The Information-Seeking Paradigm:
Moving Beyond ‘If and When’ to ‘What, Where, and How’

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Abstract – Over the past two decades, researchers have explored the question of whether animals have access to their knowledge states, and further, whether they moderate their behavior in relation to this knowledge. This paper summarizes the research that has been done using the so-called ‘information-seeking paradigm’, pioneered by Call and Carpenter in 2001. The paper describes patterns of findings that have emerged across the primate order, alternative interpretations of these findings, and remaining questions. It closes with suggestions for further investigation in the field, with a focus on exploring the following: What types of information do animals gather? Where do they access information? And, do animals modify their search behavior depending on how informative the source is?

Keywords – Metacognition, Information seeking, Primates, Animals, Knowledge state

[When] do Primates Seek Information?

Nearly two decades ago, Call and Carpenter (2001) pioneered a new hiding and locating task (the ‘information-seeking paradigm’) to explore the question of whether non-human animals were ‘metacognitive’ (aware of their own cognitive states). In the task, a researcher hid a prize (food or sticker) into one of two horizontal, opaque tubes, with the ends of the tubes in front of the participant. Chimpanzees, orangutans, and young human children were given the opportunity to select a tube; if they chose correctly, they were given the prize hidden within. Critically, on some of the trials, participants were allowed to watch as the prize was being hidden. On other trials, the hiding process was blocked from participants’ view. Thus, on half of the trials, participants already knew the location of the prize, and on half they did not. On all trials, however, they were allowed – but not required – to peer into the tubes to visually locate the hidden prize before making a selection.

The hypothesis was that if subjects were aware of their own knowledge states (knowing or not knowing the location of the prize), they should seek information only on the trials in which they had not seen the hiding process. Searching for the prize on trials in which they had watched the hiding process would be redundant, requiring extra effort and self-imposing a delay to the retrieval of the prize. Indeed, the apes and the children in the original study behaved as predicted, gathering information significantly more often on trials in which they were lacking information than on those in which they were informed. In the ensuing years, several researchers have replicated, modified, and extended this approach with a variety of primate species, including bonobos (Call, 2010), capuchin monkeys (Basile, Hampton, Suomi, & Murray, 2009; Paukner, Anderson, & Fujita, 2006; Vining & Marsh, 2015), gorillas (Call, 2010), lion-tailed macaques (Marsh, 2014), and rhesus macaques (Hampton, Zivin, & Murray, 2004; Rosati & Santos, 2016).
Alternative Explanations

This approach had a major advantage over the other dominant metacognitive paradigm at the time: the uncertainty response. Namely, because the information-seeking paradigm capitalized on a naturally occurring behavior (looking for food), extensive training and reinforcement were not required. In one study, rhesus macaques even spontaneously demonstrated the metacognitive-like behavior in a single trial test (Rosati & Santos, 2016). This made alternative explanations based on associative learning mechanisms more problematic, because there was minimal opportunity for subjects to associate cues and response patterns with rewards.

Nonetheless, the results of these studies have been met with competing alternative explanations. One such explanation is that the sight of the prize itself has hedonic value (Perner, as cited in Call, 2012). If this is the case, subjects look for the hidden prize because its sight is intrinsically rewarding, not because subjects are gathering information about its location. In a second explanation, the behavior might represent a generalized foraging strategy, in which animals that do not have food spend their time foraging for it (Call & Carpenter, 2001). Once animals have food (or know where it is located, as on a trial in which they have watched the hiding process), they retrieve it and eat it (see also Perner, 2012). A final alternative explanation involves response competition (Hampton, 2009). In this interpretation, subjects have the choice between two mutually exclusive responses: a primary response (reaching for a prize) and a secondary, purportedly ‘metacognitive’, response (looking for the location of a prize). On trials in which subjects are shown the location of a prize (i.e., visible baiting trials), the primary response is activated, and thus, the animal reaches immediately for the prize without searching for it. On trials in which the location of the prize is unknown (i.e., the hidden baiting trials), there is no predominating drive to reach for a prize, and its absence leaves the possibility for other behaviors – including searching for a prize – to occur. In this interpretation, the choice to search for a hidden prize does not require access to one’s own knowledge state; instead, the searching emerges passively during response periods in which there is no drive to reach for a prize.

