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The cognitive map debate in insects: A historical perspective on what is at stake

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A B S T R A C T

Though well established in mammals, the cognitive map hypothesis has engendered a decades-long, ongoing debate in insect navigation studies involving many of the field's most prominent researchers. In this paper, I situate the debate within the broader context of 20th century animal behavior research and 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. The expanded history of the cognitive map provided in this paper shows that more is at stake in the cognitive map debate than the truth value of propositions characterizing insect cognition. What is at stake is the future direction of an extraordinarily productive tradition of insect navigation research stretching back to Karl von Frisch. Disciplinary labels like ethology, comparative psychology, and behaviorism became less relevant at the turn of the 21st century, but as I show, the different ways of knowing animals associated with these disciplines continue to motivate debates about animal cognition. This examination of scientific disagreement surrounding the cognitive map hypothesis also has significant conse-quences for philosophers' use of cognitive map research as a case study.

1. Introduction

The cognitive map has been called an "a priori assumption" that "should be abandoned" (Benhamou, 1996, p. 211), "an unwarranted exercise of anthropomorphism" (Shettleworth, 2010, p. 310), "one of the holy grails of cognition" (Breed, 2017, p. 57), and "one of the most important neuroscientific results in recent decades" (Shea, 2018, p. 113). The idea that animals like rats use an internal, cognitive, "map-like" representation of the environment to navigate was proposed by American behavioral scientist Edward Tolman in 1948 (Tolman, 1948). Because Tolman proposed his hypothesis against the backdrop of American behaviorism, this event is often interpreted as a harbinger of the so-called "cognitive revolution" in mid 20th century psychology (Greenwood, 1999, p. 9–10; Mandler, 2002; Hobbs & Chiesa, 2011, p. 391; Gallistel, 2017, R108). 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 (Bingman, 2011; Boesch & Boesch, 1984; Bshary & Brown, 2014; Casini et al., 1997; Epstein et al., 2017; Genzel 2018; Gould, 1986; Harten et al., 2020; Liu et al., 2019; Lopez et al., 2001). Within mammalian navigation research, the cognitive map hypothesis has broad support (O'Keefe & Nadel, 1978; Gallistel, 1990; Burgess, 2014; Cheeseman et al., 2014a, p. 8949; 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. Despite the debate's longevity (or perhaps because of it) multiple hon-eybee researchers have lamented via personal communication that they have lost sight of what is at stake in the debate. In this paper, I combine historical and philosophical approaches to clarify 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, contrary to existing commentary that implies the cognitive map debate persists due to defi-nitional confusion (Bennett, 1996; Dyer, 1998, p. 146; Rescorla, 2013, p. 89), I show that competing research groups largely agree about what it would take for an insect's neurosensory representations to culminate in a cognitive map. The pro-cognitive map position holds that the animal remembers and integrates representations of their environment into a more comprehensive, map-like representation. The animal can access this map-like representation when deliberating about where to go. The anti-cognitive map position holds that neurosensory representations relating to the environment remain distributed across task-specific par-allel processes in the nervous system; the animal does not "know where they are" within a map-like representation. Rather, the outputs of various subroutines are weighted and pooled "downstream" to determine where to go next.

Instead of locating the crux of the debate within the definition of a cognitive map, 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. As a result, competing groups do not universally endorse each other's claims about how insects employ neurosensory representations to navigate their environments.

The second insight of this paper involves situating those differing epistemic aims, theoretical assumptions, investigative practices, and evidential norms within the broader history of animal behavior research. Though it has not received much attention in print, the head of the anti-cognitive map group (Rüdiger Wehner (b. 1940–)) and the head of the pro-cognitive map group (Randolf Menzel (b. 1940–)) share an interesting relationship. Wehner and Menzel were trained at the same time in the same place by the same mentor. As such, they were brought up within the same research tradition. In 1990, Wehner and Menzel (1990) agreed that ants and honeybees *do not* possess a cognitive map. 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 et al., 2000; Menzel & Giurfa, 2006; Cheeseman et al. 2014 ab; Menzel, 2019) while Wehner continued to challenge the cognitive map by developing alternative hypotheses (Cruse & Wehner, 2011; Hoinville et al., 2012; Hoinville & Wehner, 2018; Wehner, 2020; Wehner et al., 2006). By relating Wehner's and Menzel's differing investigative 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. In the 20th century, the schism between American comparative psychology and European ethology was tightly associated with the learning vs. instinct dichotomy. American comparative psychologists generally promoted learning-heavy accounts of animal behavior while European ethologists generally promoted instinct-heavy accounts. By the end of the 20th century, these disciplines grew closer and animal behavior researchers seemingly neutralized the debate by acknowledging that genetic inheritance, developmental processes, and experience interact in nuanced ways to determine behavior. Nevertheless, I argue that the instinct vs. learning dichotomy of the 20th century continues to motivate the cognitive map debate in insects. Wehner and Menzel were both trained within an ethological context. I argue that Wehner's alternative to the cognitive map draws from a German-speaking ethological tradition that relies heavily on the instinct concept while Menzel's promotion of the cognitive map represents a blend of American learning theorists and European ethology.

In the next section, I review 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 a historical narrative of the cognitive map debate in insects. Then, in sections four and five, I show how that history sheds new light on the debate and philosopher's invocation of the cognitive map as a case study.

2. Philosophy of the cognitive map

Philosophers working on problems involving mental representations and cognition have shown sustained interest in the cognitive map as a case study (Bermúdez, 1998, Chapter 8; Camp, 2007; Rescorla, 2009, 2013, 2017; Burge 2010, p. 510; Zappettini & Allen, 2013; Bechtel, 2016; Knoll & Rey, 2017; Mikhalevich, 2017, p. 432; Shea, 2018, Chapter 5; Mollo, 2020; Robins et al., 2020). This paper's examination of the cognitive map debate in insects challenges the way some philosophers have used the cognitive map as a case study.

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, p. 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, p. 18–19) has suggested that insects exclusively use pushmi-pullyu representations. Rescorla (2013, p. 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 & 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, p. 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, p. 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 use?

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. Knoll and Rey correctly recognize that the desert ant group produces results that imply a different view of how representations are used 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.

