of performance on a metacognitive task. It distinguished the firing of single cells in the frontal-orbital cortex on the basis of their responses to the difficulty of an olfactory discrimination, whether responses were correct or errors and subject's confidence that it could respond correctly on the current trial and thereby earn a reward and avoid a lengthy TO. The latter distinction suffered from the same methodological problem that was made in many behavioral studies of metacognition. In this instance, there is no way to distinguish between two interpretations: firstly, that the behavioral responses in question were based on a subject's metacognitive judgment of low confidence that it could respond correctly on a particular trial or secondly, the maximization of reward.
31. Foote AL, Crystal JD: **Metacognition in the rat.** *Curr Biol* 2007, **17**:551-555.
32. Son LK, Kornell N: **Meta-confidence judgments in rhesus macaques: explicit versus implicit mechanisms.** In *The Missing Link in Cognition: Origins of Self-Reflective Consciousness*. Edited by Terrace HS, Metcalfe J. New York: Oxford University Press; 2005:296-320.
33. Smith JD, Beran MJ, Redford JS, Washburn DA: **Dissociating uncertainty responses and reinforcement signals in the comparative study of uncertainty monitoring.** *J Exp Psychol: Gen* 2006, **135**:282-297.
34. Hampton RR: **Rhesus monkeys know when they remember.** *Proc Natl Acad Sci U S A* 2001, **98**:5359-5362.
- This was the first study of metacognition in animals that was based on the memory of previously presented stimuli, rather than on the perception of stimuli that were present at the time at which a subject responded to a high-risk or low-risk confidence icon. It was also the first experiment based on prospective judgments. A metacognitive task that is based on memory rules out the possibility that the purported metacognitive response was under the control of an external stimulus. If it were, it would be indistinguishable from other discriminative responses for which it is not necessary to postulate a metacognitive judgment.
35. Kornell N, Son LK, Terrace H: **Transfer of metacognitive skills and hint seeking in monkeys.** *Psychol Sci* 2007, **18**:64-71.
- This was the first study of metacognition in animals that was based on the memory of stimuli and the responses made to those stimuli (retrospective judgments). It was also the first experiment to use a transfer test to show that subjects were able to make metacognitive judgments on a task that was qualitatively different from the one on which they were trained. In this instance, the transfer was from a magnitude discrimination task to a short-term memory task. Another novel feature of this study was the use of a hint paradigm in which subjects learned to seek hints on a need-to-know basis. Hints were requested when subjects were making errors during initial training but not when subjects learned the task.
36. Son LK, Kornell N: **Meta-confidence judgments in rhesus macaques: explicit versus implicit mechanisms.** In *The Missing Link in Cognition: Origins of Self-Knowing Consciousness*. Edited by Terrace HS, Metcalfe J. Oxford University Press; 2005.
37. Benjamin AS, Bjork RA, Schwartz BL: **The mismeasure of memory: when retrieval fluency is misleading as a metamnemonic index.** *J Exp Psychol: Gen* 1998, **127**:55-68.
38. Janowsky JS, Shimamura AP, Squire LR: **Memory and metamemory: comparisons between patients with frontal lobe lesions and amnesic patients.** *Psychobiology* 1989, **17**:3-11.
39. Fernandez-Duque D, Baird JA, Posner MI: **Executive attention and metacognitive regulation.** *Conscious Cogn* 2000, **9**:288-307.
40. Gallo DA, Kensinger EA, Schacter DL: **Prefrontal activity and diagnostic monitoring of memory retrieval: fMRI of the criterial recollection task.** *J Cogn Neurosci* 2006, **18**:135-148.
41. Reder LM (Ed): *Implicit Memory and Metacognition*. Mahwah, NJ: L. Erlbaum; 1996.
42. Funnell M, Metcalfe J, Tsapkini K: **In the mind but not in the tongue: feeling of knowing in amnesic patient HW.** In *Implicit Memory and Metacognition*. Edited by Reder LM. Hillsdale, NJ: Erlbaum; 1996:171-194.
43. White B, Frederiksen J: **A theoretical framework and approach for fostering metacognitive development.** *Educ Psychol* 2005, **40**:211-223.
44. Reder LM, Schunn CD: **Metacognition does not imply awareness: strategy choice is governed by implicit learning and memory.** In *Implicit Memory and Metacognition*. Edited by Reder LM. Mahwah, NJ: L. Erlbaum; 1996:45-77.
45. Sussan D, Son LK: **The training of metacognitive monitoring in children.** *Columbia Undergraduate Sci J* 2007, **2**:98-112.
46. Van Zandt T: **ROC curves and confidence judgments in recognition memory.** *J Exp Psychol: Learn Mem Cogn* 2000, **26**:582-600.
47. Metcalfe J: **Novelty monitoring, metacognition, and control in a composite holographic associative recall model: implications for Korsakoff amnesia.** *Psychol Rev* 1993, **100**:3-22.
48. Morgan G, Terrace H: **Further demonstrations of metacognitive skills in rhesus macaques (*Macaca mulatta*).** In *Poster Presented at the 16th Annual Conference on Comparative Cognition; Melbourne Beach, FL*; 2009.