A common counter-argument to these accounts is that they explain at a general level why subjects look for the prize on hidden baiting trials, but reach for food on visible baiting trials, but they cannot account for the specific search patterns that are routinely found in these studies. For instance, subjects on occasion terminate their search behavior once they have looked in the empty tube, inferring that it must be in the other one without verifying so visually (Call & Carpenter, 2001). If they were driven only by a hedonic motivation of seeing a prize, or were merely foraging for food, they should continue their search until the food is spotted (Call, 2012). A hedonic explanation also cannot explain why subjects look more often on hidden baiting trials than on visible ones, as noted by Call (2012). If the mere sight of food itself was the sole motivation, one would expect to see much higher rates of so-called ‘redundant’ searching on visible baiting trials, because this would still satisfy the drive to see food. Instead, although subjects do, on occasion, look for the hidden prizes on visible baiting trials, these rates are consistently and dramatically much lower than rates of searching on hidden baiting trials.

The alternative interpretations also cannot account for the finding that rates of information-gathering increase when the risk and/or cost of error is greater (Marsh & MacDonald, 2012a; Mulcahy, 2016), or when the time between the hiding process and the subject’s opportunity to respond is increased (Call, 2010). Moreover, the generalized search response does not explain why subjects still occasionally look for the hidden food on trials in which they have been shown the baiting process (Call, 2012). Finally, although response competition could account for many of the above patterns of behavior, it cannot explain the finding that subjects look for hidden food items more often when higher-quality foods are used, even on trials with visible baiting processes (Call, 2010; Marsh & MacDonald, 2012a). Response competition would predict that a higher quality prize would increase the drive to reach for it, not to induce a delay by visually verifying its location.

Thus, in the decade following Call and Carpenter’s (2001) seminal paper, there has been an accumulation of investigations into ‘if’ and ‘when’ primates seek information about the location of a
hidden food item, with accompanying dialogue surrounding the appropriate interpretation of these results. While the preponderance of data suggest that at least most of the primate species tested thus far behave in a manner consistent with a metacognitive interpretation, questions remain.

Expanding the Boundaries: What Kind, from Where, and how Much?

Broadening the question from whether primates seek information to what types of information? Where is the information acquired from? How informative is the source? offers an opportunity to expand the boundaries of the paradigm, in terms of the cognitive complexity of tasks and the cognitive domains therein. This may help to push the field beyond explanations tied to a specific context and tease apart the phylogenetic gradations in metacognitive ability. In particular, several theorists have advocated for the idea that metacognition is likely not an ‘all-or-nothing’ phenomenon (Beran & Smith, 2011; Marsh, 2014; Morales, 2016; Vining & Marsh, 2015), and viewing it as a dichotomy – something an animal does or does not possess – is probably not a comprehensive account. Indeed, there may be nuances in ability, both between and within species, and it may thus be more productive to examine metacognition in terms of its functional elements and the capacities that they support (Beran & Smith, 2011; Morales, 2016). Below, I outline some promising new directions that have begun to emerge within the information-seeking paradigm framework.

What Type of Information?

As noted, the traditional information of value in the information-seeking paradigm is the spatial location of a hidden food item. More recent investigations have expanded the type of information that is needed to solve the task. For example, in two recent studies, the critical piece of information to be gathered was about a tool’s properties (Bohn, Allritz, & Völter, 2017; Muleahy, 2016). In these studies, apes were required to select a tool out of an array, and that tool could be used to access a food reward. In each case, multiple tools were available to subjects, but only one of the options offered the functionality required to acquire the reward (either due to the length of the tool or its structure). Otherwise, the task was structured similarly to the traditional ‘tubes’ task; on some trials, subjects were shown the properties of the tool before making a choice, and on other trials, they were not shown the properties in advance. In all cases, apes could optionally gather information about the tools’ properties before making a selection. In each of these studies, apes gathered information more often when it was necessary than when they were shown the properties in advance. These studies are critical in refuting some of the alternative explanations, as they expand the capacity for adaptive information-seeking beyond a spatial foraging context.

In Beran, Smith, and Perdue (2013), language-trained apes were tested on their ability to acquire information about a hidden food item’s identity, rather than its location. Specifically, they were required to name a food item in order to retrieve it, rather than looking for its location. On some trials they were given the identity beforehand, and on others, they were not. Once again, the apes successfully sought information more often when it was needed than when it was redundant. Researchers have also tested monkeys’ abilities to gather information about a stimulus’ identity, through repeated or extended stimulus exposure, on computerized tasks. Redford (2010) and Malassiss, Gheusi, and Fagot, (2015) both demonstrated that Old world monkeys requested greater exposure of hidden visual stimuli on difficult discrimination trials, as compared to simpler trials. In Malassis et al. (2015), baboons also responded more quickly and accurately when they had gathered more information about a stimulus’ identity. In Tu, Pani, and Hampton (2015), rhesus macaques dynamically gathered information about the identity of a hidden visual stimulus on-screen by controlling how much of the stimulus was revealed before they had sufficient confidence in their ability to make a correct response. In each of these studies, the information acquired was not directly tied to the location of a food stimulus, thus moving beyond explanations of generalized foraging strategies and hedonic motivation.
From where is the Information Acquired?