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 cognitive map research on rats, 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, p. 106, emphases added) 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 exchange between Mollo and Bechtel highlights a distinction between 1) how justified or substantive a scientist's use of a concept is and 2) the scientific heritage informing the way scientists use that concept. Although it is beyond the scope of this paper to explicitly critique this distinction, I believe that the connections this paper draws between scientific heritage and the way scientists use concepts gives reason to be

skeptical of it. 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 better-known story of the cognitive map in mammalian navigation research with a parallel narrative that traces the cognitive map's reception in insect navigation research. This parallel narrative highlights how the cognitive map debate in insects is currently motivated by and a continuation of long-standing debates from the history of animal behavior research. Although historical accounts of the cognitive map often begin with Tolman's, 1948 publication, I begin by looking back to 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 contain a common point of divergence for the ancestors of the two positions currently constituting the cognitive map 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) drew from Craig's (1918) theory of instincts to build their own theories of behavior. Comparing the different ways Tolman and Lorenz incorporated Craig's theory of instincts highlights differences that continue to influence 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. The behaviors resulting from appetitive/aversive states have the *purpose* of receiving or removing stimuli in the 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 those 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 after Craig's publication, Edward Tolman (1932) incorporated Craig's theory of instincts into his own theory of behavior called "purposive behaviorism".[1] Tolman was an American psychologist who studied learning and was influenced by American behaviorism and German gestalt psychology (Tolman, 2001). American behaviorism was famously focused on explaining behavior via theories of learning based on

observable properties of behavior. Tolman (1932, p. 271–273) 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 sense that it tends to continue until an ameliorative goal state is reached. Tolman (1932, p. 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, p. 135–136) "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, p. 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, Austrian co-founder of European ethology, completed his doctorate in zoology at the University of Vienna. Lorenz (1989, p. 265, emphasis in original) recounts how reading Tolman's book as a doctoral student caused him to doubt how much scientists like Tolman really knew animals.[2] 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.[3] 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 Craig's appetitive theory of instincts until 1935 when the ornithologist Margaret Nice urged Lorenz to begin a correspondence with Craig (Burkhardt, 2005, p. 152, 469).[4] 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 (Lorenz, 1937, p. 270, 277).[5] For Lorenz, Craig's consummatory act *is* the instinctive behavior

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[1] Tolman's (1932, p. 272) book contains a section devoted to "Craig's Doctrine of Appetites and Aversions" where he acknowledges his debt to Craig: "This doctrine of certain physiological quiescences and disturbances to be got to or from, given certain initiating physiological states, plus certain innate sign gestalt readiness as to how to get thus to or from has been borrowed almost *in toto* from Craig (although Craig himself might not perhaps be willing to recognize it when thus translated into our language)."

[2] "Bühler [Lorenz's 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" (Lorenz, 1989, p. 265, emphasis in original).

[3] Burkhardt (2005, p. 152–3) suggests that Lorenz's (1989) flair for telling a good story causes him to exaggerate his negative reaction to the purposive psychologists.

[4] See Brigandt (2005, p. 581) for more on Lorenz's Correspondence with Craig.

[5] "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" (Lorenz, 1937, p. 270, 277 emphases in original).

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, p. 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, p. 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." In other words, 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).[6] According to Lorenz (1937, p. 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 1).

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 2). In Tolman's (1932) theory, instincts drive learning. Sophisticated behaviors, like those exhibited by maze running rats, result from the way animals employ the contents of memory.[7]

Lorenz, in contrast, holds that sophisticated behaviors are often instinctive behavior patterns, especially in animals like birds and insects. Instincts do not drive learning; animals learn how to trigger instincts. According to Lorenz, scientists should not assume that animals reason their way to goals by manipulating mental representations. Rather, physiological forces motivate animals to enter situations that trigger instincts, and the triggering of the instinct is the animal's goal.

3.2. Tolman proposes the cognitive map: highlighting some definitional and methodological details
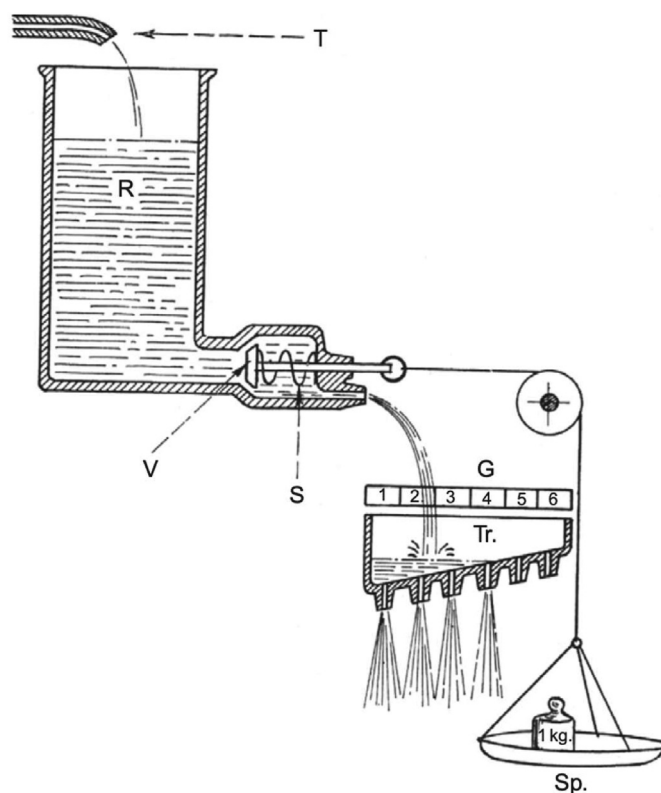
Tolman explicitly proposed his cognitive map hypothesis in his 1948 publication, "Cognitive Maps in Rats and Men". Between Tolman's 1948 paper and the present, researchers have proposed a variety of definitions for what constitutes a cognitive map (For reviews see Mackintosh, 2002 and Jensen, 2006). 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, p. 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

Figure 1. Illustration of Lorenz's (1950) 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.

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). 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, p. 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

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[6] As pointed out by Haldane (1956), Lorenz's hydraulic model of instincts also seems to draw from McDougall's (1923) *Outline of Psychology*. See Griffiths (2004) for the argument that Lorenz derived his hydraulic model from McDougal.

[7] 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, p. 143), who wrote that Tolman's rats were "buried in thought".

The Cognitive Map Debate in Insects

1930s

Purposive Behaviorism
Edward Tolman (1886–1959)

- Instincts drive animals to learn
- Animals remember goal stimuli and deliberate about how to realize goals
- Focus on learning and the content of memories
- Focus on mammals

German Ethology
Konrad Lorenz (1903–1989)

