The Meaning of Meaning in Insect Navigation Research

by

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ABSTRACT

Getting clear about what behavioral scientists mean when they invoke content presupposing concepts, like information, is necessary for understanding how humanity's own behavioral capacities do or do not relate to those of non-human animals. Yet, producing a general naturalistic definition for representational content has proven notoriously difficult. Some have argued that Claude Shannon's formal, mathematically defined notion of information is the proper starting point for building a biological theory of content. Others have sought to define content presupposing concepts in terms of the historical selection processes that drive evolution. However, neither approach has produced definitions that capture the way successful researchers in the behavioral sciences use content-presupposing concepts. In this dissertation, I examine an ethological tradition of insect navigation research that has consistently ascribed content to insects. To clarify the meaning of such ascriptions, I analyze the practices scientists use to justify new attributions of content and the way new attributions of content guide scientists' future research activities.

In chapter 1, I examine a series of insect navigation experiments performed in 2006–2007 that led to a novel ascription of content. I argue that researchers ascribe content to insects' navigation behaviors when those behaviors reliably accomplish a difficult goal-directed function. I also argue that ascriptions of content help researchers achieve their epistemic aims by guiding hypothesis formation and aiding comparative theorizing.

In chapter 2, I trace the history of the experimental strategy analyzed above back to the work of Karl von Frisch in the early 20th century. I argue that von Frisch has a complicated and understudied relationship to the discipline of ethology. I support that argument by highlighting features of von Frisch's research that both comported with and differed from the program of classical ethology.

In chapter 3, I examine the cognitive map debate in insects. I argue that the debate stems from competing research groups' endorsement of different norms for justifying claims about the dynamics of representational contents. I then situate these different norms historically to show how the cognitive map debate is a continuation of longstanding divisions within the history of animal behavior research.

Dedicated to my wife Monika, who was there for me the whole time, and to my mother Mary Jo, who always encouraged my academic pursuits, no matter how obscure.

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Introduction

1. The Circumstances and Motivations that Produced this Dissertation

This dissertation is about meaning— quite a broad topic. Anthropologists, sociologists, psychologists, linguists, political scientists, literary researchers, philosophers, and historians all grapple with problems of meaning and interpretation, problems concerning what makes a thing *about* something else and how to determine whether that is the case. If one wanted to avoid using the term *aboutness*, one could instead frame the problem in terms of *representation*, *semantic content*, or *reference*. Broadly put, this dissertation concerns the mystery of what makes some things about, represent, or reference other things.

As the above list of disciplines implies, the most familiar instances of meaning relationships come from human behavior, where people think thoughts and speak words that are about other things in the world. However, biologists also regularly attribute meaningful content to the activities of non-human systems, and that is the phenomenon that this dissertation examines. But before relating the details of this dissertation and why they matter, it will be good to give a brief account of the events and motivations that led me into this conceptual wilderness. How else am I to explain how an ambition to understand the meaning of meaning led me to scrutinize a European tradition of meddling with insects?

I come to the problem of meaning by way of linguistics and anthropology. Humans are strange animals. Anthropologists claim that our ability to produce and participate in *symbolic culture* is deeply implicated in that strangeness. I wanted to know

more about what makes something symbolic. What is a symbol, and how do they work? Given the weight cultural anthropologists put on humanity's discursive abilities, I thought linguistics would be a good place to find answers. Imagine my disappointment when I enrolled in a formal semantics course and came across the following passage eighty-four pages into a book titled *What is Meaning?* (Portner, 2005):

> "Semanticists are in a way like lawyers (sorry, fellow semanticists), who take for granted a system of right and wrong, without asking the deeper question of what makes certain things right and wrong. Philosophers get to ask that question […] Any area of inquiry which is in such a state of disarray (or fascinating openness, depending on your perspective) is generally part of philosophy."

Thus, my desire to understand meaning within the context of behavior led me into the arena of philosophical inquiry and the austere forms of argumentation that accompany it. But as the above passage implies, philosophy can be confusing. There is not much firm ground to stand upon, and it can be difficult to find the proper foothold that makes a project tractable. At the very beginning of graduate school, I thought I might produce something that combined Charles Peirce's theory of signs with insights from the life sciences (whatever that would mean). I greatly admired Peirce's semiotics for the systematic manner in which he organized a taxonomy of signs complete with schematic descriptions of how each functioned to produce meaning. However, after perusing some biosemiotics journals, I diverted and continued along the lines of a broader Peircean thesis. Namely, that philosophers can clarify the meaning of abstract concepts by examining the sensible effects people attend to when they make judgements about whether the concept applies to a given situation.

As I continued to think about Peirce's pragmatic maxim, I was also becoming familiar with contemporary literature in the philosophy of science. My advisor, Beckett

Sterner (2014), and one of my committee members, Colin Allen (2017), had both published arguments advocating for pluralistic, practice-oriented analyses of *biological information* and *cognition*, respectively. The common point that made its way through to me from these papers was that philosophers required a more dynamic, diachronic view of scientific concepts as evolving tools. The traditional approach of curating a static list of necessary and sufficient conditions was insufficient for grasping the significance of these concepts or the role they played in scientific inquiry. All this meshed nicely with Peirce's diachronic framework of belief attainment, wherein an initial state of doubt is appeased by the attainment of a belief that goes on to guide future action. By examining 1) the doubt that occasions behavioral scientists' investigations into meaning, 2) the practices and habits of reasoning that scientists use to support beliefs that appease that doubt, and 3) the modes of action that scientists engage in as a result of attaining those beliefs, I could facilitate a dynamic understanding of the meaning of meaning within the behavioral sciences. I resolved to use these methodological insights to guide my research.

As I continued to familiarize myself with the philosophy of science and the turn towards practice that the field had recently experienced, I realized that my project could not assume homogeneity across the behavioral sciences or their sub disciplines. To analyze concepts at the resolution of scientific practices, I had to choose a research program to study. Two pragmatic criteria led me to select an insect navigation research program. First, I thought it prudent to begin with basic meaning relations and work my way up to more advanced forms of meaning later. Philosophers generally agree on a rough hierarchy of meaning: propositional content is at the top as the most complex, below that is conceptual content, then at the bottom is something like perpetual content or

primitive content. As a philosopher in training drawn to bottom-up approaches, I elected to investigate researcher's ascriptions of primitive content. Second, I wanted access to people who were doing the research I would be analyzing. For my project to succeed, I needed a competent understanding of the science I would be examining, and I knew that insiders could help me achieve that competence.

This is where the insects come in. Arizona State University houses the Social Insect Research Group, a place full of accomplished behavioral researchers. Fortunately, I was able to build some inroads with them. During one of my discussions with Bert Hölldobler, he informed me that navigation studies have always been the most rigorous form of animal behavior research. When I heard that, a little light bulb went off, because as any analytic philosopher will tell you, rigor is good. Given the messiness of philosophical inquiry into meaning, I was eager to take well-defined clarity where I could find it. I finally settled on examining insect navigation research after taking an individualized reading course with Robert Page, who introduced me to the cognitive map debate and some classic navigation studies in ants and honeybees. Among such studies were Rüdiger Wehner's work on the desert ant *Cataglyphis*. Page told me that Wehner had a reputation for executing elegant experiments that produced unambiguous results. This was just what I needed for my diachronic, pragmatic approach.

Time and time again, Wehner's research program hypothesized the existence of content in *Cataglyphis*, performed a series of behavioral experiments to test that hypothesis, and then produced decisive evidence that *Cataglyphis* possessed the hypothesized content. Moreover, researchers' ascriptions of content seemed to be in the service of one of the most tangible epistemic aims within organismal research: causal

mechanistic accounts of behavior. Finally, from a philosophical perspective, navigation behavior presents a cleaner, more spartan analytical context than communication behavior, which is complicated by the potential for agents to hold conflicting interests. I had found an ideal research program for my philosophical methodology.

But this dissertation is more than a purely philosophical examination of practices that produce evidence for content ascriptions within a scientific community and the actions the result from those ascriptions. This dissertation also has a strong historical dimension. As one contemplates the thesis that the practices and habits of reasoning tied to appropriate ascriptions of a concept are a significant aspect of what that concept means, new avenues of inquiry become apparent. The story cannot end with scientific practice because scientific practices do not come from nowhere. Scientific practices are developed and propagated by people, and their character is contingent on a vast array of historical circumstances. Thus, one way to delve deeper into the pragmatic meaning of a scientific concept is to become a historian of science, and I have decided to do that here. By tracing the pedigree of Wehner's *Cataglyphis* research program, this dissertation provides a fuller, more contextualized understanding of the notion of semantic content employed within this exceptional research program. And conversely, my philosophical focus on the epistemology of biologists' ascriptions of meaning has informed the historical problems this dissertation addresses.

Having provided that background, I now turn to a more detailed summary of this dissertation's three chapters and how they fit together.

2. Wehner's *Cataglyphis* Research Program and the Stilts and Stumps Experiment

The first chapter of this dissertation is primarily philosophical and focuses on Rüdiger Wehner's *Cataglyphis* research program. Wehner's research makes heavy use of behavioral experiments and is often engaged in what Wehner (2020, pp. 146) has called "classical neuroethology," wherein 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, Wehner and colleagues engage in the mechanistic research strategies of decomposition and localization articulated by Bechtel and Richardson (1992/2010). The behavioral traits that Wehner's group seeks to mechanistically explain are navigational traits that *Cataglyphis* express when foraging.

Cataglyphis foragers search for food during the hottest part of the day. 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). Despite their circuitous searches for food, *Cataglyphis* foragers consistently return home from foraging runs via the most direct route.

To explain that navigational trait—that capacity to consistently return to a goal location via the most direct route—Wehner hypothesized early on that *Cataglyphis* navigate via path integration (Wehner 2013). I will save the details of how path integration works for the chapter itself. The important thing is that the path integration hypothesis ascribes content-carrying functions to *Catalglyphis*. If the path integration hypothesis is true, it follows that *Cataglyphis* has some means of recording content about

distance and direction of travel. Wehner and colleagues perform behavioral experiments to produce evidence bearing on the path integration hypothesis, and when they confirm that hypothesis, they formulate new hypotheses that trace the content-carrying functions down to deeper mechanistic levels. For instance, after attaining the belief that *Cataglyphis* does navigate via path integration, Wehner and colleagues asked what sensory mechanisms allow *Cataglyphis* to record content about distance and direction of travel? What material cues are the ants picking up on that reliably correspond to these abstract categories of "distance travelled" and "directed of travel"? What parts of the ant are sensitive to these cues, and how are those sensory signals processed to control navigation behavior? The first chapter examines the role of content ascriptions in this investigatory context through use of a case study.

Specifically, Chapter 1 examines the case of the stilts and stumps experiments, a series of experiments that confirmed the hypothesis that *Cataglyphis* foragers *record content* about distance travelled via some kind of step-counter mechanism (Wittinger et al. 2006, 2007). In keeping with the diachronic perspective of this dissertation, I look at the experimental practices and habits of reasoning that researchers use to produce evidence bearing on the step-counter hypothesis. Then, after researchers have attained the belief that the step-counter hypothesis is true, I examine how that belief guides their future research actions. There are two significant upshots to this chapter.

First, in clarifying the evidential norms that govern the way researchers confirm the step-counter hypothesis, I create an account of content ascription that holds that researchers are justified in ascribing content to some neurophysiological process if the process *reliably achieves a difficult goal-directed function*. Teleosemantic theories of

content make the ontological claim that semantic properties supervene on functional properties[1], and the account I produce shows how the epistemological endeavors of navigation researchers comport with that ontological claim. The account I produce departs from traditional teleosemantic accounts of content by reserving a privileged role for goal-directed function over etiological selected-effects function. This account of content attribution provides a definite means of assessing researchers' ascriptions of content while respecting the inferential reasoning of researchers.

The account I produce is not comprehensive in the sense that it does not answer all of the questions that have traditionally interested philosophers who think about biological content. For instance, the account does not offer in principle solutions to the content determinacy or content localization problems. Rather, it clarifies an investigative strategy that allows researchers to justify increasingly specific claims about where content is and what content is about for particular target systems.

Though the account I produce is not comprehensive in the way traditional ontology-oriented accounts of content are, the account has the significant virtue of articulating a productive epistemological role for ascriptions of content. Given my

[1] There is disagreement over what defines teleosemantic theories. According to Neander (2017; p. 19–22), teleosemantic theories of content are defined by a commitment to the claim that semantic content supervenes on some notion of function that permits the possibility of malfunction and has "a teleological flavor". Unlike Millikan's teleosemantics, Neander's informational teleosemantics remains open to the possibility that semantic content supervenes on non-etiological notions of function. According to Shea (2018; p. 15), the defining feature of teleosemantic theories is that they reserve a content-fixing role for an etiological notion of function. Thus, Shea does not consider his latest varitel semantics theory of content to be a teleosemantic theory of content because his varitel semantics allows non-etiological notions of function to determine content.

clarification of the norms governing content ascriptions, I argue that ascriptions of content contribute to researchers' aim of producing mechanistic explanations by guiding the mechanistic research strategies of localization and decomposition. I also argue that ascriptions of content help researchers achieve their epistemic aim of cross-taxa comparative theorizing.

The practice of ascribing internal, content-carrying states to animals has been a longstanding source of debate in behavioral research. Both 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. The first chapter 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.

3. Karl von Frisch and Ethology

The second chapter is primarily historical and examines the origins of the experimental strategy Wittlinger et al. used in the stilts and stumps experiment. When I asked, "Where does Wehner's approach to justifying content ascriptions come from?" I discovered that I could trace the strategy back to Karl von Frisch, an Austrian zoologist famous for the way he used behavioral experiments to demonstrate sophisticated sensory capacities in fish and insects. One of von Frisch's most influential students was Martin Lindauer (Seeley et al. 2002), who also focused on honeybees. Martin Lindauer then trained Wehner, whose doctoral research also utilized behavioral experiments to produce

evidence about honeybee perception (Wehner 1967). As I researched von Frisch and the circumstances under which he developed the experimental strategy in question, I discovered a historiographic riddle. In chapter 2, I provide an answer to that riddle, and in doing so, I uncover historical evidence that corroborates a key argument from chapter 1.

The riddle I discovered concerns a deceptively simple question: "What is von Frisch's relationship to the discipline of ethology?" In addition to his scientific findings, von Frisch is also remembered for being vaguely integral to the founding of European ethology, a distinct discipline of animal behavior research that emerged in the 1920s and 1930s. For example, in 1973, von Frisch was awarded a 1/3 share of the Nobel Prize in Physiology or Medicine along with Nikolaas Tinbergen and Konrad Lorenz. These three men did not receive the award for any particular discovery. Rather, they won the award for their ethological approach to animal behavior research. Historians have shown how Lorenz and Tinbergen's work was central to the practical and theoretical innovations that came to define ethology. Von Frisch is rarely mentioned in such histories, and when he is, he is often framed as an expert practitioner of ethology rather than a founding influence. Yet, it seems strange to consider von Frisch as following the ethological example set by Tinbergen and Lorenz when von Frisch was significantly older than Tinbergen and Lorenz and had already developed his approach to animal research by the time Tinbergen and Lorenz began promoting ethology in the 1930s. So, what exactly was von Frisch's relationship to ethology?

In keeping with this dissertation's emphasis on experimental practices and reasoning, I examine von Frisch's science by examining von Frisch's experimental practices. By comparing von Frisch's experiments with the experiments of

contemporaries who sought to answer the same questions about sensation with the same animal subjects at the same time, I highlight the features of von Frisch's approach that made him stand out in his own time. Then, I show how the features that made von Frisch's experimental approach stand out comported with the disciplinary niche Tinbergen and Lorenz sought claim for ethology prior to WWII. Specifically, Tinbergen and Lorenz promoted ethology as a discipline that would reconcile reductionist and holist approaches to animal behavior studies, and von Frisch's experiments demonstrated how successful such a reconciliation could be.

In addition to this abstract correspondence, there is a more concrete connection between von Frisch's early career research and the figureheads of ethology. As a university student and early career researcher, Tinbergen was markedly influenced by von Frisch's experimental style. To support that claim, I show how Tinbergen's early research on digger wasp navigation mirrored von Frisch's work on honeybees. I also rely on the first-person recollections of Tinbergen and his students.

Thus far, it seems as though von Frisch's relationship to the discipline of ethology was that of an early exemplar. However, despite the conceptual correspondence and influential relationship linking von Frisch's research with Tinbergen and Lorenz's ethological program, Tinbergen and Lorenz did not refer to von Frisch's work as exemplary in the way one would expect. The question has now evolved from, "What was von Frisch's relationship to the discipline of ethology?" to "Given the significant affinities between von Frisch's work and Tinbergen and Lorenz's programmatic ambitions, why didn't Tinbergen and Lorenze treat von Frisch's experiments as an exemplar of the ethological program?"

Chapter 2 concludes by providing two answers. First, the niche Tinbergen and Lorenz sought to carve out for ethology prior to WWII differed from von Frisch's research in a few key respects. Von Frisch's experiments required conditioning or training animals to perform learned behaviors while Tinbergen and Lorenz emphasized studies on "naïve" instinctive behavior. Von Frisch was not engaged in the project of reconstructing phylogenies via comparative studies of instinctive behaviors, yet Lorenz saw that project as a key contribution of his new science. Finally, von Frisch did not work with birds, which were an important experimental subject for Tinbergen and especially Lorenz.

The second answer concerns the changing relationship between evolutionary theory and ethology. In short, although von Frisch's work had strong affinities with Lorenz and Tinbergen's pre-WWII vision for ethology, those affinities became much less obvious as ethology reconstructed itself post-WWII. Whereas Tinbergen and Lorenz had promoted mechanistic explanations of behavior in terms of underlying physiology as a hallmark of ethology prior to WWII, after WWII, ethology became more tightly associated with investigations into the survival value of behavioral traits. After WWII, Tinbergen emerged as ethology's international figurehead and proselytizer, and his move from Leiden University to Oxford University in 1949 was emblematic of this shift from physiological causation to adaptive significance. Von Frisch's use of behavioral experiments to investigate sensory physiology did not fit with post-WWII ethology as well as they did with pre-WWII ethology. As result, von Frisch already looked like the odd man out by the time von Frisch, Tinbergen, and Lorenz won the Nobel Prize in 1973.

How does this conclusion corroborate a key argument from the Chapter 1? It provides a historical complement to Chapter 1's philosophical conclusion about the respective roles goal-directed function and etiological function play in justifying content ascriptions in the stilts and stumps experiment. In Chapter 1, I argue that Wehner's group specifies the privileged goal outcome of a behavior type according to some notion of etiological function. Then, to justify a content ascription, they design experiments that produce evidence about goal-directed properties of a behavior type. Chapter 2 complements this argument by showing how the same division of conceptual labor took place in von Frisch's experiments on animal sensation, experiments that also justified ascriptions of content. The difference in how these two chapters discuss the topic is terminological. Chapter 2 talks about the influence of "evolutionary theory" and "evolutionary thinking" while about Chapter 1 talks about "etiological selected-effects function." Both clarify what role thinking about historical selection processes have within a particular experimental strategy for justifying content ascriptions.

Thus, an important connection between the first two chapters is that chapter 2 shows why a major conclusion of chapter 1 makes sense from a historical perspective. The experimental strategy employed by Wittlinger et al. in the stilts and stumps experiment is extremely similar to the experimental strategy developed by von Frisch nearly a century previous. This is no coincidence—the research strategy was passed down from doctoral mentor to doctoral advisee, from von Frisch to Lindauer to Wehner to Wittlinger. Chapter 1 gets into the conceptual weeds about how content ascriptions are justified and how those ascriptions affect the future actions of researchers. Chapter 2 provides a partial answer to why the picture painted in Chapter 1 looks the way it does.

Part of the reason Wehner's *Cataglyphis* research program justifies ascriptions of content in the manner they do is because they come from a Frischean ethological tradition.

4. The Cognitive Map Debate in Insects

Finally, chapter 3 takes a philosophical and historical approach to examine the bigger picture of how Wehner's *Cataglyphis* research program fits into contemporary cognitive research. Specifically, I examine a strategy the Wehner group has developed for challenging *the cognitive map*, a well-established cognitive trait in animal navigation research. During the latter half of the 20th century, mammalian navigation researchers established the existence of a cognitive map in rats (Tolman 1948; O'Keefe and Nadel 1978; Bechtel 2016). As scientists uncovered the neuro-cellular basis of the cognitive map in rats, insect navigation researchers began to ask whether animals like ants and honeybees might also possess a cognitive map (Gould 1986; Benhamou et al. 2011; Bshary & Brown 2014; Epstein et al. 2017; Genzel 2018). Wehner was an early skeptic of the idea that ants and honeybees possess a cognitive map (Wehner 1981), and so was his colleague, Randolf Menzel (Wehner & Menzel 1990).

It is not surprising that Menzel and Wehner were on the same side of this debate. Both were trained in the same ethological tradition of honeybee research by the same doctoral mentor (Lindauer) at the same time (1960s). What is surprising is that as the scientists continued to investigate insect navigation and develop their own prominent research programs, Menzel changed his position and began to argue that honeybees do possess a cognitive map (Menzel, 2000; Menzel and Giurfa 2006; Cheeseman et al. 2014; Menzel 2019) while Wehner continued to develop alternatives to the cognitive map

(Cruse and Wehner 2011; Hoinville et al. 2012; Hoinville and Wehner 2018; Wehner 2020). How can two scientists pursuing such similar problems within the same disciplinary context go from agreeing with each other about insect cognition to disagreeing with each other as more evidence became available? And what, if anything, can this debate teach philosophers about the prospects of cognitive research converging on big picture accounts of cognitive traits that span a wide variety of taxa?

The historical upshot to this manuscript corresponds to the first question. Through personal communication with insect navigation researchers, I have found that some are exasperated by the cognitive map debate in ants and honeybees. They have lost the thread and are not sure what is really at stake anymore despite the fact that both sides feature well respected researchers. In this chapter, I use an historical, epistemological perspective to show how the terms used to articulate distinctions at the crux of the cognitive map debate are themselves contested in nonobvious ways. Competing research groups adhere to different evidential norms when determining whether the results of behavioral experiments justify claims about the dynamics of neural representations. Thus, there is more at stake in the debate than the truth value of propositions characterizing insect cognition. What is at stake for participants of the debate are competing constellations of epistemic aims, evidential norms, preferred animal subjects, investigative practices, and theoretical assumptions that are often orthogonal rather than conflicting. The general take away is that the cognitive map debate between Wehner and Menzel has become a proxy war over the future of neuroethology, or how best to perform neuroethology.

The philosophical upshot to Chapter 3 concerns the problem of synthesizing a big picture understanding of how a scientific concept (e.g. the cognitive map) applies to the

world from the heterogeneous ways distinct research communities use that concept. Wehner has coined a term for this problem within the context of neuroethological research: the chimera problem. The chimera problem, as described by Wehner, results from the fact that to reveal the neurophysiological mechanisms behind behavioral traits, researchers must often investigate different aspects of those mechanisms in different taxa due to practical constraints. Chapter 3 introduces and clarifies the chimera problem as a philosophical problem facing cognitive model organism research. I show how disagreements over the chimera problem figure into the cognitive map debate in insects and how those disagreements over the chimera problem involve deeper disagreements about what makes a hypothesis more or less parsimonious and whether anthropomorphism or anthropodenial is a greater threat to neuroethological researchers.

I see this as the other side of the coin to Love and Travisano's (2013) paper on model organisms, where they argue that biologists studying embryogenesis should use single-celled organisms as an experimental model for multi-cellular organisms because of the practical advantages to experimenting on single-celled organisms. That paper celebrates the pragmatic use of diverse taxa in comparative research, and it also seems to assume that researchers will be able to put all the pieces back together at the end of the day to make general taxa-spanning claims about embryogenesis. The cognitive map debate in insects is an interesting case of researchers struggling to put the pieces back together again after exploiting the practical advantages of using ants and honeybees as experimental subjects.

As with the previous two chapter, I take a practice-based approach to the cognitive map debate and examine a research strategy that Wehner's group has developed

for discrediting the pro-cognitive map arguments of Menzel's group. However, unlike the previous two chapters, Chapter 3 examines researchers' modeling practices in addition to their experimental practices.

In the 2000s, Wehner's group developed Navinet, a computational network model that simulates central place foraging behavior and, importantly, does not operate according to the rules of a cognitive map. When Menzel's group publishes the results of behavioral experiments on honeybees and argues that those results support the existence of a cognitive map, Wehner's group counters by showing how their non-cognitive map network model is sufficient to account for those results. These are proof of concept demonstrations, and I draw on Elliot's (forthcoming) account of proof of concept demonstrations to describe Wehner's strategy. I also draw on Dietrich and Skippers' (2007) work on "manipulating underdetermination" as a framework for understanding scientific controversies.

A key reason Menzel's group is not swayed by Wehner's proof of concept demonstrations is that some parameters of the Navinet model are based on the results of Wehner's *Cataglyphis* experiments, and Menzel maintains that there are important differences between those desert ant studies and his own honeybee studies. By examining 1) how Wehner's group transforms the results of behavioral experiments into parameters for Navinet and 2) why Menzel's group is not swayed by this strategy, Chapter 3 clarifies a challenge for scientists seeking to synthesize particular cognitive models of widely-realized goal-directed behaviors such that they converge on general mechanisms or principles.

5. So What?

How does this in-depth examination of content ascriptions relate to contemporary problems that people care about? In this section, I show how the results of this dissertation are relevant to the work of humanists, behavioral scientists, cognitive scientists, AI researchers, roboticists, and historians.

Humanists: This dissertation contributes to the interdisciplinary project of understanding semantic content in general, and as noted at the beginning of this introduction, problems of semantic meaning are central to the humanities. Humans perform fascinating behaviors like making promises, painting pictures, telling stories, and performing rituals. We recognize those behaviors as being meaningful in a way that other behaviors are not, and the sophistication of such behaviors can make it seem like this special class of human behaviors bear no relation to the behavior of other animals. But people are not separate from the rest of biology; our evolutionary history blends with the histories of other life forms. Like other animals, people are agents whose actions are directed toward goals, and when scientists set out to study the goal-directed actions of non-human animals, they cannot seem to avoid attributing some notion of meaning to certain kinds of animal behavior.

This dissertation clarifies the opaque yet familiar distinction between neurobehavioral processes that deal in meaning and neurobehavioral processes that do not, and it does so in terms of *biological functions* and *agents who make decisions* within *naturally-occurring contexts*. Although these notions may seem exclusively biological, various humanist traditions have valuable perspectives on what makes an agent, the

importance of decisions, and the function of an action. As a philosopher of science, I have concerned myself with epistemological issues of evidence, justification, belief, and inference. Other branches of the humanities can examine other dimensions of these concepts to provide richer understanding of how humanity fits into the rest of the living world.

Behavioral Scientists: 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; Buckner 2013). This dissertation advances the discussion by articulating how exactly ascriptions of content actually aid neuroethologists' efforts to provide causal physiological understandings of animal navigation.

