

COMPARATIVE COGNITION & BEHAVIOR REVIEWS

Situated Cognition and the Function of Behavior

David J. Pritchard

*School of Biology
University of St Andrews*

In his review of “situated cognition” Cheng reminds us that the properties of cognition can be influenced by much more than what is going on in the brain. In this commentary, I focus on the lessons that this situated approach can teach those of us using behavior as a tool for investigating animal cognition. Rather than just a measure telling us about hidden cognitive processes, the details of behavior can provide important clues about how animals are solving a task. By looking in more detail at the behavior of our animals, and the possible sensory consequences of these behaviors, we can not only learn more about how animals do what they need to do but also explore how situated cognition shapes the structure of behavior.

Keywords: active vision, active sensing, ethology, computational biology, spatial cognition.

Introduction: What's the Point of Situated Cognition?

As someone who has debated the value of embodied and extended cognition with my friends and colleagues, I found Cheng's review of “situated cognition” incredibly helpful. For most biologists and psychologists interested in understanding natural behavior, the usefulness of situated cognition depends on what it adds that current perspectives don't. Does situated cognition get us closer to understanding how animals do what they need to do in nature?

Based on Cheng's overview in his target article, I would say the answer to that question is yes. Situated cognition not only explicitly links animal cognition with ecology and morphology but also raises intriguing evolutionary questions. For example, are there limits to where and when distributed cognition can evolve, similar to those discussed in studies of altruism and eusociality (Gardner & Grafen, 2009)? In this commentary,

however, I focus on what I think situated cognition has to offer those of us who study animal cognition through behavioral experiments. In my opinion, situated cognition does more than just challenge our ideas about what counts as “cognitive”: It tells us that we could benefit from looking much more closely at behavior.

Don't We Already Look at Behavior?

Although traditional approaches to animal cognition have always measured behavior, I would argue that these measurements have been shaped by the assumed relationship between cognition and behavior. Behavior is considered either an opportunity to learn, for example, in exploration or information seeking, or an output of cognition. As a result, most experiments on animal cognition focus on the *end points* of behavior, such as where a bird digs (Kelly, Kamil, & Cheng, 2010) or which arm a rat runs down (M. F. Brown, 1992). These behaviors are thought to reflect “decisions,” and our experiments test the effect

of manipulations on these decisions. In my own research, for example, I have studied where a hummingbird probes for sucrose (Pritchard, Scott, Healy, & Hurly, 2016) and where a hummingbird stops when searching for a removed flower (Pritchard, Hurly, & Healy, 2015). In both cases, I have assumed that a decision to probe or hover is the result of the spatial cognition of the hummingbirds, and by measuring where these events take place, I can understand how that cognition operates.

Situated cognition challenges this assumption and suggests that by focusing on the end points of behavior, we might be missing out on clues to how animals are actually solving these tasks. When choosing between two stimuli, for example, chickens follow repeated paths to the chosen object. Along this path, chickens make an idiosyncratic sequence of head movements, viewing the object with different parts of the eye at different points along their path. When the chickens are forced to take a different path, their ability to discriminate between the objects decreases (Dawkins & Woodington, 2000). By focusing only on the end points of the discrimination task, whether a chicken chooses the “correct” object or not, we would be missing an important part of how these birds were solving this task.

Detailed examinations of behavior are much more common in studies of navigating Hymenoptera. Since the 1970s, studies of navigating bees, wasps, and ants have analyzed not only *where* an insect goes but also how she moves *during* navigation (e.g., T. S. Collett & Land, 1975). As a result, we now know that insects use specialized behaviors, such as learning flights and scanning head movements, to acquire and use visual information to navigate (M. Collett, Chittka, & Collett, 2013; Zeil, 2012). There are signs that a similar, descriptive approach to spatial cognition could be used to study “enactive” cognition in vertebrates. Birds, for example, also show prominent head movements: Pigeons bob their heads (Green,

Davies, & Thorpe, 1994; Troje & Frost, 2000), owls peer side to side (Ohayon, Van Der Willigen, Wagner, Katsman, & Rivlin, 2006; Van Der Willigen, Frost, & Wagner, 2002), and terns scan scenes with different parts of their retina (Land, 1999). You only need to watch birds at a feeder in your garden to see that birds are constantly using behavior to shape what they see. Although insect navigation strategies have been presented as efficient solutions for animals with poor resolution vision and small brains (e.g., Chittka & Skorupski, 2017), I don’t see any reason why similar “enactive” strategies might not be used by birds, despite their larger brains and higher resolution vision. Currently, however, we haven’t looked to see if this is the case. Studies of spatial cognition in birds have focused mostly on the end points of behavior, such as the location of digging or pecking, and much less on how birds reach these locations in the first place. If enactive and extended cognition encourages more people to look more closely at the behavior of their animals, then these approaches are already adding something important to our traditional approaches.