- Animals learn how to trigger instincts
- Animals do not have insight about goals of behavior. The performance of instincts is the goal
- Focus on physiological causation of behavior (psychohydraulic model)
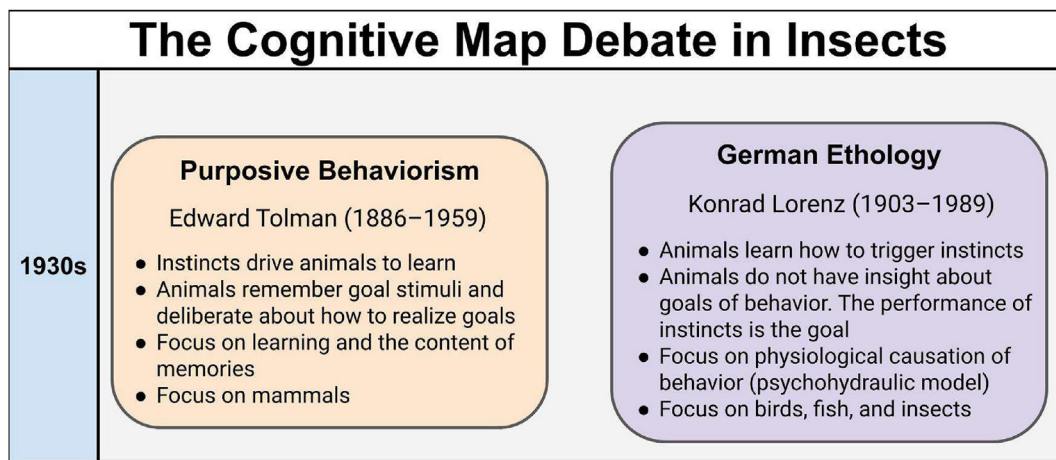- Focus on birds, fish, and insects

Figure 2. Visual summary of the cognitive map debate in insects.

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 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), 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 deliberate about future navigation decisions, and 3) exploiting novel shortcuts is evidence that a navigator employs such map-like representations (See Figure 3).

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

Between Lorenz's 1937 publication and the beginning of WWII, he and the Dutch scientist 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 straight-forward relationship with the discipline (Dhein, 2021). 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 un-prepossessing 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 founded a lineage of social insect researchers who continue to self-identify as ethologists, and this lineage produced Wehner and Menzel (Dhein, 2022). After WWII, von Frisch gained public notoriety for his discovery of the honeybee dance "language"[8] (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 university. Thus, when Wehner and Menzel joined Lindauer , 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 as a mentor for different reasons. Menzel wanted to study the neurophysiological mechanisms behind learning, and it was suggested to him that he seek out Lindauer in Frankfurt for such a project (Menzel, 2004, p. 462–463). Given von Frisch's instinct-heavy thinking about honeybees, it may seem odd that Menzel went to von Frisch's former student, Lindauer, to study learning. However, according to Menzel (2004, p. 465), Lindauer was a good fit for the kind of research he wanted to perform because Lindauer's research diverged from von Frisch's in ways that corresponded to Menzel's interests.[9] 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 2004; 2007; 2020). For example, remembering his time as a doctoral student with Lindauer in the mid 1960s, Menzel (2004, p. 463, emphases added) cites Tolman's 1932 book on purposive behaviorism as a key influence

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[8] 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).

[9] "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, 2004, p. 465).
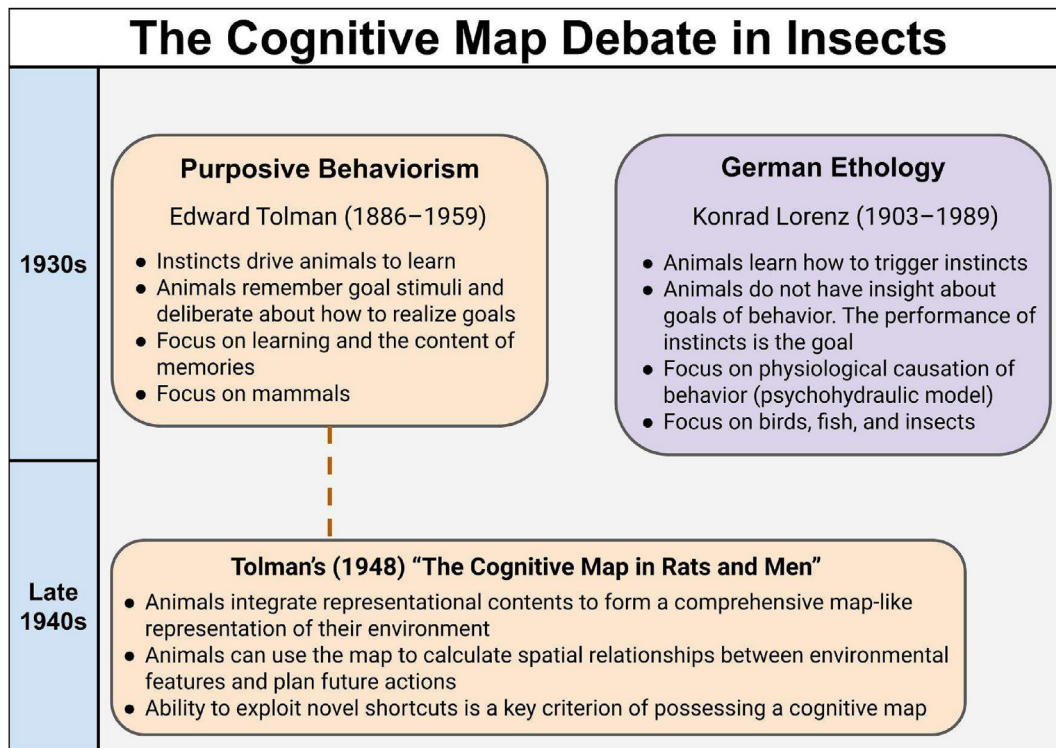
Figure 3. Visual summary of the cognitive map debate in insects.

while questioning von Frisch's reluctance to investigate neural mechanisms.[10]

What about Wehner? In contrast to Menzel, who was frustrated by Frischean ethology's focus on peripheral sensory physiology, Wehner was attracted by it. 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 (Wehner, 2013, p. 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 dissertation focused on visual pattern recognition in honeybees (Wehner, 1967). This line of research led Wehner to propose a retinotopic-template matching hypothesis for honeybee pattern recognition (Srinivasan, 2010; Wehner 1969, 1981, p. 586–592). The hypothesis is notable for its emphasis on 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 via some central brain process, Wehner's theory held that honeybees evaluate the similarity of visual 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 with the actual retinal image of the new pattern. This early line of research is an 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.[11]

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 than others 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.[12]

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

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[10] "The role models I found in my readings were Karl von Frisch (1965), Thorpe (1983), Lashley (1950), Thorndike (1932), Pavlov (1927), von Holst (1935), Tolman (1932), and Köhler (1921), a colorful mixture, representing conflicting schools within behavioral biology. […] 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*" (Menzel, 2004, p. 463, emphases added).

[11] For a representative articulation of this commitment, see Wehner (1987, p. 528–529): "[N]atural 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."

[12] Given the different sorts of conclusions Wehner and Menzel drew from their dissertation research, it is interesting to note that Wehner and Menzel used the same experimental methodology originally developed by von Frisch. For more on the history of this experimental methodology and the versatile ends to which ethologists and neuroethologists have used it, see Dhein (2022, Section 3). For a more philosophical look at Wehner's research program see Dhein (2020).

doctorate. The exchanges Menzel remembers from his interactions with von Frisch illustrate both Menzel's theoretical commitment to not discounting central processing mechanisms and the way Menzel sees his research diverging from Frischean ethology.[13]

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, p. 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, p. 4–5) remembers noticing solitary foraging ants. He began performing navigation experiments on the ants, and Menzel eventually joined him.