Cognitive Scientists: This dissertation demonstrates that the way scientists justify claims about representational content matters for the larger project of synthesizing general cognitive mechanisms or cognitive principles from the results of diverse research programs. Furthermore, the way researchers justify scientific claims is partially a product of the way they were trained to justify scientific claims. Thus, one productive avenue for clarifying what is at stake in conflicts about how widely realized cognitive traits are is to examine the disciplinary history of competing research groups.

Artificial Intelligence Researchers and Roboticists: Artificial intelligence researchers and roboticists have already looked to Wehner's *Cataglyphis* research program for inspiration when building robots that can navigate. Part of the reason roboticists are attracted to Wehner's research program is that Wehner's group builds computational network models to simulate *Cataglyphis* behavior, and these models are translatable to robotics applications. Additionally, research on ant and honeybee navigation is interesting to artificial intelligence researchers because ants and honeybees have small brains (less than 1 million neurons). When researchers seek to build biologically plausible models of the neural dynamics controlling navigation behavior in ants and honeybees, they are limited by the computational constraints imposed by small brains. That leads to the construction of computationally efficient algorithms, which is a major desideratum of many roboticists. In sum, Wehner's *Cataglyphis* research program has already provided roboticist with a useful target for biomimetic designs.

This dissertation can help expand such projects by providing a computationally tractable account of content that can be translated between biological and computational applications. Indeed, the account of justified content ascriptions I provide in Chapter 1 has clear affinities with Shannon's theory of communication and decision theory. An important difference is that my account of content ascription focuses on the semantic dimension of information, whereas information theory assumes the existence of semantic content but does not directly address the semantic dimension of information.

One of the major promoters of Claude Shannon's theory of communication, Warren Weaver (1949, pp. 9), wrote that "The concept of information applies not to individual messages (as the concept of meaning would), but rather to the situation as a

whole […]". Contra Weaver, this dissertation has shown that although ascriptions of content are localized to particular processes, to justify those ascriptions, researchers must attend to a variety of features characterizing a whole behavioral situation. By incorporating those relevant features into their biomimetic algorithms, roboticists may get closer to reproducing the remarkable feats of *Cataglyphis* navigation.

Finally and more speculatively, the diachronic account of content ascriptions I provide may have machine learning applications. The idea here is that computer scientists can go beyond biomimicry by creating machine learning algorithms that model the evidential norms governing appropriate content ascriptions in neurobehavioral research. By feeding such a learning algorithm the right sorts of cases, one may be able to produce novel answers to questions concerning the content of neural representations. In practice, computer scientists often face the problem of specifying content when they have to make decisions about how to define variables. Learning algorithms that model the process of inquiry that scientists use to uncover the dynamics of neural representations in ants may provide a novel means of defining variables for biomimetic algorithms.

Historians of Science: This dissertation identifies an understudied tradition of ethological research and begins the project of characterizing that tradition. The bulk of historical work on ethology has focused on Tinbergen and Lorenz and the research traditions they initiated. This dissertation traces the ethological research stemming from von Frisch to uncover a tradition of predominantly German-speaking ethologists focused on causal physiological accounts of sophisticated navigation and orientation behavior. The aspects of von Frisch's research that distinguished him from Tinbergen and Lorenz largely persist among von Frisch's academic progeny, who continue to use Frischean

research strategies on honeybees and ants to produce novel conceptions of animal cognition.

Chapter 1: What Makes Neurophysiology Meaningful? Semantic Content Ascriptions in Insect Navigation Research

(This chapter is a slightly modified version of Dhein (2020), an article I published as sole author in the journal *Biology & Philosophy*.)

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.[2]

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?

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

[2] 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.

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 food 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 researchers' 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 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.[3]

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

[3] 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.

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.

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.[4]

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 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

[4] 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.

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.

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.

Chapter 2: Karl von Frisch and the Discipline of Ethology

(This chapter is a slightly modified version of an article I authored that is currently under review at *Journal of the History of Biology*.)

1. Introduction

In 1973, the discipline of ethology came into its own when three of its most prominent practitioners—Konrad Lorenz, Niko Tinbergen, and Karl von Frisch— jointly received the Nobel Prize for Physiology or Medicine. The award was unusual because instead of commending a particular discovery of major importance, it seemed to broadly endorse a disciplinary style of investigating animal behavior (Hinde and Thorpe 1973; Marler and Griffin 1973; Hein 1976, p. 243; Burkhardt 1981, p. 65; Lorenz 1985, p. 283; Kruuk 2003, p. 268–269). Tinbergen (1973a) called the Nobel Foundation's decision "unconventional" and reasoned that "Since at least Konrad Lorenz and I could not really be described as physiologists, we must conclude that our *scientia amablilis* is now being acknowledged as an integral part of the eminently practical field of Medicine." I begin with Tinbergen's reaction to the Nobel Prize because it illustrates the primary question motivating this paper.

What is von Frisch's relation to the discipline of ethology? In the above quote, Tinbergen singles out von Frisch for being more of a physiologist than he or Lorenz. That compartmentalization is also reflected in the historiography of ethology. Others have shown how Lorenz and Tinbergen's work was central to the practical and theoretical innovations that came to define ethology as a distinct form of animal behavior research in

the 20th century (Burkhardt 1981, 1983, 1997, 1999, 2005; Beer 1975; Kalikow 1975; Heinroth & Burghardt 1977; Burghardt 1982; Baerends 1991; Jamieson & Bekoff 1992; Dewsbury 1992; Brigandt 2003, 2005; Kruuk 2003; Beale 2008; Munz 2011; Schulze-Hagen & Birkhead 2015, p. 14–15). Von Frisch is rarely mentioned in such histories (Jaynes 1969; Beer 1975; Heinroth 1977; Lea 1984, chapter 1), and when he is, he is often framed as an expert practitioner of ethology rather than a founding influence (Bates 1953; Thorpe 1979; Dewsbury 1992; Jamieson and Bekoff 1992, p. 111–112; Kruuk 2003; Greenberg 2012; Radhakrishna 2018).

However, as this paper demonstrates, von Frisch's relationship to ethology is not that of an acolyte or skillful early adopter. Von Frisch was 17 years older than Lorenz and 21 years older than Tinbergen. By the time Tinbergen and Lorenz began promoting ethology in the 1930s, von Frisch had already developed his own experimental approach to animals and established himself as a prominent academic. The most obvious alternative—that von Frisch was a co-founder of ethology alongside Tinbergen and Lorenz—also seems to be ruled out. As Burkhardt (2005, p. 6) writes in the introduction to his comprehensive history of ethology, von Frisch "essentially took no direct part in the efforts that constituted ethology as a new discipline in the middle decades of the [20th] century." This paper resolves the tension between historians' inability to articulate a clear relationship between von Frisch and ethology and the pervasive sense that von Frisch was somehow important to ethology. To resolve that tension, I begin by exploring the idea that von Frisch was an *exemplar* for the nascent discipline of ethology.

By questioning whether von Frisch was an exemplar for classical ethology, this paper uncovers previously neglected affinities between von Frisch's early research and

the program of classical ethology. In the 1930s and 1940s, Tinbergen and Lorenz were eager to frame ethology as a discipline that reconciled certain reductionist and holist commitments. On the one hand, Tinbergen and Lorenz promoted reductive, causal-physiological explanations of behavior over psychological explanations. On the other hand, they saw animals as complex collections of interdependent parts whose behaviors bore nuanced relationships to environmental context and phylogenetic history, and they were keen to incorporate an awareness of those relationships into behavioral studies. Von Frisch's grey card experiments, performed in the 1910s, modeled how productive a reconciliation between such reductive and holist commitments could be. To complement that conceptual perspective on the history of science with a more concrete examination of interpersonal relationships, I also demonstrate how von Frisch's grey card experiments influenced Tinbergen while Tinbergen was a university student and early career academic in the 1920s and 1930s.

All this seems to indicate that von Frisch was an exemplar for classical ethology; his experimental approach had action-guiding force for young Tinbergen and demonstrated the reconciliation of reductionist and holist commitments that Tinbergen and Lorenz promoted as a hallmark of their new science. However, the problem with this conclusion is that Tinbergen did not treat von Frisch as exemplary of the ethological program. That is, after Tinbergen joined forces with Lorenz and began promoting ethology, he did not reference von Frisch's work in the way one would expect a discipline-builder to reference an exemplar. Instead of asking, "What is von Frisch's relationship to ethology?" the question now becomes more pointed. Given these

significant affinities with von Frisch, why did Tinbergen not present von Frisch as an exemplar of ethology?

To answer that question, I examine Tinbergen's references to von Frisch's grey card experiments between 1938 and 1951 and show how Tinbergen and Lorenz's vision for ethology differed from von Frisch's work in key respects. Those differences concerned the proper way to interpret experimental results, preferred animal subjects, the use of conditioning in experiments, choice of explanatory targets, and the practice of reconstructing phylogenies through behavioral traits. Put briefly, von Frisch performed his most famous work on honeybees, those experiments required von Frisch to condition the bees to perform learned behaviors, his experiments produced evidence about the physiology underlying sensory capacities, and he did not engage in the project of reconstructing phylogenies through behavioral traits. These aspects of von Frisch's research did not cleanly mesh with Tinbergen and Lorenz's vision for ethology.

In the next section, I introduce the notion of a scientific exemplar and clarify what it would take for something to achieve that status. In section 3, I provide a close examination of von Frisch's grey card experimental technique that demonstrates how his approach to animals reconciled holist and reductionist commitments. In section 4, I show how von Frisch's grey card experiments influenced Tinbergen and emphasize the affinities between von Frisch's early career research and the program of classical ethology. Finally, in section 5, I answer the question, "Given those affinities, why did Tinbergen not treat von Frisch's work as exemplary?" I conclude by exploring the multifaceted relations von Frisch holds with the discipline of ethology.

2. What Does It Mean to Be an Exemplar for a Developing Scientific Discipline?

Nikolaas Tinbergen and Konrad Lorenz are generally acknowledged as the two primary figures in the founding and promotion of 20th century European ethology. In examining the emergence of ethology as a distinct scientific discipline, Burkhardt (1981, p. 63; 1983, p. 440) has employed an ecological perspective in which scientific disciplines occupy niches and compete for resources. For instance, Burkhardt (1981, p. 63) writes that "The history of scientific disciplines, it would seem, involves the carving out of niches, the defense and expansion of territories, the management of boundary disputes with neighbors, and the placing of demands on contemporary and future resources." Applying that perspective to the emergence of ethology, Burkhardt (1983, p. 440 emphasis in original) writes that "instead of viewing the ethologists as having simply moved into a previously unoccupied niche in the domain of scientific knowledge, it appears more instructive to think of them as having actually *constructed* a niche, and shaped their own ideas in the process." This paper adopts Burkhardt's ecological perspective to explore whether von Frisch's work played an exemplary role in Tinbergen and Lorenz's early efforts to construct a niche for ethology.

To judge whether or not von Frisch's work played that exemplary role, I use Woody's (2003, p. 24) definition of a scientific exemplar: "Exemplars […] display, without explicitly articulating, what a scientific community judges to be explanatory, what model of intelligibility it has chosen to embrace […] An exemplar is an example that, through community sanction, we are urged to follow. It has action-guiding force." The traditional home for scientific exemplars is textbooks. To reproduce themselves,

scientific disciplines must familiarize students with the methodological practices, habits of reasoning, and types of explanations that the discipline deems appropriate. Identifying exemplars is especially important for young disciplines because such disciplines need to inculcate new students to persist and grow. Additionally, exemplars can lend credibility by demonstrating a discipline's ability to successfully solve scientific problems. Exemplars show how the practitioners of a discipline achieve their epistemic aims, and in doing so, they communicate practical details often left unarticulated by general disciplinary definitions.

Using this definition of exemplar, I build the case over the next two sections that von Frisch's early experimental work on animal sensation was well suited to play an exemplary role for ethology as the discipline carved out its own niche in the 1930s and 1940s. The first part of that case is conceptual; von Frisch's grey card experiments embodied some of the key tenets that Tinbergen and Lorenz advertised as the hallmark of ethology prior to WWII. The second part of the case is material; von Frisch's grey card experimental technique had "action-guiding force" for young Tinbergen and demonstrably influenced Tinbergen's approach to experimental research before Tinbergen and Lorenz met in 1936. However, as the fifth section of the paper shows, von Frisch did not satisfy an important criterion of a scientific exemplar. Tinbergen and Lorenz did not fully sanction von Frisch's work as a model to be replicated by ethologists.

In the next section, I argue that von Frisch's grey card experiments exemplified a reconciliation of reductionist and holist commitments that corresponded to Tinbergen and Lorenz's vision for ethology. However, there are a plurality of ways for scientific

investigations to be more or less reductive or holistic, and scientific investigations are only more or less reductive or holistic relative to other scientific investigations. Therefore, to highlight how the practices and habits of reasoning that comprised von Frisch's grey card experiments reconciled reductionist and holist commitments in their own time, I compare von Frisch's grey card experiments with the experiments of two of his contemporaries. Multiple animal researchers in the beginning of the 20th century sought a middle path between controlled experiments directed at reductionist explanations and naturalistic observations that remained sensitive to holistic aspects of animals.[5] What makes the two comparisons I draw in the next section especially relevant to a practice-based analysis of von Frisch's grey card experiments is how uncannily similar they are to von Frisch's experiments. Each experimentalist examined in the next section sought to answer the same question with the same animals via similar methods within five years of each other. Comparing and contrasting these experiments highlights the different ways von Frisch could have implemented and interpreted his experiments on animal sensation and therefore provides contemporaneous benchmarks for assessing what was reductionist and holistic about the investigative decisions von Frisch made with his grey card experiments.

3. Can Fish and Honeybees See Colors? How von Frisch's Grey Card Experiments Reconciled Reductionist and Holist Approaches to Animal Sensation

[5] See, for example, the work of German scientist Wolfgang Köhler (1971) and American scientist Gladwyn Kingsley Noble (Noble 1939; Milam 2010, p. 55–7).

In the early 1910s, multiple researchers were asking the same questions: Can fish see colors? Can honeybees see colors? Von Frisch is remembered as definitely answering both questions in the affirmative. To defend his finding that fish and honeybees can see colors, von Frisch engaged in a public and well-documented feud with the German ophthalmologist Carl von Hess (Hess 1912a, 1912b, 1913; von Frisch 1912, 1913a, 1913b, 1913c, 1914; For commentary, see Warner 1931; von Frisch 1967, p. 48–49; Thorpe 1983, p. 198; Hölldobler 1985; Menzel and Backhaus 1989; Autrum 1990; Kelber et al. 2003; Kelber & Osorio 2010; Munz 2016, Chapter 2; Dröscher 2016). By contrast, von Frisch was largely unaware of the work of Charles Henry Turner (1910, 1911), an American comparative psychologist whose experiments on honeybee color vision anticipated von Frisch's (1914) own experiments (von Frisch 1914, p. 79–80; West-Eberhard 1986; Wehner 2016). Using Hess' and Turner's approaches as a historically relevant comparison class allows one to make more concrete, practice-based claims about what exactly distinguished von Frisch's investigations as being more or less reductive or holistic.

Von Frisch employed multiple experimental strategies aimed at producing evidence for different sorts of explanations throughout his career. Here, I focus on von Frisch's grey card experiments, a strategy that von Frisch used to investigate color vision in honeybees and fish. Von Frisch's grey card experiments were well received by fellow zoologists and influenced other researchers to execute their own versions of the grey card experiment, especially in Germany during the 1920s and 1930s (Kelber et al. 2003). In fact, animal behavior researchers throughout the 20th century continued to perform variations of von Frisch's grey card experiment, solidifying the strategy's reputation as a

scientifically respectable means of answering questions about animals' sensory capacities (Kelber et al. 2003; Horridge 2009, Chapter 1; Kelber & Osario 2010, p. 1621). As I show in the next section, Tinbergen was influenced by von Frisch's grey card experiments prior to his collaboration with Lorenz.

Von Frisch's grey card experiment allows researchers to make inferences about animals' sensory capacities by observing animals' orientation behavior under controlled circumstances. To begin, researchers need an animal that will reliably orient itself toward a goal in a reproducible situation. Often, researchers accomplish that by training animals to orient toward a feeding site. Once the animals are primed to orient themselves to a feeding site, researchers begin training the animal to associate food with a particular color. To achieve that, researchers set out a series of potential food-holders at the feeding site, all of which are various shades of grey, except for one potential food-holder that is colored. When feeding the animals, the researchers only put food in the colored food-holder. If the animal can indeed see the color in question, researchers reason that the animal will come to associate the color with food. Alternatively, if the animal cannot see the color in question, the animal should systematically confuse the colored food-holder with the grey colored food-holder of corresponding brightness. After training the animal to associate the colored food-holder with food, researchers perform the decisive experiment by presenting the animal with the many grey and one colored food-holder, except this time, none of the food-holders contain food. If the animal still orients to the colored food container, researchers have good evidence that the animal can recognize the color in question because the color was the critical cue directing the animal toward the colored food-holder, as opposed to some confounding cue emanating from the food.

3.1 Can Fish See Colors? Contrasting von Frisch's Grey Cards with Hess' Light Box

After defending his thesis in the winter of 1909/1910, von Frisch (1913a) demonstrated that freshwater minnows (*Phoxinus laevis*) can recognize colors by performing the grey card experiment as a research assistant to Richard Hertwig at the University of Munich's Zoological Institute. To train the fish, von Frisch used "rather expensive" custom glass test tubes (Fig. A) that had either grey-scale or colored pieces of paper melted into the walls of each tube. Von Frisch purchased the paper from Ewald Hering's laboratory, where they produced standardized colors for experiments on color perception (von Frisch 1913a, p. 47–48; Munz 2016, p. 41). The tubes had little eyelets at the lip so that von Frisch could hang them in a row by threading a wire through them. To ensure the tubes stayed right-side up when submerged in water, von Frisch weighted the bottom of each tube with balls of shot. Von Frisch then trained the fish for "a few weeks" in diffused daylight coming from the window of his laboratory by submerging the tubes in his fish tanks with food in the colored tube (von Frisch 1913a, p. 44, 48). In his research report, von Frisch advises the reader that "shy" fish are unsuitable, but that such fish can be made tame by keeping them in glass tanks that have no hiding places (von Frisch 1913a, p. 46). He also advises readers not to house too many fish per tank lest the fish begin orienting toward the excited movements of other fish and not the color in question. Once von Frisch had trained the fish to associate a particular color with food, he submerged the tubes with no food and found that the fish reliably swam to the colored tube. Thus, von Frisch concluded that fish possess color vision.

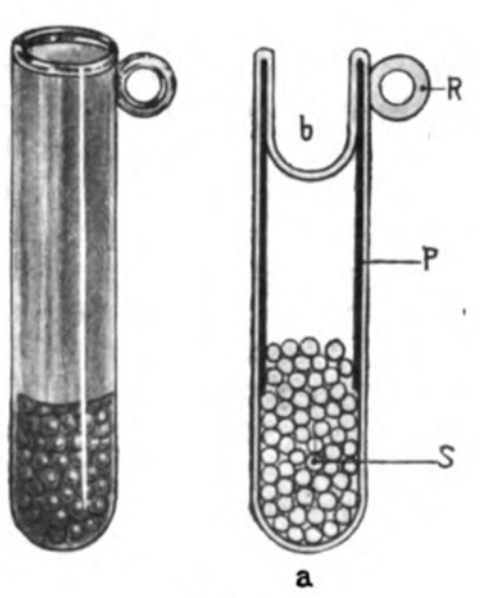

Fig. 1 A black and white illustration of von Frisch's custom glass test tubes. One of the test tubes gives the reader a cross-section view. The little well labeled *b* is where von Frisch placed the food. *R* is the eyelet that allowed von Frisch to hang the test tubes on a wire. The black line along the walls of the tube labeled *P* represents the colored paper melted into the glass. The little balls at the bottom of the tube labeled *S* represent the balls of shot von Frisch used to weigh down the tubes and keep them upright in the water (von Frisch 1913a, p. 47)

That result squarely contradicted the work of Hess (1909), whose experiments on the Mediterranean sand smelt (*Atherina hepsetus*) at the Anton Dohrn Zoological Station in Naples had indicated that fish do not possess color vision. For his experiments, the zoological station provided Hess (1909, p. 2) with one hundred or more fish every two or three days for weeks so that he had worked with over a thousand fish by the end of his trials. Hess only used young fish because older fish tended to be too shy to properly

participate in his experiments. Hess required fresh fish every two or three days because many of the fish died after a day of being held in captivity, and those that survived were often too weak to use in further experiments. The general experimental strategy employed by Hess (1909, p. 3) involved keeping fish in tanks and subjecting them to a dark environment "for at least thirty minutes". Then, using tightly controlled sources of artificial light including incandescent light bulbs, arc lamps, and Nernst lamps, Hess illuminated different portions of the tank with light of varying color and brightness. By observing where the fish swam under different lighting conditions, Hess made inferences about their capacity to see colors.

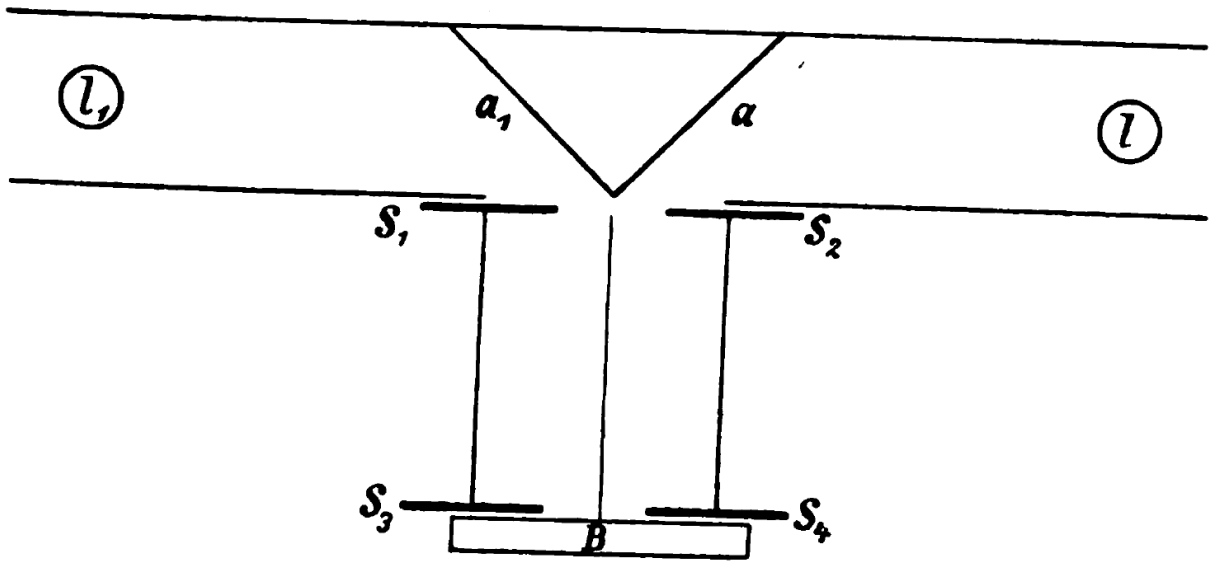

Fig. 2 An illustrated cross-section view of the T-shaped device Hess used to direct different sources of light in the same direction (Hess 1909, p. 31)

One of the most striking versions of Hess' (1909) experiments involved a T-shaped device that allowed Hess to direct light from two different sources in a common direction while keeping the two lights distinct (Fig. B). To use the device, Hess shone light into the two openings facing each other (l, l_1). Two surfaces sprayed with magnesium oxide (a_1,a) then reflected the lights in a common perpendicular direction. The channel into which the light was reflected had a dividing wall that kept the reflected lights separate until they exited the opening. Hess directed the divided lights at his fish tanks and systematically manipulated the color and brightness of each light. He found that the fish generally swam to the brighter of the two lights, irrespective of color, so that he could manipulate the movements of the fish through subtle contrasts in brightness. In Hess' (1909, p. 35) words, "All the facts so far established by us would be in good standing with the assumption that the examined fish are totally color blind, indeed, according to such an assumption one could have predicted the behavior actually observed in detail.[6]"

Hess' and von Frisch's different experimental strategies also led to conflicting results regarding color vision in honeybees. Von Frisch (1914) found honeybees could discriminate between colors while Hess (1913) found they could not. Looking back, the dispute largely resulted from von Frisch and Hess' failure to contextualize their findings (Tinbergen 1942, p. 45, 1951, p. 8; Hölldobler 1985; Menzel & Backhaus 1989, p. 281; Menzel 2004, p. 466; Dröscher 2016, p. 4; Gadagkar 2018b). In his light box

[6] "Alle von uns bisher ermittelten Thatsachen würden gut in Ein klang stehen mit der Annahme, dass die untersuchten Fische total farbenblind seien, ja, nach einer solchen Annahme hätte man das thatsächlich gefundene Verhalten in allen Einzelheiten voraussagen können."

experiments, Hess had created an emergency situation where the animals fled toward the brightest source of light. Von Frisch's grey card experiments, on the other hand, caused animals to exhibit feeding type behavior. Taken together, Hess' and von Frisch's results showed that in the context of feeding, fish and honeybees exhibit an ability to discriminate between colors; in the context of fleeing, fish and honeybees seem to disregard color and move in the direction of the brightest light. So, fish and honeybees can see colors, or to put it more precisely, under some circumstances their behavior indicates that they can distinguish different colors of the same brightness.

Since Hess and von Frisch's dispute centered on the question of whether fish and honeybees can see colors simpliciter, commentators acknowledge von Frisch as the winner and attribute his success to his differing methods. For instance, Dröscher (2016, p. 3–4) argues that von Frisch's and Hess' approaches were "profoundly different" because Hess "acted as an experimentalist, measuring reactions and drawing reductionist conclusions" while von Frisch "acted as a naturalist" and tried to keep the fish "in an environment that was a natural as possible" to "pose biologically meaningful questions". Hess' and von Frisch's experimental strategies did differ, but the difference does not come down to reductionist vs. naturalist. Both von Frisch and Hess were reductionists.

To put it more exactly, both von Frisch and Hess deployed their respective experimental strategies as part of research programs that sought reductionist explanations of animal's sensory capacities. As an ophthalmologist, Hess was deeply familiar with the physiology of eyes and sought to understand how the histological and physiological properties of eyes enable and constrain sensory capacities (Hess 1902, 1905, 1911, 1912b). Von Frisch received his doctoral training in zoology, but he came from a family

of academics who had made significant contributions to neuro-sensory physiology and color theory (Exner, K. 1881; Exner, S. 1885; Exner, S. 1889; Exner, S. 1891; Exner F. S. (II) 1902; Exner F. S. (II) & Exner S. 1910; von Frisch 1989; Coen 2006, 2007). Indeed, von Frisch performed his first formal university research as a first or second year university student under the guidance of his uncle Sigmund Exner, the director of the Institute of Physiology at Vienna University. Exner guided von Frisch through investigations into how nervous stimulation affects eye pigmentation in invertebrates (von Frisch 1967, 32–33). Though von Frisch is most remembered for establishing the existence of unexpectedly sophisticated capacities in animals (e.g. minnows change body pigmentation by perceiving light through a translucent window in their cranium, honeybees can perceive ultraviolet and polarized light, honeybees communicate the distance and direction of food sources to nest mates via a "dance language") von Frisch also sought causal explanations for animal capacities in terms of lower-level physiological dynamics (von Frisch 1908, 1910, 1911; Munz 2017). Furthermore, he trained his doctoral students to pursue research oriented at such reductionist explanations (Baumgärtner 1928; Scharrer, E. 1930; von Frisch & Dijkgraaf 1935; Scharrer, B. 1935, 1937; Löwenstein 1932; Jander & Waterman 1960; Dijkgraaf 1963; Hug et. al. 1964; Boch & Shearer 1971). The difference between Hess' and von Frisch's work is not that one pursued reductionist explanations while the other did not; both Hess and von Frisch sought such explanations.

