Slow Progress with the Most Widely Used Animal Model: Ten Years of Metacognition Research in Rats, 2009-2019

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Abstract – Until recently, demonstrations of metacognition in primates have been frequent and robust, while in rodents they have been few and equivocal. However, the past few years have seen a change in this trend with the introduction of novel methods to determine whether metacognitive responding is governed by internal or external sources of stimulus control in rats. Such studies suggest that like primates, rats can indeed use internal assessment of memory strengths to guide metacognitive responding. Strong behavioral paradigms suitable for rodents support the development of easily-accessible animal models for the neurobiology of metamemory and translational studies on diseases of memory. They also allow for a more complete comparative study of the evolution of metacognition, as the presence of this ability in rodents would suggest that metacognition evolved ~80 rather than ~25 million years ago.

In a 2009 special issue on metacognition in *Comparative Cognition & Behavior Reviews* (CCBR), leaders in the field reviewed the literature to date on the ability of nonhuman animals to think about thinking (Crystal & Foote, 2009; Hampton, 2009a, 2009b; Jozefowiez, Staddon, & Cerutti, 2009; Smith, Beran, Couchman, Coutinho, & Boomer, 2009). For the most part, everyone agreed: alternative explanations can often explain putative metacognition. For example, after reviewing the last 15 years of research on metacognition in nonhuman animals, Hampton (2009b) concluded that many demonstrations of metacognitive responding could be explained by associative learning or other mechanisms in which the stimulus guiding metacognitive responding is external rather than internal, private, or introspective. There were a few demonstrations of metacognitive responding, however, that were mostly immune to these criticisms, including situations in which the metacognitive choice was made prior to the primary task, the discriminada was mnemonic, and multiple generalization tests were run (e.g., Hampton, 2001; Smith, Redford, Beran, & Washburn, 2006). Since then, and perhaps driven by the call for "sharper paradigms and safer inferences" (Smith, Beran, Couchman, & Coutinho, 2008), evidence for introspective metacognitive behavior in which alternative mechanisms can be ruled out has mounted, with the most robust evidence coming from work with primates (e.g., Basile, Schroeder, Brown, Templer, & Hampton, 2015; Beran, Smith, & Perdue, 2013; Brown, Basile, Templer, & Hampton, 2019; Call, 2010; Smith et al., 2018; Templer, Brown, & Hampton, 2018).

In 2009 we were not sure if rats were capable of internally-guided metacognitive responding. Crystal's group had recently published the first study investigating the possibility of metacognitive responding in rats, which showed that in a perceptual task, rats adaptively declined difficult trials (Foote & Crystal, 2007). Subjects were required to make the metacognitive choice before the psychophysical

discrimination, thereby preventing behavioral cues, such as response latencies or vacillating, and ruling out that response competition alone was guiding behavioral responding (see Hampton, 2009b, for detailed explanations of mechanisms for metacognitive responding). While the results of this initial study were promising and exciting, the new way of examining metacognition after the 2009 CCBR discussion created many new questions that remained unanswered. Firstly, the fact that the task did not involve generalization tests to novel stimuli left open the possibility that subjects could have used external cues in the environment to guide metacognitive responding, such as associating cue delay length with declining the test (Hampton, 2009b). Secondly, at this same time, quantitative models based on response-strength and reinforcement were proposed that mirrored the cognitive behavioral explanations Hampton proposed as external sources of stimulus control. These models (Le Pelley, 2012; Smith et al., 2008) could explain adaptive use of the decline response and the Chosen-Forced performance advantages shown by Crystal's rats without invoking cueing by internal cues (Crystal & Foote, 2009, 2011).

Since that time, a few more attempts were made to determine if rats were indeed capable of metacognitive responding, but few efforts have been made to dissociate potential sources of internal or external stimulus control. Expanding upon the paradigm in which rats classified tone durations as either long or short, rats were sometimes allowed to repeat the stimulus and were sometimes forced to hear it again (Foote & Crystal, 2012). Less than half of the rats were more accurate at making the duration discrimination when they were forced to repeat it than when they chose to repeat it, and rats were not more likely to repeat the stimulus on difficult trials. Moreover, the authors were unable to eliminate the possibility that rats learned to associate intermediate durations with trial-decline responses. Mixed results were collected by other groups that also failed to test rats on generalization tests that could have tested for the possibility of environmental cue associations (Kirk, McMillan, & Roberts, 2014).