Wehner & 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.

The following spring, Wehner travelled to Tunisia to continue his *Cataglyphis* 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. 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 represent 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 use allocentric representations of space.

Importantly, path integration and map navigation presuppose different underlying mechanisms. Map navigation requires mechanisms that combine memories about the environment into an extensive map-like representation, faithfully preserve and update that map-like representation, and keep track of where the navigator is within that representation. Alternatively, path integration only requires mechanisms that record the distance and direction of a navigator's journey and integrate those values into a single vector. Whereas map navigation does not specify the content of the memories being combined, path integration specifies the content as being about distance and direction of travel. Additionally, map navigation does not specify the sense in which mechanisms "combine" memories to form a map-like representation. With path integration, the relevant notion of "integration" is mathematical. In summary, the functions of the mechanisms underlying path integration are more tightly specified and seem to require less computational work than those underlying map navigation.

Between 1969 and the turn of the 21st century, Wehner turned *Cataglyphis* into a model organism for navigation studies by attracting new researchers to the growing group constituting his 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, p. 166; Cheng & Freas, 2015, p. 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 (Cheng & Freas, 2015; Wehner & Srinivasan, 1981).

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 methodology for investigating classical conditioning in honeybees (Bitterman et al., 1983; Kuwabara, 1957; Menzel, 2020). 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 experimental method "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, p. 118). While Wehner was investigating a potential alternative to the cognitive map with ants, Menzel was producing evidence that honeybees are surprisingly sophisticated learners.

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 (Dhein, 2022; Seeley et al., 2002), and he employed experimental strategies associated with behaviorist theories of learning. Wehner, on the other, continued to work within the Frischean tradition of German ethology, but instead of

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[13] For example, when Menzel (2004, p. 466–467) described his dissertation work to von Frisch, he remembers that despite von Frisch being encouraging.

"He [von Frisch] didn't want to follow my core argumentation […] which was the differentiation between peripheral and central mechanisms of estimating color […] 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."

More recently, Menzel (2020) has recalled 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."
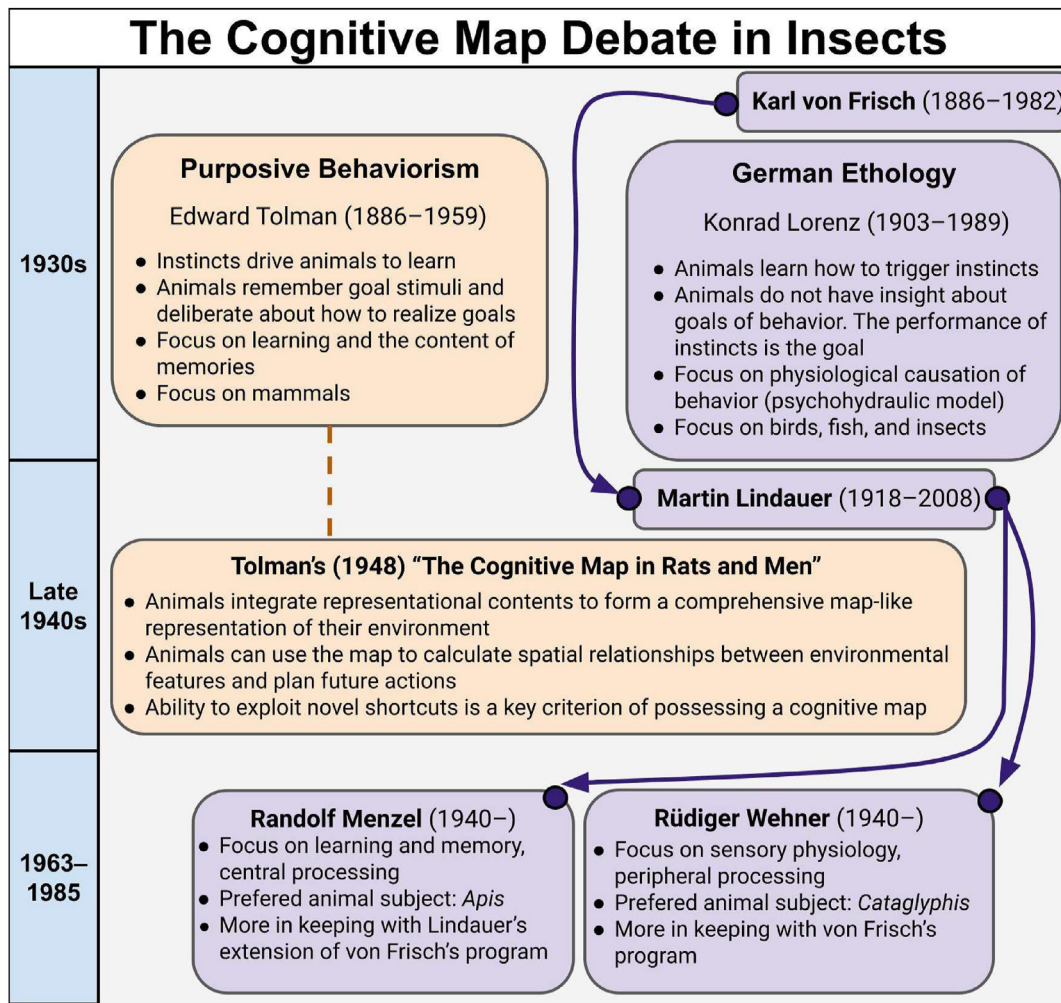
Figure 4. Visual summary of the history of the cognitive map debate in insects.

continuing von Frisch's and Lindauer's focus on honeybees, he began applying that approach to *Cataglyphis* (See Figure 4).

3.4. The cognitive map comes to insects

In the mid 1980s, a Tolmanian framing of the cognitive map hypothesis moved from mammalian navigation research to insect navigation research, where it immediately caused controversy. In 1986, American scientist James Gould (1986) published a paper purporting to provide experimental evidence for a Tolman-like cognitive map in honeybees.[14] Multiple insect navigation researchers offered rebuttals to Gould's pro-cognitive map paper (Cartwright & Collett, 1987; Dyer & Seeley, 1989a; Dyer and Seeley, 1989b; Dyer, 1991; Dyer, 1996) including Wehner and Menzel (Menzel et al., 1990; Wehner et al., 1990; Wehner & Menzel, 1990; Wehner & Wehner, 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. In Gould's (1986, p. 861) 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."

The second way Gould's (1986) paper calls 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, p. 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 wrong when he 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 used. 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

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[14] 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 1989a,b; Dyer, 1991; Dyer 1996).

