What Makes Neurophysiology Meaningful? Semantic Content Ascriptions in Insect Navigation Research

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Abstract

In the course of investigating the living world, biologists regularly attribute semantic content to the phenomena they study. In this paper, I examine the case of a contemporary research program studying the navigation behaviors of ants and develop an account of the norms governing researchers' ascriptions of semantic content in their research practices. The account holds that researchers assign semantic content to behaviors that reliably achieve a difficult goal-directed function, and it also suggests a productive role for attributions of semantic content in the process of animal behavior research.

1. Introduction

In the course of investigating the living world, biologists regularly attribute semantic meaning to the phenomena they study, though it remains unclear how to make sense of this practice (Allen and Hauser 1991; Sarkar 1996; Burghardt 2007; Griffiths and Stotz 2013; Sterner 2014; Bechtel 2016). Geneticists have claimed DNA carries content about how to build organisms, physiologists say sense organs provide animals with content about their environment, and animal behavior researchers describe communicative actions as conveying content to others. Given the practice's longstanding role in successful areas of biological research, a charitable assumption is that attributing meaning to living systems somehow helps biologists realize their epistemic goals because the practice is based on objective features of the phenomena under investigation. However, when philosophers set out to examine whatever notion of semantic content this involves, they rarely find a straightforward state of affairs.

Traditionally, philosophers have sought to make sense of the usage of semantic content in biology by determining whether biologists' invocations of content are justified. A popular approach to justifying the notion of content is to produce a comprehensive, metaphysical account of content that grounds content in objective natural properties. This ontology-centered approach to making sense of semantic content often abstracts away from scientific practice in favor of reconstructed scientific explanations. Instead of analyzing the way biologists identify content in practice and the research activities caused by their identifications of content, ontology-focused philosophers look to the theoretical knowledge encapsulated in scientific explanations to guide and constrain their metaphysical accounts of content.

As a result, a gap has emerged between the metaphysical accounts of content that ontology-focused philosophers produce to make sense of content *in principle* and the way

biologists utilize the notion of content *in practice*. This gap is especially apparent in the neurobehavioral sciences. Ontological, teleosemantic theorists like Millikan (1990) and Neander (2017) maintain that content supervenes on properties constituting etiological selected effects functions, in part because such etiological functions allow a crucial distinction between representing and *mis*representing in a way that alternative theories of function, such as cybernetic goal-directed function, do not. However, as multiple philosophers have noted (Bigelow & Pargetter 1987; Kitcher 1993; Godfrey-Smith 1993, 200; Amundson and Lauder 1994; Walsh 1996, 558; Boorse 2002, 73; Wouters 2003, 656), physiologists investigating how mechanisms within organisms causally contribute to interesting capacities seem to ascribe functions to traits without any detailed knowledge of those traits' etiologies. Much work in the neurobehavioral sciences falls into this gap since some notion of biological function seems to figure prominently into neurobehavioral researchers' ascriptions of content, yet researchers' do not seem to justify their ascriptions of content in the ways that etiological, ontology-focused accounts of content suggest.[1]

If neurobehavioral researchers investigating the physiological basis of behavior do not ascribe content according to the criteria articulated by philosophers' ontological accounts, then what criteria do they follow? And are these practical criteria justified by the role ascriptions of content play in helping neurobehavioral researchers achieve their epistemic aims?

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[1] Within the functions debate, some philosophers have argued the stronger claim that biological usage warrants a totally ahistorical theory of function, not just a non-etiological theory of function (Amundson and Lauder 1994; Walsh 1996, 558; Boorse 2002, 73). However, Garson (2019) has recently argued that there are no ahistorical theories of biological function on the grounds that purportedly ahistorical theories actually retain a historical dimension. Garson's point that theories of function can reference history in nonobvious ways is well taken, and this paper addresses the question of how history figures into researchers' ascriptions of content in section 4.

This paper answers those questions within the context of neuroethological research into animal navigation by examining a new case study where researchers assign semantic content to the neurophysiological processes enabling ant navigation. In the late 1960s, Rüdiger Wehner began a research program focused on the navigation behaviors of desert ants in the genus *Cataglyphis*. Wehner's research program continues into the 21st century, and its success has transformed *Cataglyphis* into a model organism for animal navigation studies.

By analyzing the experiments that Wehner and colleagues use to test their hypothetical ascriptions of content, I produce an account that clarifies the evidential norms governing their ascriptions of content. The account holds that researchers assign semantic content to neurophysiological mechanisms that 1) possess a goal-directed function and 2) reliably achieve this function despite the difficulty of the goal. The result is not a full-blown, comprehensive theory of content. Researchers' practices and pronouncements do not specify solutions to all the metaphysical problems that have traditionally interested philosophers (e.g. the content localization and content determinacy problems). Rather, the result of my analysis is a local account of content attribution that has the virtue of clarifying how researchers' ascriptions of content figure into the diachronic progression of their research program to help them achieve their epistemic aims. Thus, this paper demonstrates how attributions of content can aid researchers in achieving their epistemic goals even when researchers' standards for ascribing content remain indeterminate in relation to a full theory of content.

Before situating this practice-based approach within the literature and showing how the results of this approach are of philosophical interest to existing projects, I need to explain a terminological point. I have chosen to use "semantic content" or "content" throughout this paper, terms from the biological information literature, because the researchers I analyze often frame

their attributions of meaning in terms of information processing and storage. However, "semantic content" is sometimes thought to imply theoretical claims about levels of intentionality or the symbol-mediated nature of semantic processes. In referring to researchers' attributions of meaning as attributions of semantic content, I am not picking out a theoretical subtype of meaning attribution nor assuming that all of researchers' attributions of meaning presuppose claims about intentionality or symbols. The phenomenon of interest is researchers' practice of identifying some minimal notion of content within biological phenomena.

2. The Value of Clarifying How Successful Researchers Identify Content in Practice

This paper is primarily concerned with illuminating the epistemological value of content ascriptions in animal navigation research. Historically, behavioral scientists have doubted whether ascribing content carrying states to animals has any epistemic value (Watson 1913; Skinner 1977). Currently, even researchers skeptical of content ascriptions accept the minimal claim that content ascriptions have the potential to aid behavioral research under some circumstances (Wynne 2004). However, the problem of when and how ascriptions of content are useful to researchers remains an open question (Gould and Gould 1982; Dennett 1988; Allen and Hauser 1991; Newen and Bartels 2007; Cameron 2013). This paper advances the discussion by articulating how exactly ascriptions of content actually aid neuroethologists' efforts to provide causal physiological understandings of animal navigation.