Situated Cognition and Active Sensing

The “active” visual strategies of navigating insects and discriminating chickens highlight the role that “active sensing” could play in situated cognition. Active sensing involves animals using energy to sense their environment, either in terms of behavior (in the case of active vision or whisker movements) or by producing signals (e.g., echolocation or electroreception; Nelson & MacIver, 2006). By definition, active sensing informs an animal’s cognitive state (it is sensing, after all), but many examples of active sensing also show signs of being influenced by an animal’s cognition. Rats will modify their whisker movements in anticipation of objects (Grant, Mitchinson, Fox, & Prescott, 2009), bats adjust the direction and structure of their echolocation calls based on their experience (Moss & Surlykke, 2010), and electric fish actively scan areas where they have previously found food (Jun, Longtin, & Maler, 2016). All of these examples potentially pass the mutual manipulability criterion (MMC) as discussed by Cheng. As in the spiders of Japyassú and Laland (2017), these animals are using behavior not only to sense their environment but also to direct and focus their attention.

The line between active sensing and situated cognition can, however, be quite slippery. Barn owls, for example, use “peering” head movements to assess distances before attacking prey (Ohayon et al., 2006). These

Author Note: David J. Pritchard, Centre for Biological Diversity, University of St Andrews, Greenside Place, St. Andrews, Fife, UK, KY16 9TH.

Correspondence concerning this article should be addressed to David J. Pritchard at djp4@st-andrews.ac.uk.

Acknowledgments: I would like to thank Shoko Sugawara for her useful comments on a previous version of this manuscript, and Marcia Spetch and Lauren Guillette for giving the opportunity to write this commentary.

movements generate motion parallax and so provide owls with information about depth and distances, a form of active sensing. I suspect peering would also pass the MMC, although I don't know if this has been tested directly. Barn owls can, however, also perceive depth using stereo vision and can use stereo vision to recognize distances they previously learned via head movements (Van Der Willigen et al., 2002). This would suggest that, once acquired, depth information is represented independently of how it was perceived, which would seem to support the traditional Cartesian view. Even if peering was found to pass the MMC, it might therefore be difficult to classify peering as truly part of an enactive cognitive system. But does this matter? Under natural conditions, owls automatically make peering movements when inspecting visual scenes and, indeed, had to be actively trained not to make peering movements in Van Der Willigen et al.'s (2002) experiments. Peering seems to have evolved as part of the package of mechanisms that owls use to inspect the world. Rather than drawing a hard line separating behaviors such as peering from "true" examples of situated cognition, it might be more productive to embrace the fact that cognition (like all biology) is a bit messy around the edges. Indeed, it might be in the gray areas between cognition, behavior, perception, and morphology in which we discover the most interesting comparative data.

Cognition and the Organization of Behavior

If an animal's behavior is involved in processing information, then what consequences does this have for the evolution of behavior? Many unusual behaviors in animals function as a way to simplify sensory processing. Head bobbing in birds, for example, reduces visual blur by restricting head movements to rapid thrusts forward (Necker, 2007), whereas flies restrict head rotations to short saccades to better separate translational optic flow (which contains useful depth information) from rotational optic flow (which doesn't; Hateren & Schilstra, 1999). If the need to process other information influences how an animal behaves, then we might expect to see a similar adaptation in the structure of behaviors used in enactive or extended cognition.

How would we identify the influence of cognition on the structure of behavior? In the case of vision, the sensory "consequences" of behavior can be worked out based on the function of the eye (Zeil, Boeddeker, & Hemmi, 2008). For cognition, however, the consequences of behavior are likely to depend on the task

that the animal faces. The "best" behavior for learning about space, for example, might look very different from the "best" behavior for learning about material properties, or for inspecting a conspecific. Instead, perhaps we could start by looking for any patterns in behavior at all. The computational analysis of behavior has recently become a hot topic in neuroscience and has resulted in a suite of computational methods to identify patterns in behavior (Anderson & Perona, 2014; A. E. Brown & de Bivort, 2017; Egnor & Branson, 2016). Although designed for computational neuroscience, these methods could provide a valuable new tool for comparative cognition researchers looking to broaden their measures of behavior. By identifying patterns in how animals behave during, for example, a spatial memory task, these computational methods could highlight candidate behaviors that could then be examined in more detail. In this manner, descriptive analyses of the structure of behavior could complement traditional experiments in comparative cognition and lead to a more integrative study of animal cognition.