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.[15] Furthermore, as argued by other critics of Gould (Cartwright & Collett, 1987; Dyer & Seeley, 1989a; Dyer and Seeley, 1989b; Wehner and Menzel (1990), p. 407–409) claim that *even if* Gould's results were accurate, they can be explained without appealing to cognitive maps (See Figure 5).

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 (Hammer & Menzel, 1995; Hammer & Menzel, Randolf, 1998; Menzel, 1999; ; Menzel, 2001; Galizia & Menzel, 2000; Ganeshina & Menzel, 2001; Menzel et al., 2001) and began to conclude that honeybees integrate their vector memories to guide navigation in previously unexpected ways (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,b; Lambrinos et al., 1998; Wehner, 1998; Collett et al., 1999; Möller et al., 1999; Ronacher et al., 2000; Wolf & Wehner, 2000; Wohlgemuth et al., 2001; Sommer & Wehner, 2005). Around 2000, Menzel (2012) 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.

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. performed displacement experiments on two groups of honeybees. The first group was trained to forage at a stationary feeding site while the second group was trained to forage at a feeding site that was moved around the hive in a circle so that it orbited the hive every 3 h. Menzel et al. (2000) then captured the trained honeybees in little glass vials at their respective feeding sites and displaced them to new, unfamiliar locations.

Menzel et al. (2000) reasoned that the first group of bees used path integration to develop an egocentric route-specific memory of how to

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[15] There is insufficient space to relate the methodological details of all the experiments referenced here and in the following section. I encourage those interested to review the research reports referenced here to sample the impressively imaginative ways scientists have exploited ant and honeybee foraging behavior to produce evidence about the neurosensory physiology of these animals.

return to the hive. Thus, when displaced to an unfamiliar location, bees from the first group should fly in the same direction they would have flown from their stationary feeding site. Alternatively, Menzel et al. reasoned that the second group of bees lacked route-specific memories about how to return from their feeding site to the nest because the location of the feeder was always moving. Thus, Menzel et al. expected the bees to take a while to navigate back to their hive after being displaced. If the second group of honeybees slowly improved their ability to navigate to the hive from an unfamiliar location, then Menzel et al. (2000) would interpret that result as supporting the idea that honeybees build general, allocentric representations of space via latent learning.

As expected, the first group of honeybees appeared to navigate according to an egocentric route-specific memory. To Menzel et al.'s (2000) 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. Menzel et al. (2000, p. 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 full conversion to the idea that honeybees use "map-like" representations was facilitated by a technological innovation. In prior displacement experiments, researchers could not track honeybees during their flights. To draw conclusions about the actuals flight paths of honeybees, researchers timed how long it took bees to fly between observation points and relied on vanishing bearings—the direction a honeybee was flying before it was no longer visible. But in 2005, Menzel et al. (2005) published the results of displacement experiments that used harmonic radar to track honeybees in midair. According to Menzel (2012; 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 Menzel et al. (2000). Path integration vector memory takes precedence over other memories, but once a honeybee has "run out" her path integration vector, she is not lost. She does an orientation flight to gain her bearings and then uses 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 of the cognitive processes underlying insect navigation whose current iterations are called Navinet. Navinet is a "toolkit" model in the sense that it represents different navigational strategies (e.g. path integration and landmark recognition) as independent modules. Each module takes sensory and motivational input and then outputs a 2D vector representing an action command about where to walk. These output vectors then undergo a weighted summation that generally leads to a winner-take-all result. 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 their Navinet model predicts the actual 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
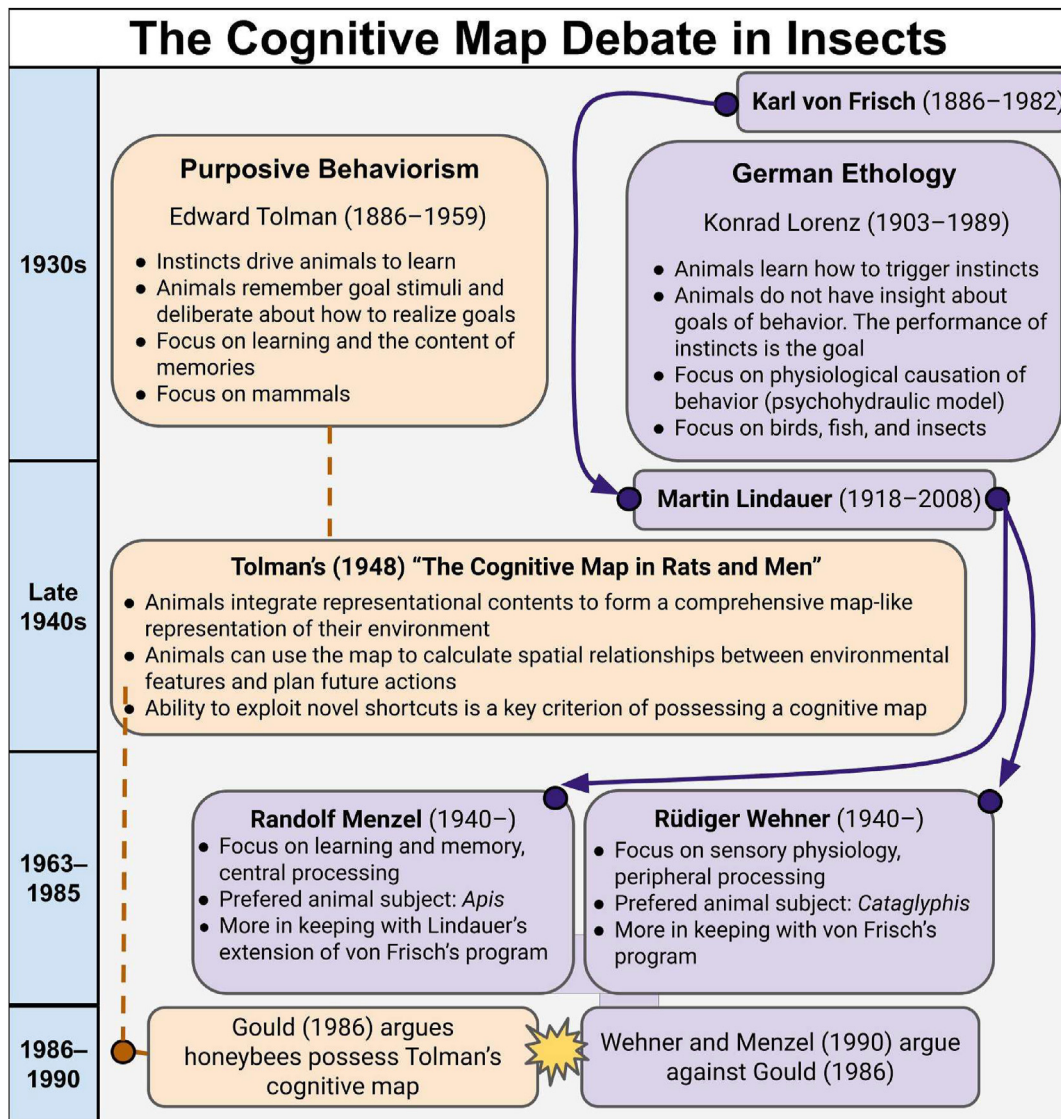
Figure 5. Visual summary of the history of the cognitive map debate in insects.

assumes learning processes because it assumes that insects possess visual memories of landmarks, but as Cruse and Wehner (2011, p. 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, p. 3) also 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, p. 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, p. 241 See also Menzel & Fischer, 2011, p. 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 (Menzel & Giurfa, 2006, p. 27).[16] 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, not honeybees.