When investigating the role of content ascriptions in behavioral research, one must distinguish between the role such ascriptions play in explanation versus in producing evidence since it is not obvious that scientists' content ascriptions play the same role in both contexts. Ontological accounts of content are usually built to capture the theoretical role of content

ascription in explanation. For example, in building an ontological account of content, Shea (2018; p. 230) sets himself the task of showing "why representational properties underpin better explanations of behaviour than would otherwise be available." In contrast, this paper sets itself the task of clarifying whether and how neuroethologists' ascriptions of content figure into the process of successful navigation research.

Bechtel (2016) engaged in a project similar to the one pursued here when he analyzed ascriptions of content within a neurobehavioral research program investigating mammalian navigation. After analyzing how the notion of neural representation figures into the progression of that research program, Bechtel argues that researchers are committed to the ontological reality of semantic content. Furthermore, Bechtel (2016, p. 1291) makes the epistemological argument that ascriptions of content are a necessary component of the research process because they allow researchers to formulate hypotheses that guide research. In particular, Bechtel argues that ascriptions of content help researchers employ the mechanistic research strategies of localization and decomposition described by Bechtel and Richardson (1992/2010).

This paper builds on the results of Bechtel (2016) with a novel case study that provides a more detailed analysis of the experimental practices and habits of reasoning that researchers use to justify their ascriptions of content, illuminating how exactly ascriptions of content figure into the mechanistic research strategies of localization and decomposition. Briefly put, there is a reciprocal relationship between researcher's specifications of content-carrying vehicles and the content carried by those vehicles. Experiments that produce evidence about the nature of content-carrying vehicles help researchers formulate tractable hypotheses about the nature of the content carried by those vehicles, and vice versa.

Finally, although this paper is primarily concerned with illuminating the epistemological value of content ascriptions, the account of content ascription provided here also has value for a bottom-up style of ontological theorizing about semantic content and cognition.

Bergstrom and Rosvall (2011a; 2011b) modeled this approach when they built a transmission account of biological information that does not reference semantic content. The account draws on scientific practice, and Bergstrom and Rosvall argue that it justifies biologists' ascriptions of information independently of semantic justifications. In response to critiques that their account does not address the semantic dimension of information that has traditionally interested philosophers (Shea 2011; Maclaurin 2011), Bergstrom and Rosvall (2011b) make the crucial point that the objective criteria they provide for diagnosing biological information have implications for the semantic dimension of information even though they do not directly reference the semantic dimension of information.

This approach to ontological theorizing is in keeping with more recent calls from philosophers to engage with the concepts of content and cognition at a level of analysis that is relevant to the concerns of practicing biologists. For instance, Sterner (2014) developed Bergstrom and Rosvall's approach into a broader methodology for naturalizing semantic content. Just as biologists do not require a complete, naturalized account of semantic content to productively investigate biological phenomena as being potentially semantic, Sterner (2014) argues that philosophers do not need to produce a complete account of biological information for the account to be philosophically interesting. Instead, philosophers can begin with a provisional set of criteria for identifying cases of biological information. Those cases then provide a neutral starting point for developing and distinguishing different naturalized views of content in a comparative manner. Allen (2017, p. 4240) outlines a similar approach to defining cognition,

arguing for a "relaxed pluralism" that is motivated by "a commitment to letting the productivity of research programs in cognitive science guide the extension of [cognitive] language to new contexts." Contrast these approaches with that of Thompson and Piccinini (2018), who assume an account of content and then argue that the existence of neural representations is an empirical fact by demonstrating how the work of neurobehavioral researchers satisfies the criteria of that account.

Rather than assuming that philosophers are in a position to build comprehensive ontological accounts of content or cognition, bottom-up approaches begin with provisional notions of content or cognition that are informed by ongoing empirical research. The account of content ascription offered here figures into this bottom-up style of ontological theorizing by providing a provisional set of criteria that philosophers can use to identify semantic content in animal navigation research. Although I do not discuss the relationship in this paper, the criteria I enumerate in section 5 have clear affinities with Bergstrom and Rosvall's appeal to Shannon information, and I similarly draw on the idea that information theory provides a means of diagnosing phenomena in need of an explanation.

3. Navigation Behavior in the Desert Ant *Cataglyphis*

Neuroethologist Rüdiger Wehner and his colleagues have consistently made hypothetical ascriptions of content and then performed behavioral experiments that produced decisive evidence supporting those ascriptions. The research program has employed a variety of experimental strategies to this end. In this section, I elucidate the aims and practices characterizing a particularly prevalent experimental strategy. Then, I outline a series of experiments conducted according to that strategy that caused Wehner and colleagues to endorse

a novel attribution of semantic content. All this provides a backdrop that allows the role of semantic content ascriptions to be examined in the context of a particular community of researchers successfully pursuing common research goals via a common research strategy.

In the deserts of Northern Africa and Israel, ants of the genus *Cataglyphis* forage for food during the hottest part of the day. Often, their prey takes the form of other insects who have succumbed to heat death. Relative to their size, the foraging ants can travel vast distances from their subterranean nest in search of food, and because the ants are solitary foragers, they do not use the pheromone trails of nest mates to navigate as many other species of ant do (Wehner and Srinivasan 1981, 316; Ronacher 2008; Steck et al. 2009; Wehner and Rössler 2013). Despite their circuitous searches for food, *Cataglyphis* foragers consistently return home from foraging runs via the most direct route.

All these traits attracted the attention of Rüdiger Wehner in the late 1960s. In the roughly five decades since, Wehner has spent his career building a research program around *Cataglyphis'* sensory capacities, neurophysiology, and navigation behaviors. That research program has transformed *Cataglyphis* from a largely unknown genus of ant to a model organism in navigation studies. (For *Cataglyphis* as model organism, see Lenoir et al. 2009; Steck et al. 2009; Wehner and Rössler 2013, 514; For a review of *Cataglyphis* navigation research prior to Wehner's career, see Wehner 2016). From both a sociological and traditional epistemic view of science, Wehner's research program has been a success: the research is highly regarded by the scientific community and has furthered scientists' understanding of how insects' neurosensory physiology enables them to navigate their environments.