Although it was alluded to in the original Call and Carpenter (2001) paper in 2001, researchers have begun to explicitly test primates’ abilities to seek information metacognitively when the information is provided in different modalities. For instance, Call (2010) demonstrated that great apes adapted their information-seeking behavior when provided auditory information about a food item’s location.

Moving beyond perceptual modalities, several studies have investigated whether subjects refrain from seeking information when the location of the hidden prize can be inferred by logical exclusion (Marsh, 2014; Marsh & MacDonald, 2012b; Perdue, Evans, & Beran, 2018; Vining & Marsh, 2015). In these cases, rather than showing subjects were the food is, they are shown where the food is not. ‘Success’ on these types of tasks would argue against explanations related to generalized foraging strategies, response competition, or the hedonic sight of a food reward.

Interestingly, although all of the species tested thus far have shown the ability to infer logically (e.g., Call, 2004, 2006; Marsh, Vining, Levendoski, & Judge, 2015), only the great apes have shown the ability to use this information in order to adaptively control their information gathering behavior (Marsh, 2014; Marsh & MacDonald, 2012b; Perdue et al., 2018; Vining & Marsh, 2015). That is, even though the monkeys tested in these studies had demonstrated the ability to correctly locate a hidden food item using logical exclusion, if they were given the option to look for the hidden food before making a selection, they did so (Marsh, 2014; Vining & Marsh, 2015). Even among the great apes, there has been wide individual variation in the ability to use inference to guide information seeking behavior (Marsh & MacDonald, 2012b; Perdue et al., 2018). Thus, this may be an instance in which there is variation within and between species; is it the case that monkeys know what they have seen, but apes know what they have inferred?

How Informative is the Source?

A third variation involves manipulating the informative value of a source. Can subjects discriminate between and adaptively use information sources, according to their informational value? Thus far, this question has received relatively minimal empirical attention. In the aforementioned study by Malassis et al. (2015), when given the choice between two different informative sources about a stimulus’ identity (a ‘repeat exposure’ button for the more difficult stimulus and one for the simpler stimulus, respectively), they chose the more helpful one, from an informational perspective. Thus, they not only gathered information adaptively, but discriminated based on the value of different information sources and selected the one that provided the information they needed the most.

A similar pattern was found in the ‘revelation’ study by Tu et al. (2015), in which rhesus monkeys gradually revealed ‘blockers’ to expose a picture that they were then required to classify. Specifically, in one experiment, the size of the visual blockers was manipulated, relative to the image they were blocking, such that there was only one critical blocker that provided all of the information necessary to make the discrimination. In that experiment, monkeys continued to search for the information until the critical blocker had been removed, suggesting that they continued to gather information until they had the critical information they needed to solve the task, regardless of how many sources of information they were required to expose.

While this is still a relatively new area of study within studies on primate metacognition, it should be noted that similar concepts have been tested in other non-human species. McMahon, Macpherson, and Roberts (2010) found that dogs selectively sought information from an informative human (who provided information about the location of a hidden prize), rather than a human that provided no information. In addition, Roberts, Marsh, and Strang (2015) tested whether rats showed a preference for informative over non-informative stimuli on a radial arm maze, with equivocal results.

Although it has not yet been widely adopted, testing subjects with multiple information sources simultaneously would allow researchers to manipulate additional variables; information sources might vary in terms of their level of information (providing complete information, partial information, or no
information); the information-gathering process could be simultaneous (consult all sources at once) or sequential (serially consulting sources over time); and the type of information could differ between sources (e.g., one source provides information about identity whereas another provides information about location). Providing multiple simultaneous ‘metacognitive response options’ would provide further evidence against the possibility of ‘response competition’ as a driving force behind this behavior.

**Conclusion**

The information-seeking framework has allowed the field to move beyond associative learning mechanisms and has demonstrated with relatively remarkable consistency the ability of primates to gather information when required, but not when redundant. By broadening the types of questions we investigate around primate information-gathering, varying the type of information gathered, the modality within which it is gathered, and the number and value of information sources, we may further delineate the flexibility with which primates can adaptively monitor and control their knowledge states. Pushing these boundaries will allow the field to move beyond what Call (2012) terms ‘narrow beam’ explanations of this behavior, such as response competition and a generalized foraging strategy. Perhaps more importantly, by elevating the complexity of the tasks, we may capture more elemental abilities (or lack thereof) across the primate order (particularly as the number and range of species tested expands). If metacognition is, indeed, not an all-or-nothing phenomenon, it is incumbent on the field to develop tasks that are dexterous enough to capture the nuance within.

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