The key difference between Hess' and von Frisch's experiments is the degree to which those experiments employed a holistic perspective on animal capacities as phenomena that is exhibited in particular contexts for adaptive purposes. Von Frisch's

grey card experiments differed from Hess' light box experiments in that that employed more evolutionary thinking. Von Frisch (1967, p. 48) was initially skeptical of Hess' claim that fish are color-blind because his PhD thesis research had shown that minnows change color according to luminescent properties of their environment, and von Frisch reasoned that an animal exhibiting that capacity would be able to perceive color patterns themselves (Thorpe 1983, p. 198). Similarly, von Frisch (1914, p. 1–5) believed that insects who feed on the nectar of flowering plants would be likely to possess color vision as a means of recognizing food sources. In other words, von Frisch hypothesized that minnows and honeybees can see colors because the way minnows and honeybees interact with their environment suggested that such a capacity would be adaptive. Von Frisch then used that evolutionary reasoning to design experimental situations that caused minnows and honeybees to exhibit their color discriminating capacity.

A brief anecdote from von Frisch's time as director of the Zoological Institute of Rostock University in the early 1920s further illustrates the sense in which von Frisch's research was holistic in its incorporation of evolutionary reasoning. Because the ears of fish lack any structure analogous to the cochlea of terrestrial vertebrates, many scientists at the beginning of the 20th century believed fish were deaf. In his autobiography, von Frisch (1967, p. 83) remembers how one such scientist "whistled to them [catfish] in many different ways, with his mouth, through his fingers, on penny whistles, high or low, but in vain. He even asked a famous singer to sing to them, but the fish were no more moved by her trills and shakes than by his own common or garden whistling. They did not give the slightest sign of sound perception." In response, von Frisch (1967, p. 83–84) reasoned that "If I were a small fish, I should be interested in earthworms and other

delicacies of the kind, but hardly in the coloratura of a famous soprano which normally would not be in the least relevant to my survival." By blinding a captive catfish and training the fish to associate his whistling with food, von Frisch (1923) was able to demonstrate that catfish can hear. Von Frisch did not go on to investigate the specifics of how hearing contributes to the fitness of catfish. He used basic evolutionary reasoning to design an experiment that established the existence of a sensory capacity because the establishment of such a capacity had interesting implications for research on the physiological mechanisms underlying hearing.

The sense in which von Frisch's grey card experiments exhibited a holistic understanding of animals is also reflected in his use of relatively natural environments. As a background condition, keeping aquatic animals in tanks requires extensive maintenance (Muka 2014). Von Frisch kept his freshwater minnows alive for weeks as he trained them, and he attempted to modify the environments of shy fish in a way that would make them experimentally useful. Hess discarded shy fish and was less successful keeping his Mediterranean smelt alive, a species accustomed to brackish water. Nevertheless, Hess overcame that limit on his control by persistently resupplying his stock, a strategy that required the extensive resources of the Anton Dorn Zoological Station and the labor of the "extraordinarily accommodating gentlemen" who worked at the station and supplied Hess (1909, p.2) with fish. Von Frisch's ability and desire to acclimate his fish to his laboratory environment makes his experiments more holistic than Hess' in the sense that he attended to the relationship between his experimental subjects and their environment. However, there is still quite a difference between the paradigmatic image of the naturalist as observing animals in their naturally-occurring environment and

von Frisch's grey card experiments. Like Hess, von Frisch required the artificial technologies of the laboratory to exert the control necessary for his experimental strategy.

When considering von Frisch's and Hess' means of controlling the independent variable of colored light, one reaches a similar conclusion. Both Hess and von Frisch invested in custom technologies to manipulate light. Hess (1909) employed multiple sources of artificial light and light manipulating devices, such as arc lamps, Nernst lamps, filters, mirrors, and lenses. Von Frisch (1913a, p. 48) commissioned custom feeding tubes exhibiting standardized colors for vision research. The difference is that von Frisch conducted his experiments in diffused daylight from his laboratory window. By allowing his fish to become familiar with their laboratory environment and subjecting them to normal daylight, von Frisch was able to make his fish exhibit feeding behavior as needed for his experimental training and trials. Hess' finer control over properties of light allowed him to quantify his results along an extra dimension. But the extreme lights to which he subjected his fish paired with the fact that his laboratory environment caused fish to die within a few days likely contributed to the outcome that his fish performed fleeing type behavior and therefore did not exhibit their capacity to distinguish colors. Von Frisch's experiments were more holistic in the way they attended to the relationship between animals and their environment, but again, keeping fish in aquaria next to a laboratory window is significantly less naturalistic than experimenting on minnows in the fresh water lakes they naturally inhabit.

3.2 Can Honeybees See Colors? Contrasting von Frisch's Grey Cards with Turner's Colored Cornucopias

The von Frisch-Hess comparison highlights holistic features of von Frisch's work. The next comparison highlights reductive features of von Frisch's work. Though von Frisch (1914, p. 79–80) was unaware of it at the time, the American comparative psychologist Charles Henry Turner (1910, 1911) was performing experiments in St. Louis, Missouri, that also indicated honeybees can see color and were very similar to the grey card experiments.

To begin, von Frisch's grey card experiments on honeybees were very similar to his previously described experiment on minnows. To train the bees to associate some color with food, von Frisch set out grey-scale or colored tiles from Hering's laboratory on a table and placed little glass bowls on the tiles (Fig. C). He then placed honey or sugar solution in the bowls on top of the non-grey tiles. Once von Frisch had trained the honeybees to associate a particular color with food for a few days, he set out empty bowls, or no bowls at all on the grid. Demonstrating an ability to discriminate colored squares from grey squares of corresponding brightness, the honeybees reliably navigated to the colored square to which they had been trained. Thus, von Frisch concluded that like minnows, honeybees can recognize colors.

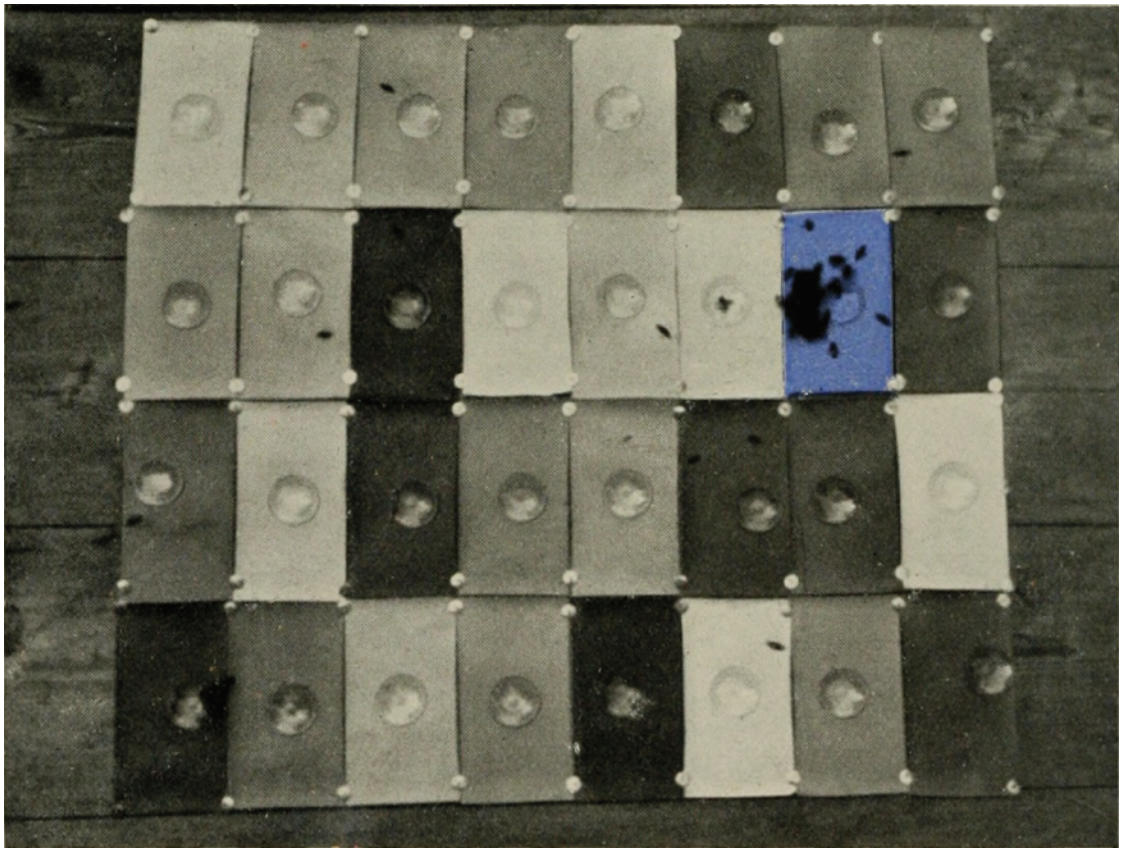

Fig. 3 A photograph of the feeding station used in one of von Frisch's grey card experiment trials. The photograph is black and white and depicts an array of grey scale tiles laid on a table, except for one tile that is colored blue. A little glass food bowl has been placed in the center of every tile. When the photograph was taken, von Frisch had already trained honeybees to associate the blue tile with food. The experimental trial captured in the photograph depicts a group of honeybees congregating exclusively on the blue tile feeding bowl they had been conditioned to associate with food, despite the fact that all of the food bowls on the grey scale tile contain sugar water while the bowl on the blue tile is empty (von Frisch 1914, p. 190)

Unlike with his minnow experiment, von Frisch (1913b, 1913c, 1914) performed his grey card honeybee experiments outdoors at his family's summer property in

Brunnwinkl, Austria. Beginning a pattern that he continued for much of his career, von Frisch studied honeybees when they were active in the summer and fish in the winter. The honeybees von Frisch experimented on came from the domesticated hive of an apiary. In his Munich laboratory, von Frisch was able to feed his captive minnows whenever he wanted, but the honeybees presented more of a challenge. If von Frisch (1914, p. 11–12) filled the feeding bowl every time the foraging honeybees emptied it, he found that his feeding site attracted an unmanageable number of foraging bees. However, when the feeding bowl became empty, he found that most bees quickly flew away from the site. By marking each bee that came to his feeding site with paint to avoid double counting, von Frisch determined that by refilling the bowl every thirty minutes, he could repeatedly attract the same group of roughly 200 individual foragers. To record every instance of a honeybee landing on any of the tiles, von Frisch (1914, p. 9; 1967, p. 56) enlisted help from friends and family vacationing at the Brunnwinkl property. In this way, von Frisch was able to manipulate honeybees' foraging behavior into discrete experimental trails whose results could be quantified with reasonable accuracy.

In stark contrast to von Frisch, who was born into the scientific dynasty of the Exner family in *fin-de-siècle* Vienna (Coen 2006, 2007), Charles Henry Turner was an African American man born in Cincinnati, Ohio, in 1867, two years after the American Civil War (Turner 1902; See also Abramson 2003, 2006, 2009). Turner was probably the first African American to publish in *Science* (Turner 1892), and when Turner earned his Ph.D. in zoology from the University of Chicago in 1907, he was probably the first African American to earn such a degree from that institution (Abramson 2009). Nevertheless, due to the pervasive racism of American academics, Turner was unable to

secure a professorship at a major research university (DuBois 1929; Abramson 2009, p. 348–350). Instead, Turner (1910) performed his experiments on honeybee color vision in a field near Sumner High School in St. Louis, Missouri, a segregated school for African American students where he taught biology.

Rather than work with honeybees from an apiary, Turner (1910) sought to attract wild honeybees for a series of experiments he performed over the course of five consecutive summer days. He began by placing honey on red cardboard discs that he either pinned to existing plants at various heights or attached to stem-like rods he staked in the ground. Initially, the honeybees ignored his feeding site, even after he caught a forager in a bottle and attempted to force the bee onto his honeyed disc. Eventually, Turner succeeded in attracting foragers. He had red colored discs and blue colored discs, but he only placed honey on the red discs. Before ending his first day of experiments, he left three red discs in the field with all the honey they could hold. When he returned the following day, the honey was gone. Over the next four days, Turner continued to reinforce the association between food and the color red by placing honey on red feeding vessels but rarely placing honey on his blue or green vessels. After using discs, he designed cardboard "cornucopia" vessels (Fig. D) that resembled flowers, and then cardboard boxes with little portico entrances. When Turner did put honey on blue or green vessels, the bees mostly ignored them in favor of the red vessels. When Turner (1910, p. 270–271) presented the bees with two empty vessels, one red and one green, the green was mostly ignored while the red became "packed almost full" of bees so that "it was impossible for those that reached the inner depths [of the vessel] to leave […]".

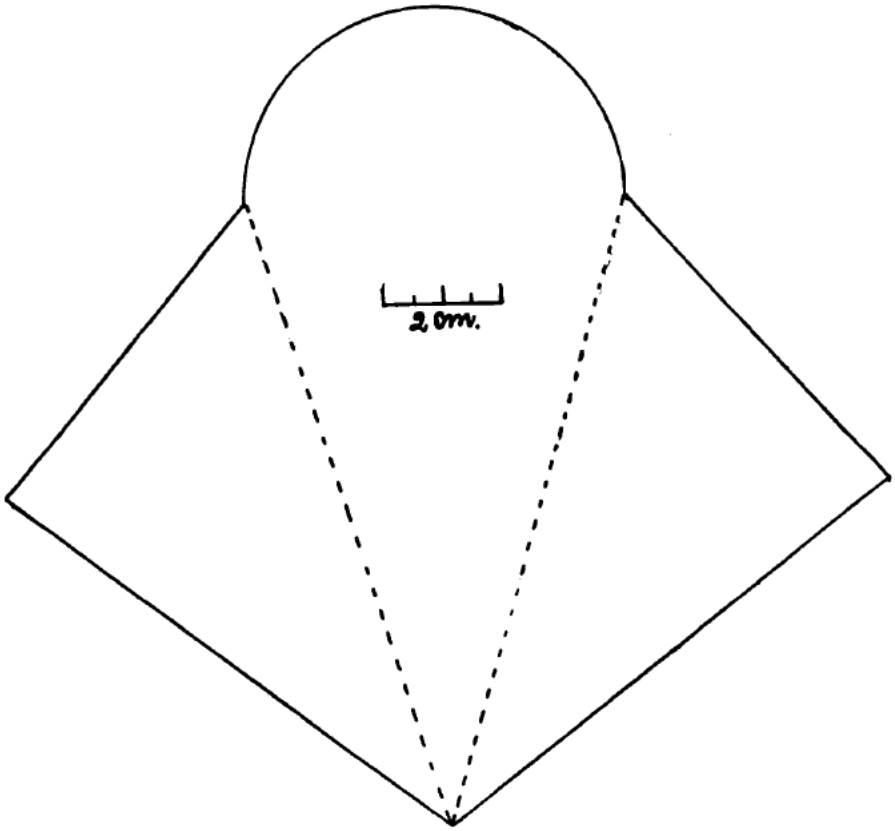

Fig. 4 A black and white illustration of the cardboard cornucopia vessels used by Turner. Turner constructed the vessels by folding along the dotted lines and fastening the overlapping corners to each other to form a funnel with a protruding, semicircular lip (Turner 1910, p. 268)

Turner conceded that his results could be explained by honeybees' ability to discriminate between different shades of grey rather than true color vision. But because he had observed honeybees fly directly to his red vessels when the vessels were in the shade, direct sunlight, or cloud-diffused sunlight, Turner reasoned that the bees could

recognize the color red as distinct from blue or green by means that did not rely on discriminating different shades of grey.

In comparing Turner's and von Frisch's experiments, the most striking contrast has to do with resources and experimental control. In a footnote, Turner (1910, p. 264) writes that "When these experiments were first planned, it was my intention to mark each bee that participated; but, at this stage of the work, I realized that such a procedure would be impracticable and my paint and brush were put away." Such a procedure was quite practicable for von Frisch, who used a paint dot notation technique and timed interval feedings to structure the foraging runs of a known quantity of bees. Like von Frisch, Turner attempts to count the number of bee-landings on each of his feeding vessels to quantify his results into tables. However, unable to produce discrete foraging runs with wild honeybees and lacking assistants to help him count the number of bees landing on his various vessels, Turner has fewer and less reliable quantifications. For instance, the tables Turner (1910, p. 269) does produce contain X's that mean "that the bees were so numerous that it was impossible to make an accurate count." Finally, though both men worked outside, von Frisch used standardized colors and grey-scale tiles to systematically control for the possibility that honeybees discriminate colors solely according to brightness. Turner crafted flower-like feeding vessels, pinned them to existing plants in the honeybee's naturally-occuring environment, and relied upon naturally-occurring variations in brightness. Von Frisch's enhanced control allowed him to produce more decisive, quantitative results; Turner's use of happenstance variations in brightness and wild honeybees made his experimental conditions more similar to naturally occurring conditions and his results less decisive and quantitative.

A subtler contrast between von Frisch and Turner concerns their willingness to make claims about the mental experiences of animals. At the end of his paper on honeybee color vision, Turner (1910) writes, "These experiments prove that, to the bee, my colored discs, my colored cornucopias, and my colored boxes were something more than mere sensations; it seems to me that they were true percepts. To the bees those things had acquired a meaning; those strange red things had come to mean 'honey-bearers,' and those strange green things and strange blue things had come to mean 'not-honey-bearers.'" Based on his observations of sophisticated behaviors in ants and snakes, Turner (1907, 1909) also ascribed "practical judgements" to those animals, a notion Turner (1907, p. 343) described in one paper as "[responding] to stimuli, not as ends in themselves, but rather as means to ends."

Turner's willingness to make inferences about mental operations driving the behaviors he observes is in keeping with his admiration of George Romanes (1883, p. 1–2), an evolutionary biologist whose book, *Animal Intelligence*, contains the following dictum: "Starting from what I know subjectively of the operations of my own individual mind, and the activities which in my own organism they prompt, I proceed by analogy to infer from the observable activities of other organisms what are the mental operations that underlie them." Turner's esteem for Romanes is exhibited by the extraordinary name he gave to his second son, Darwin Romanes Turner.

Von Frisch, by contrast, displayed a career-long reluctance to make claims about the mental life of animals. As Munz (2007, p. 47) argues, von Frisch "believed that the workings of other minds, be they human or non-human, were not accessible to reliable scientific methods, which for him amounted to those of experimental physiology." In a

pronouncement characteristic of his stance on animal minds, von Frisch (1937, p. 9; From Munz 2007, p. 41–47) wrote, "If I have taken to speaking of the psychology of the bees, I still want to make one thing clear up front: I cannot speak of what goes on in the bee's soul, but only of those things which manifest themselves externally." This reserved attitude toward the mental life of animals is also evident in the way von Frisch wrote about his most celebrated and sensationalized discovery. Though von Frisch dubbed certain communication behaviors between honeybee nest mates "the dance language", he was always careful to put the word "language" in scare quotes lest he be interpreted as making deeper claims about honeybees' mental faculties.[7] Unlike Turner, von Frisch's (1914) work on honeybee color vision does not speak to what colors may mean "to the bee."

To sum up, comparing von Frisch's grey card experiments with the work of Hess and Turner shows how von Frisch reconciled reductionist and holist approaches to the problem of animal sensation. The von Frisch-Turner comparison highlights von Frisch's reductionist commitment to explaining animals' sensory capacities in terms of their underlying physiology, and it shows how he used domesticated animals in a tightly controlled environment to generate decisive evidence for those explanations. The von Frisch-Hess comparison, on the other hand, highlights how von Frisch's holistic understanding of organisms as entities affected by environmental context and

[7] For an explicit discussion of von Frisch's justification for using the term "dance language", see von Frisch's (1953) response to a critic who argued that honeybees' communication behaviors do not fulfill the criteria of a true language.

evolutionary history helped him design experiments that caused animals to exhibit the capacities under investigation.

4. The Case for von Frisch as Early Exemplar of Ethology: How von Frisch's Experiments Influenced Young Tinbergen and Embodied an Important Element of the Ethological Program

This section progresses in roughly chronological order. I start by establishing the influence of von Frisch's grey card experiments on young Tinbergen. Then, I establish the conceptual affinities between von Frisch's grey card approach to studying animals and the disciplinary niche Tinbergen and Lorenz sought to claim for early ethology.

In 1925, Tinbergen was 18 years old. He was unsure about attending university until his parents sent him to an ornithological field station for the summer, an experience that helped convince him to enter the University of Leiden as a zoology student (Tinbergen 1985, p. 437; Burkhardt 2005, p. 190; Munz 2005, p. 543). Von Frisch, by contrast, was 39 years old. He had just replaced his former mentor, Richard Hertwig, as the director of the Munich Zoological Laboratory, and during the previous year, he had co-founded *Zeitschrift für vergleichende Physiologie,* a journal that continues to thrive under the title *Journal of Comparative Physiology* (Heldmaier et al. 2014). When Tinbergen was just beginning his academic training in zoology, von Frisch had already established himself as one of the most prominent researchers in the field.

Tinbergen's first contact with von Frisch came through von Frisch's research reports. As a university student, Tinbergen was generally more interested in observing animals and performing experiments than reviewing scientific literature on animal

behavior and identifying influences (Baerends 1991, p. 3–4; Burkhardt 1999, p. 504–5; Kruuk 2003, p. 58–59, 78–81). In light of that tendency, Tinbergen's explicit identification of von Frisch as an early influence during his time as a student is all the more striking. In an autobiographical essay, Tinbergen (1985, p. 440) recalls reproducing some of von Frisch's experiments on animal sensation as a student, experiments which "seemed (and still seem) to me methodologically faultless and beautifully elegant in their sophisticated simplicity […] I had a tremendous admiration not only for his style of research, but also for the way he described it." As shown in the previous section, von Frisch persistently refrained from making inferences about the subjective experiences of animals. This omission must have further endeared von Frisch's research to Tinbergen the student, who was developing a suspicion that he harbored for the rest of his life, that the subjective experiences of animals are inaccessible to scientific investigation (Tinbergen 1985, 439–440, Burkhardt 1997, Kruuk 2003, p. 76–81). Contrary to Dutch animal psychologists like Johannes Abraham Bierens de Haan, Tinbergen sought causal, physiological explanations of animal behavior over psychological explanations. The action guiding influence of von Frisch's research becomes especially evident in Tinbergen's Ph.D. thesis on the orientation behavior of the digger wasp *Philanthus Triangulum*, a thesis that Tinbergen (1932) published in von Frisch's *Zeitschrift für vergleichende Physiologie*.

Digger wasps reproduce by laying eggs in small, self-made burrows that they supply with honeybees whom they have paralyzed and captured. When the wasp's eggs hatch, the larvae eats the paralyzed honeybees. In his thesis, Tinbergen investigated the sensory capacities that enable digger wasps to identify both their honeybee prey and their

nest burrows. Tinbergen (1932, p. 312, 320) explicitly states that his experiments are inspired by von Frisch's grey card training method, and he (ibid., p. 310) calls von Frisch's (1914) research on color vision in honeybees a "classic work," an honorific not bestowed on any other citations. By marking wasps via von Frisch's paint dot technique, Tinbergen (1932, p. 307) was able to keep track of individual wasps and observe that they make multiple burrows (Burkhardt 2005, p. 194). That observation further supported Tinbergen's hypothesis that wasps require some means of remembering and recognizing the locations of their hidden burrows.

To determine whether the wasps used visual cues to recognize their burrows, Tinbergen waited until the wasps constructed a burrow. Then, he placed pinecones around the burrow in a circle. If the wasps used visual cues to identify their burrows, then Tinbergen reasoned that the wasps should come to associate the pinecone formation with their burrow. After allowing the wasps time to make this association in their coming and going from the next, Tinbergen created a decoy burrow about 30 cm away and moved his pinecone formation to the decoy burrow. When wasps returned, they oriented to the decoy surrounded by pinecones, not their actual burrow. In an attempt to control for the possibility that the wasps used scent cues emanating from the pinecones to orient to their burrow, Tinbergen repeated the experiment, but instead of training the wasps to associate a pinecone formation with their burrow, he attempted to train wasps to associate pine-scented oil with their burrow. In another experiment meant to control for scent cues, Tinbergen employed von Frisch's (1921) method of using "bee scissors" to amputate the antennae of the wasps. Both the pine oil and amputated antennae experiments indicated that wasps do not use scent cues to orient to their burrows.

Finally, in a clear reproduction of von Frisch's grey card experiments, Tinbergen (ibid, p. 320) uses the same standardized colors and grey-scale tiles from Hering's laboratory to test whether the wasps can discriminate between colors. He trained wasps to associate a colored square with the location of their burrow. Then, he replaced the colored square with a grey square of corresponding brightness and placed the colored square next to a decoy burrow. The wasps continued to orient to the real burrow with the grey square, indicating they may not be able to recognize colors. However, Tinbergen (1932, p. 324; translation from 1933, p. 122) remains cautious and avoids the over generalizations that characterized the Hess-von Frisch feud when he writes that "It must be emphasised that this in no way implies that *Philanthus* is unable to perceive colour; it is quite possible that, with the aid of 'natural' landmarks, colour vision could be demonstrated." This seemingly minor divergence between the way Tinbergen and von Frisch interpret their grey card experiments will come to play a major role in the way Tinbergen references von Frisch after Tinbergen partners with Lorenz to promote ethology.

After completing his Ph.D., the newly married Tinbergen left for an expedition to Greenland with his wife, Elisabeth Amélie Rutten. When he returned in the fall of 1933, Tinbergen stayed on at the University of Leiden as an assistant. Here, Tinbergen began training his own group of university students. He established a summer field site at Hulhorst where he brought students to continue digger wasp experiments along the lines of his thesis work (Tinbergen 1935; Tinbergen & Kruyt 1938; Tinbergen & van der Linde 1938; Baerends 1941). One of Tinbergen's students during this time, Gerard Baerends (1991, p. 12–13) remembers how the work of von Frisch influenced their studies: "For

the study of causal mechanisms, the work of behavioural physiologists such as Von Uexküll and Kühn, but above all that of Karl von Frisch, was even more important. Von Frisch can be said to have founded the art of making an animal answer questions; this was exactly what Niko needed and wanted to extend to his own experiments. Von Frisch's approach inspired various studies of the Leiden group on how animals perceive and recognize those stimulus situations in their environment that are of biological significance to them." Von Frisch's work had action-guiding force not just for Tinbergen during his doctoral research, but also for the community of young researchers coalescing around Tinbergen immediately after his doctorate (Baerends 1985, p. 18). In the remainder of this section, I establish the affinity between the way von Frisch reconciled holist and reductionist approaches to animal behavior and Tinbergen's and especially Lorenz's theoretical characterization of ethology.