Menzel and colleagues fully endorse the cognitive map hypothesis in 2014 and frame their endorsement of the hypothesis as an extension of the

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[16] "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 & Giurfa, 2006, p. 27).

"[…] 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, p. 8949). Again, Menzel and colleagues use displacement experiments to support their argument.

Cheung et al. (2014) argued against Cheeseman et al.'s (2014a) interpretation of the experiments on the grounds that a non-cognitive map interpretation of the results is still possible and that Cheeseman et al.'s (2014a) experimental interventions 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 their interventions is 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 (Menzel & Greggers, 2015; See also Jacobs & Menzel, 2014, p. 6; Wiener et al., 2011, p. 74; Bursten & Dhein, Forthcoming).[17] 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 & Menzel, 2014, p. 19). For these reasons, Menzel continues to maintain that the Cheeseman et al. (2014a) displacement experiments show that honeybees possess a cognitive map (Menzel, 2020).

Meanwhile, Wehner and colleagues continue to develop Navinet (Hoinville & Wehner, 2018; Wehner et al., 2016) (See Figure 6). Incorporating the results of cue conflict experiments caused Wehner et al. (2016) to make Navinet less hierarchical and more heterarchical. Whereas the vector outputs of different modules used to be combined in a way that led to winner-take-all outcomes, the new Navinet is more heterarchical in the sense that its optimal combination procedure tends to blend the vector outputs from different modules into intermediate vectors. Different modules representing different "tools" in the "toolkit" influence action simultaneously. 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 displacement experiments. Menzel is unmoved by this demonstration for reasons already explained.

In 2018, Harald Wolf, Matthais Wittlinger, and Sarah Pfeffer performed cue conflict experiments on *Cataglyphis* and used the results of those experiments to further develop the 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 he invited Wolf to join him at his Tunisian field site (Wehner, 2019; For a publication resulting from their early collaboration, see; Wolf & 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, p. 11) explicitly call back to Lorenz's (1937) psycho-hydraulic model of instincts (See Figure 7).

Having already traced the cognitive map hypothesis from Tolman to Menzel, this Wolf et al. (2018) publication further highlights the influence of German ethology on the toolkit hypothesis. In Lorenz's original psycho-hydraulic model, the liquid represents action-specific energy that drives instinctive patterns of behavior. Traditionally, memories and instincts are considered incompatible because memories are formed through learning, and instincts are, by definition, unlearned. However, Wolf et al.'s (2018) hydraulic model of content integration adapts the Lorenzian framework for thinking about instincts to the domain of memory and cognition. This development reflects the split between Tolman and Lorenz in the 1930s. Tolman argued learning was responsible for sophisticated behaviors while Lorenz argued that many sophisticated behaviors are instinctive. Correspondingly, Wolf et al. (2018) seek to account for the sophisticated navigation behavior of *Cataglyphis* by articulating an alternative to the cognitive map that draws on ethological theorizing about instincts (See Figure 8).

4. Historical upshots

How does this history 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, p. 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 hinges on how insects use those representations.

This history also highlights how background norms guiding cognitive theorizing cause Wehner and Menzel to endorse conflicting positions about how insects use representations. Concerns about anthropomorphism and anthropodenial figure prominently in many debates over animal cognition (Andrews & Huss, 2014; Buckner, 2013; Burghardt, 2004; De Waal, 1999; Wynne, 2004), and the cognitive map debate in insects is no exception. Bringing the anthropomorphism vs. anthropodenial framework to bear on the cognitive map debate in insects clarifies the contrast between Wehner and Menzel's norms for theorizing about animal cognition. 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 & Wehner, 1990; Wehner et al., 1994; Wehner, 2003, p. 582). For Menzel, one must be on guard against anthropodenial—the tendency to discount similarities between animals and humans (De Waal, 1999). Menzel (2004, p. 479–480) frames this stance