Throughout the history of this program, researchers have utilized a behavioral research strategy to determine whether hypothesized ascriptions of content are justified. Though details of

the research strategy vary according to its particular application, there are general defining features. Fundamentally, the strategy exploits the fact that *Cataglyphis* are central place foragers and enables researchers to use *Cataglyphis*' navigation behavior to make inferences about neurophysiological phenomena they cannot directly observe *in situ*. Researchers begin by training the animal to navigate to particular location, often using food. Having reached the trained location, the animal then attempts to return to the nest. Together, the outbound and inbound run present researchers with the opportunity to observe navigation behavior whose outcomes can be safely assumed. Researchers are then able to manipulate features of the animal's body or environment bearing on the animal's sensory capacities to make inferences about how those sensory capacities causally contribute to navigation behavior. Those inferences sometimes lead researchers to assign semantic content to states or processes within the animal.

For instance, Wehner and colleagues have used the above research strategy to investigate path integration in *Cataglyphis*, and those investigations have led researchers to assign semantic content to *Cataglyphis* neurophysiological processes. Path integration, or dead-reckoning, is a navigational strategy that allows navigators to determine their location relative to a point of origin. To perform path integration, a navigator must record the distance and direction of each segment of their outgoing journey relative to a point of origin. Formally, modelers represent the outgoing journey as a series of vectors where the paired values of each vector represent the distance and direction of each segment of the outgoing journey. Recording distance and direction of travel are prerequisites for path integration, which is performed when a navigator integrates all the vectors representing their outgoing journey into a single vector. That single vector then represents the most direct route back to the point of origin (in the case of *Cataglyphis* navigators and other central place foragers, the point of origin is the nest). By constantly recording distance

and direction of travel and then constantly integrating those values, a navigator maintains

constant access to how far away and in what direction their point of origin is.

Early on, Wehner hypothesized that *Cataglyphis* foragers used path integration to reliably

return home via the most direct route after their circuitous searches for food (Wehner 2013, 5).

For an early example of the research program's use of content-laden terms to describe path

integration in *Cataglyphis*, consider this quote featuring both informatic and intentional terms

from Wehner and Srinivasan (1981, 316):

"In relying on such a dead-reckoning system it [the foraging ant] must keep track of all of

its motions during foraging, and using this information it must continually compute the mean

vector pointing from its actual position towards home […] No vector integration system would

allow the ant to be absolutely sure about the position of the nest."

For a more recent example, consider Wehner and Rössler (2013):

"A desert ant (*Cataglyphis fortis*) is endowed with a 0.1-mg brain and has an outdoor life

expectancy of approximately 6 days. Nevertheless, it is able to acquire, store, retrieve, handle,

and use amazing amounts of spatial information."

The above quotes provide vague specifications of where content vehicles are located and

what the contents of those vehicles are. In the first quote, researchers speak of content that is

about "motions during foraging" and content that is about "the position of the nest", while the

second quote speaks generally of "spatial information." Regarding the location of content, the

second quote implies that the content is generally localized to processes within the ant's nervous

system. For philosophers interested in building a comprehensive theory of content, these

ascriptions may seem too vague to be of import. However, as researchers investigate the

neurophysiological processes that produce *Cataglyphis'* impressive navigation behavior, their ascriptions of content become more specific.

For example, in 2006 and 2007, Wehner, his colleague Harald Wolf, and their joint doctoral student Matthias Wittlinger performed a series of experiments to test the more specific hypothesis that *Cataglyphis* foragers record *information about* distance traveled via some kind of step-counting mechanism (Wittlinger et al. 2006, 2007). The idea that ants could use walking behavior as a proxy for distance travelled stems from the idea that ants walk in such a consistent way that some regular unit of walking, like a step, corresponds to some regular unit of distance. Thus, if the ants recorded how many steps they took on each segment of an outgoing journey, they could record the distance they had walked on each segment of their outgoing journey, which is exactly the input successful path integration requires.

In the experiment, Wittlinger et. al (2006) began by training ants to walk on a linear metal channel from their nest to a feeder. Once ants were trained to forage at a specific feeder site using the route provided by the metal channel, researchers captured foraging ants at the feeder site, manipulated the length of the ants' legs, and released the ants into a second metal channel running parallel to the original channel each ant had traversed on her outbound journey. The difference between the two channels was that the first channel led from the ants' nest to the feeder site while the second parallel channel began near the feeder site but continued on past the ants' nest. To manipulate the length of ants' legs, researchers either shortened them by snipping the legs down to stumps or elongated them by supergluing stilts made of pig bristles to the end of each leg. Once the trained ants had reached the feeder site and were ready to return to their nest with food, researchers captured the ants, manipulated their legs, released them into the second channel, and observed the nest-bound navigation behavior of the manipulated ants.

Researchers manipulated the length of the ants' legs to manipulate the distance ants cover per step. The longer an ants' legs, the more distance that ant travels per step; the shorter the legs, the less distance an ant covers. If the ants indeed relied upon a correspondence between some unit of locomotion and some unit of distance traveled, researchers' manipulations would have broken that correspondence, causing ants with stumps to cover less distance on their incoming journey than they had on their outgoing journey and causing ants with stilts to cover more distance on their incoming journey than they had on their outgoing journey. If the hypothesis that step-counting mechanism produces semantic content about distance travelled were true, then ants with stilts should systematically overshoot the nest on their return journey while ants with stumps should systematically undershoot the nest on their return journey.

Researchers could not directly observe when an ant's path integrator indicated that the ant has navigated back to her nest. Instead, researchers used the ants' looping search pattern behavior as a means of inferring when the ant's path integrator indicated that the ant had reached her nest (Wehner and Srinivasan 1981; Wittlinger et al. 2007). By observing where ants began looping search behavior and scrutinizing the distances covered in that looping search, researchers made inferences about where ants "expected" their nest to be.