Tinbergen began the project of promoting ethology as a distinct discipline in 1936 after meeting Lorenz, who had already formulated the theoretical basis for the new discipline of ethology prior to their meeting. Lorenz received his first doctorate in medicine from the University of Vienna in 1927 and his second doctorate in zoology from the same institution in 1933. Like Tinbergen, Lorenz the student was an unsystematic reader (Brigandt 2005, p. 580–581; Burkhardt 2007, p. 142). He drew more from personal mentors like the anatomist Ferdinand Hochstetter and the ornithologists Oskar Heinroth and Erwin Stresemann. In contrast to Tinbergen, whom his colleagues have described as "pathologically modest" (Kruuk p. 11), Lorenz developed an early conviction that he "knew animals" to a greater degree than most scientific authorities and that he possessed an extraordinary ability to observe and make intuitive judgements about

animal behavior. In a monograph published in 1935, Lorenz (1935, p. 151) wrote that outside his own observations of animals, he could only trust the observations of a few animal researchers whom he personally knew and trusted. Tinbergen quickly became one of those trusted researchers after the two met at a 1936 symposium on instinct at Leiden University. The two agreed that Tinbergen's experimental work provided an ideal counterpart to Lorenz' theoretical work,[8] and they began to plan future collaborations that would further Lorenz's well-developed programmatic ambitions to grow ethology into a major discipline.

A key element of Lorenz's vision for ethology was a reductionist commitment to causal physiological explanations over psychological explanations (Brigandt 2005). In tracing the influences behind this commitment, Brigandt (2005, p. 593) suggests that Lorenz's training in medicine at the University of Vienna predisposed him to favor physiological explanations. In light of that suggestion, it is interesting to note that like Lorenz, von Frisch also began his university studies as a medical student at the University of Vienna before switching to zoology. Concerning his time as a medical student at the same institution a few decades earlier, von Frisch (1967, p. 33–34) recalls that "What one is taught about the histology, anatomy, and physiology of the human body during the first 2 years of a medical course is far more detailed and thorough than anything one learns about any one animal in the course of normal zoological studies, and I have always rated this knowledge as pure gain. It provided me with a solid foundation

[8] In an interview with Burkhardt (2007, p. 203, 526, emphasis in original) Tinbergen remembers that upon introducing Lorenz to his experimental work, Lorenz exclaimed, "This is just what *I* need!"

and a permanent point of reference for all investigations into the structure and function of animal organs." Though Lorenz's research was more observational and much less experimental than either von Frisch's or Tinbergen's, Lorenz characterized ethology as a discipline that would produce decisive evidence for causal physiological explanations. As demonstrated in the previous section, von Frisch and his students were already performing that kind of research.

Tinbergen also stressed the link between ethology and reductionist physiology. In a 1939 practicum he designed for his animal behavior students at Leiden University, he wrote, "The scientific approach of this analytic ethology, as it is used in this practicum, is thus in principle the same as that of physiology, when this is viewed as the study of the actions of the animals, and there is no objection to considering this ethology a branch of physiology."[9] Additionally, Tinbergen's (1942) last publication before becoming a prisoner of war during WWII, titled "An Objectivistic Study of the Innate Behaviour of Animals." features many explicit arguments tying ethology to physiological reduction. Finally, Tinbergen and Lorenz's efforts to associate classical ethology with experimental physiology also bolstered their discipline building efforts in a more sociological way by conferring the prestige of experimental physiology to the new the science of ethology (Burkhardt 1981, p. 79–80; 1999, p. 502; 2005, p. 218). In an unpublished and undated manuscript for a talk Lorenz delivered at the end of his career, he stated that "The further progress of ethology was due mainly to Niko Tinbergen whose inspired yet circumspect experimentation did much to make ethology recognized as a 'respectable' branch of

[9] From Burkhardt (2005, p. 218–219, 530–531).

biological science."[10] The respectability of reductive experimental physiology served as an important counter weight to another key element of Lorenz's vision for ethology: the importance a holistic perspective and naturalistic observations.

One month prior to meeting Tinbergen for the first time, Lorenz sent a letter to Stresemann where he lamented the fact that so many physiological chemists are unable to see animals as an "organic whole."[11] The word "Ganzheit," which has been translated here as "whole," often appears in Lorenz's arguments for a holistic conception of animals (Brigandt 2003), especially in Lorenz's Russian Manuscript, a strikingly philosophical work that Lorenz wrote while a prisoner of war during WWII. The English translator of that manuscript writes in a foreword that "Ganzheit" might better be translated as "totality" (Martin 1996, p. xxi). Lorenz (1996, p. 209) is quite clear about how overly mechanistic research suffers from an inability to view animals in their totality, and he situates the ethological approach to animal behavior as a middle ground between such overly mechanist schools and the vitalist school: "If the vitalists created a supernatural 'factor' on the basis of the holistic Gestalt or organic phenomena, in the face of which any attempt at analysis would have been tantamount to sacrilege, the mechanists retreated almost voluntarily into blindness to the [Ganzheit] accompanied by an extreme, methodologically fallacious atomism." (Russian manuscript, p. 209; "Ganzheit" left untranslated). Despite the failings of overly mechanistic approaches, Lorenz (1996, p. 195 emphasis in original) is clear about his desire to reconcile holistic understandings of

[10] From Burkhard (2005, p. 203, 526).
[11] Original text of letter from Brigandt (2005, p. 588): ''Ich kenne aber so viele Physiologische Chemiker, die alle ganz unfähig sind, im Tier eine organische Ganzheit zu sehen.'' (Lorenz, letter to Stresemann, October 4, 1936).

behavior with reductionist analyses: "Because of their [the mechanists] fearless—one is almost tempted to say disrespectful—causal analytical approach to the most complex of problems, indeed because of their conscious simplism, they have achieved major and lasting success in their research. Seen merely as a working hypothesis, mechanism is not only enormously fertile; it is simply the only legitimate approach available to the research worker […] It is a *question of belief* whether one feels in one's heart that there is something supernatural that is immune to research. As a *researcher*, however, one *must* be a mechanist."

As demonstrated by the von Frisch-Hess comparison, von Frisch's research successfully incorporated a holistic understanding of animal behavior in the sense that von Frisch considered the effect that environmental context has on animal behavior when designing his experiments. He also considered how a particular behavior or capacity fit into an animal's general life strategy, and that holistic perspective informed the way von Frisch formulated and tested hypotheses. The major conclusion of this section, then, is that von Frisch's work influenced young Tinbergen and prefigured two key elements of the ethological approach to animals that Tinbergen and Lorenz championed in the 1930s and 1940s. Thus, there seems to be a strong case for viewing von Frisch as an exemplar for early ethology. The problem with that case, as I will show in the next section, is that Tinbergen did not treat von Frisch's work as exemplary.

5. Why Did Tinbergen Not Treat von Frisch as an Exemplar of the Ethological Program? A Multifaceted View of von Frisch's Relationship to the Discipline of Ethology

Remember that scientific exemplars achieve their exemplary status when a scientific community urges its practitioners to follow them. Remember also that exemplars are likely to be found in textbooks or other places where disciplinary programs are summarized and promoted. Given the trajectory of this paper so far, it is surprising to see that although Tinbergen referenced von Frisch's work after joining with Lorenz to promote ethology, Tinbergen did not refer to von Frisch's work as exemplary. Instead, Tinbergen framed von Frisch's interpretations of grey card experiments—the same experiments Tinbergen had recreated as part of his doctoral thesis—as an object lesson in what not to do. Specifically, Tinbergen invoked von Frisch's feud with Hess as a cautionary tale about the mistakes experimentalists make when they do not adopt the ethologist's observational methods or holistic approach to behavioral analysis.

Classical ethology lacked texts that were comprehensive and accessible enough to qualify as textbooks prior to WWII. The best candidate for ethology's first textbook comes after WWII, in the form of Tinbergen's 1951 book, *The Study of Instinct*. Here, Tinbergen (1951; 1969, p. 7–8) references von Frisch's work in a section titled, "Ethograms." Ethograms describe and catalogue an animal's behavioral repertoire, or the actions an animal normally performs in a variety of naturally-occurring situations. As characterized by Tinbergen, a properly ethological approach to animal behavior begins with the creation of an ethogram. Without a baseline understanding of an animal's behavioral repertoire, researchers are ill equipped to analyze the significance of any particular behavior type.

Tinbergen uses the von Frisch-Hess feud over color vision to illustrate this point. Tinbergen (1951; 1969, p. 7–8) writes: "Special emphasis should be placed on the

importance of a complete inventory of the behaviour patterns of a species. It is a natural tendency of the experimental worker to select a special problem, as, for instance, colour vision, or homing, or the delayed response. This specialization is often accompanied by a narrow point of view and a neglect of other aspects of behaviour. The resulting generalizations, based on too limited a foundation, may give rise to sterile controversies." Then, after summarizing von Frisch's and Hess' approach to the problem of color vision, Tinbergen (1951; 1969, p. 8) concludes that "a species may be able to distinguish between colours and, in a way, be colour-blind as well […] Knowledge of the whole behaviour pattern helps us to recognize the relative value of each one of these conclusions and prevents us from describing as incompatible the conclusions drawn from the study of what prove to be two differs sorts of behaviour." Von Frisch considered the adaptive value color vision would have for foraging honeybees and feeding minnows, and he used those considerations to design experiments that demonstrated those animals' capacity to discriminate between colors, but he did not acknowledge the possibility that those animals do not exercise that capacity in all behavioral contexts.

Though *The Study of Instinct* may have been ethology's first textbook, it was not the first place Tinbergen used the von Frisch-Hess controversy to construct a niche for the new discipline of ethology. In 1938, two years after meeting Lorenz, Tinbergen became the first to personally promote European ethology in the United States when he presented at a conference titled "Plant and Animal Communities" at Cold Spring Harbor, New York (Burkhardt 2005, p. 215–217). Tinbergen's (1939, p. 228) presentation was published one year later, and just like his 1951 reference of the von Frisch-Hess dispute, Tinbergen uses the controversy to make the point that "no experiments should be started

before simple observation of behavior in natural surroundings has discovered the outlines of the behavior pattern." Finally, Tinbergen referenced the von Frisch-Hess dispute over color vision to make the same point in his 1942 paper "An Objectivist Study of the Innate Behaviour of Animals" and in a lecture Tinbergen (1947) gave upon assuming the chair of experimental zoology at the University of Leiden in 1947. I have argued that the von Frisch-Hess comparison highlights the holistic aspects of von Frisch's experimental approach to animals, yet when Tinbergen the discipline builder looked back to that conflict, he found that von Frisch's approach was not holistic enough.

There are a few other broad differences between von Frisch's research and the disciplinary niche Tinbergen and Lorenz sought to claim for ethology that help explain why von Frisch was not explicitly identified as an exemplar of early ethology. First, Tinbergen and Lorenz promoted ethology as a discipline that investigated instinctive or innate patterns of behavior, and to produce evidence about such behaviors, they championed the study of wild, undomesticated, or unconditioned animals (Lorenz 1935, 1937; Tinbergen 1942; Tinbergen 1985, p. 444–446; Brigandt 2005). Much of von Frisch's work, on the other hand, focused on sensory physiology, and to produce evidence about animals' sensory capacities, he designed behavioral experiments that required researchers to train animals to perform conditioned behaviors. Thus, both the explanatory target and methodology of von Frisch's work were askew from the advertised focus of early ethology.

Second, Lorenz was clear that part of the theoretical foundations of ethology included the idea that instinctive behaviors could be used to reconstruct phylogenies in the same way biologists used morphological traits to reconstruct phylogenies (Lorenz

1932, 1935, 1955; Burkhardt 2005, p. 134). After WWII and in collaboration with one of his students, von Frisch hypothesized about the phylogenetic age of different versions of the honeybee dance language (von Frisch and Lindauer 1956, p. 48), but reconstructing phylogenies via instinctive actions was not a major part of von Frisch's research. In contrast, the two men whom Lorenz credited with the insight that instincts can be used to reconstruct phylogenetic relationships—Charles Otis Whitman and Oskar Heinroth—were often framed as exemplary forerunners of classical ethology.

The final difference between von Frisch's work and the program of early ethology can also be highlighted by contrasting von Frisch with Whitman and Heinroth. Although ethology was never promoted as a science that exclusively focused on bird behavior, birds were one of the most favored animal subjects of early ethology, especially for Lorenz (Burkhardt 2005, p. 140–1, 147; Munz 2011). Many of Lorenz's early manuscripts were published in the ornithological journal, *Journal für Ornithologie* (Lorenz 1927, 1931, 1932, 1933a, 1933b, 1934, 1935). And again, Whitman and Heinroth, the two men whom Lorenz often referenced as forbearers of ethology, specialized on birds. Von Frisch, by contrast, primarily worked with fish and honeybees.

So far, this paper has focused on fleshing out von Frisch's relationship to ethology via his relationship to Tinbergen in the period between Tinbergen's doctoral work in the 1930s and Tinbergen's publication of *The Study of Instinct* in 1951. The story has been that von Frisch's grey card experiments influenced Tinbergen prior to Tinbergen's 1936 meeting with Lorenz. Once Tinbergen became a fellow discipline builder alongside Lorenz, Tinbergen began referencing von Frisch's work as a cautionary tale that highlighted one of ethology's contributions to animal behavior studies. Before

concluding, I will briefly look forward to make the point that von Frisch not only meant different things at different times to Tinbergen, but also to different researchers working under the ethological banner.

The subject deserves a paper of its own, but it is clear that von Frisch is regarded as a pioneering figure by a German speaking tradition of social insect researchers who continue to lead prominent research programs. This lineage largely passes through Martin Lindauer, one of von Frisch's most influential students who completed his doctoral training under von Frisch in 1947 (Marler and Griffin 1973, 464; Seeley et al. 2002; Menzel 2004, 464; Wehner 2013, 3). In the 1960s, Lindauer mentored Berthold Hölldobler, Rüdiger Wehner, and Randolf Menzel, three prominent social insect researchers who explicitly view Lindauer and von Frisch as exemplary figures for their style of investigation (Hölldobler 1985; Lindauer 1985; Menzel 2004, 2007; Smith 2013; Wehner 2013; Dyer et al. 2015; Dhein 2017). The disciplinary label of "ethology" continues to be promoted by Wehner and Menzel, who claim the title of "neuroethologist".

Finally, to include one more strand to the story, it is interesting to see how, after WWII, Lorenz looked back to von Frisch's research program and, as he did with many things (Burghardt 1982; Burkhardt 2005, p. 179; Schulze-Hagen & Birkhead 2015, p. 14–15), attempted to incorporate its success into his own overarching theory of animal behavior research. Arguing for the importance of animal watching via his theory of Gestalt perception, Lorenz (1962) wrote:

> The accumulation of facts stretching across long periods of time which represents the analogy of the inductional basis for the ratiomorphic perceptional

> achievement, offers an explanation of the fact that great discoveries by the same scientist dealing with the same subject are often several decades apart. For example, Karl von Frisch published his first work on bees in 1913; in 1920 he wrote for the first time on their ability of communication by dances; in 1940 he discovered the mechanisms of orientation according to the position of the sun, which presumes an 'inner chronometer,' as well as a means of indicating direction in the hive. (This operates through transposing the direction of the sun by 'symbolizing' it in the dances by the vertical direction.) In 1940 he discovered the amazing 'computer' which can ascertain the position of the sun by the polarization plane of the light from the blue sky. However much diligent experimenting and conscientious verifying is contained in these great discoveries of a great scientist, it is not accidental that they took place during the scientist's vacation and were made with his own beehives in his summer home [Brunnwinkl]. For one of the most pleasant properties of gestalt perception is that it is most active in gathering information when the perceiver, absorbed in the beauty of his object, imagines himself to be enjoying the most profound spiritual peace.

Lorenz's narrative represents a reflexive reinterpretation of von Frisch's work. Whereas Tinbergen criticized von Frisch between 1938 and 1951 for not bringing a holistic understanding of an animal's behavioral repertoire to bear on the interpretation of grey card experiments, Lorenz looked back on von Frisch's research in the 1960s to exalt von Frisch's supposedly immersive style of animal observation and thereby bolster his own theory of gestalt perception. Surely, one of the reasons Tinbergen and Lorenz's

relationship to von Frisch's research changed over time is the fact that von Frisch's research also changed and developed over time. This paper has largely focused on von Frisch's early career grey card experiments. But after WWII, von Frisch became tightly associated with his discovery of the honeybee dance language, a discovery that was widely popularized outside academia (Munz 2016). Given von Frisch's rise to prominence, it makes sense that Lorenz sought to capitalize on von Frisch's increased notoriety. The way Tinbergen and Lorenz related to von Frisch's work was historically mobile and defies easy encapsulation.

6. Conclusion

So, what is von Frisch's relationship to the discipline of ethology? The conclusion of this paper is that there is no single category that captures von Frisch's multi-faceted relationship to the discipline, a fact that is reflected by historians' inability to articulate a consensus account of why von Frisch's work was important for ethology. Although von Frisch never seems to have used the term "ethology" himself (Thorpe 1979, p. 64), his work meant different things at different times to different figures within the ethological tradition. For Tinbergen the university student and early career academic, von Frisch's grey card experiments were a formative influence. Then, once Tinbergen assumed the role of fellow discipline-builder alongside Lorenz, von Frisch's interpretation of the grey card experiments became a cautionary tale that helped Tinbergen claim a disciplinary niche for ethology by highlighting the need for a properly ethological approach to animals. While Tinbergen became the figurehead of ethology after WWII (especially in the English-speaking world), von Frisch produced a lineage of

students, some of whom currently identify as neuroethologists and treat von Frisch as a pioneering figure. Finally, for Lorenz in the 1960s, von Frisch's research program was a case study whose illustrious reputation reinforced Lorenz's own theory of animal behavior research. This paper has provided grounds for the pervasive sense that von Frisch was important to the discipline of ethology and has begun the task of specifying how exactly von Frisch fits into the larger story of ethology.

Chapter 3: The Cognitive Map Debate in Insects: A Historical Perspective on What Is at Stake

1. Introduction

The cognitive map has been called "one of the holy grails of cognition" (Breed 2017, 57), "an unwarranted exercise of anthropomorphism" (Shettleworth 2010, 310), "one of the most important neuroscientific results in recent decades" (Shea 2018, 113), and an "a priori assumption" that "should be abandoned" (Benhamou 1995, 211). Mammalian navigation researchers have long held the cognitive map to be an established fact (O'Keefe and Nadel 1978; Gallistel 1990; Lisman et al. 2017). However, in insect navigation research, the cognitive map hypothesis has engendered an ongoing, decades-long debate featuring many of the field's most prominent researchers. Others have examined the history of the cognitive map in mammalian navigation research (Jensen 2006; Johnson and Crowe 2009; Burgess 2014; Pfeiffer and Foster 2015), but that story has yet to be connected to its latest development in insects. Philosophers of science have scrutinized the cognitive map (Bermudez 1998, Chapter 8; Camp 2007; Rescorla 2009, 2013, 2017; Bechtel 2016; Knoll and Rey 2017; Shea 2018, Chapter 5; Mollo 2020; Robins et al. 2020), but instead of examining the cognitive map as a contested concept shaped by its own history of inquiry, they invoke the cognitive map as an established scientific case study ready to inform theorizing about content and cognition. In this paper, I remedy both of these gaps by combining historical and philosophical approaches to

provide a new perspective on the following question: What is at stake in the cognitive map debate in insects?

My focus on the disciplinary and methodological dimensions of the cognitive map debate produces two insights. First, I argue that the crux of the debate is methodological rather than definitional. Contrary to existing commentary that implies the cognitive map debate persists due to definitional confusion (Bennett 1996; Dyer 1998, 146; Rescorla 2013, 89), I argue that the debate persists because competing research groups are guided by different constellations of epistemic aims, theoretical commitments, preferred animal subjects, and investigative practices when justifying claims about how insects utilize neurosensory representations. As a result, competing groups do not universally endorse each other's claims about the way insects employ representations. Despite the variety of definitions scientists have proposed for the cognitive map, the competing research groups constituting the debate still largely agree about how neurosensory representations interact to produce a cognitive map.

The second insight of this paper involves situating those different epistemic aims, theoretical assumptions, investigative practices, and evidential norms within the broader history of animal navigation research. From a historical and sociological perspective, the heads of the pro-cognitive map group and the anti-cognitive map group in insects have an interesting relationship. Rüdiger Wehner (b. 1940–) and Randolf Menzel (b. 1940–) were trained in the same ethological research tradition by the same mentor at the same time, and in 1990, they agreed that ants and honeybees *do not* possess a cognitive map (Wehner and Menzel, 1990). But as the scientists continued to develop their own prominent research programs through the 2000s, Menzel changed his position and began

to argue that honeybees do possess a cognitive map (Menzel, 2000; Menzel and Giurfa 2006; Cheeseman et al. 2014; Menzel 2019) while Wehner continued to challenge the cognitive map by developing alternative hypotheses (Wehner et al. 2006; Cruse and Wehner 2011; Hoinville et al. 2012; Hoinville and Wehner 2018; Wehner 2020). By relating Wehner's and Menzel's justificatory practices to larger disciplinary themes in the history of animal behavior research, I show that more is at stake in the cognitive map debate than the truth value of propositions characterizing insect cognition. Wehner and Menzel's competing ways of knowing animals represent competing visions for the future of their shared research tradition.

An added benefit to examining the history of major scientific debates is that it provides genealogical insight into why a debate looks the way it does (Lennox 2001). Why, for instance, has the debate fixated on desert ants and honeybees? Why are so many of the participants associated with research institutions in German speaking countries? As evidenced by the range of attitudes scientists and philosophers hold toward the cognitive map, the concept has different standing in different academic communities. It is my hope that examining the genealogy of events that led to the cognitive map debate in insects will provide academics with a common foundation for making sense of the confusion surrounding the cognitive map.

In the next section, I review historical and philosophical treatments of the cognitive map hypothesis and indicate how the expanded history provided by this paper advances that scholarship. In section three, I present my expanded history of the cognitive map debate in insects. Then, in sections four and five, I show how that

expanded history sheds new light on the debate and philosopher's invocation of the cognitive map as a case study.

2. The History and Philosophy of the Cognitive Map

When commentators introduce the cognitive map hypothesis, they usually provide an account of the hypothesis' origin that list the same string of events (Jacobs 2003; Shettleworth 2010, 296–312; Bechtel 2016, 1296–1297; Breed 2017, Chapter 17; Gallistel 2017; Oess et al. 2017; Zhao 2018; Lahr and Donato 2020; Robins et al. 2020). Taken together, these accounts have coalesced into a canonical narrative of the cognitive map's origin and rise. The account begins with American behavioral scientist Edward Tolman's 1948 publication, "Cognitive Maps in Rats and Men," where Tolman argues that rats possess a trait called a "cognitive map" after reviewing the results of multiple laboratory maze experiments. Because Tolman proposed his hypothesis against the backdrop of American behaviorism, this event is often interpreted a harbinger of the so-called "cognitive revolution" in mid 20th century psychology (Greenwood 1999, 9–10; Mandler 2002; Hobbes and Chiesa 2011, 391; Gallistel 2017, R108). Tolman's cognitive map hypothesis received renewed attention in 1978 when John O'Keefe and Lynn Nadel published *The Hippocampus as a Cognitive Map*. The cognitive map was then formally vindicated in 2014 when John O'Keefe, May-Britt Moser, and Edvard Moser won the Nobel Prize in Physiology or Medicine for their work on the neuro-cellular basis of rats' cognitive maps. In the 70 years since Tolman's (1948) original proposal, scientists have argued that chimpanzees, honeybees, sea turtles, pigeons, bats, fish, frogs, and humans navigate by means of cognitive maps (Boesch and Boesch 1984; Gould 1986; Casini et

al. 1997; Lopez et al. 2001; Bingman 2011; Bshary & Brown 2014; Epstein et al. 2017; Genzel 2018; Liu et al. 2019; Harten et al. 2020). Thus, on the canonical account, the cognitive map appears to be one of the oldest, most established, and most widely investigated cognitive traits in experimental behavior research.

This paper expands upon the canonical account of the cognitive map. Thus far, the historiography surrounding the cognitive map hypothesis has focused on mammalian navigation research. I supplement that story by connecting it with the history of the cognitive map debate in insect navigation research. Given the cognitive map's high status and longstanding influence, the expanded history provided by this paper contributes to the broader project of illuminating the historical and conceptual foundations of cognitive science. More immediately, an important upshot of the expanded history is that it counterbalances the canonical account's triumphalist view of the cognitive map with a narrative that emphasizes scientific disagreement surrounding the cognitive map hypothesis. This shift has significant consequences for philosophers' use the cognitive map as a case study.

Philosophers tend to treat the cognitive map as a successful case study ready to inform theorizing about mental representations and cognition (Bermudez 1998, Chapter 8; Camp 2007; Rescorla 2009, 2013, 2017; Bechtel 2016; Knoll and Rey 2017; Shea 2018, Chapter 5; Mollo 2020; Robins et al. 2020).[12] This attitude makes sense given the

[12] Burge (2010, 510) acknowledges the debate more than most and Zappettini and Allen (2013) and Mikhalevich (2017, 432) engage directly with the controversy surrounding the cognitive map hypothesis in insects.

canonical account of the hypothesis' rise. Furthermore, Gallistel's (1990) work on learning and memory seems to have been especially influential among philosophers interested in the cognitive map, likely because Gallistel engages with philosophical issues surrounding mental representation and cognition so explicitly. However, Gallistel is a pro-cognitive map partisan, and the influence of his work contributes to philosopher's acceptance of the cognitive as a well-established hypothesis. The expanded history of the cognitive map provided here challenges philosopher's use of the cognitive map, especially when philosophers appeal to literature from insect navigation literature.

For example, although Rescorla (2013) acknowledges that the cognitive map hypothesis has been contested in insect navigation, he ultimately sides with the pro-cognitive map honeybee group. He then draws on that honeybee research to critique Millikan's teleosemantics. One of his critiques focuses on Millikan's (1984, 99) "pushmi-pullyu" representations, which are supposed to combine imperative and indicative content in a way that "connect states of affairs directly to actions, to specific things to be done in the face of those states of affairs". Millikan (2004, 18–19) has suggested that insects exclusively utilize pushmi-pullyu representations. Rescorla (2013, 99) objects that "Current science supports a clean division between 'informational' and 'motivational' elements in honeybee cognition." The problem with Rescorla's objection is that the current science he appeals to heavily favors pro-cognitive map honeybee research (e.g. Menzel 2008) while excluding competing anti-cognitive map models of insect navigation that do not cleanly divide motivational and informational elements (i.e. Cruse and Wehner 2011; Hoinville et al. 2012). Rescorla's objection loses force because it ignores the anti-cognitive map side of the cognitive map debate in insects.