More recently, one group did test for generalization of metacognitive responding and found that rats used the decline response when the sample in the delayed-match-position tests was omitted. Importantly, adaptive use of the decline response was only obtained when the test was at the optimal level of difficulty (six-choice task) but not when the task was relatively easy (two-choice task), and the resulting utility of declining trials was low (Yuki & Okanoya, 2017). Indeed, students of metacognition often appropriately titrate difficulty level during training so that subjects experience uncertainty or forgetting; performance on the primary task should be above chance but below ceiling, so that use of the decline response has the opportunity to be advantageous (e.g., Brown, Templer, & Hampton, 2017; Hampton, 2001; Templer, Lee, & Preston, 2017). Nonetheless, evaluating the utility of metacognitive judgments has led to fruitful results, especially in elucidating the neural mechanisms underlying them in humans (Yuki, Nakatani, Nakai, Okanoya, & O.Tachibana, 2019).

While Yuki and Okanoya (2017)'s findings certainly progressed the field of rodent metacognition, results consistent with metacognitive responding were presented with just two rats in one generalization test. Since the extent to which rats demonstrate metacognitive responding remained an open question, we aimed to answer questions about whether potential metacognitive responding is governed by internal or external sources of stimulus control in a large cohort of rats that was given multiple generalization tests (Templer et al., 2017). We developed a new paradigm (Lee, Preston, Wise, & Templer, 2018) for testing metacognition in rats that was adapted after existing paradigms in primates (Hampton, 2001; Templer & Hampton, 2012). Positive results in an olfactory-based delayed matching-to-sample (DMTS) task with nine rats clarified that even when environmental (external) contingencies were inconsistent and could not serve as discriminative cues, rats transferred adaptive use of the decline response. All nine subjects continued to selectively utilize the decline response when memory was weak or nonexistent and refrained from using it when memory was strengthened. This pattern suggested that rats used an internal assessment of memory strength to guide responding in this task.

This most recent study in rats adds a critical piece to the phylogenetic picture of the evolution of metacognition across species (Templer et al., 2017) and provides us with a better understanding that rats are capable of guiding behavior based on cognitive and memory awareness. Humans share a common ancestor with rats that existed approximately 80 million years ago (Gibbs et al., 2004) while the common ancestor between humans and Old World monkeys existed about 25 million years ago (Stevens et al.,

2013). Positive demonstrations of internal cues or memory states guiding metacognitive responding in Old World monkeys are both frequent and robust, and while worth doing and informative, the field of nonhuman metacognition would also benefit greatly if we could answer more questions about the more distant evolution of metacognitive abilities. Using rodents has this advantage given that we are more distantly related. Recent studies in other species such as pigeons (Iwasaki, Watanabe, & Fujita, 2018) have added to this picture and point to the possibility of convergent evolution.

Metamemory, a type of metacognition, is the ability to access and monitor the contents of one's memory, a hallmark of the explicit or declarative memory system. Here, cognitive access of the explicit memory system and memory awareness do not necessitate a state of conscious awareness (e.g., Templer, 2016). Despite the fact that evidence is accumulating that rats have explicit memory systems that function at the same basic level as humans (Crystal & Smith, 2014; Eacott & Easton, 2010; Eichenbaum, 2011; Panoz-Brown et al., 2016, 2018), progress in the field of rat metamemory has been relatively slow. This might be due to the fact that finding a paradigm suitable for rats has been difficult and the sensory modality has varied widely across tasks (auditory: Foote & Crystal, 2007, 2012; visual: Kirk et al., 2014; Yuki & Okanoya, 2017). It is worth noting that the most robust results were obtained from a task that used odor as the discriminada (Templer et al., 2017), so future research endeavors might benefit from such ecologically relevant stimuli and testing procedures (Lee et al., 2018). However, titrating individual performance on the primary memory task such that subjects forget about 30-40% of the time is labor-intensive, especially in a non-automated task. Future studies may, therefore, benefit from using an automated olfactory-based task, such as a match-to-sample procedure in an operant box (e.g., Lu, Slotnick, & Silberberg, 1993).

Using rodents in the comparative study of metacognition has the considerable benefit of creating a better model of cognitive accessibility and memory function and dysfunction in the most commonly used animal model. Such an easily accessible animal model readily lends itself to neurobiological investigation, which is critical to uncovering neurobiological underpinnings of complex cognition and memory awareness that degrade in diseases of memory and old age. Hopefully, the next ten years will bring faster progress in the field of rodent metacognition with focus on examining multiple sources of stimulus control and combining cognitive behavioral manipulations with neurobiological techniques (Templer, 2016; Templer & Hampton, 2013). Future data from rodents would be especially compelling if we focus on dissociating the source of internal cues, such as working memory, ease of processing, familiarity, and heuristic cues, as researchers have recently begun to study and in some cases dissociate in monkeys (Brown et al., 2019; Ferrigno, Kornell, & Cantlon, 2017; Kornell, 2014). Such studies will inform the evolution of metacognition in crucial ways and will provide a necessary model for better understanding the neurobiology of cognitive control and memory awareness.

Acknowledgements

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