Upon performing the stilts and stumps experiment, researchers found that ants with stilts did systematically overshoot the location of the nest while ants with stumps systematically undershot the location of the nest. Furthermore, researchers repeated the experiment but allowed the ants to go on both outgoing and incoming journeys with manipulated legs so that the ants left their nest for the feeder walking on stilts or stumps, were relocated by researchers to the parallel channel, and then attempted to navigate home to their nest. In this variation of the experiment, the ants successfully navigated to the location their nest should have been. That result further

supported researcher's hypothesis because it indicated that the ants could successfully perform

path integration with legs of different lengths so long as the distance covered by each step was

consistent from the outgoing journey to the incoming journey. Based on those series of stilts and

stumps experiments, researchers concluded that the ants received semantic content *about units of

locomotion characterizing a journey* from *some kind of step-counter*. In Wittlinger et al.'s (2006,

1967) words, "Future studies will have to address the mechanism of the proposed step integrator,

for example, whether it actually registers steps by means of proprioceptors, or whether it

integrates activity of a walking pattern generator, and to what extent sensory feedback regarding

stride length and walking performance is considered."

  In the next section, I examine the practices and habits of reasoning that allow

experiments like the stilts and stumps experiment to generate evidence supporting novel,

increasingly specific ascriptions of content. As it turns out, biological functions play a central

role in those habits of reasoning. Then, in section 5, I introduce two more conceptual distinctions

that bear on researchers' ascriptions of content: the *difficulty* and *reliability* of a function. The

major argument is that researchers attribute content to processes that reliably accomplish difficult

goal-directed functions.

4. The Stilts and Stumps Experiment Justifies a Goal-Directed Notion of Function

  A central tenet of teleosemantic theories is that representational properties supervene on

functional properties. The stilts and stumps experiment shows how the epistemological

endeavors of navigation researchers comport with that ontological claim. To determine whether a

neurophysiological process is content-bearing, Wittlinger et al. investigate the functional

properties of neurophysiological processes via behavioral experiments. In this section, I argue

that those experiments are governed by evidential norms that are best captured by a goal-directed notion of function rather than the etiological, selected-effects notion of function traditionally championed by teleosemantic theorists.

To see the deep connection between function and content in the *Cataglyphis* research program generally and the stilts and stumps experiment in particular, consider where the stilts and stumps experiment fits into the dialectic between hypotheses and experiments driving that research program. In the beginning, researchers observe that ants possess the behavioral capacity to reliably return home via the most direct route. That observation causes them to infer that the ants possess internal mechanisms that are causally responsible for realizing that capacity. Next, the content-ascribing hypothesis that ants perform path integration is formulated in functional terms: ants are able to navigate home via the most direct route by *integrating content about* distance and direction of travel. The path integration hypothesis specifies content but not content vehicles; it remains an open question what neurophysiological processes serve as vehicles for content about distance and direction of travel. The stilts and stumps experiment is designed to address part of that question by determining whether the vehicles that carry content about distance traveled are located in a step-counting mechanism. To support the step-counter hypothesis, researchers need to demonstrate that some neurophysiological process records content about some locomotion parameter corresponding to distance travelled. By examining the things researchers do to determine whether or not the physiological process in question actually exists and possesses the function of recording content, it will become clear that researchers justify their ascriptions of content according to a goal-directed notion of function.

Before demonstrating how the stilts and stumps experiment produces evidence for a goal-directed notion of function, it is worth re-examining the nature of goal-directed functions. A

common trait shared by accounts of goal-directed function is that they use modal language to define directedness (Braithwaite 1953; Sommerhoff 1969; Boorse 1976). Generally, such accounts hold that a system exhibits goal-directed function if the system's behavior is flexible or plastic enough to realize the goal within a stipulated set of circumstances. To determine whether a dynamic system has a function on such an account, one needs to know about the outcomes of modal variations of the system's behavior. When the modal variations of behavior all realize their goal within the possible worlds stipulated by the account, then one can rightfully assign goal-directed function to that behavior.

The fundamental point of correspondence between the stilts and stumps research strategy and goal-directed accounts of function is the shared emphasis on assessing behavioral outcomes according to a predefined goal and comparing behavioral outcomes of the same type. Goal-directed accounts ground function in a trait's ability to achieve a privileged outcome across a range of heterogeneous circumstances. Similarly, the stilts and stumps experiment supports the hypothesis that a trait possesses a content-carrying function by comparing the outcomes of that trait across a range of heterogeneous circumstances to a privileged outcome.

4.1 Developing A Notion of Goal-Directed Function that Captures the Notion of Function Justified by the Stilts and Stumps Experiment

To develop a goal-directed notion of function that captures the notion of function supported by the stilts and stumps experiment, I modify Boorse's (1976) modal account of goal-directed function. I use this account as a starting point because it provides such a minimal, unadorned articulation of goal-directed dynamics. Boorse (1976, 78) puts forward his definition in a single sentence: "To say that an action or process A is directed to the goal G is to say not

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only that *A* is what is required for *G*, but also that within some range of environmental variation, *A* would have been modified in whatever way was required for *G*." To convert Boorse's account of function into something that captures the epistemic activities of Wittlinger et al., the account needs to be modified.

First, to determine whether some system possesses some function, Boorse's account requires one to know the outcomes of modal variations of that system's behavior. Lacking empirical access to alternate possible worlds, biologists cannot compare modal variations of the same behavioral instance. However, in the stilts and stumps experiment, Wittlinger et al. approximate that activity. First, Wittlinger et al. acquired a homogenous group of animals. That meant finding and training a group of ants that had matured to the developmental stage at which ants leave the nest to forage outdoors. By training those ants in an identical manner, researchers condition the ants to perform behaviors of the same type under controlled circumstances. That arrangement allows researchers to observe the outcomes of the same behavioral type under a variety of controlled circumstances. Instead of observing modal variants of the same behavior, researchers approximate that activity by observing various instantiations of the same behavioral type.

Second, Boorse's (1976, 78) account of function holds that for a behavior to have a function, the behavior must be both "required for" the realization of the goal and plastic in the sense that the behavior would have been modified "in whatever way was required" to achieve its goal, within some range of environmental variation. Both of these strong requirements need to be weakened. Wehner's *Cataglyphis* program recognizes that foragers possess redundant means of achieving the same navigational goals (Wehner 2020, Chapter 7), and they ascribe content-bearing functions to traits that are sufficient but not necessary for achieving such goals.