A similar problem affects Knoll and Rey's (2017) analysis of insect navigation research. Although Knoll and Rey do not explicitly analyze the cognitive map hypothesis, the scientific literature they appeal to is taken from the cognitive map debate in insects. After analyzing this literature, Knoll and Rey (2017, 20) "tentatively conclude" that desert ants lack intentional representations while honeybees possess fully-fledged intentional representations. The problem with this argument is that the scientific literature Knoll and Rey appeal to comes from two opposed groups: the anti-cognitive map desert ant group and the pro-cognitive map honeybee group. This discrepancy matters because the points at issue in the scientific debate bear directly on Knoll and Rey's typology of representations. Knoll and Rey (2017, 21 footnote 15) acknowledge that they are drawing from conflicting sources of evidence and they justify this discrepancy by claiming that they are exploring the implications of each group's research "[f]or the sake of clarifying the distinctions we are after". But if the goal is only to clarify conceptual distinctions, then why draw tentative conclusions about the sorts of representations ants and honeybees actually utilize?

The historical context provided by this paper suggests a different framing for Rescorla's objection to Millikan and Knoll and Rey's argument that avoids the dilemmas described above while providing a fresh interpretation of their conclusions. As it stands, Knoll and Rey gloss over scientific disagreement to highlight conceptual distinctions while Rescorla ignores the anti-cognitive map work of desert ant researchers to critique the way Millikan mixes motivation with information. However, the historical context provided by this paper shows how Knoll and Rey's conceptual distinctions and Rescorla's objection actually capture important differences at the heart of the cognitive

map debate in insects. Knoll and Rey correctly recognize that the desert ant group produces results that imply a different view of how representations are utilized than the honeybee group. Instead of taking this discrepancy at face value, I provide a historical perspective on why these competing research groups perform work that supports different conceptions of mental representation and cognition in the first place. Similarly, Rescorla identifies an important fault line in the cognitive map debate when he examines the relationship between motivational states and informational states. Instead of endorsing one side of the debate and using that position to critique or support a general theory of content, I provide a historical narrative that shows why the relationship between motivation and information is so central to the cognitive map debate in insects. In short, this paper undermines philosopher's appeals to insect cognitive map research while providing a novel perspective that vindicates their conclusions as capturing key distinctions driving the debate.

A final exchange worth noting concerns Bechtel's (2016) and Mollo's (2020) conflicting interpretations of mammalian cognitive map research. After performing a detailed examination of the research referenced by the canonical narrative of the cognitive map, Bechtel (2016) argues that scientists' ascriptions of representational content are not mere explanatory glosses. Rather, Bechtel argues that scientists are committed to the ontological reality of neural representations and that their ascriptions of content drive research forward. Mollo (2020) counters that a deflationary, pragmatic interpretation of representations captures the cognitive map case study just as well. In Mollo's (2020, 106) words, Bechtel must "[…] establish that talk of representation is

justified and substantive, and not a mere matter of scientific heritage" to successfully argue that a realist account of representational content best captures scientific practice.

This paper gives reason to be skeptical of Mollo's distinction between ascriptions of content that are justified and substantive and ascriptions of content that are matters of scientific heritage. Indeed, this paper shows how "mere matters of scientific heritage" exert significant influence on the way researchers think about representational processes. Scientific investigations are not discrete events that can be comprehensively analyzed in isolation. Their character is inevitably informed by the history of research that preceded them. Thus, historical examinations of the scientific traditions informing a case study have the potential to reveal previously concealed aspects of that case study. This paper engages in such historical examination to reveal novel aspects of the cognitive map debate in insects, aspects that would remain concealed given less historical "snapshot" case studies of the debate.

3. Expanding the Story of the Cognitive Map

In this section, I supplement the canonical account of the cognitive map with a parallel narrative that incorporates a German speaking tradition of European ethology. This parallel narrative highlights how the cognitive map debate in insects is currently motivated by and a continuation of long standing problems from the history of animal behavior research. This parallel narrative also broadens the story of the cognitive map to include the concept's reception by insect navigation researchers. Although the canonical account of the cognitive map begins with Tolman's 1948 publication, I begin by looking

back the 1930s, a decade before Tolman explicitly proposed the cognitive map hypothesis.

3.1. Prologue to the Cognitive Map: Tolman's Purposive Behaviorism and Lorenz's Ethology

The 1930s is an important decade for understanding what is at stake in the cognitive map debate in insects because it displays a common point of divergence for the ancestors of the two positions currently constituting the debate. The primary characters in this prologue are Wallace Craig (1876–1954), Edward Tolman (1886–1959), and Konrad Lorenz (1903–1989). In the 1930s, both Tolman (1932) and Lorenz (1937) incorporated Craig's (1918) theory of instincts into their own theories of behavior. Comparing the different ways Tolman and Lorenz incorporated Craig's theory of instincts highlights differences that I trace to the current cognitive map debate between Wehner and Menzel.

Craig's (1918) theory of instincts proposed that "appetites" and "aversions" set instinctive patterns of behavior into motion. An appetitive state causes agitation until a particular stimulus is received and an aversive state causes agitation until a particular stimulus is removed. Appetitive/aversive states cause animals to perform appetitive/aversive behaviors. These behaviors have the *purpose* of receiving or removing particular stimuli in the objective sense that animals tend to perform variations of these behaviors until the stimuli in question has been received or removed, at which point the received or removed stimuli may trigger a "consummatory reaction." Craig argued that animals must often learn how to seek or avoid appetitive or aversive stimuli through trial and error, but that the consummatory act that terminates an instinctive

behavior pattern is innately determined. For example, a chicken may experience an appetitive state that can only be assuaged by particular stimuli, like bugs on the grass. To receive that stimuli, the chicken performs appetitive behavior. The chicken may have to learn through experience what parts of the lawn are most likely to contain bug-in-the-grass stimuli. But once the chicken orients itself to the appetitive bug-in-grass stimuli, the consummatory reaction of pecking at the ground and swallowing is innately determined and may be a rigid chain of reflexes.

Fourteen years later, Tolman (1932) incorporated Craig's theory of instincts into his own theory of behavior called "purposive behaviorism." Tolman was an American psychologist who studied learning and was influenced by American behaviorism and German gestalt psychology (Strickland 2001). American behaviorism was famously focused on explaining behavior via theories of learning based on observable properties of behavior. Tolman (1932, 271–3) brought the seemingly anathema concepts of *purposiveness* and *cognition* to behaviorism by transforming Craig's theory of instincts into a theory of ultimate drives. For Tolman, appetitive and aversive states motivate all behavior (hence their transformation into *ultimate* drives), so behavior is purposive in the objective sense that it tends to continue until an ameliorative goal state is reached. Tolman (1932, 273) argues that behaviors motivated by ultimate drives are cognitive when "they express […] sign-gestalt-readiness, however vague, about how to get thus to or from [a privileged stimulus] in 'short' fashion." Tolman's (1932, 135–6) "sign-gestalts" are memorized associations of stimuli that include "means-end-relations" about how past interactions with one set of stimuli led to interactions with the other privileged set of stimuli. Tolman's (1932, 143–154) sign-gestalts go beyond behavioristic accounts

of associative conditioning in that Tolman describes maze running rats as integrating sign gestalts to create more comprehensive representations of their environment.

Tolman's 1932 book on purposive behaviorism was published one year before Konrad Lorenz completed his doctorate in zoology at the University of Vienna in 1933. Around that time, Lorenz (1985, 265) recounts how his teacher

> […] made me discuss at his main seminar the most important books of the purposivistic school, W. McDougall's *An Outline of Psychology* and Edward Chase Tolman's *Purposive Behavior in Animals and Men*, and in a subsequent lecture, a book by Watson. […] I suffered a really shattering disillusion: none of these people really *knew* animals. None was familiar with them as Heinroth [Lorenz's mentor] was or as even I was at the age of just over twenty years. I felt crushed by the amount of work that was still to be done and that obviously devolved on a new branch of science that, I felt, was more or less my own responsibility.

Perhaps Lorenz's disillusionment with the work of learning theorists like Tolman really did help inspire him to promote a new science of animal behavior, and perhaps this quote also evidences Lorenz's penchant for self-mythologizing.[13] Whatever the case, the quote shows that Lorenz was aware of Tolman's purposive behaviorism in the 1930s and that he was critical. Still, despite Tolman's (1932) explicit invocation of Craig's ideas and despite Lorenz's fixation on instinctive behavior patterns, Lorenz did not appreciate

[13] Burkhardt (2005, p. 152–3) suggests that Lorenz's (1985) flair for telling a good story causes him to exaggerate his negative reaction to the purposive psychologists.

Craig's appetitive theory of instincts until 1935 when the ornithologist Margaret Nice urged Lorenz to begin a correspondence with Craig (Burkhardt 2005, 152).[14] Lorenz's most explicit development of Craig's ideas comes two year later in Lorenz's 1937 paper, "Über die Bildung des Instinktbegriffes" ["The Establishment of the Instinct Concept"].

In that paper, Lorenz uses Craig's distinction between appetitive behaviors and consummatory actions to draw a sharp distinction between instinctive behaviors and all other types of behavior. In Lorenz's (1937, 270, 277 emphases in original) words:

> Wallace Craig, in his *Appetites and Aversions as Constituents of Instincts*, was the first to point out that an animal brings about, or 'attempts' to bring about, the performance of its instinctive behaviour patterns by means of what we term *purposive behaviour*. Following Tolman, this term is taken to cover all behaviour patterns which *exhibit adaptive variability whilst the goal remains the same*. This objective definition of purpose is extremely useful for the separation of conditioned and insight-determined behaviour from the instinctive behaviour pattern and provides us with a governing concept which incorporates all non-instinctive behaviour patterns. But it must at once be said that neither Craig nor Tolman perform a separation of this kind. Instead, the purposive behaviour through which the animal endeavors to enter the necessary stimulus situation for the elicitation of its instinctive behaviour pattern is interpreted as a *component* of the pattern concerned. I, on the other hand, separate these two types of behaviour as *fundamentally different* constituents."

[14] See Brigandt (2005, 581) for more on Lorenz's correspondence with Craig.

For Lorenz, Craig's consummatory act *is* the instinctive behavior pattern while the appetitive behavior that purposively seeks the appetitive stimuli may result from acquired or "insight-controlled" behavior.

This segregation of instinct type behavior from all other types of behavior clears the way for Lorenz's idiosyncratic account of instincts (Brigandt 2005). Lorenz (1937, 290) argues that it is "impossible for an animal to improve its own instinctive behaviour patterns through learning or insight." Instincts are innately determined actions. Lorenz (1937, 309) also argues that there is no "relationship between the adaptive function of an instinctive behaviour pattern and the goal which is actually sought by the animal subject." Animals need not be aware of the adaptive outcomes caused by their instinctive actions. The performance of instinctive behavior patterns is a goal and reward in itself. Lorenz also borrows Craig's talk of "energy" flowing through "channels" when describing his psycho-hydraulic model of instincts (Burkhardt 2005, p. 49). According to Lorenz (1937, 308), "response-specific energy *accumulates*" when an instinctive behavior pattern is not performed. As this energy accumulates, it affects the conditions that would release the instinct. If the energy builds for too long, the animal may perform the instinctive behavior pattern without any triggering stimuli, thereby releasing the energy (See Figure A).

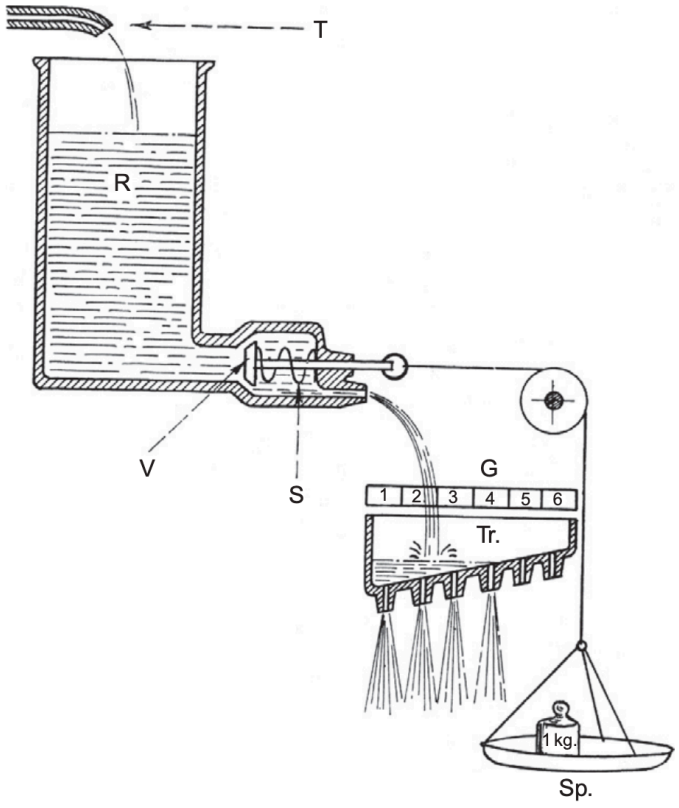

Fig. 5: Illustration of Lorenz's psycho-hydraulic model of instinctive behavior. Although this illustration was published over a decade after Lorenz's (1937) instinct paper, it remains a useful tool for visualizing the way Lorenz (1937) conceives of instincts. The tap *T* supplies a constant flow of liquid representing the endogenous production of action-specific energy. Reservoir *R* represents the amount of this energy that has built up in the animal. Cone valve *V* represents the instinct-releasing mechanism, and spring *S* represents inhibitory pressure stopping the instinct from being released. Pan *SP* represents the perceptual aspects of the instinct-releasing mechanism, and the 1 kg weight represents impinging stimulation (the heavier the weight, the more intense the releasing stimuli). The instinctive behavior pattern is the jet of liquid pouring out of the reservoir, and measuring stick *G* indicates the intensity of the behavior pattern. The slanted bottom

of trough *Tr* shows how different intensities of instinctive behavior patterns cause sequences of different activities (Lorenz 1950).

Within the larger context of cognitive map debate in insects, the key differences between Tolman's and Lorenz's theories of behavior are 1) the role of learning, 2) the level of insight animals possess about goal-directed actions, 3) their respective focuses on the contents of memories vs. the physiological causation of behavior, and 4) their focuses on different taxa of animal (See Figure B). In Tolman's (1932) theory, Craig's instincts serve as an engine that drive rats to learn about their environment. As presented by Tolman, rats' competence at navigating mazes is largely a result of the way rats integrate the contents of memories about their environment. For Tolman, rats running mazes develop representations of their environment and manipulate those representations to reach their goal.[15] Lorenz, in contrast, uses Craig to completely separate instinct from learning. Learning still has a place in Lorenz's theory: animals may have to learn how to put themselves into situations that trigger their instincts, and "higher mammals" may reduce their use of instinctive behavior patterns by relying on purposive insight-determined behavior. However, in animals like birds and insects, Lorenz is more likely to see sophisticated behaviors as instances of instinctive behavior patterns than as instances of insight-determined purposive behavior. According to Lorenz, scientists should not assume that animals reason their way to goals by manipulating representations. Rather,

[15] The agency and apparent intentionality that Tolman's (1932) purposive behaviorism gives to rats was captured by the criticism of the American behaviorist Edwin Guthrie (1935, 143), who wrote that Tolman's rats were "buried in thought".

physiological forces motivate animals to enter situations that trigger instincts, and the triggering of the instinct is the animal's goal.

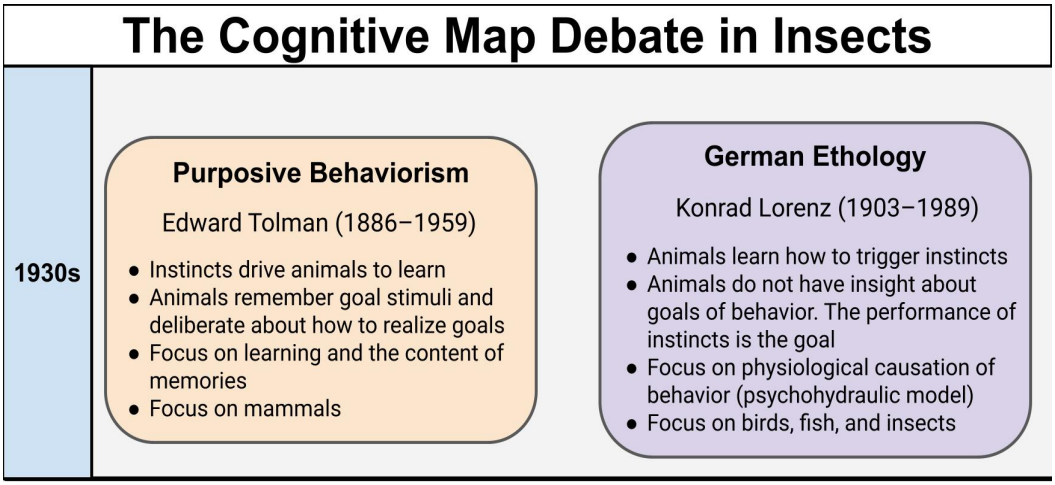

Fig. 6: Visual summary of the cognitive map debate in insects (first iteration).

All of the above differences distinguishing Lorenz's development of Craig's theory from Tolman's development of Craig's theory continue to motivate the contemporary cognitive map debate in insects. To show the continuity of these differences through time, I track two developments. First, I look forward to Tolman's 1948 proposal of the cognitive map hypothesis and the adoption of that hypothesis by an American honeybee researcher in the 1980s. Second, I follow the tradition of German ethology that produced Wehner and Menzel, both of whom initially argued against the cognitive map hypothesis in honeybees. These two developments collide in the 2000s, when Menzel begins arguing for Tolman's cognitive map in honeybees while Wehner continues to argue against the cognitive map. The next section briefly notes a few key points about Tolman's cognitive hypothesis that continue to shape the cognitive map debate in insects. After that, I pick up the parallel narrative of German ethology.

3.2. Tolman Proposes the Cognitive Map: Highlighting Some Definitional and Methodological Details

Tolman explicitly proposed his cognitive map hypothesis in his 1948 publication, "Cognitive Maps in Rats and Men." Between Tolman's 1948 paper and the present, researchers have proposed a variety of definitions for what constitutes a cognitive map (For reviews, see: Mackintosh 2002; Jenson 2006; cite). In this section, I highlight two features of Tolman's proposal that continue to characterize the cognitive map debate in insects: the way Tolman defined the cognitive map and the behavioral evidence Tolman took to support the cognitive map hypothesis.

I will start with the definition. As articulated by Tolman (1948, pp. 192 emphasis added), the cognitive map theory holds that,

"[…] something like a field map of the environment gets established in the rat's brain […] Although we admit that the rat is bombarded by stimuli, we hold that his nervous system is surprisingly selective as to which of these stimuli it will let in at any given time […] The stimuli, which are allowed in, are not connected by just simple one-to-one switches to the outgoing responses. Rather, the incoming impulses are usually *worked over and elaborated in the central control room* into a tentative, cognitive-like map of the environment. And it is this tentative map, indicating routes and paths and *environmental relationships*, which finally determines what responses, if any, the animal will finally release."

Tolman's points about "elaborating" stimuli in a "central control room" to produce a map-like representation that indicates "environment relationships" continue to

shape the cognitive map debate in insects. For a representation of space to be useful to a navigator, the representation must have a frame of reference. Tolman did not use these terms in his original definition, but his articulation of the cognitive map has since been developed into the more precise claim that cognitive maps utilize an allocentric frame of reference that allows animals to extract information about the relationships between environmental features (e.g. landmarks) (cite). Allocentric frames of reference represent objects relative to an environment that is independent of the navigator. Contrast that with egocentric frames of reference, where objects are represented relative to the position of the navigator.

This definitional issue is closely related to a second feature connecting Tolman's (1948) publication to current debates about insect cognition: how do the results of behavioral experiments justify inferences about animal learning? Tolman (1948, pp. 191–192) situates his cognitive map theory of rat navigation in opposition to what he calls the "telephone switchboard school" of animal learning likely represented by Hull's 1930 publication, "Knowledge and Purpose as Habit Mechanisms." Specifically, Tolman argues that the learning involved in rat navigation cannot be fully accounted for by hard behaviorist theories that characterize learning in terms of the strengthening or weakening of atomistic connections between stimuli and response via conditioning. In challenging the hard behaviorism of the telephone switchboard school, Tolman (1948) reviews various maze experiments and argues that their results indicate that a) rats seem to remember seemingly unreinforced environmental stimuli for later use, b) rats seem to actively compare those remembered stimuli when making navigation decisions at bifurcation points in mazes, c) rats seem to execute systematic search strategies in

unfamiliar mazes, and d) rats seem to be able to select novel routes to a previously discovered goal. Taken together, Tolman argues that these interpretations of behavioral experiments support the existence of a cognitive map in rats. The last of these interpretations, (d), has become the most explicit criterion in the insect cognitive map debate (Menzel 2020, cite), although the (b) criterion also continues to be a less obvious point of contention (Menzel 2020).

The key points to remember, the points that continue to shape the cognitive map debate in insects, are: 1) that Tolman's cognitive map requires animals to integrate representations of environmental features into a cohesive, map-like representation, 2) this representation is map-like in the sense that navigators can use the map to deduce spatial relationships between environmental features and deliberating about future navigation decisions, and 3) exploiting novel shortcuts is evidence that a navigator employs such a map-like representations (See Figure C).

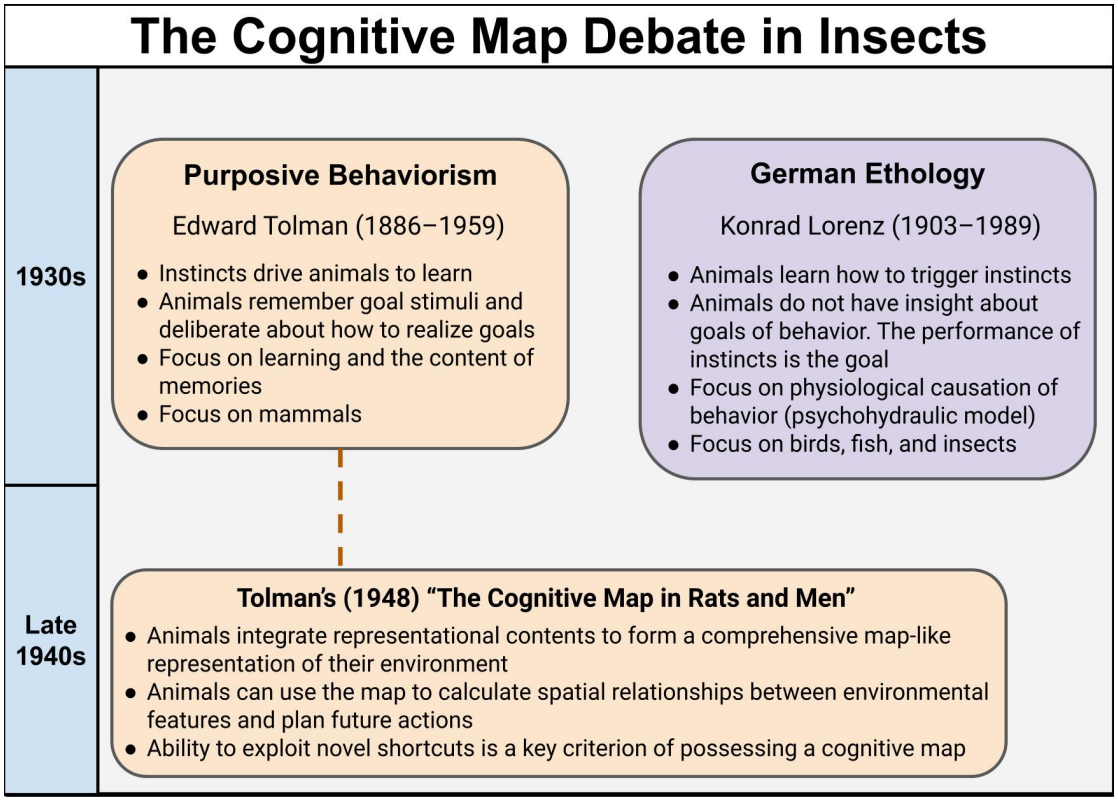

Figure 7: Visual summary of the cognitive map debate in insects (second iteration).

I now return to the parallel narrative of German ethology to introduce the heads of the pro-cognitive map and anti-cognitive map positions in the insect cognitive map debate.

3.3. Rüdiger Wehner, Randolf Menzel, and German Ethology

We left Lorenz in 1937 with his publication characterizing a novel instinct concept for his new science of ethology. Between Lorenz's 1937 publication and the beginning of WWII, he and Nikolaas Tinbergen promoted ethology as a distinct form of behavioral research representing a genuinely biological (as opposed to psychological) approach to behavior (Burkhardt 2005). The Austrian scientist Karl von Frisch (1886–

1982) has also become tightly associated with ethology, though he has a much less straightforward relationship with the discipline (Dhein 2021*if JHB accepts* (a.k.a. the second chapter of this dissertation)). Despite the differences separating von Frisch's research from the program of early ethology, von Frisch shared Lorenz's view that instincts can account for most of the behavior of "lower" organisms, even behaviors that seem too sophisticated to be instinctive. For instance, von Frisch (1959) wrote, "Insects have—even in relation to their body size—a very unprepossessing brain, not created to reflect or make inventions. They too accomplish astonishing intellectual feats, complex and meaningful actions. But they do not consider what they should sensibly do in any given case. How they should behave, that is essentially something they are born with. Innate behavior, 'instincts,' guide them on their way through life."

Von Frisch's connection to ethological ideas is relevant because he founded a lineage of social insect researchers who continue to self-identify as ethologists, and this lineage produced Wehner and Menzel. After WWII, von Frisch gained public notoriety for his discovery of the honeybee dance "language" [16] (Munz 2016), and in 1973, he was awarded a 1/3 share of the Nobel Prize in Physiology or Medicine alongside Lorenz and Tinbergen for their ethological approach to behavior. Von Frisch's most influential student was Martin Lindauer (1918–2008), who continued to research communication in honeybees. In 1963, Lindauer became director of the Institute of Zoology at the University of Frankfurt in West Germany, and Wehner and Menzel became some of Lindauer's first doctoral students at the new university. Thus, when Wehner and Menzel

[16] Von Frisch always put the word "language" in scare quotes lest he be interpreted as making deeper claims and honeybees' communicative abilities (von Frisch 1953).

joined Lindauer at the University of Frankfurt, they were entering into a Frischean tradition of German ethology. The different ways Wehner and Menzel responded to that tradition prefigure the pair's opposing stances in the cognitive map debate.

To begin, Wehner and Menzel's autobiographical recollections show that they were drawn to Lindauer for different reasons. Menzel (2004, 462) left University of Frankfurt due to "deficiencies in the animal physiology degree program" to study for one semester at the University of Tübingen. There, he became interested in combining behavioral and neurological analyses to investigate mechanisms of learning. In Menzel's (2004, 463) words, "I got a vague idea of what direction I wanted to go, but how could I combine this direction with my interests in the mechanisms of learning processes? Huber didn't want to get involved with such a project; he recommended Martin Lindauer, who had taken up the professorship for zoology in Frankfurt. So I returned to Frankfurt and began my doctoral work on color learning in bees."