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[17] "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 & Greggers, 2015, p. 554 and 561).
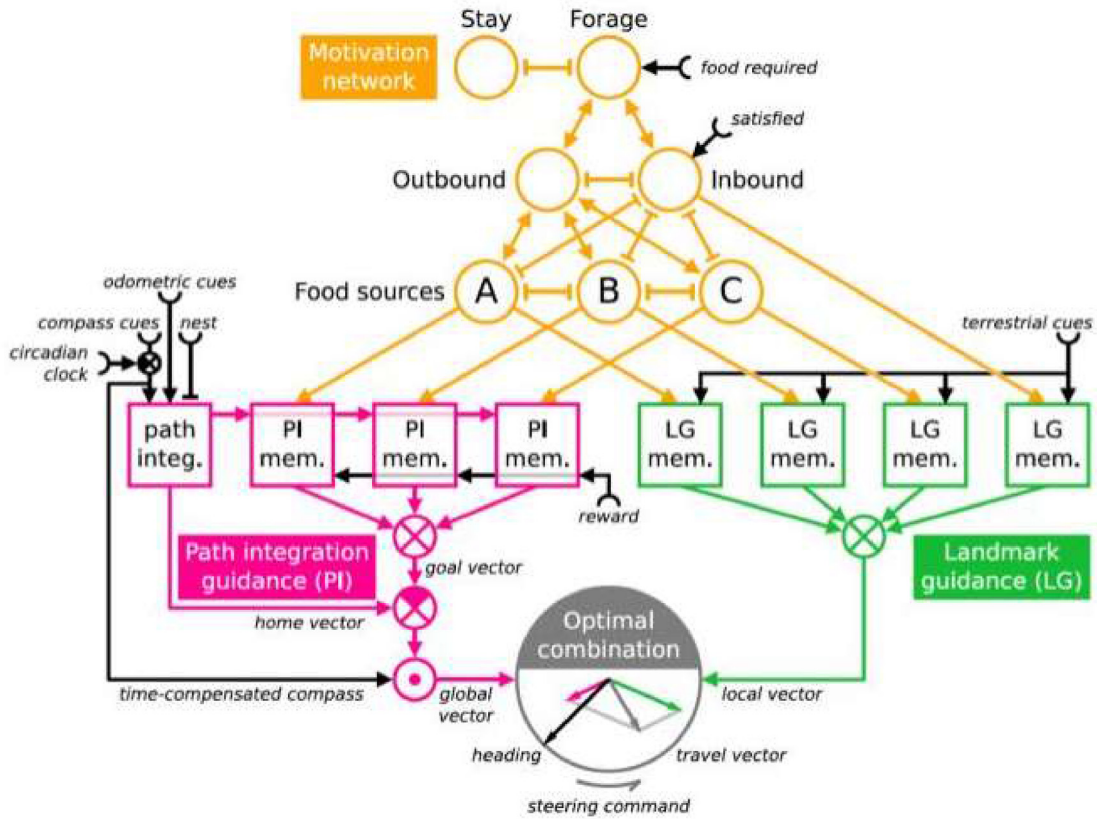
Figure 6. Navinet model of the cognitive processes underlying *Cataglyphis* navigation (Hoinville & Wehner, 2018, p. 2825).
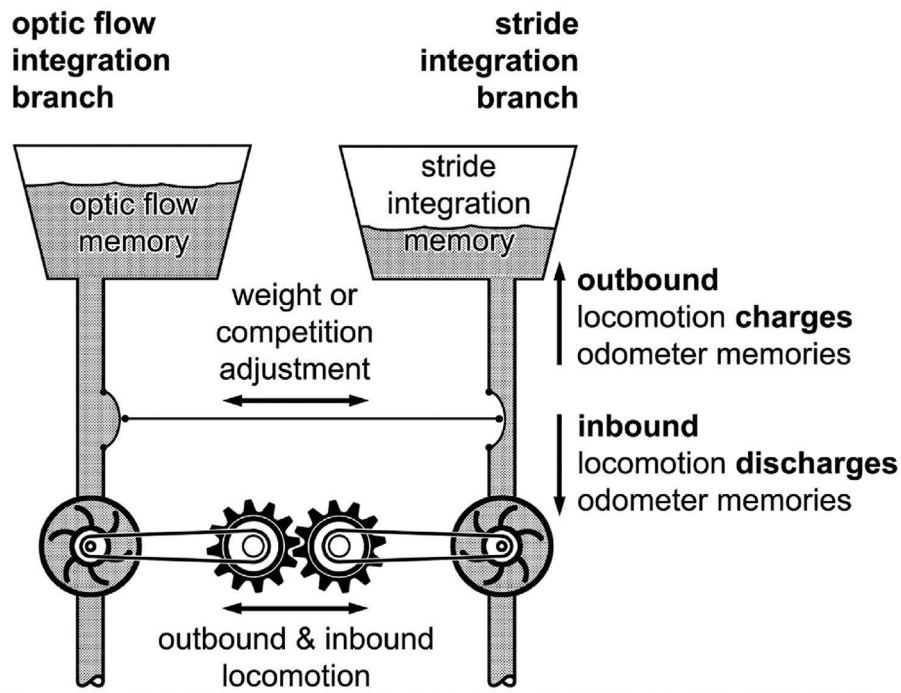

Figure 7. Wolf et al.'s (2018) hydraulic model of content integration for optic flow and stride integration mechanisms in *Cataglyphis*. Note the similarity to Figure A.

as a reaction against the presumed simplicity of small-brained invertebrates.[18]

Furthermore, the expanded history provided above gives 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 modulized, 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 use 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 (Dhein, 2022). 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 (Jacobs & 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 (Dhein, 2021; Munz, 2016). 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 the Frischean tradition's focus on instincts, sensory physiology, and behavioral experiments.

Additionally, the expanded history provided above 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.

The historical narrative presented above also shows how Wehner and Menzel's choice of model organism offered distinct experimental affordances that helped place them at opposing ends of the cognitive map debate. Wehner's adoption of the desert ant *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. Wehner and his colleagues have leveraged this advantage to design behavioral experiments that produce quantitative parameters for their computational toolkit model of insect navigation. For example, as discussed in section 3.5, Wehner and colleagues perform cue conflict experiments where they subject foraging ants to stimuli that indicate conflicting routes (Bregy et al., 2008; Wehner et al., 2016). When subjected to such stimuli, ants sometimes take a comprise route somewhere between the two conflicting routes. By precisely measuring the direction and distance of the ant's comprise route, they calculate the relative influence of each stimulus on the ant's behavior. These calculations then become parameters used to develop computational toolkit models of insect navigation. Menzel's honeybee, on the other hand, was more amenable to experimental paradigms from classical learning theorists (Kuwabara, 1957). For instance, 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 use the proboscis extension reflex to investigate how honeybees learn to associate stimuli with rewards. As noted in section 3.5, these sorts of experiments have led Menzel and colleagues to speculate that honeybees form and use memories in a similar way to vertebrates (Bitterman et al., 1983, p. 118). In both Wehner and Menzel's case, choice of model organism was not sufficient to determine their current position on the cognitive map debate, but it was also not completely unrelated. When scientists develop a research program around a model organism, the resulting experimental system can take on a momentum of its own, and part of that momentum involves scientists exploiting experimental affordances of their animal subjects (Hacking, 1983; Rheinberger, 2010).

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 persists due to a clash of 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 historical narrative presented in this paper shows how ways of knowing 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

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[18] "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" (Menzel, 2004, p. 479–480).

The Cognitive Map Debate in Insects

Karl von Frisch (1886–1982)

1930s

Purposive Behaviorism

Edward Tolman (1886–1959)

- Instincts drive animals to learn
- Animals remember goal stimuli and deliberate about how to realize goals
- Focus on learning and the content of memories
- Focus on mammals

German Ethology

Konrad Lorenz (1903–1989)

- Animals learn how to trigger instincts
- Animals do not have insight about goals of behavior. The performance of instincts is the goal
- Focus on physiological causation of behavior (psychohydraulic model)
- Focus on birds, fish, and insects

Martin Lindauer (1918–2008)

Late 1940s

Tolman's (1948) "The Cognitive Map in Rats and Men"

- Animals integrate representational contents to form a comprehensive map-like representation of their environment
- Animals can use the map to calculate spatial relationships between environmental features and plan future actions
- Ability to exploit novel shortcuts is a key criterion of possessing a cognitive map

1963– 1985

Randolf Menzel (1940–)
- Focus on learning and memory, central processing
- Prefered animal subject: *Apis*
- More in keeping with Lindauer's extension of von Frisch's program

Rüdiger Wehner (1940–)
- Focus on sensory physiology, peripheral processing
- Prefered animal subject: *Cataglyphis*
- More in keeping with von Frisch's program