Conclusion: Description and Diversity in Animal Cognition

One of my favorite aspects of the animal kingdom is its diversity, what Darwin (1859) referred to as its "endless forms most beautiful" (p. 490). By emphasizing the role that behavior, environment, and morphology can play in cognitive processing, Cheng presents a version of animal cognition that embraces this diversity. Situated cognition does not just evolve through changes in the brain or via tweaks in the accuracy, capacity, or duration of general processes. Situated cognition could evolve and adapt through changes in bodies, or in behavior, or even in social structure. At the beginning of one of the key early texts on embodied cognition, James J. Gibson (1979) wrote, "We are told that vision depends on the eye, which is connected to the brain. I shall suggest that natural vision depends on the eyes in the head on a body supported by the ground" (p. 1). Given the diversity in senses, anatomy, ecology, and behavior seen in the animal kingdom, we might therefore expect that diversity in cognition might be the norm.

A necessary step for those of us wishing to investigate this situated cognition will be to look much closer at *how* animals are behaving, and how this changes during our experiments. This is not a new suggestion. One of the first sections of Tinbergen's (1963) seminal "On Aims and Methods in Ethology" was on the need

for “Observation and Description.” But although Tinbergen’s four questions have been embraced by ecologically minded researchers in comparative cognition (e.g., B. Gibson & Kamil, 2009; Kamil, 1998), his warnings about the need for description and observation seem to have had less impact. The triumph of Tinbergen and the early ethologists was to expand animal behavior beyond the handful of model species studied in psychology laboratories in order to include the diverse range of species and behaviors seen in the wild. Although comparative psychology today is very different to that faced by the early ethologists, Tinbergen’s (1963) warning about the danger of recording only behavior we consider relevant and overlooking “trivial” behavior still rings true: “We might forget that naïve, unsophisticated, or intuitively guided observation may open our eyes to new problems. Contempt for simple observation is a lethal trait in any science” (p. 412).

We are now living in a time in which computational approaches are revolutionizing how we can study behavior, providing tools that can capture, quantify, and analyze behavior like never before. Observation and description can now be carried out automatically and in incredible detail. But technology itself is not necessary for looking closer at behavior. Studies of navigating insects have been using film and video to measure the details of behavior since the 1970s (T. S. Collett & Land, 1975). What is needed is a reason to look closer, and I think that situated cognition could provide one.

References

- Anderson, D. J., & Perona, P. (2014). Toward a science of computational ethology. *Neuron*, *84*, 18–31. doi:10.1016/j.neuron.2014.09.005
- Brown, A. E., & de Bivort, B. (2017). The study of animal behaviour as a physical science. *BioRxiv*, 220855. doi:10.1101/220855
- Brown, M. F. (1992). Does a cognitive map guide choices in the radial-arm maze? *Journal of Experimental Psychology. Animal Behavior Processes*, *18*, 56–66. doi:10.1037/0097-7403.18.1.56
- Chittka, L., & Skorupski, P. (2017). Active vision: A broader comparative perspective is needed. *Constructivist Foundations*, *13*, 128–129.
- Collett, M., Chittka, L., & Collett, T. S. (2013). Spatial memory in insect navigation. *Current Biology*, *23*(17), R789–R800. doi:10.1016/j.cub.2013.07.020
- Collett, T. S., & Land, M. F. (1975). Visual spatial memory in a hoverfly. *Journal of Comparative Physiology A*, *100*, 59–84. doi:10.1007/BF00623930
- Darwin, C. (1859). *On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life*. London, England: J. Murray.
- Dawkins, M. S., & Woodington, A. (2000). Pattern recognition and active vision in chickens. *Nature*, *403*(6770), 652–655. doi:10.1038/35001064
- Egnor, S. E. R., & Branson, K. (2016). Computational analysis of behavior. *Annual Review of Neuroscience*, *39*, 217–236. doi:10.1146/annurev-neuro-070815-013845
- Gardner, A., & Grafen, A. (2009). Capturing the superorganism: a formal theory of group adaptation. *Journal of Evolutionary Biology*, *22*, 659–671. doi:10.1111/j.1420-9101.2008.01681.x
- Gibson, B., & Kamil, A. (2009). The synthetic approach to the study of spatial memory: Have we properly addressed Tinbergen’s ‘four questions’? *Behavioural Processes*, *80*, 278–287. doi:10.1016/j.beproc.2008.11.013
- Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston, MA: Houghton Mifflin.
- Grant, R. A., Mitchinson, B., Fox, C. W., & Prescott, T. J. (2009). Active touch sensing in the rat: Anticipatory and regulatory control of whisker movements during surface exploration. *Journal of Neurophysiology*, *101*, 862–874. doi:10.1152/jn.90783.2008
- Green, P. R., Davies, M. N. O., & Thorpe, P. H. (1994). Head-bobbing and head orientation during landing flights of pigeons. *Journal of Comparative Physiology A*, *174*, 249–256. doi:10.1007/BF00193791