Concerning the latter half of Boorse's account, even within a given set circumstances, the requirement that animals always modify behavior to successfully achieve a privileged goal outcome is too strong. It is difficult to account for the wide range of variables that potentially affect an animal's behavior, even in meticulously controlled settings. Discrepancies in behavior may come down to apparently similar animals having different developmental life histories, animals receiving different treatment from researchers, or other experimental contingencies. Whatever the cause of behavioral discrepancy, researchers generally accept the results of non-unanimous experiments. That is, it does not need to be the case that every animal modifies their behavior in whatever way was necessary to achieve some goal for researchers to assign goal-directed function to that behavior type. Given the complexities of using animals as objects of research, scientists tolerate non-unanimous data.

Third, Boorse (1976, 78 emphasis added) writes that "[…] within some range of *environmental variation*, *A* would have been modified in whatever way was required for *G*." However, in the stilts and stumps experiment, Wittlinger et al. varied both the environment foragers navigated and the physiology of the foragers themselves. Instead of testing directedness solely by observing behavioral outcomes in different environments, Wittlinger et al. also test directedness by observing the behavioral outcomes of altered animals. Instead of speaking of *environmental* variations, it would be more appropriate to speak of *circumstantial* variations.

The final and most substantial modification has to do with specifying goals, a crucial aspect of the goal-directed notion of function. Within an epistemic context, evidence supporting an ascription of goal-directed function is produced by comparing outcomes to a pre-defined, privileged goal outcome. Without specifying that outcome, evidence for goal-directed function cannot be produced. However, Boorse's (1976) account doesn't tightly specify what counts as a

goal. To adapt Boorse's account to the epistemic activities of Wehner's *Cataglyphis* research program, one must recognize that in practice, researchers specify goals according to some etiological selected effects notion of function.

Evidence for this comes from the way scientists involved in Wehner's *Cataglyphis* research program talk. Describing his methodology, Wehner (2013, 8) has written that "[I]t is only by considering a given navigational tool in the wider context of the animal's behavioral ecology that the proper questions can be asked—the ones that *Cataglyphis* itself, rather than the human investigator, had to answer during its evolutionary history" (See also Wehner 1987, 511). Furthermore, researchers introduce their research reports on path integration in ways that imply that path integration is a long-established species-level capacity that has provided ants with adaptive benefits relative to their environment (Wehner and Srinivasan 1981; Ronacher 2008; Wehner and Rössler 2013).

To be clear, I am not arguing that Wehner's research program investigates the adaptive significance of past instances of traits to specify privileged goal outcomes for their experiments. To specify what outcomes count as the hypothesized goal of some behavioral or neurophysiological trait, Wehner's research program makes *assumptions* concerning the adaptive significance of past instances of that trait. My appeal to selected-effects function here is analogous to the way Kitcher (2016) appeals to selected-effects function to modify Cummins' causal role function. Kitcher argues that the explanatory role of function ascriptions in physiology can be captured by restricting Cummins functions so that instead of a part's function being its contribution to some capacity of interest to an observer, a part's function is its contribution to some capacity that has been shaped by unspecified evolutionary selection processes. Kitcher and I develop hybrid notions of function for different purposes, but we agree

that evolutionary considerations play a background role in specifying the privileged outcomes investigated by physiologists.[2]

4.2 Why the Notion of Goal-Directed Function Developed Above Best Captures the Notion of Function Justified by the Stilts and Stumps Experiment

Having proposed a modified account of goal-directed function, I now turn to demonstrating how this account captures the evidential norms governing ascriptions of content in the stilts and stumps experiment. Researchers begin with a hypothetical ascription of a content-bearing function: ants possess a step-counter whose function is to record content about a locomotion related parameter that maintains a reliable correspondence with distance traveled. The connection between the way researchers justify such hypothetical ascriptions of a content-bearing function and goal-directed function has to do with the act of comparing behavioral outcomes. On goal-directed accounts, to determine whether a system possesses a function, one must know the outcomes of that system's behavior across a variety of possible worlds; In the stilts and stumps experiment, to determine whether ants possess a content-bearing function, researchers must observe the outcomes of ants' navigation behavior across a variety of experimentally controlled circumstances.

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[2] Neander (2016) concedes that Kitcher's hybrid account of function has the potential to ground the crucial function/malfunction distinction in objective phenomena, but she critiques Kitcher's account for leaving important questions unanswered. Namely, how are adaptive capacities assigned to trait types? Within what environmental contexts must a trait type be adaptive? And how are those trait types individuated? A major point of this paper is that researchers do not require comprehensive answers to such questions for their ascriptions of content-bearing functions to play a productive role in the development of a successful research program. Still, as the next section demonstrates, the evidential norms governing researcher's ascriptions of content-bearing functions suggest partial answers to such questions.

In both cases, the act of comparing behavioral outcomes to privileged goal outcomes plays a central justificatory role. Consider a traditional example of goal-directed function: the heat-seeking missile. On a goal-directed account, the missile possesses the function of homing toward high temperatures by virtue of the fact that across a range of circumstances, the missile would alter its course to home toward high temperatures. In this example, counterfactual outcomes (what the missile in question would do) are compared to a privileged goal outcome (what a heat-seeking missile does) to determine whether the missile possesses heat-seeking function. If the two sorts of outcomes are sufficiently similar, the missile in question possesses the function. The stilts and stumps experiment progressed in a similar manner. Researchers predict where ants would navigate if their hypothesis is true. Then, they observe where experimental ants actually navigate. If the two are sufficiently similar (e.g. ants' whose legs were shortened to stumps before returning home from a foraging journey undershot the nest by 3.86 meters), then researchers have evidence supporting their hypothetical ascription of a content-bearing function.

At this point, an apparent problem arises concerning researchers' specifications of privileged goal outcomes. If researchers specify goals according to background evolutionary considerations, as I argued earlier, then how can undershooting the nest by 4 meters be an example of a privileged goal outcome? Overshooting or undershooting the nest seem like maladaptive behavioral outcomes for homing ants. The solution is to remember that the stilts and stumps experiment is focused on the step-counter mechanism, not homing behavior in general. Usually, when all the component mechanisms controlling homing behavior in an ant function properly, the ant performs successful homing behavior and navigates back to her nest. One of the reasons the stilts and stumps experiment is so remarkable is that it severs the connection that

usually obtains between the proper functioning of neurophysiological mechanisms and successful behavioral outcomes. Wittlinger et al. designed situations where ants *would not* successfully navigate to their nests if a hypothesized component mechanism *was* functioning properly. The privileged goal outcomes specified in the stilts and stumps experiment (i.e. undershooting or overshooting the nest) only seem problematic when viewed as privileged goal outcomes for navigation behavior, not when viewed as privileged goal outcomes for step-counting.