According to Menzel (2004, 465), this was a good suggestion since Lindauer's research diverged from von Frisch's in ways that corresponded to Menzel's interests: "Although Lindauer himself never made the switch to neurophysiological studies, he prepared his pupils for them. For him, receptor and communication tasks in the bee were not exclusively carried out by receptors, but included brain processes. He began to think about learning and memory formation and, in doing so, distanced himself from two strong traditions which had been a firm basis for his previous work: sensory physiology from the behavioral-analytical point of view, and ethology […]." Menzel emphasizes this difference between von Frisch's focus on peripheral sensory physiology and his own interest in centralized learning processes in several places (Menzel 2000, 2004, 2007,

2020). For example, remembering his time as a doctoral student with Lindauer in the mid 1960s, Menzel (2004, 463) writes (emphases added):

"The role models I found in my readings were Karl von Frisch (1965), Thorpe (1963), Lashley (1950), Thorndike (1932), Pavlov (1927), von Holst (1935), *Tolman* (1932), and Köhler (1921), a colorful mixture, representing conflicting schools within behavioral biology. I could understand how important it was to use objective and quantifiable criteria to record behavior; my own experimental work was an intensive effort in this direction, but I was disappointed that behavioral biology did not refer to the brain. The American learning psychologists caught my eye, but they were also the most disappointing because they thoroughly dismissed any connection to brain mechanisms. Ethologists, on the other hand, disappointed me because they ignored learning processes and instead developed such rather strange concepts as "release mechanism modified by experience" as the only possible explanation for learning, even though learning quite obviously consists of acquiring totally new skills. *Despite being enthralled with Karl von Frisch and having devoured his book with unflagging interest, I couldn't quite understand why he concentrated exclusively on sensory mechanisms when successful decision-making during nectar search, dance communication, navigation, social coordination, and more is clearly the result of brain mechanisms* (Emphases Added)."

What about Wehner? In contrast to Menzel, who was frustrated by Frischean ethology's focus on peripheral sensory physiology, Wehner was attracted by Lindauer's research on honeybee sensory physiology. Like many ethologists, Wehner grew up loving birds. But he remembers his interests moving to insects after Lindauer joined the University of Frankfurt in 1963: "[Lindauer's] studies on the sensory physiology of

honey bees struck me immediately. Here was a field of research in which a freely moving organism could be subjected to rigorous experimental tests, i.e., presented with well-defined physical stimuli, while the animal's behavioral responses could be recorded and evaluated quantitatively (Wehner 2013, 3)." The difference between Wehner and Menzel's interests becomes more apparent in their doctoral research projects, which they both completed in 1967.

Wehner's work focused on visual pattern recognition in honeybees (Wehner 1967). He found that honeybees can be trained to distinguish the angular orientation of a striped pattern on a vertical screen. This line of research led Wehner to propose a retinotopic-template matching hypothesis for honeybee pattern recognition (Wehner 1969; Wehner 1981; Srinivasan 2010). Wehner's hypothesis emphasized peripheral neurosensory mechanisms. Instead of evaluating the similarity of patterns by extracting characteristic parameters like size or contrast and then comparing the values of those parameters, Wehner's theory held that honeybees evaluate the similarity of patterns by remembering a "snapshot" template of the learned pattern. The template is snapshot-like because it preserves retinotopic coordinates of the learned pattern, and to compare the similarity of the learned pattern with a new pattern, honeybees orient themselves in such a way that they evaluate the overlap of their retinal template pattern with the actual retinal image of the new pattern. This is an early expression of a theoretical commitment that has guided Wehner's career: all things being equal, one should assume that insects' behavioral capacities are significantly determined by peripheral, task-specific neuro-sensory processes. In Wehner's (1987, 528–529) words:

"[A]n animal's solution reflects a unique nervous system with adaptive limitations, biases, and distortions. Similar problems may be solved by different animals in different ways depending on the animal's evolutionary past. Anachronisms in neural circuitry may persist as long as they do their job […] natural selection favours whatever works, however short the final solution may fall of the investigator's optimal design criteria […] in [insects] much of the processing of information occurs at rather peripheral neural levels, at both the sensory and the motor side. Of course, such 'peripheralisation' of the insect's nervous system limits the versatility with which information can be handled and used, but eases the way the information can be processed. These potentialities and constraints inherent in the design of the insects' nervous system are certainly related to the small body sizes and narrow ecological niches characterizing all insect species."

Menzel's (1967) doctoral work, in contrast, vindicated his suspicion that such peripheral-focused perspectives miss important determining factors of honeybee behavior. Menzel tested honeybees' ability to associate different colors with rewards. He found that honeybees learned some colors more quickly and that this discrepancy cannot be accounted for by properties of the honeybee eye. Menzel reasoned that there must be learning mechanisms relevant to color/food associations that are more centrally located in the honeybee brain.

In fall 1967, just after Menzel and Wehner had graduated, Menzel remembers that Lindauer brought his research group to von Frisch's summer home in Austria, where von Frisch (then 81 years old) gave an additional oral exam to those who had recently completed their doctorate. The exchanges Menzel remembers and relates from his

interactions with von Frisch illustrate both Menzel's theoretical commitment to not discounting central processing mechanisms in insect behavior and the way Menzel sees his research diverging from Frischean ethology:

"After the exam, we told him [von Frisch] about our experiments, and he encouraged us with tips that proved he understood the underlying problem. I reported that bees learn violet spectral light especially quickly, and this effect cannot be due to a sensory mechanism, but rather must be based on an evaluation process made by the central nervous system. […] Since my attempts to explain things relied on many details from the psychophysics of color vision, I feared the discussion would become a bit sticky. Nothing of the kind: von Frisch was exceptionally well informed, wanted to learn from me, and gave numerous tips for further experimentation. He didn't want to follow my core argumentation, however, which was the differentiation between peripheral and central mechanisms of estimating color." (Menzel 2004, 466–467)

Menzel also remembers discussing von Frisch's feud with Carl von Hess from the early 1910s over whether honeybees possess color vision (Hess 1912a, 1912b, 1913; von Frisch 1912, 1913a, 1913b, 1913c, 1914; For commentary, see Warner 1931; von Frisch 1967, p. 48–49; Thorpe 1983, p. 198; Hölldobler 1985; Menzel and Backhaus 1989; Kelber et al. 2003; Kelber & Osorio 2010; Munz 2016, Chapter 2; Dröscher 2016; Dhein 2021). The details of the feud are less important than what Menzel (2004) remembers from his discussion of the feud with von Frisch:

"My theory (speculative back then, but in the meantime experimentally proven, see Menzel und Greggers, 1985) was that […] the bee has various central chromatic integration systems that are assigned to various behaviors. This way of thinking was alien

to von Frisch, which told me that he, following the tradition of sensory physiology from the first half of the 20th century, equated perception with peripheral (mostly receptor) performance. This mindset was surely remarkably successful and had led to great discoveries by Karl von Frisch and his students (i.e., seeing UV light, seeing polarized light, odor perception, and differentiation between acoustic and vibratory mechanosensory perception). The limitations of this way of thinking seemed obvious to me, but I could not satisfy von Frisch; he could not accept the existence of central evaluating mechanisms as a basis for an explanation. He was right with that, of course, as long as nothing is known about these hypothetical central mechanisms. I took this as a challenge to work on exactly this problem and to search for these central mechanisms."

Finally, in a separate recollection, Menzel (2020) recalls that "In 1967, I asked Karl von Frisch where he would expect to find the memory for flowers in the bee brain, and he responded with a skeptical look: 'Why in the brain? Isn't it much too small?' With this answer, von Frisch stayed true to himself."

Thus far, I have demonstrated an early difference concerning the way Wehner and Menzel theorize about insect cognition. The next difference concerns Wehner and Menzel's preferred animal subjects.

After graduating, a serendipitous series of events led Wehner to change his focus from honeybees to desert ants of the genus *Cataglyphis* (Wehner 2013, 4–6). In spring of 1968, Lindauer helped Wehner and Menzel travel to Israel, where (unlike central Europe) it was warm enough to begin conducting foraging experiments on honeybees. The problem was that the test site was located next to a blossoming orange orchard, and since the honeybees preferred the orange blossom nectar over artificial sucrose solution,

researchers could not implement their intended experimental setup. While trying to attract honeybees, Wehner (2013, 4–5) remembers that he "noticed some long-legged ants that were frantically running about my apparatus. They seemed to be solitary foragers not depending on scent trails and thus navigating visually. Free of any devotion to the world of ants, these fast runners caught my eye immediately. They fascinated me to such an extent that I finally even hoped that no bee would arrive—and none did! Together with two students, who had accompanied me during this two-month trip, I now started to do some pilot experiments on the navigational abilities of these ants, which taxonomically were completely unknown to me […] Finally, Randolf Menzel, my colleague and friend from university days, who had traveled with me and in the meantime had observed the flower-visiting behavior of bees in the orchard, joined our endeavors."

Wehner and Menzel (1969) turned their unexpected encounter with the desert ant *Cataglyphis* into a coauthored paper. They argued that *Cataglyphis* uses the sun and visual landmarks to navigate home from foraging journeys, and that when sun cues conflict with cues from visual landmarks, the landmark cues take precedence in determining the ant's navigation behavior. But they briefly consider an alternative: "If, however, *Cataglyphis* does not possess any sun orientation mechanism, [visual] pattern recognition and learning abilities ought to be highly developed in order to enable this extraordinarily vagrant species to perform its high orientation achievements." This dichotomy between sophisticated learning abilities on the one hand and a nested hierarchy of more task-specific navigation mechanisms on the other hand continues to characterize the cognitive map debate in insects, and although the relative contributions

of each author are unclear, it is easy to imagine Menzel as the motivating force behind the above suggestion that *Cataglyphis* possesses highly developed learning abilities.

Wehner returned from his 1968 trip to Israel with the intention of continuing his *Cataglyphis* navigation research. The following spring, he travelled to Tunisia to continue that work. There, Wehner (2013) "came across a lonely forager of what later turned out to be *Cataglyphis fortis*. The ant meandered around in search of food and after having found a dead fly, grasped it and ran straight back over more than 100 m to an inconspicuous nest hole. Impressed by this feat of navigation, I immediately decided that path integration, the classic dead reckoning applied in nautical navigation, should become our first *Cataglyphis* research topic." According to Wehner (2013), this new line of research is "what really let me shift my research priorities from *Apis* to *Cataglyphis* […]."

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. Path integration is a cognitive hypothesis in the sense that it ascribes representational contents to navigators. However, path integration does not require navigators to integrate information about the spatial relationships between environmental features like the cognitive map hypothesis does. Path integration could exclusively provide navigators with egocentric representations of space whereas the cognitive map requires navigators to utilize allocentric representations of space.

Wehner did not abandon his honeybee work upon finding *Cataglyphis*, but he began to shift his focus to *Cataglyphis*. Between 1969 and the turn of the 21st century, Wehner turned *Cataglyphis* into a model organism for navigation studies by attracting new researchers to his growing annual Tunisia field site trips (Wehner 2019). This *Cataglyphis* research is what currently forms the basis of the anti-cognitive map group's attacks on the cognitive map hypothesis. As multiple navigation researchers have commented (Mackintosh 2002, 166; Cheng and Freas 2015, 519), O'Keefe and Nadel's (1978) influential book, *The Hippocampus as a Cognitive Map*, did not pay much attention to path integration as a potential navigational strategy. Around the time O'Keefe and Nadel's book was causing renewed interest in the cognitive map hypothesis, Wehner was investigating path integration in *Cataglyphis*, raising the profile of both in animal navigation research (Wehner and Srinivasan 1981; Cheng and Freas 2015).

Meanwhile, Menzel continued to use the honeybee as his primary experimental subject. In keeping with his focus on learning mechanisms and his interest in classical learning theorists, Menzel began to develop and implement an existing experimental paradigm for investigating classical conditioning in honeybees (Kuwabara 1957;

Bitterman et al. 1983; Menzel 2020). The paradigm exploits the fact that honeybees have a reflex that causes them to extend their proboscis when they are hungry and their antennae are stimulated with sucrose solution. By restraining individual honeybees in little tubes so only their heads protrude, researchers are able to use the proboscis extension reflex to investigate how honeybees learn to associate stimuli with rewards (See Figure D). Menzel found that these experiments with honeybees produced results that were analogous to similar experiments performed on vertebrates, causing he and his colleagues to speculate that the proboscis extension reflex paradigm "gives access to some fundamental mechanisms of information storage and retrieval evolved in a remote common ancestor" shared by vertebrates and invertebrates (Bitterman et al. 1983, 118). While Wehner was investigating sensory physiology and path integration in *Cataglyphis*, Menzel was investigating learning and memory in honeybees.

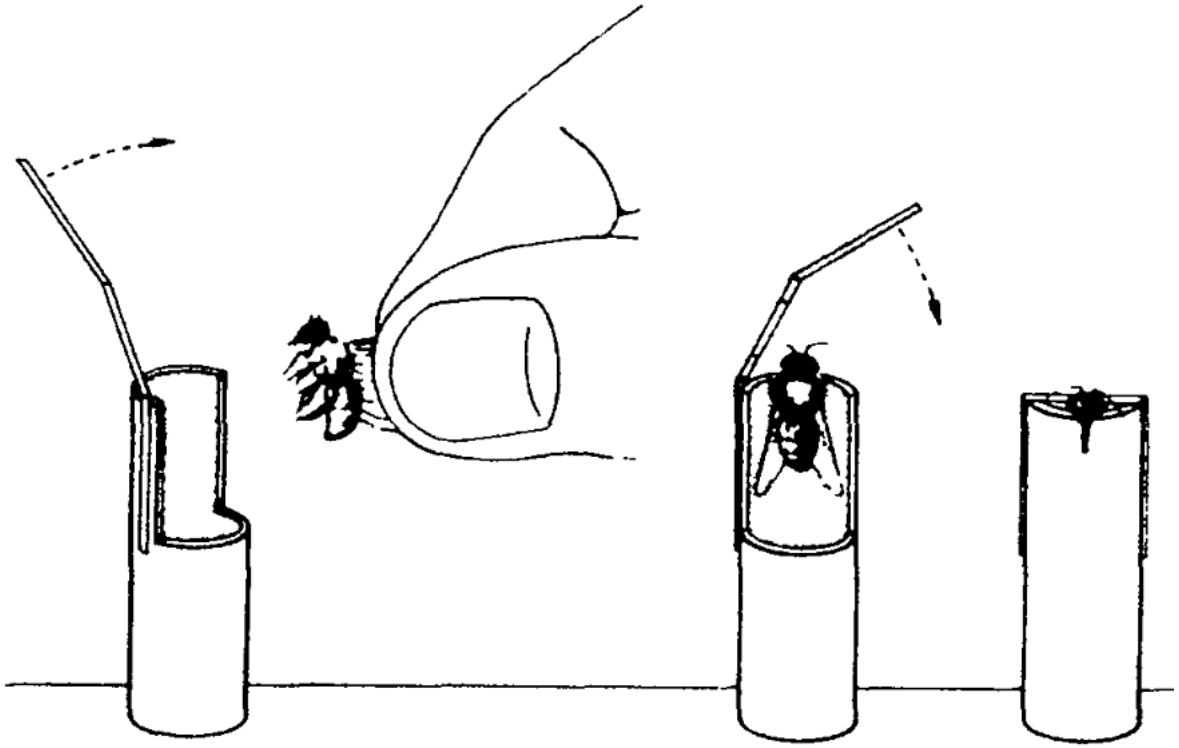

Fig. 8: Illustration of the Proboscis Extension Response Conditioning Paradigm (Bitterman et al. 1983).

The key point to take away is that Menzel and Wehner entered into the same tradition of animal behavior research at the same time via the same mentor, and they responded to that tradition differently. Menzel reacted against Frischean ethology's emphasis on instinct, peripheral processing, and sensory physiology. His work was more in keeping with Lindauer's extension of von Frisch's research program (Seeley et al. 2002), and he employed experimental paradigms associated with behaviorist theories of learning. Wehner, on the other, continued to work within the Frischean tradition of German ethology, but instead of continuing von Frisch's and Lindauer's focus on honeybees, he began applying that approach to *Cataglyphis* (See Figure E).

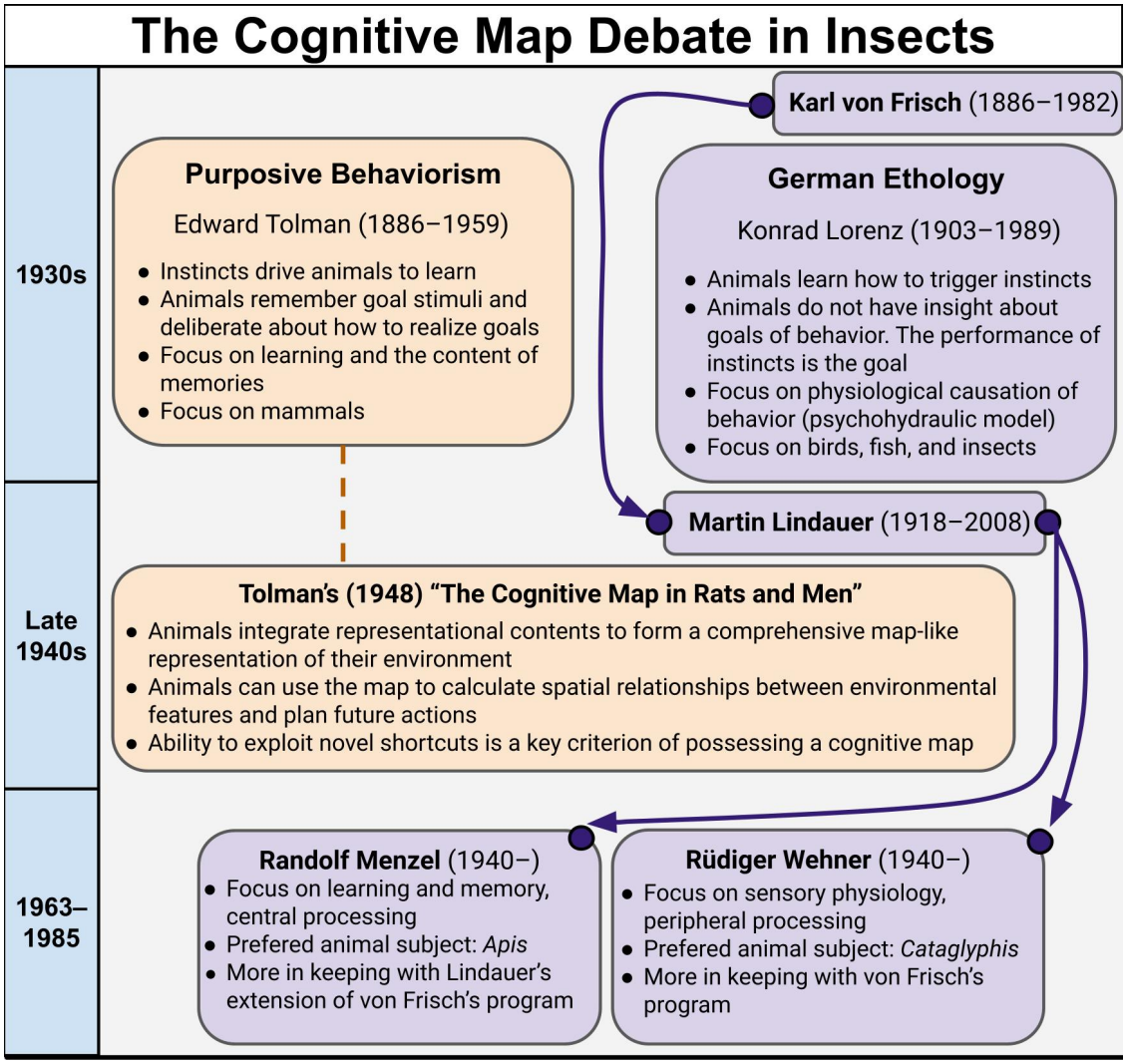

Fig. 9: Visual summary of the history of the cognitive map debate in insects (third iteration).

3.4. The Cognitive Map Comes to Insects

In the mid 1980s, the cognitive map moved from mammalian navigation research to insect navigation research, where it immediately caused controversy. In 1986, American scientist James Gould (1986) published a paper claiming to provide

experimental evidence for a Tolman-like cognitive map in honeybees.[17] Multiple insect navigation researchers offered rebuttals to Gould's pro-cognitive map paper (Cartwright and Collett 1987; Dyer and Seeley 1989a, 1989b; Dyer 1991; Dyer 1996)) including Wehner and Menzel (Menzel et al. 1990; Wehner and Menzel 1990; Wehner and Wehner 1990; Wehner et al. 1990). The points at issue in Gould's original promotion of the cognitive map hypothesis show the continuity between Tolman's (1948) original proposal and the current cognitive map debate in insects.

First, Gould (1986) uses an animal's ability to perform shortcuts as the key piece of evidence supporting the cognitive map hypothesis. Gould began by training honeybees to forage at feeding stations. After training the bees to forage at a particular feeding station, Gould captured bees in a beaker just as they were about to depart their hive to forage at the trained feeding station. Gould then transported the honeybees in the dark to a new location and released them. Once released, Gould reports that the honeybees flew directly to the feeding station to which they had been trained. According to Gould, this result supported the cognitive map hypothesis because it showed that honeybees could use familiar landmarks to plot a novel route to their goal. In Gould's (1986, pp. 861)

[17] It has been claimed that the experiments referenced in Gould's (1986) paper were performed by Gould's then doctoral student, Fred Dyer, and that Gould provided his own interpretation of Dyer's results and published that interpretation unbeknownst to Dyer. Whatever the case, Dyer was dissatisfied with Gould's interpretation of the experiments in question and repeated the experiments himself after completing his Ph.D. (Dyer and Seeley 1989; Dyer 1991; Dyer 1996).

words, “the relative location of familiar landmarks is understood—presumably stored in the brain as a map—so that novel routes based on new combinations of landmarks may be used, freeing the animal from dependence of route-specific combinations.” If honeybees lack a cognitive map, Gould reasoned that they would have to use route specific landmark memories to navigate back to hive and then, once at the hive, depart for their intended feeding station.

A major hurdle in honeybee navigation research concerns the difficulty of tracking honeybees as they fly long distances. From an experimenter’s point of view, when one releases honeybees, one can only visually track them for so long before they become little specks in the sky and eventually vanish. When Gould published his pro-cognitive map paper, the custom for representing the flight path of a displaced honeybee involved recording “vanishing bearings”. Vanishing bearings are the point at which a researcher can no longer see the traveling honeybee, they represent the last observed compass direction in which a departing honeybee was flying. By averaging the vanishing bearings of multiple honeybees across different experimental trails, researchers calculate the general direction honeybees flew after being released. Gould and other researchers of this time also timed how long it takes honeybees to travel from a release point to their eventual destination. Between a honeybee’s vanishing bearing and a honeybee’s landing at a destination, however, researchers could not accurately track a honeybee’s flight path.

The second way Gould’s (1986) paper called back to Tolman’s cognitive map is that Gould situates the debate over whether insects possess cognitive maps within the same broader dialectic identified by Tolman. Gould (1986, pp. 862–863) argues that existing non-cognitive map theories of insect navigation (he cites Wehner 1981 in

particular) are "analogous to the original formulations of learning theory, in which animals were supposed to be incapable of learning out the context of performing the specific behavior that was being conditioned". It is true that part of Tolman's argument for cognitive maps is that rats seem to learn unreinforced environmental stimuli that they put to later use. However, in light of the expanded history provided by this paper, Gould gets it exactly wrong when likens Wehner's path integration account of insect navigation to the original formulations of learning theory.

The ethological framework influencing Wehner is not opposed to the cognitive map hypothesis because the hypothesis implies unreinforced learning. The issue is not how memories are formed so much as how memories are utilized. Wehner's ethological framework is opposed to the cognitive map because it implies that behavior is determined by a deliberative process in which the animal is—to some degree—*aware* of the goal their behavior is directed toward and that the animal synthesizes a comprehensive representation of their environment to help them compute a plan for realizing that goal. For the purposive behaviorism that birthed the cognitive map hypothesis, instincts drive learning, and sophisticated behaviors are the product of learning. In the German ethological tradition Wehner inherited, animals learn how to enter situations that trigger instincts, and sophisticated behaviors are the product of instincts, especially in insects. Thus, for Wehner, it does not make sense to assume that the more or less peripheral neurosensory mechanisms that implement different navigation strategies pool their outputs into a general map; it makes more sense to think of navigation behaviors as being triggered by the way the insect's innate motivations and physiology interface with

environmental cues. But at this early stage of the cognitive map debate in insects, these theoretical fault lines are not as obvious as they later become.

Wehner and Menzel (1990) performed similar experiments to those referenced in Gould's (1986) paper and could not replicate his results. Instead, Wehner and Menzel found that displaced honeybees depart in the compass direction one would expect given a path integration model of navigation. According to the path integration model, honeybees departing their hive to navigate toward a trained feeding station are following a remembered vector representing direction and distance of travel. When these bees are displaced, their motivation to follow that vector memory is unchanged, and so they depart in the direction they would have departed from the hive. This is exactly what Wehner and Menzel observed. Furthermore, as argued by other critics of Gould (Cartwright & Collett 1987; Dyer and Seeley 1989), Wehner and Menzel note that Gould's reported results can be explained without appealing to cognitive maps hypothesis (See Figure F).

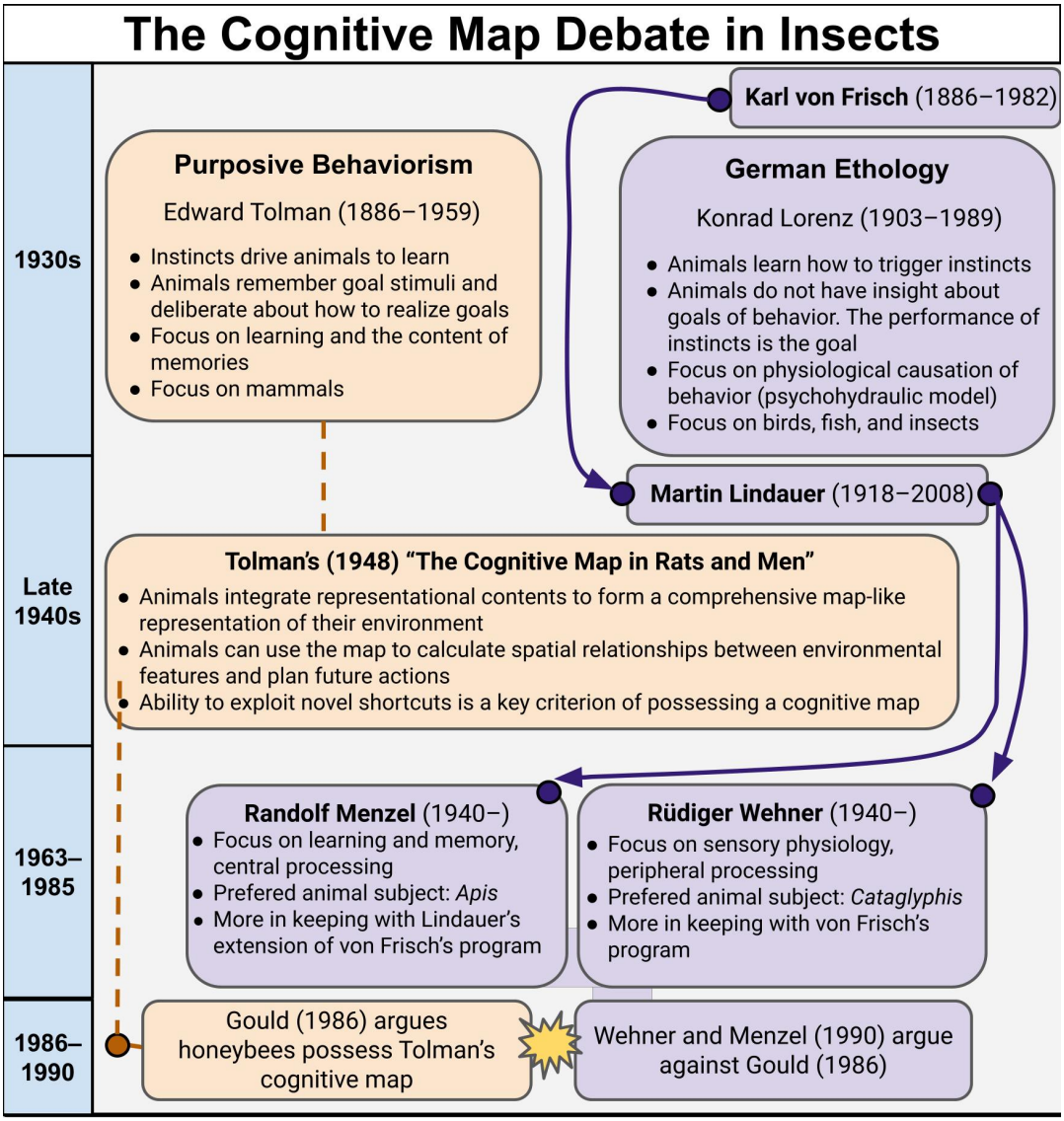

Figure 10: Visual summary of the history of the cognitive map debate in insects (fourth iteration).