- Hateren, J. H., & Schilstra, C. (1999). Blowfly flight and optic flow. II. Head movements during flight. *Journal of Experimental Biology*, *202*, 1491–1500.
- Japyassú, H. F., & Laland, K. N. (2017). Extended spider cognition. *Animal Cognition*, *20*, 375–395. doi:10.1007/s10071-017-1069-7
- Jun, J. J., Longtin, A., & Maler, L. (2016). Active sensing associated with spatial learning reveals memory-based attention in an electric fish. *Journal of Neurophysiology*, *115*, 2577–2592. doi:10.1152/jn.00979.2015
- Kamil, A. C. (1998). On the proper definition of cognitive ethology. In R. Balda, I. Pepperberg, & A. C. Kamil (Eds.), *Animal cognition in nature. The convergence of psychology and biology in laboratory and field* (pp. 1–28). New York, NY: Academic Press.
- Kelly, D. M., Kamil, A. C., & Cheng, K. (2010). Landmark use by Clark's nutcrackers (*Nucifraga columbiana*): Influence of disorientation and cue rotation on distance and direction estimates. *Animal Cognition*, *13*, 175–188. doi:10.1007/s10071-009-0256-6
- Land, M. F. (1999). The roles of head movements in the search and capture strategy of a tern (Aves, Laridae). *Journal of Comparative Physiology A*, *184*, 265–272.
- Moss, C. F., & Surlykke, A. (2010). Probing the natural scene by echolocation in bats. *Frontiers in Behavioral Neuroscience*, *4*, 33. doi:10.3389/fnbeh.2010.00033
- Necker, R. (2007). Head-bobbing of walking birds. *Journal of Comparative Physiology A*, *193*, 1177–1183. doi:10.1007/s00359-007-0281-3
- Nelson, M. E., & MacIver, M. A. (2006). Sensory acquisition in active sensing systems. *Journal of Comparative Physiology A*, *192*, 573–586. doi:10.1007/s00359-006-0099-4
- Ohayon, S., Van Der Willigen, R. F., Wagner, H., Katsman, I., & Rivlin, E. (2006). On the barn owl's visual pre-attack behavior: I. Structure of head movements and motion patterns. *Journal of Comparative Physiology A*, *192*, 927–940. doi:10.1007/s00359-006-0130-9
- Pritchard, D. J., Hurly, T. A., & Healy, S. D. (2015). Effects of landmark distance and stability on accuracy of reward relocation. *Animal Cognition*, *18*, 1285–1297. doi:10.1007/s10071-015-0896-7
- Pritchard, D. J., Scott, R. D., Healy, S. D., & Hurly, A. T. (2016). Wild rufous hummingbirds use local landmarks to return to rewarded locations. *Behavioural Processes*, *122*, 59–66. doi:10.1016/j.beproc.2015.11.004
- Tinbergen, N. (1963). On aims and methods of ethology. *Ethology*, *20*, 410–433. doi:10.1111/j.1439-0310.1963.tb01161.x
- Troje, N. F., & Frost, B. J. (2000). Head-bobbing in pigeons: How stable is the hold phase? *The Journal of Experimental Biology*, *203*(Pt. 5), 935–940.
- Van Der Willigen, R. F., Frost, B. J., & Wagner, H. (2002). Depth generalization from stereo to motion parallax in the owl. *Journal of Comparative Physiology A*, *187*, 997–1007. doi:10.1007/s00359-001-0271-9
- Zeil, J. (2012). Visual homing: An insect perspective. *Current Opinion in Neurobiology*, *22*, 285–293. doi:10.1016/j.conb.2011.12.008
- Zeil, J., Boeddeker, N., & Hemmi, J. M. (2008). Vision and the organization of behaviour. *Current Biology*, *18*(8), 320–323. doi:10.1016/j.cub.2008.02.017