No other account of function captures the notion of function justified by the stilts and stumps experiment as well as this modified account of goal-directed function developed in this section. Consider two alternate accounts of biological function: propensity functions and selected-effects functions. One might object that a modified version of Bigelow and Pargetter's (1987) propensity account of function would work just as well for capturing the notion of function supported by the stilts and stumps experiment. After all, the stilts and stumps experiment seems to produce evidence that satisfies the criteria of the propensity account by supporting the claim that the hypothesized step-counter confers "a survival- enhancing propensity" to foraging ants (Bigelow and Pargetter 1987, 192). Similarly, given a few background assumptions and inferences, one could interpret the results of the stilts and stumps experiment as satisfying the criteria of a selected-effects account of function. That is, the experiment could be interpreted as supporting claims about the history of selection that caused the step-counting trait to exist in contemporary ants. However, such objections miss what makes goal-directed function so well suited to the research strategy in question.

It is not merely that researchers' experiments produce evidence bearing on the criteria of goal-directed function. Goal-directed function best captures the notion of function supported by

the stilts and stumps experiment because the experiment consists of actions that closely correspond to the function-making criteria enumerated in goal-directed accounts of function. In other words, goal-directed accounts outline a procedure for determining whether something has a function, and that procedure closely matches the procedure used by Wittlinger et al. to determine whether ants possess the content-bearing function of step-counting.

Alternatively, selected-effects accounts of function do suggest procedures for identifying function, but those procedures do not match the stilts and stumps experiment as well as goal-directed function. Consider Millikan's (1989, 199) tight articulation of selected-effects function, "A trait's function is what it actually did—did most recently—that accounts for its current presence in the population, as over against historical alternative traits no longer present." To determine whether a trait has a function on such an account, one must know things about ancestral traits. However, Wittlinger et al. do not investigate ancestral traits in the stilts and stumps experiment, and as I argued in section 4, traits' history of selection does not play a primary role in the evidential norms governing researchers' ascriptions of content-bearing functions. Additionally, some accounts of selected-effects function, like Millikan's above, feature a comparative element. To specify a trait's function, one must compare what an ancestral homologue of a trait did to what historical alternatives did and focus on the difference between the two. This is a totally different style of comparison than the comparative procedure outlined by goal-directed accounts of function and practiced by Wittlinger et al. in the stilts and stumps experiment. With selected-effects accounts of function, the *difference* between the effects of alternative traits helps specify function; in the stilts and stumps experiment, the *similarity* of behavioral outcomes supports the ascription of a pre-specified function.

5. Researchers Ascribe Content to Neurophysiological Processes that *Reliably* Achieve a *Difficult* Goal-Directed Function

A context where animal behavior researchers tend to invoke content is when describing how animals coordinate their behaviors with their environment in sophisticated ways, and Wehner's work on *Cataglyphis* navigation is an instance of that trend. The ant's ability to return home via the most direct route is impressive in the sense that one would not expect it to happen by accident. The ant must have some means of coordinating herself with the environment that explains how she reliably achieves her extraordinary navigational feats. In what follows, I articulate the norms governing this distinction between difficult goal-directed functions and easier, more mundane functions. Then, I argue that those norms play a role in dictating appropriate ascriptions of content. Wehner's *Cataglyphis* research program only ascribes content to neurophysiological processes that *reliably* achieve a *difficult* goal-directed function.

5.1 Difficult Goals and Behavioral Repertoires

Why do researchers treat the function of returning home via the most direct route as difficult in a way that a more mundane function, like gaining traction on the ground while walking, is not? In the most general terms, it comes down to (a) the number of ways an ant could attempt to achieve a goal that would causally contribute to it versus (b) the number of ways an ant could attempt to achieve a goal that would not causally contribute to it. The larger (a) is relative to (b), the easier the goal-directed function; the larger (b) is relative to (a), the more difficult the goal-directed function.

This articulation of difficulty relies upon the ethological notion of a behavioral repertoire, or a finite set of potential behaviors. Ethologists generally treat categories of animals as

possessing behavioral repertoires (Lorenz 1950; Tinbergen 1963; Hinde 1982, 43). Those animal categories can be quite general, like the taxonomic category of species, or they can be narrower, like a particular developmental stage of a certain sex in a species.

In addition to relying upon ethologists' practice of treating animals as possessing finite behavioral repertoires, the notion of difficulty articulated above also relies upon ethologists' practice of categorizing animal dynamics according to types. In the course of their investigations, ethological researchers in general and Wehner's *Cataglyphis* research program in particular exhibit the ability to reach consensus about what instances of animal dynamics belong to what behavioral or neurophysiological types (Allen and Bekoff 1997, 47; Hinde 1982, 30–32; Lehner 1996, 110–14; Love 2009, 61–62). For example, an ethologist may divide behaviors into ontogenetic types so that behaviors are categorized according to the developmental stage at which an organism exhibits those behaviors. Alternatively, ethologists also categorize neurophysiological dynamics into functional types, as I argued Wittlinger et al. did in the stilts and stumps experiment with "step-counting." Researchers interpret animal dynamics as belonging to types, and though researchers studying ant behavior tend to reach consensus about what actions count as instances of what types, researchers lack an explicit, comprehensive account of how they make those interpretations and reach consensus (Gordon 1992). In analyzing ethologists' research practices, I will therefore assume the availability of an appropriate typology of behaviors but leave a full analysis of its basis for another context.

To see how the notion of difficulty articulated above distinguishes between goal-directed functions, consider ant locomotion behavior. To move around, ants' tarsomeres need to gain traction with the ground so the ants can generate thrust in a particular direction. Gaining traction is a component goal necessary for achieving the higher-level goal of walking. Ants possess a

behavioral repertoire, and researchers interpret some subset of that repertoire as stepping-type behavior that possesses the function of gaining traction on the ground. The exact size of that subset is unclear. As stated in Lehner's (1996, 109) *Handbook of Ethological Methods*, "The choice of an appropriate behavior unit is generally based on experience, tradition, logistics, and intuition." Surely, the choice of an appropriate behavior unit is also influenced by the questions under investigation. It may be the case that researchers treat stepping behavior as highly stereotyped so that there are a small number of actions that count as step-taking. Alternatively, researchers may examine step-taking behavior at high resolution so that they distinguish many variations of step-taking behavior. In either case, a large majority of step-taking behaviors will causally contribute to the goal of gaining traction on the ground: due to the stable morphological features of an ant's foot, it gains traction in most instances of step-taking behavior regardless of variations in angle or velocity of impact. Thus, though the behavior type's goal is reliably achieved, it is not difficult. Accordingly, researchers do not posit content-carrying functions as somehow mediating the metatarsal's ability to gain traction.