Finally, Gould (1986) sets the cognitive map hypothesis in opposition to overly restrictive attitudes about insect's cognitive capacities. Gould expresses this point by framing the "vertebrate-invertebrate dichotomy" as a parochial distinction that should not prejudice researchers against the existence of complex cognitive traits in invertebrates

like honeybees. Menzel has never agreed with Gould's argument for a cognitive map in honeybees, but once Menzel changes his stance in the 2000s and begins arguing for cognitive maps in honeybees, Menzel also argues that parochial attitudes about the simplicity of insects wrongly prejudice scientists against the cognitive map hypothesis in insects.

3.5. Wehner's Toolkit vs. Menzel's Map: The Contemporary Cognitive Map Debate in Insects

After Wehner and Menzel's (1990) publication critiquing Gould (1986), Menzel continued to focus on memory and learning processes in honeybees. He investigated the neuro-cellular basis of learning and memory in honeybees (Hammer and Menzel 1995; 1998; Menzel 1999; Galizia and Menzel 2000; Ganeshina and Menzel 2001; Menzel 2001; Menzel et al. 2001) and he began to conclude that honeybees integrate their vector memories to guide navigation in previously unexpected ways (Menzel et al. 1995; Menzel et al. 1996; Menzel et al. 1998). Wehner, on the other hand, continued to investigate the sensory physiology of *Cataglyphis*, the way that physiology contributes to different navigational subroutines, and the way those subroutines interact to determine behavior (Wehner et al. 1994; Wehner et al. 1996; Wehner 1997a; 1997b; 1998; Lambrinos et al. 1998; Collett et al. 1999; Möller et al. 1999; Ronacher et al. 2000; Wolf and Wehner 2000; Wohlgemuth et al. 2001; Sommer and Wehner, 2005). Around 2000, Menzel (2000) begins to shift toward the view that honeybees do possess a cognitive map. The resulting debate between Wehner and Menzel over whether insects possess cognitive maps has produced many publications over the last twenty years. In this

section, I focus on Menzel's conversion to the cognitive map hypothesis and a strategy Wehner's anti-cognitive map group has developed for discounting the claims of Menzel's pro-cognitive map group. Namely, I examine how Wehner's group developed their toolkit model of insect navigation as an explicit competitor to the cognitive map.

In Menzel et al.'s (2000) paper, "Two Spatial Memories for Honeybee Navigation", Menzel and colleagues argue that in addition to utilizing route-specific egocentric representations of space, honeybees also utilize general allocentric representations of space. To support their argument, Menzel et al. perform displacement experiments on two groups of honeybees. The first group is trained to a particular feeding station before being displaced in similar manner to Gould (1986) and Wehner and Menzel (1990). As expected, Menzel et al. (2000) get the same result with this group as Menzel and Wehner (1990): the honeybees vanishing bearings support an egocentric route-specific path integration model of navigation. This is the first kind of spatial memory referenced in the article title.

The second group of bees, however, is not trained to a particular feeding location. Instead, they are allowed to feed at a station near their hive that slowly orbits their hive. When these bees are displaced outside the orbit of this moving feeding station, Menzel et al. expected them to take a while to navigate back to their hive since they lacked route-specific memories of how to return to the hive from the displacement location. If the second group of honeybees slowly improved in their ability to navigate to the hive from a displacement location, Menzel et al. reasoned that result would support the idea that honeybees build general, allocentric representations of space via latent learning. To Menzel et al.'s surprise, however, the second group of honeybees did not require multiple

displacements to improve their navigation performance. They navigated back to their nest on the first displacement much faster than expected. To explain this result, Menzel et al. hypothesize that the second group of honeybees engaged in latent learning during orientation flights prior to the experiment, and that they drew on those memories to guide their flights back to the hive after displacement. This is the second kind of spatial memory referenced in the article. Menzel et al. (2000, 967) do not conclude that this second kind of memory proves honeybees possess a cognitive map, but they consider that possibility along with competing hypotheses and end the paper with a provocative suggestion "[…] what appears as parsimonious on logical grounds might, in a mechanistic sense, not be the simpler solution."

Menzel's conversion to the idea that honeybees utilize "map-like" representations was facilitated by a technological innovation. In prior displacement experiments, researchers relied on vanishing bearings and the temporal duration of honeybee flights to draw conclusions about the actual paths honeybees navigate. But in 2005, Menzel et al. published the results of displacement experiments that used harmonic radar to track honeybees in midair. According to Menzel (2005; 2011), the results of those displacement experiments showed that after displaced honeybees navigate according to their path integration vector memory (and are no longer visible to observers), they enter a search phase followed by a direct flight to either their hive or the feeding station. Menzel et al. interpret these results along the lines of the Menzel et al. (2000) publication. Path integration vector memory takes precedence over other memories, but once a honeybee has "run out" their path integration vector, they are not lost. They do an orientation flight

to gain their bearings and then utilize a map-like representation to *choose* between different navigational goals.

Wehner, however, rejected Menzel et al.'s (2005) interpretation, and the way in which Wehner sought to discount Menzel's interpretation began a general strategy that the desert ant anti-cognitive map group continues to develop. In response to Menzel et al. (2005), Cruse and Wehner (2011) built a computational neural network model whose current iterations are called Navinet. Navinet is a "toolkit" model in the sense that it utilizes different navigational strategies (e.g. path integration and landmark recognition) and these strategies largely operate independently and in parallel. Thus, Navinet is not a cognitive map because it does not integrate spatial representations and memories in the appropriate way. Cruse and Wehner (2011) use Navinet to undercut Menzel et al.'s (2005) interpretation by demonstrating that Navinet predicts the experimental results obtained by Menzel et al. (2000).

Navinet embodies the theoretical commitments and epistemic aims driving Wehner's *Cataglyphis* research program. The primary inputs to Navinet are stimuli and motivation, and "the whole motivation network is assumed to be an innate structure" (Hoinville et al. 2012). Navinet also assumes learning processes because it assumes that insects possess visual memories of landmarks, but as Cruse and Wehner (2011, 4) explain, "To keep the simulation as simple as possible, learning processes as such are not simulated, but memories may be switched off or on by hand to simulate different learning states." The parameters that determine how different aspects of the model interact with each other are taken from Wehner's experimental work on *Cataglyphis*. Still, Cruse and Wehner (2011) argue that Navinet is relevant to insect navigation generally, not just

Cataglyphis navigation. Cruse and Wehner (2011, 3) argue that their proof of concept demonstration replicating Menzel et al.'s (2005) results refute the cognitive map hypothesis since the cognitive map "represents a more complex hypothesis" than the Navinet toolkit model. Wehner and colleagues continued to elaborate Navinet in subsequent years (Hoinville et al. 2012; Schilling et al. 2013)

Menzel et al. (2012, 241) agree that Navinet can account for the results of the Menzel et al. (2005) harmonic radar experiments, and they agree that Navinet is not a cognitive map, but they push back against the idea that Navinet is more parsimonious than the cognitive map: "Whether the model captures a more parsimonious neural implementation is a different question and must be kept open as long as we do not have any data on the neural processes in the insect brain allowing the animal to navigate over long distances in a highly flexible way and to communicate about locations using the same spatial reference frame" (Menzel et al. 2012, 241 See also Menzel and Fischer 2011, 2).

Furthermore, prior to Cruse and Wehner's (2011) publication, Menzel had already cast doubt on the idea that the results of navigation experiments on walking ants are relevant to flying honeybees: "Most experiments adopting the toolbox model were performed with ants (mostly the wood ant *Formica rufa*, the desert ant *Cataglyphis*, and the Australian desert ant *Melophorus bagoti*). The data were generalized to bees, implying that navigation strategies in running and flying Hymenoptera are similar. Bees fly over distances of kilometers, cruising well above ground with a bird's-eye view, whereas ants run over a few tens of meters and have only close-up views of the terrain. The biology of these groups of insects is so different that different forms of learning and

different structures of spatial memory are quite likely" (Menzel and Giurfa 2006, 27). Menzel is unmoved by Cruse and Wehner's Navinet demonstration because Menzel believes that Wehner's parsimony arguments are misguided and because Navinet's parameters are derived from experiments on ants.

Menzel and colleagues fully endorse the cognitive map hypothesis in 2014 and frame their endorsement of the hypothesis as an extension of the "[…] broad consensus that the brains of mammals, and perhaps even all vertebrates, compute a metric cognitive map of the experienced environment on which they maintain a continuously updated representation of the animal's position" (Cheeseman et al. 2014a, 8949). Again, Menzel and colleagues use the displacement experimental paradigm to support their argument.

At this point in the debate, it is mutually agreed that when researchers capture and displace honeybees that are foraging at a familiar site, the honeybees will, upon release, fly in the direction they were going to fly before being displaced according a path integration strategy. The point at issue is what happens after the honeybee has travelled to where the hive or feeding station should have been. In Cruse and Wehner's (2011) toolkit model, the honeybee recognizes a landmark that is associated with a vector memory indicating how to get to their goal. If the honeybee recognizes multiple landmarks, the associated vectors are averaged and the honeybee flies the averaged route. Alternatively, the cognitive map hypothesis holds that when honeybees recognize landmarks, they are able to locate themselves within an allocentric map that they can use to plan a course from any represented feature to any other represented feature. On the Navinet model, honeybees use their sun compass to determine the directional component of the vectors associated with landmarks; on the cognitive map hypothesis, honeybees determine the

directional component of their next journey by using landmarks to place themselves in a terrain-referenced map. To test whether honeybees possess a cognitive map, Cheeseman et al. (2014) design a displacement experiment where these competing hypotheses predict different results.

By anesthetizing honeybees, Cheeseman et al. (2014a) create a mismatch between the honeybees' circadian clock and the actual time of day. On the toolkit model, this mismatch should cause honeybees to become even more lost after they recognize familiar landmarks. Honeybees should become more lost because they will execute the associated vector memories according to an erroneous reading of their sun compass. According to the cognitive map hypothesis, the mismatch will not affect honeybees because once they recognize a familiar landmark, they use their cognitive map system of reference to determine the direction of their next flight. After performing the experiment, Cheeseman et al. (2014a) report that the anesthetized honeybees were able to fly in the proper direction after recognizing landmarks, a result they argue supports the cognitive map hypothesis.

Cheung et al. (2014) argued against Cheeseman et al.'s (2014a) interpretation of the experiment on the grounds that a non-cognitive map interpretation of the results is still possible and that the anesthesia may not have affected the honeybees in the ways Cheeseman et al. assume. Cheesemen et al. (2014b) reply that their assumptions about the effects of anesthesia are supported by previous research and by dismissing Cheung et al.'s (2014) non-cognitive map interpretation of the results because it "[…] is predicated on data from walking insects rather than flying insects."

In addition to rejecting Wehner's parsimony arguments and emphasizing the difference between walking insects and flying insects, Menzel offers more rebuttals to anti-cognitive map researchers. First, he argues that the cognitive map debate in insects must be resolved at the level of neuro-cellular or neuro-molecular mechanisms, not via behavioral experiments. In Menzel's words, "The content of memory is not directly accessible by behavioral means because only retrieved and expressed memory controls a particular behavior. However, the memory content not directly controlling the movement may still be of high relevance for decision making. Different behaviors may lead to differently retrieved memories and thus may give the impression that these memories are separated and independent […] Innate components are tightly combined with learning. Thus, the acquisition and use of the animals' knowledge base for navigation transcends the study of the perceptual capacities and the description of the expressed behavior" (Menzel and Greggers 2015; See also Jacobs and Menzel 2014, 6; Wiener et al. 2011, 74). Menzel also suggests that the anti-cognitive map stance is a consequence of Wehner's preferred experimental subject: "If an animal such as the desert ant *Cataglyphis* is studied in an environment lacking extended landmarks, and each individual performs a rather limited number of foraging/exploration runs, then it is not surprising that only rather limited navigational strategies can be detected" (Jacobs and Menzel 2014, 19). For these reasons, Menzel continues to maintain that the Cheeseman et al. (2014a) anesthesia displacement experiments show that honeybees possess a cognitive map (Menzel 2020).

Meanwhile, Wehner and colleagues continue to develop Navinet (Wehner et al. 2016; Hoinville and Wehner 2018). In 2016, Wehner and colleagues updated Navinet according to the results of cue conflict experiments on ants (Wehner et al. 2016). Cue

conflict experiments involve setting two navigational strategies, such as landmark recognition and path integration, against each other. By observing which cue the animal follows, researchers make inferences about how the contents of different cognitive systems influence behavior. Incorporating the results of cue conflict experiments caused Wehner et al. (2016) to make Navinet less hierarchical and more heterarchical. The idea is that all of an insect's navigational strategies are running simultaneously, and the different outputs of those strategies are reconciled "downstream" where they are integrated into navigation behavior. To use Wehner et al.'s (2016, 470) turn of phrase, the integrated outputs of Navinet indicate "What to do?" whereas the cognitive map hypothesis holds that the contents of different navigational mechanisms are resolved centrally, farther "upstream" into a representation that indicates "Where am I?". Wehner et al. (2016) provide evidence for their new version of Navinet by demonstrating how the model predicts the results of actual cue conflict experiments on ants. Hoinville and Wehner (2018) then demonstrate how their new version of Navinet predicts the results of Menzel's 2014 anesthesia displacement experiments. Menzel is unmoved by this demonstration for reasons already explained. Again, Hoinville and Wehner (2018, 2828) distinguish Navinet from the cognitive map hypothesis according to forms of knowledge each produces: "At any one time, the animal knows where to go rather than where it is on some kind of cognitive map."

The expanded history of the cognitive map has nearly reached the present. Before getting into the lessons one can learn from this history, I will examine a recent development that shows how the debate has been passed down to a new generation of

researchers while also demonstrating the continuity of this expanded history from the 1930s to the present.

In 2018, Harald Wolf, Matthais Wittlinger, and Sarah Pfeffer performed cue conflict experiments on *Cataglyphis* and used the results of those experiments to develop the parallel toolkit model of insect navigation (Wolf et al. 2018). By looking to mentor-mentee relationships, one can see how this work is a continuation of the Wehner lineage. Wehner introduced Wolf to *Cataglyphis* in the 1990s when Wehner invited Wolf to join him at his Tunisian field site (Wehner 2019; For a publication resulting from their early collaboration, see Wolf and Wehner 2000). Then, in the 2000s, Wolf and Wehner co-advised Mathias Wittlinger while he was a Ph.D. student. The three discovered a step-counting odometer mechanism in *Cataglyphis* for recording distance travelled (Wittlinger et al. 2006; 2007).

The research described in Wolf et al. (2018) is striking for two reasons. First, they are clearly contributing to and thereby continuing the proof of concept strategy Wehner and colleagues have developed for fleshing out the toolkit hypothesis and undercutting the cognitive map hypothesis. Second, when theorizing about how *Cataglyphis* integrates representations, Wolf et al. (2018, 11) explicitly call back to Lorenz's (1937) psycho-hydraulic model of instincts (See Figure G).

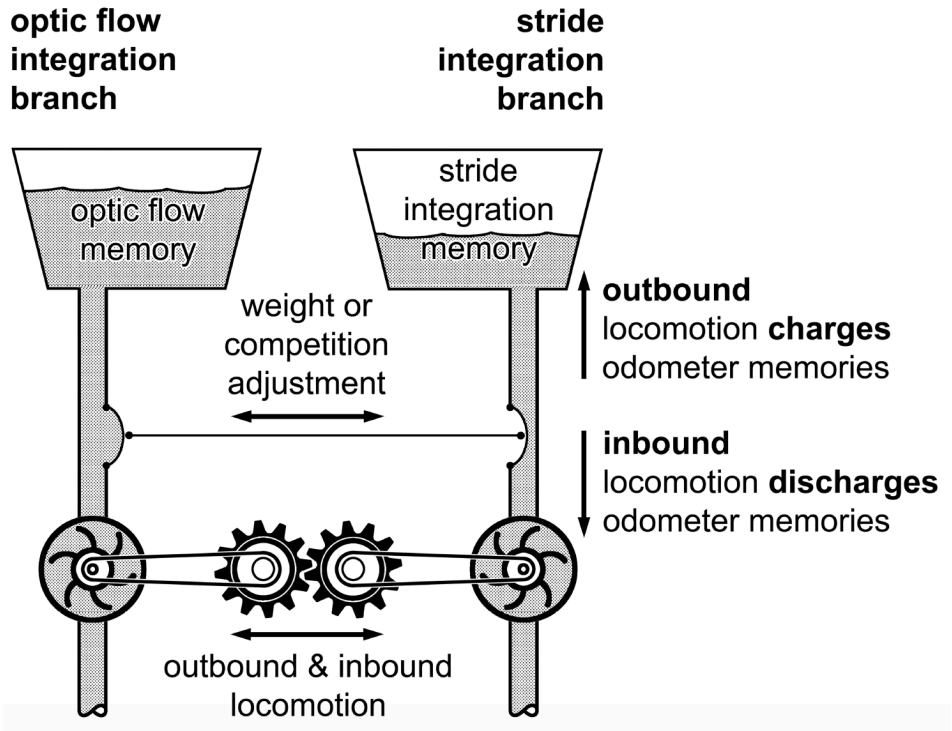

Fig. 11: Wolf et al.'s hydraulic model of content integration for optic flow and stride integration mechanisms (Wolf et al. 2018).

This is a clear visual representation of the way Wehner's brand of German ethology blends Lorenz's idea of action-specific energy with the contents of memory. (See Figure H).

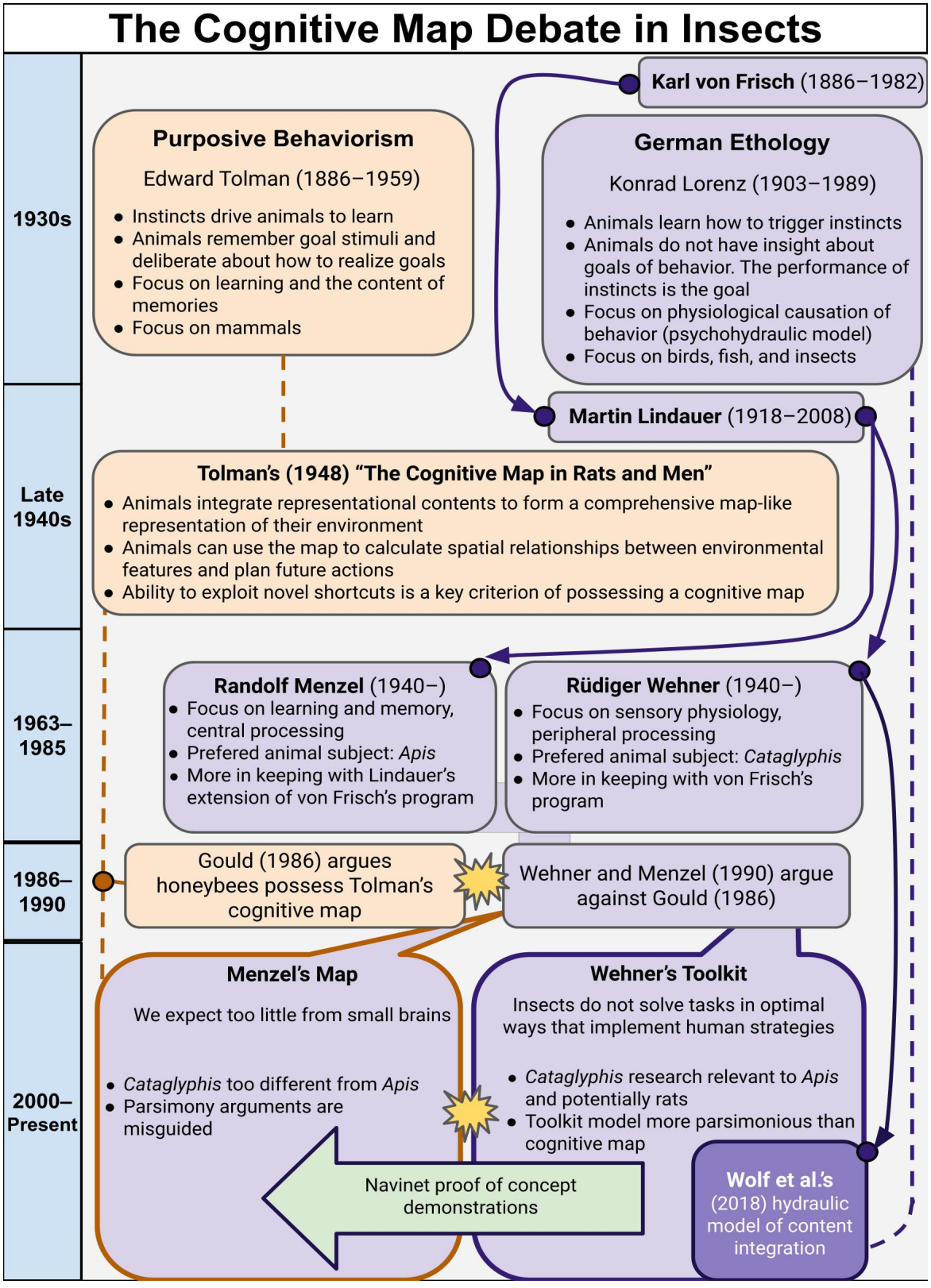

Fig. 12: Visual summary of the cognitive map debate in insects (fifth iteration).

4. Historical Upshots

How does this expanded history of the cognitive map illuminate what is at stake in the cognitive map debate in insects? First, it shows that despite the definitional complexities surrounding the cognitive map hypothesis, the cognitive map debate in insects is not motivated by definitional disagreements or confusion, and it never has been. Menzel and Wehner agree about the key distinctions that separate the cognitive map hypothesis from the toolkit hypothesis. To use Wehner's (2020, 301) colloquial phrasing, on the toolkit model, insects know *where to go*, not *where they are*. Alternatively, on Menzel's (2019) cognitive map hypothesis, honeybees know *where they are* according to an allocentric map with a terrain-based system of reference, and they form expectations about the outcomes of potential behaviors by utilizing this map. Both Wehner and Menzel ascribe representational contents to insects. The debate largely hinges on how insects utilize those representations.

The expanded history also highlights how background norms guiding cognitive theorizing cause Wehner and Menzel to endorse conflicting positions about how insects utilize representations. For Wehner, one must be on guard against the anthropomorphic temptation to assume that animals solve navigation problems the way humans solve navigation problems. Animals evolve solutions that work for particular problems presented by the local environment, and human ideas of what constitutes an "optimal" solution are often misleading (Wehner and Wehner 1990; Wehner 1994; Wehner 2003, 582). For Menzel, one must be on guard against anthropodenial—the tendency to discount similarities between animals and humans (de Waal, 1999). Menzel (2004, pp.

479–480) frames this stance as a reaction against the presumed simplicity of small-brained invertebrates:

"When I ask myself what I have learned so far from my studies of how the nervous system works, I can suggest this answer. We expect too little from small brains […] Little brains do not appear to produce more stereotyped behavioral patterns than big brains. There is also no indication that a small brain, by necessity, has a more limited memory capacity, at least within the boundaries of its cognitive faculties. Experience-dependent neural plasticity, and the memory trace resulting from it, is such a basic property of nervous systems that it does not require any particular level of network complexity or total number of neurons. Similar environmental demands are made of small and big brains. Are different neural strategies implemented in small and big brains to solve similar problems? I do not believe so, and in particular, I do not consider small brains to be less flexible and less quick to adapt […] This does not mean that the neural and cellular mechanisms are the same in small and big brains, but the mechanisms should be related to each other because of common phylogenetic histories."

Furthermore, the expanded history provides context that allows one to situate these background norms about cognitive theorizing within the broader history of animal behavior research. Wehner's suspicion of anthropomorphic theorizing is in line with the German ethological tradition he inherited as represented by the work of Lorenz and von Frisch. For Lorenz and von Frisch, a genuinely biological approach to behavior conflicts with anthropomorphic perspectives in the sense that it emphasizes physiological causation and evolutionary processes over the psychological intentions people normally appeal to when explaining human behavior. Lorenz and von Frisch believed that

instinctive behavior patterns could account for more of an animal's behavioral repertoire than learning psychologists were willing to grant.

In this light, one can see how the Navinet toolkit model continues some of the modularized, instinct-heavy theorizing of German ethology. In Navinet, an innate motivational system interfaces with external stimuli to trigger different cognitive subroutines, and the representational contents of those subroutines are "charged" and "discharged" in a manner reminiscent of Lorenz's psycho-hydraulic model of instincts. As Lorenz stressed, an animal need not be aware of the adaptive value of a properly executed instinctive behavior pattern; the performance of instinctive behavior patterns are ends in themselves. Similarly, on Wehner's toolkit model, insects are not aware of their navigational goals and they do not make choices about how to utilize representations to realize those goals. Historical context also sheds light on Wehner's investigative practices and epistemic aims. Similar to von Frisch, Wehner's primary investigative target is sensory physiology and his primary style of investigation involves behavioral experiments that exploit central place foraging.

Menzel, on the other hand, reacted against aspects of his German ethological heritage and became interested in the theories and experimental paradigms of animal psychologists as a doctoral student. Seen in this context, his pro-cognitive map research represents a synthesis of German ethology and American animal psychology. His work takes after Lindauer's research more than von Frisch's in its focus on more central, neurophysiological mechanisms. Another manifestation of Menzel's ethological heritage is his conviction that behavioral approaches to animal navigation must include field experiments that allow an animal to move freely across spatial scales that the animal

would normally traverse in the wild (Jacob and Menzel 2014). On the American psychological side, Menzel subjects honeybees to laboratory conditioning experiments that he believes provide evidence about deeply conserved learning mechanisms. More obviously, he has also extended Tolman's cognitive map hypothesis to insects.