1986– 1990

Gould (1986) argues honeybees possess Tolman's cognitive map

Wehner and Menzel (1990) argue against Gould (1986)

2000– Present

Menzel's Map

We expect too little from small brains

- *Cataglyphis* too different from *Apis*
- Parsimony arguments are misguided

Wehner's Toolkit

Insects do not solve tasks in optimal ways that implement human strategies

- *Cataglyphis* research relevant to *Apis* and potentially rats
- Toolkit model more parsimonious than cognitive map

Navinet proof of concept demonstrations

Wolf et al.'s (2018) hydraulic model of content integration
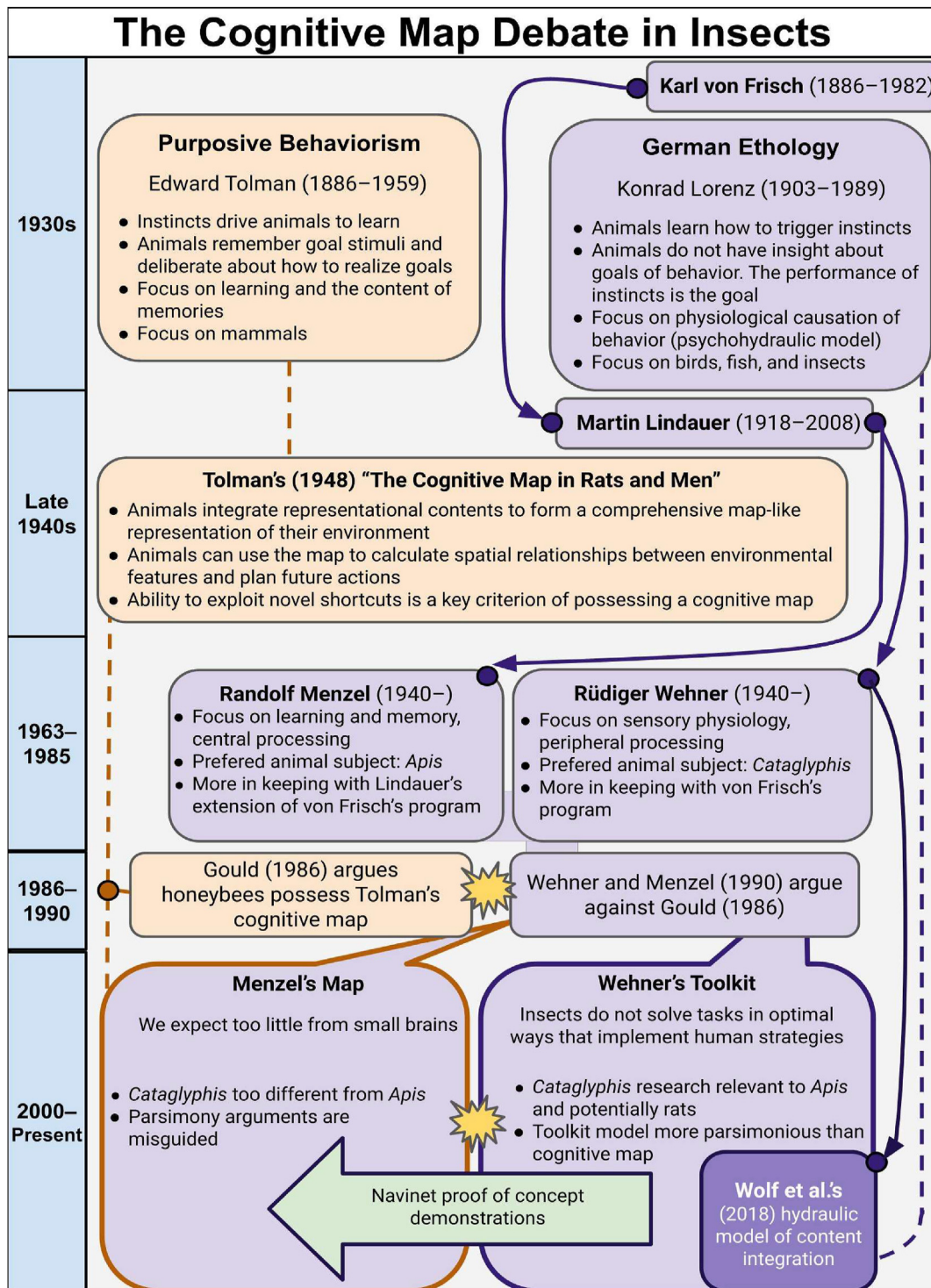
Figure 8. Visual summary of the cognitive map debate in insects.

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 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.
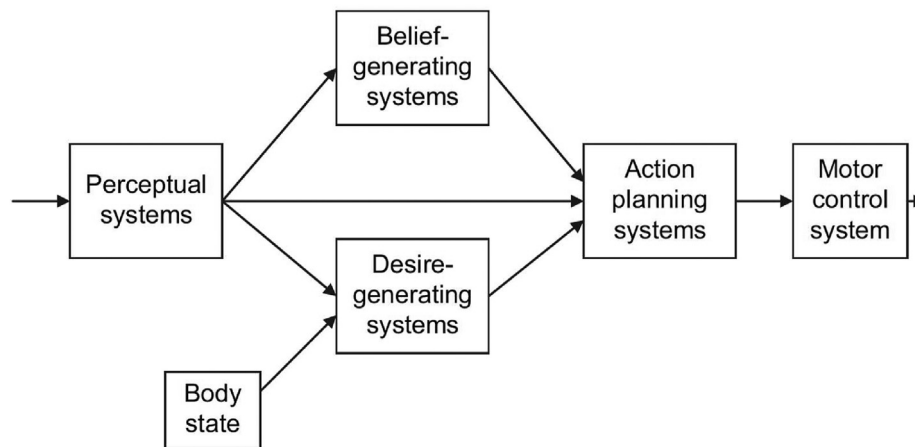
Figure 9. The cognitive structure of the honeybee brain (From Menzel, 2008, 272; after Carruthers 2006, 66).

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 Carruthers' (2006, p. 66) model of cognition (See Figure 9).

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 Carruthers (2006) model of cognition endorsed by Menzel with Wehner's Navinet toolkit model (Figure 6), which is just as current as Menzel's work. 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 to 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.[19] 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, p. 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.

Similarly, Knoll and Rey's (2017) distinction between non-intentional representations and intentional representations points to issues that are at the crux of the cognitive map debate in insects. Following Burge (2010, Chapter 10), Knoll and Rey (2017) argue that a system uses 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, p. 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 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, p. 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

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

important historical context is when selecting case studies from cognitive science for philosophical purposes. Without such context, philosophers 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 (Dewsbury, 1992; Hinde, 1966). This paper shows how pre-synthesis debates continue to motivate controversy in animal navigation research.

Declaration of competing interest

None.

Acknowledgments

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