Now consider Wittlinger et al.'s ascription of content to step-counting type processes. As they hypothesize, the step-counter is some neurophysiological mechanism that has the goal-directed function of assuming different states corresponding to different distances travelled by the ant. So, the step-counter must have the capacity to record at least as many distances as foraging ants regularly walk in their searches for food. If the step-counting hypothesis is true, then those distances are likely individuated according to some unit of locomotion, like a step. Furthermore, for any particular instance of navigation, the goal of the step-counter is tightly specified: it must assume the state corresponding to the units of locomotion actually travelled by the navigating ant. Thus, in any instance of *Cataglyphis* navigation, the step-counter has a

difficult goal-directed function. There are many states the step-counter can assume that reflect the many distances ants can walk, but there will always be just a small number of states that accurately reflect the distance the ant has actually travelled for the purposes of returning to the nest.

This notion of difficulty applies just as well to higher-level ascriptions of content made by Wehner's *Cataglyphis* research program. Just like the step-counter, the path integrator is hypothesized to be some neurophysiological process that assumes different states corresponding to the distance and direction of the ant relative to her nest. In their meandering foraging journeys, ants can find themselves in many different locations relative to their nest, so the path integrator must be able to assume a large number of potential states. However, for any instance of actual navigation, the ant will find herself in a particular location that a properly functioning path integrator must accurately represent by assuming the proper state. Thus, the path integrator has a difficult goal. Accordingly, researchers define the path integrator in terms of content-carrying functions.

5.2 Reliably Achieved Goals and Naturally-Occurring Contexts

Before moving on to the productive role content ascriptions play in Wehner's *Cataglyphis* research program, the relevant notion of reliability also needs to be clarified. The reliability with which an ant achieves a goal-directed function varies with the proportion of instances in which the ant performs goal-directed behavior that causally contributes to achieving that function. A process that rarely achieves a difficult goal may depend on luck more than sophisticated systems of coordination, but a process that reliably achieves a difficult goal provides grounds for positing content carrying properties. Hence just as the norms governing

appropriate ascriptions of content are sensitive to the difficulty of a goal-directed function, so too are they sensitive to how reliably a goal-directed function is achieved. The more difficult the goal and the more reliably it is achieved despite that difficulty, the more justified ascriptions of content are to the processes that causally contribute to that goal.

Of course, both the difficulty of a goal-directed function and the reliability with which an animal achieves that function is affected by the context in which the function is attempted. Furthermore, as noted in Neander's critique of Kitcher's hybrid account of function, the adaptiveness of a trait's outcome is also relative to environmental context. The evidential norms governing researcher's ascriptions of content-baring functions are also sensitive to context. Just as ethologists generally treat animals as possessing behavioral repertoires, ethologists also treat animals as having naturally-occurring environments and physiologies, and ascriptions of content-bearing function are justified in relation those naturally-occurring environments and physiologies. Indeed, one of the interests that has historically distinguished ethology from other fields of animal behavior research is ethologists' emphasis on understanding animal behavior in the animal's naturally-occurring context. In Wehner's *Cataglyphis* research program, the difficulty and reliability of a goal-directed function are appropriately assessed within the context of naturally-occurring circumstances.[3]

Briefly, I need to address a potential source of confusion concerning the naturally-occurring contexts just discussed and the experimental circumstances implemented in the stilts and stumps experiment. In the stilts and stumps experiment, ants are induced to perform

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[3] Again, as with researchers' individuation of trait types, researchers seem to lack an explicit, comprehensive account of how they individuate naturally-occurring contexts. Still, it is clear that researchers recognize the distinction between naturally-occurring and non-naturally occurring circumstances.

navigation behavior under manipulated circumstances that do not constitute a naturally-occurring context for *Cataglyphis*. Foragers' legs do not grow or shrink over the course of a single foraging run under naturally-occurring circumstances. Still, researchers use the evidence produced by the sticks and stumps experiment to make inferences about the functioning of non-manipulated foragers in naturally-occurring contexts. Indeed, researchers take great pains to ensure that their experimental manipulations do not create confounding variables (See Wittlinger et al. 2007 for an examination of how the stilts and stumps manipulations affected other parameters of forager locomotion). By making precise interventions, researchers produce evidence for goal-directed functions that apply not just to the animals experimented on, but to *Cataglyphis* foragers generally. Thus, although the range of circumstances implemented in experiments differs from the range of circumstances relevant to justified ascriptions of content, the two are epistemically connected since evidence produced within experimental circumstances also supports ascriptions of goal-directed function within naturally-occurring contexts.

5.3 Difficulty and Reliability Come in Degrees

Finally, it is important to note that difficulty and reliability come in degrees. The upshot for researchers' attributions of semantic content is that the appropriateness of those ascriptions also come in degrees. The more difficult a function is and the more reliably an animal achieves that function, the more appropriate an attribution of semantic content is. Researchers' investigations into the neurosensory physiology underlying *Cataglyphis* navigation do not result in unequivocal determinations of processes that deal in semantic content and processes that do not. Rather, their investigations result in gradations of evidence for or against a given process's dealing in semantic content.

For a borderline case, consider how this account handles another component goal necessary for the function of successful locomotion. In addition to gaining traction with the ground, ants must also time their steps properly to move in a particular direction. Due to the technical notion of difficulty developed in this account, whether or not researchers are justified in ascribing content to whatever neurophysiological process is responsible for controlling step timing depends on both how researchers specify the goal of step timing and how many walking rhythms researchers treat ants as possessing in their step timing repertoires. Highly specific goals and large repertoires make for difficult functions while more general goals and smaller repertoires make for less difficult functions. If researchers take the goal of step timing to be that steps are timed so that the ant never stumbles and its body never contacts the ground, then it seems that the neurophysiological mechanism controlling step timing has a difficult function. Alternatively, if researchers treat the goal of step timing behavior to be timing steps in such a way that the ant moves forward, then the goal becomes more general and the function becomes less difficult.