Despite Menzel's rejection of some aspects of German ethology, one should not confuse Menzel's suspicion of anthropodenial as anti-ethological. Indeed, a defining theme of von Frisch's career was his ability to demonstrate unexpectedly sophisticated capacities in fish and honeybees (Munz 2016; Dhein 2021). Furthermore, in addition to pitting itself against psychological, introspective approaches to animal behavior, European ethology also challenged the idea that animals are mere reflex machines. Menzel continues the Frischean tradition of challenging people's preconceptions about the simplicity of honeybees. However, he does so in a way that also challenges Frischean ethology's focus on instincts, sensory physiology, and behavioral experiments.

The expanded history provided above also shows how the investigative dispositions Wehner and Menzel developed early in their careers prefigured certain aspects of the cognitive map debate in insects. Wehner's doctoral research contributed to a theory of visual pattern recognition that appealed to peripheral sensory processes rather than central processing while Menzel's doctoral research indicated that central processing affects the way insects learn to associate colors with rewards. Correspondingly, Wehner's toolkit model emphasizes peripheral processing while Menzel's cognitive map emphasizes central processing. Wehner discovered *Cataglyphis* shortly after completing his doctorate and the large body of work he has produced on *Cataglyphis* has turned the ant into a model organism for navigation studies. On the one hand, Wehner's adoption of

Cataglyphis has allowed him to exert a greater amount of control in his navigation experiments relative to honeybees, since ants travel less distance on a 2D plane while honeybees fly greater distances in three dimensions. On the other hand, the fact that Navinet's parameters are largely informed by Wehner's *Cataglyphis* research has provided an opening for Menzel to discount Wehner's proof of concept demonstrations on the grounds that walking ants are too different from flying honeybees.

Finally, this historical perspective on the cognitive map debate in insects shows that more is at stake in the debate than the truth value of propositions characterizing insect cognition. What is at stake are different constellations of epistemic aims, preferred model organisms, investigative practices, and theoretical commitments. Situating these competing constellations within the history of 20th century animal behavior research shows how the cognitive map debate in insects is a clash between different ways of knowing animals. These different ways of knowing animals used to be associated with different schools of animal behavior research. But between the end of WWII and the end of the 20th century, these competing schools of animal behavior research began to blend and disciplinary labels like "comparative psychology", "behaviorism", and "ethology" became less relevant. The expanded history of the cognitive map debate in insects shows how the different ways of knowing animals associated with these school continue to influence major developments in cognitive science.

Viewed in this light, the cognitive map debate in insects is also a debate about the future of Wehner and Menzel's shared research tradition. Both are successful senior scientists who have the right pedigree and research record to exemplify modern incarnations of the German ethological tradition stemming from von Frisch. Despite the

pluralistic inclination to let a hundred insect navigation research programs blossom, there are a limited number of students to train, a limited number of academic positions to fill, and a limited amount of grant money to award. As shown at the end of section 3.5, the cognitive map debate in insects is being passed on to a new generation of scientists. If one side were to win the debate, it would not just be a vindication of the toolkit theory or the cognitive map theory, it would also vindicate a vision for the future of an extremely productive tradition of behavioral research.

5. Philosophical Upshots

In section 2, I claimed that the expanded history presented above would provide a novel perspective that reframes Rescorla's (2013) and Knoll and Rey's (2017) conclusions as capturing key distinctions driving the debate. I begin with Rescorla.

Rescorla argued that current science supports a clean division between motivational states and informational states in insect cognition. To support that claim, he references Menzel's cognitive map research and Menzel's (2008) endorsement of Caruthers (2006, 66) model of cognition (See Figure I).

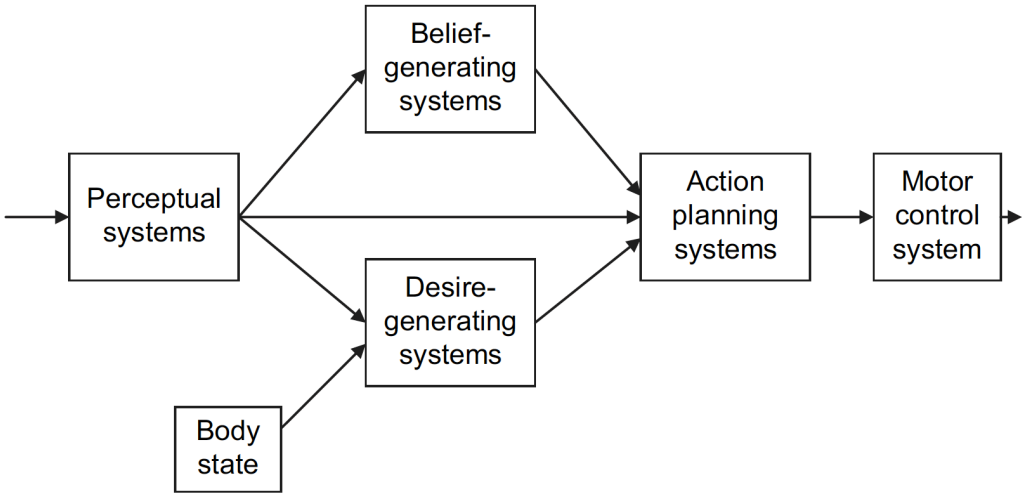

Figure 13: The cognitive structure of the honeybee brain (From Menzel 2008, 272; Menzel 2019, 671; after Caruthers 2006, 66)

Menzel's position about motivation and information being separate is linked to his endorsement of the cognitive map hypothesis. The cognitive map hypothesis maintains that animals make decisions about where to go based on their motivations and where they believe themselves to be. The cognitive map contains the same information regardless of the motivations an animal brings to their reading of the map in a particular situation. Thus, motivation and information are separate in the sense that different motivations do not give the animal access to different information.

However, contrast the Caruther (2006) model of cognition endorsed by Menzel with Wehner's Navinet toolkit model, which is just as current as Menzel's work (See Figure J).

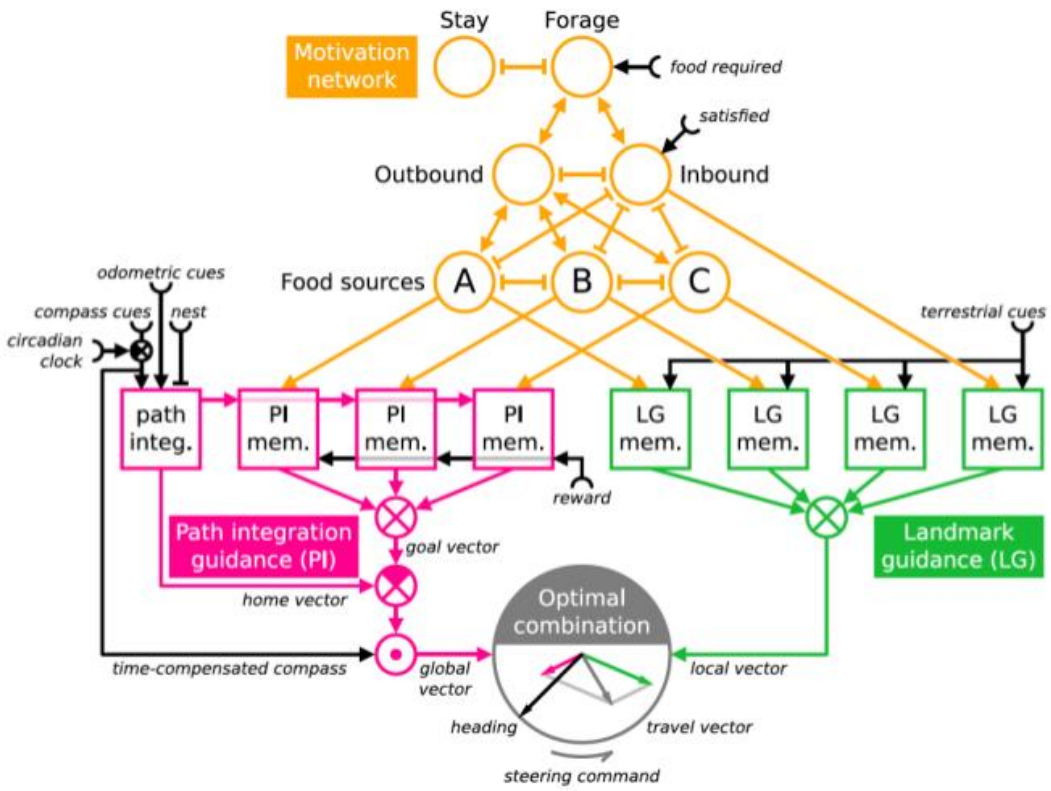

Figure 14: Navinet model of the cognitive processes underlying *Cataglyphis* navigation. The yellow is the motivation network (Hoinville and Wehner 2018, 2825).

In Wehner's toolkit model, different motivational states activate or preferentially weight the outputs of different informational states. Thus, motivation and information are connected in the sense that whether or not an informational state has the potential to influence action depends, in part, on what motivational states are activated. On the toolkit model, an insect does not bring their motivations to a buffet of information and deliberate over what informational contents are necessary for achieving their desire. Rather, motivational states and informational states blend in a way that broadly comports with Millikan's description of pushmi-pullyu representations as combining imperative and

indicative content.[18] That is, on Wehner's toolkit model, *Cataglyphis*' cognitive architecture connects "states of affairs directly to actions, to specific things to be done in the face of those states of affairs" (Millikan 1984, 99). Remember that for Wehner, insects know where to go, not where they are.

Rescorla's (2013) focus on the relationship between motivation and information highlights a key difference between Wehner's toolkit and Menzel's cognitive map. However, the correspondence between Rescorla's objection to Millikan and the points at issue in the scientific literature may be obscured by terminology. In the cognitive map debate in insects, the relationship between motivation and information is usually not at the forefront. Instead, the pro-cognitive map and anti-cognitive map groups tend to debate a) whether representations of spatial relations are synthesized into a general map-like representation and b) whether the outputs of various navigational strategies are pooled upstream before an action has been planned or pooled downstream to determine the actions that will take place. The philosopher's linguistic terminology of "indicative" or "imperative" contents is absent. Nevertheless, as this paper has demonstrated, the relationship between motivation and information is central to cognitive map debate in insects.

Similiarly, Knoll and Rey's (2017) distinction between non-intentional representations and intentional representations points to issues that are at the crux of the

[18] Given the historical connections made by this paper, it is interesting that Millikan (2004, 18–19) likens her pushmi-pullyu representations to the fixed action patterns of Lorenz and Tinbergen's (1939) classical ethology.

cognitive map debate in insects. Following Burge (2010, Chapter 10), Knoll and Rey (2017) argue that a system utilizes genuinely intentional representations when ascriptions of representational contents play an irreplaceable role in explaining the dynamics of that system. After scrutinizing Wehner's *Cataglyphis* research and Menzel's honeybee research, Knoll and Rey (2017, 19) argue that ascriptions of representations play an irreplaceable explanatory role in honeybee navigation research (but not *Cataglyphis* research) because honeybees' "navigational capacity seems to elude generalization in terms of proximal stimuli alone. Exposure to the waggle dance eventuates not just in a particular motor routine, but rather a capacity that seems capable of taking the bee to the same location via indefinite different routes." Again, like Rescorla's focus on the relationship between motivation and behavior, Knoll and Rey's focus on whether representations "eventuate particular motor routines" or provide a basis for the planning motor routines according to distal stimuli captures a key difference between the toolkit model and the cognitive map hypothesis.

6. Conclusion

The development of scientific knowledge is a dynamic process, and at any given moment, different scientists may endorse conflicting views. This is especially true of cognitive science, which encompasses a diverse plurality of research programs that may make incompatible claims (Allen 2017). Given the non-uniform nature of cognitive approaches to brains and behavior, historical perspectives have a special role to play in making sense of scientists' invocations of representational content. Namely, historical

context connects scientists' use of representational concepts to scientist' use of other, more familiar concepts.

For philosophers, such connections provide an opportunity to draw on extant scholarship when making sense of cognitive science's seemingly novel use of representational concepts. For example, philosophers have suggested a connection between cognitive scientists' practice of ascribing representational contents and Shannon's (1949) mathematical theory of communication (See Bergstrom & Rosvall 2011 for a general account; See Burge 2010, 529 and Dhein 2020 for the specific suggestion that the ascriptions of content in Wehner's *Cataglyphis* research program are tied to information theory). The historical context provided by this paper points to another productive angle for philosophical inquiry: the connection between ethological notions of instinct and representational contents. Additionally, this paper demonstrates how important historical context is when selecting case studies from cognitive science for philosophical purposes. Without such context, philosopher's appeal to "the current science" at their own peril.

Historically, connecting the cognitive map debate in insects to the larger history of animal behavior research shows the continuity between classic themes like instinct vs. learning and contemporary debates in cognitive science. In the decades surrounding WWII, practitioners of behaviorism, comparative psychology, and ethology were engaged in explicit debates about the proper way to know animals. As the 21st century drew nearer, these disciplinary labels became less relevant (Beer 1975; Denenberg 2004) and the traditions associated with these labels grew closer (Hinde 1966; Dewsbury 1992).

This paper shows how pre-synthesis debates continue to motivate controversy in animal navigation research.

Conclusion: What Does It All Mean?

Nietzsche asserted that concepts with histories cannot be defined. This warning against ahistorical approaches to clarifying ideas is especially relevant to the concept of meaning, which has surely been shaped by a long and intricate history of use. Thus, rather than produce a traditional analytic account of the meaning of meaning in animal behavior research, I have situated the scientific act of ascribing meaning within a specific historical context and research tradition. This diachronic perspective on meaning ascriptions allowed me to adopt a pragmatic, broadly Peircean framework for clarifying the meaning of content ascriptions (Figure A).

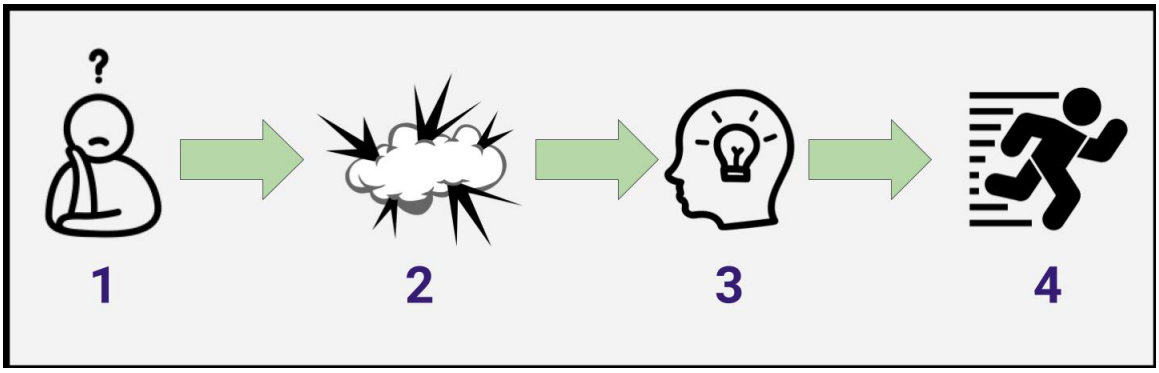

Fig. 15: A broadly Peircean framework for belief formation. A situation causes doubt (1), which leads scientists to engage in activities to appease that doubt (2) with the fixation of a belief (3). The belief then guides future action (4), especially in the sorts of situations that occasioned the initial state of doubt. Within this Peircean framework, the meaning of a belief (e.g. honeybees can *recognize* the color blue) is wrapped up in all four of the above stages, especially stages (2) and (4). The meaning of belief is constituted by the

things scientists do to produce evidence justifying that belief (2) and the way that the adoption of the belief guides future action (4).

In this conclusion, I synthesize the findings of Chapters 1–3 by filling in the blanks of Figure A for the ethological tradition of eusocial insect research stretching from Karl von Frisch through Rüdiger Wehner. The three chapters of this dissertation have not told a continuous story linking von Frisch's work to Wehner's work, so this conclusion is somewhat speculative in its broad scope. Another important caveat is that the Peircean framework I have adopted for clarifying concepts is specific to particular epistemic aims and experimental practices, and I do not claim that my filling in of the blanks of Figure A captures all content ascriptions in the research tradition. I have picked out a package or cluster of epistemic aims, experimental practices, and habits of reasoning that consistently surround scientists' ascriptions of content. I now suggest that this cluster is an enduring feature of the research tradition. In connecting the dots between the chapters of this dissertation, I articulate novel historical and philosophical hypotheses. The gist of these historical and philosophical hypotheses is that von Frisch engendered a distinct ethological tradition, and that (within a particular investigative context) the meaning of meaning has been quite consistent within that tradition. I will now flesh out these directions for future research by filling in the blanks of Figure A with the results of Chapters 1–3.

First, as shown by Chapters 1 and 2, the initial state of doubt that eventually leads researchers to ascribe content to insects concerns behavioral capacities and the physiological underpinnings of such capacities. In chapter 2, von Frisch's (1910) grey

card experiments were motivated by doubt over whether or not honeybees can see colors. To put the doubt in more philosophical terms, von Frisch questioned whether or not honeybees are capable of utilizing a special kind of perceptual contents. Likewise, in chapter 1, Wittlinger, Wehner, and Wolf (2006, 2007) questioned whether or not *Cataglyphis* has the capacity to record content about distance travelled via some kind of odometer mechanism. In both cases, scientists' doubt concerns an animal's sensory capacities and the way those capacities contribute to navigation or orientation behavior. To rephrase in terms of epistemic aims, the scientists want an account of how lower neuro-physiological mechanisms causally contribute to the performance of navigation or orientation behavior.

These two examples are separated by nearly a century. Still, Wittlinger, Wehner, and Wolf (a group that includes 3rd and 4th generation members of the von Frisch lineage) used the same experimental paradigm as von Frisch to produce evidence to appease their doubt. The stilts and stumps experiments and the grey card experiments both rely on training central place foragers to a feeding station. Researchers manipulate aspects of the experimental subjects and/or setup, observe the outcomes of foraging behavior under these manipulated circumstances, and use those outcomes as evidence to appease their doubt. This research tradition does not exclusively utilize the experimental paradigm embodied by the grey card and stilts and stumps experiments, but such experiments are a hallmark of the tradition. Furthermore, such experiments consistently mediate the transition between scientists' doubt and scientists' ascriptions of content.

Though it remains to be thoroughly argued, I believe the philosophical insights about the stilts of stumps experiment from Chapter 1 apply to von Frisch's grey card

experiments. That is, the account of content ascription developed in Chapter 1 also captures von Frisch's grey card experiments. Similarly, the historical insights about von Frisch's work from Chapter 2 continue to characterize Wehner's research program. Chapter 2 highlighted features of von Frisch's early career research that distinguished von Frisch from both Tinbergen and Lorenz's program of classical ethology and other contemporaneous experimental approaches aimed at the same questions (i.e. Turner and von Hess' work on animal sensation). Those same features continue to characterize Wehner's neuroethological approach to insect navigation.

The third stage in Figure A is belief fixation, and the beliefs of interest in this dissertation are beliefs about the semantic properties of neuro-sensory mechanisms. Scientists announce such beliefs via ascriptions of content (e.g. Honeybees *recognize* the color blue, *Cataglyphis records content about* distance travelled via an internal odometer). Chapter 1 showed how beliefs about the semantic properties of neurosensory mechanisms guide the future actions of researchers in a productive manner. Namely, they guide hypothesis formation and facilitate comparative theorizing. Regarding hypothesis formation, Chapter 1 argues that ascriptions of content help researchers drill down into increasingly lower mechanistic levels to identify mechanisms that causally contribute to an animal's ability to reliably achieve difficult goals. Broadening this point into a more general hypothesis, ascriptions of content have played this productive role throughout the Frischean tradition. In accordance with this hypothesis, the lineage of mentor/mentees I examined (von Frisch → Lindauer → Wehner → Wittlinger → etc.) have investigated lower and lower mechanistic levels over the generations. Von Frisch's honeybee work

largely focused on sensory physiology while more recent members of lineage trace content from sensory organs to the neuro-cellular level.

Chapter 3 introduces a bifurcation in the research lineage discussed so far. Instead of focusing exclusively on the von Frisch → Lindauer → Wehner lineage, it compares that lineage with the von Frisch → Lindauer → Menzel lineage. Within the broader context of the dissertation, chapter 3 shows that norms for ascribing content do not determine norms for characterizing the dynamics of contents. Wehner's Navinet toolkit model and Menzel's cognitive map both appeal to the same collection of contents (e.g. contents about direction of travel, contents about the location of landmarks). The key difference between the models is the how they characterize the processing or utilization of those contents. Are the contents integrated into more complex representations by central processes or are they kept separate and retrieved by more peripheral, task-specific processes? Chapter 3 shows how two scientists who were inducted into the same tradition at the same time by the same mentor came to embrace different norms for justifying claims about the dynamics of contents. Wehner's side draws from ethological ideas about physiological instinct while Menzel's side draws on purposive beahaviorist ideas about learning and memory.

I embarked on this dissertation to learn something about the meaning of meaning in the context of scientific investigations of behavior. I conclude the dissertation by listing what I have learned as concisely as possible:

I. (Chapter 1): Scientists do not need a philosophically comprehensive theory of content for their ascriptions of content to play a productive role in the process of inquiry.

II. (Chapter 1): Ascriptions of content can aid scientific investigations outside the context of explanation. For example, I have argued they aid hypothesis formation and comparative theorizing.

III. (Chapter 1): A cybernetic or goal-directed notion of biological function is intimately tied to the meaning of meaning in the research tradition stretching from von Frisch through Wehner. Scientists justify ascriptions of content by designing behavioral experiments that bear on goal-directed properties of behavioral functions. Scientists are justified in ascribing content to a state or process when they demonstrate that the state or process causally contributes to the reliable accomplishment of difficult goals.

IV. (Chapter 2): Karl von Frisch has a complicated and understudied relationship to the discipline of ethology. He and his work meant different things to different ethologists at different times.

V. (Chapter 3): The evidential norms guiding appropriate invocations of content need not determine the evidential norms guiding characterizations of content.

VI. (Chapter 3): The cognitive map debate in insects is not about cognition *per se* but how to characterize cognition. Specifically, it is about how characterize the dynamics of contents. Scientists' conflicting characterizations of insect cognition do not stem from conflicting philosophical positions about the nature of cognition or mental contents. Rather, scientist's conflicting characterizations of cognition

are a continuation of longstanding themes from the history of animal behavior research.

VII. (Hypothesis): The features of von Frisch's work that made it stand out from the founders of classical ethology persist in the work of a Frischean lineage of neuroethologists. This German-speaking lineage of ethologists represents a distinct and understudied branch of European ethology. Examining their development will broaden our understanding of ethology's impact on contemporary animal behavior research.

VIII. (Hypothesis): The cluster of epistemic aims, experimental practices, and ascriptions of content examined here is present in von Frisch's early career research and persists to the present day within the von Frisch → Lindauer → Wehner lineage.

When I started this project, I was just as fascinated by the concept of meaning as I was baffled by it. It seemed as though meaning were something entirely different than every other sort of thing I was familiar with. Looking forward, this dissertation has furnished me with a collection of concepts and practices that I now believe to be intimately tied to the notion of meaning in behavioral contexts: agency, motivation, comparative theorizing, behavioral repertoires, hypothesis formulation, goal-directed function, and purpose. Historically, I have come to appreciate how fractured the implicit pragmatics surrounding claims about meaning are. Scientists who seem to agree on norms for justifying ascriptions of content may disagree on norms for justifying

characterizations of content. I look forward to pursuing these themes in my next research project, "Humans, Animals, Machines: Behavior in the Information Age."

This next project continues to look at the scientific practice of ascribing content to animals, but it has a broader scope than this dissertation. Instead of examining a single research tradition over a century, I will examine two different traditions between the end of WWII and the present. I begin at the end of WWII because biology entered the information age after WWII when a communications engineer named Claude Shannon (1949) produced a theory of communication that bestowed the prestige of physics and engineering upon a new formal conception of information. That allowed physicists and mathematicians to bring the concept of information to bear on biological problems, and it created an opportunity for biologists to borrow the language of information theory (Shannon 1956; Aspray 1985; Kay 2000; Kogge 2012). In the late 1940s, the coming information revolution was most clearly heralded by the newly mobilized science of cybernetics, which promised to synthesize human, animal, and machine behavior using recently formalized notions of information, feedback, and control (Wiener 1948, 1950/1989).[19] Meanwhile, American comparative psychology and European ethology—two major traditions of animal behavior research that had emerged prior to WWII—

[19] Weiner (1950/1986, p. 16–17): "When I give an order to a machine, the situation is not essentially different from that which arises when I give an order to a person […] the theory of control in engineering, whether human or animal or mechanical, is a chapter in the theory of messages. Naturally there are detailed differences in messages and in problems of control, not only between a living organism and a machine, but within each narrower class of beings. It is the purpose of Cybernetics to develop a language and techniques that will enable us indeed to attack the problem of control and communication in general, but also to find the proper repertory of ideas and techniques to classify their particular manifestations under certain concepts."

continued to hold conflicting positions about when it is appropriate to make inferences about human behavior from non-human systems (Lehrman 1953). Accordingly, ethologists and comparative psychologists interpreted and responded to the synthetic ambitions of the cybernetics movement differently. As the 21st century drew nearer, all of these research traditions began to dissipate; comparative psychology and ethology grew closer (Hinde 1966; Dewsbury 1992), their disciplinary labels became less relevant (Beer 1975; Denenberg 2004), and most academics came to regard cybernetics as a dead movement.

Nevertheless, the epistemological problems involved with using the concept of information to compare behavior remain. Animal behavior researchers continue to grapple with the problem of human/nonhuman comparisons (Burghardt 2007; Wynne 2007; Buckner 2013; de Waal 2016), some continue to see revolutionary potential in the concept of information for synthesizing understandings of behavior (Lord et al. 2016; Pica et al. 2017; Neri et al. 2017; Porfiri 2018; Xiong & Proctor 2018), and philosophers continue to investigate the role that the concept of information plays in behavioral research (Allen 1992; Newen and Bartels 2007; Chemero 2009; Sterner 2014; Bechtel 2016; Shea 2018; Ganson 2020; Dhein 2020). My next project situates contemporary efforts to use the concept of information (and, inevitably, informational *content*) to compare human/non-human behavior within the larger history of that endeavor. Specifically, I examine the evidential relationships connecting researchers' experimental results, researchers' informatic claims about behavior, and researchers' practice of comparative theorizing. Then, I bring the concept of information back down to earth by

connecting these practices to the material, interpersonal, and political conditions that influenced their creation (Longino, 1990).

The concept of meaningful content has been and continues to be used in different ways by behavioral scientists. The dawning of the information age brought the pervasive sense that the concept of information harbors untapped revolutionary potential. My next project provides much needed context to that sentiment by relating the origins of the information age to the problem of comparative theorizing in the behavioral sciences.

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