6. How Ascriptions of Semantic Content Help Researchers Achieve Their Epistemic Aims

This section steps back from the details of researchers' evidential norms and experimental practices to consider the larger picture of how their ascriptions of content figure into the diachronic progression of their research program. First, I argue that ascriptions of content contribute to researchers' aim of producing mechanistic explanations by guiding the mechanistic research strategies of localization and decomposition. Then, I argue that ascriptions of content also help researchers achieve their epistemic aim of cross-taxa comparative theorizing.

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The role I articulate for ascriptions of content here is inferential. Justified ascriptions of content serve as warrants for inferences—inferences that go on to guide hypotheses about how neurophysiological mechanisms causally interact to generate and control navigation behavior. Given my characterization of the evidential norms governing appropriate ascriptions of content, they promote an increasingly specific two-step between content and content vehicles that produces increasingly detailed accounts of the neurophysiological phenomena responsible for ants' ability to reliably achieve difficult functions.

Wehner's (2020, 146) research program is largely engaged in what he has called classical neuroethology. In classical neuroethology, one begins with a behavioral trait and then endeavors to explain how the behavioral trait is causally generated and controlled by its underlying neurophysiological mechanisms. To do that, they engage in the mechanistic research strategies of decomposition and localization articulated by Bechtel and Richardson (1992/2010).

It all begins with a hypothetical ascription of content that decomposes a behavioral trait into physiological mechanisms (e.g. Ants navigate home via the most direct route by means of a mechanism that integrates content about distance and direction of travel.) The evidential norms governing researchers' ascriptions of content mean that when researchers decompose a behavioral trait with hypothetical ascriptions of content, they formulate hypotheses that would account for the reliability with which the behavior achieves its difficult function (e.g. navigating home via the most direct route). This initial, hypothetical ascription of content says little about content vehicles. It remains an open question what sort of neurophysiological entities within the ant carry content about distance and direction of travel. Crucially, however, this specification of content *constrains and guides hypothesizing* about content vehicles. Researchers must ask

themselves what phenomena *Cataglyphis* could potentially exploit that would serve as a reliable proxy for distance traveled.

Prior to the stilts and stumps experiment, researchers hypothesized that insects record distance traveled by monitoring the energy they consume for locomotion (Heran and Wanke 1952). They also hypothesized that ants record distance traveled via an optic flow mechanism that records the rate at which objects move across their visual field (Ronacher et al. 2000). Eventually, Wittlinger et al.'s (2006, 2007) stilts and stumps experiment provided decisive evidence that ants record distance traveled via some mechanism related to locomotion, like a step-counter.

That further specification of content vehicles then reciprocally informs hypothesizing about content. Once researchers know that the vehicles carrying content about distance travelled are related to locomotion, they can formulate more specific hypotheses about the content in question. Instead of carrying content about "distance travelled", the ants are now hypothesized to be recording content about "Some parameter associated with rhythmic leg movement in walking" (Wittlinger et al. 2007). That specification of content then guides hypotheses further specifying content vehicles (e.g. mechanoreceptor hair plates at the base of the legs or proprioceptors in leg muscles (Wehner 2020, 154)), and so on.

Researchers' goal-directed style of justifying content ascriptions also helps them transfer hypotheses and experimental designs across taxa. After examining the role mental content ascriptions play in cognitive ethology, Allen (1992, 8) concluded that "Content-bearing terms, which allow functional descriptions of cognitive abilities, permit generalizations across species which implement them differently, and, as mentioned above, species comparison is one of the basic aims of ethology." This point nicely fits the present case study. Wehner's *Cataglyphis*

research program belongs to a tradition of ethological research that has focused on ants and honeybees and shares this epistemic aim of producing knowledge via comparisons across taxa. In Wehner's research program, hypothetical ascriptions of content in one taxonomic family are sometimes imported to the other, and because both ants and honeybees are central place foragers, the goal-directed experiments designed to test those hypotheses can also be transferred.

To see this, consider the way investigations into the celestial compass of *Cataglyphis* and honeybees have advanced in tandem. Karl von Frisch (1949) was the first to demonstrate that honeybees record content about direction of travel by monitoring patterns of polarized UV sunlight in the sky. Later, Wehner and Duelli (1973) established that *Cataglyphis* can do the same by transferring this content-ascribing hypothesis to *Cataglyphis* and testing it via similar experiments. Then, one of Wehner's doctoral students, Paul Herrling (1976), discovered specialized sensory cells along the dorsal rim of *Cataglyphis'* eye that seemed morphologically suited to detecting patterns of polarized UV light. This constituted a further specification of content vehicles involved in recording direction of travel by localizing a pattern sensing mechanism to the dorsal rim of *Cataglyphis'* eyes. Wehner and colleagues (1975) subsequently transferred that hypothesis to honeybees, where they also found specialized sensory cells along the dorsal rim of honeybee eyes. Behavioral experiments indicated the shared feature was necessary and sufficient for detecting polarized light in *Cataglyphis* and honeybees (Wehner 1997; Rossel and Wehner 1984a, 1984b; Wehner and Müller 2006).

7. Conclusion

The practice of ascribing internal, content-carrying states to animals has been a perennial source of debate in behavioral research. In this paper, I clarified the evidential norms governing

ascriptions of content within a successful, well-established neuroethological research program. Then, I examined the historical trajectory of that research program to determine whether and how such attributions help researchers achieve their epistemic aims. The result has been a longitudinal analysis of content ascriptions that begins with experiments designed to justify hypothetical ascriptions of content and ends with the way justified ascriptions influence future investigations. The account of content attribution resulting from this analysis provides a definite means of assessing researchers' ascriptions of content while respecting the inferential reasoning of researchers.

Scientists and philosophers lack a comprehensive theory of what it takes in principle for something to be a genuine instance of content. For some, the absence of such a theory indicates a state of disarray that makes researchers' ascriptions of content suspect. This paper should alleviate such suspicions by demonstrating that the evidential norms governing appropriate ascriptions of content can secure a productive role for content ascriptions even though those evidential norms do not add up to a comprehensive theory of content. To see how the goal-directed style of justifying content ascriptions articulated in this paper figures into the broader context of behavioral research, philosophers will have to examine the actions and habits of reasoning that precede and follow the justification of content ascriptions in other areas of the behavioral sciences.

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