

## Millikan on Honeybee Navigation and Communication

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### §1. Insect cognition

A central task for philosophy and psychology is to identify mental continuities and discontinuities across species. Current science attributes sophisticated mental activity to simple insects, such as bees and ants. Clearly, though, such creatures differ profoundly from higher-level animals, including humans. To what degree does insect cognition resemble our own? In what sense, if any, do insects “represent” the world? How do higher-level animals, including humans, differ in their representational capacities from lower-level creatures, including insects?

Ruth Millikan has pursued these questions throughout her career, delineating a view of mental representation so powerful and systematic that it commands attention from all who study animal cognition. She frequently illustrates her view with empirical case studies, ranging from bacteria to insects to lower mammals to humans. She deploys the case studies to propose various mental continuities and discontinuities across species.

I will explore one of Millikan’s favorite examples: the remarkable *honeybee waggle dance*. Her discussions of this example are quite illuminating. However, I will question certain aspects of her analysis. I will suggest that Millikan blurs important distinctions and elides important commonalities, generating a misleading picture of the overlap between human and insect mental capacities.

## §2. The science of honeybee navigation and communication

In Nobel prize winning work, von Frisch (1967) discovered that the honeybee (*Apis mellifera*) performs a “waggle dance” whose properties reliably correlate with direction and distance from the hive to the location of some resource, such as nectar. Does the waggle dance have representational content? Do production and reception of the dance involve representational mental states? Answering such questions requires scrutiny of the empirical science.

### §2.1 Honeybee cognitive maps?

Honeybees explore large open terrain, reliably returning to the hive. During exploratory flights, they locate profitable food sources, which they can revisit from the hive or elsewhere. What cognitive mechanisms underlie these navigational feats? I will review three widely discussed navigational paradigms: *dead reckoning*, *route following*, and *map-based navigation*. ***Dead reckoning***: Also called *path integration*, dead reckoning maintains a running record of the creature’s position, regularly updated by monitoring the creature’s current motion. Using dead reckoning, animals can travel long, circuitous routes and then return directly home along a straight path. Dead reckoning is ubiquitous among vertebrates and invertebrates (Gallistel, 1990, pp. 57-102). To employ dead reckoning, an organism must detect its speed and its direction. Honeybees detect speed mainly by monitoring optic flow (Srinivasan, Zhang, and Bidwell, 1997), (Srinivasan, Zhang, Lehrer, and Collett, 1996). They detect direction through a “sky-compass” attuned to the sun’s position and to patterns of light polarization (Wehner, 1994). Converting speed and direction into displacement requires elementary integration or the discrete equivalent: iterated vector summation.

Dead reckoning is noisy and fallible. Errors are cumulative, rendering it unreliable over long distances. Moreover, in the special case of honeybee navigation, an overcast sky renders the sky-compass inoperative. Accordingly, the honeybee must supplement dead reckoning with additional navigational mechanisms.

**Route following:** During route following, the organism implements *sensorimotor vectors* that correlate sensory stimulations with motor instructions. A given stimulation triggers a given motor behavior. A simple example, displayed even by bacteria, is *beaconing*: the organism navigates towards a target by exploiting sensory input emanating from the target. A more sophisticated strategy, implemented by honeybees, is retinal image matching to a stored “snapshot” of the environment as seen from some location (Collett and Collett, 2002). Another example: honeybees can learn to fly some direction when confronted with a certain stimulation.

Honeybees can chain together sensorimotor vectors: an initial stimulus induces some motor behavior until a new stimulus induces a new motor behavior, and so on. In this manner, the bee divides its route into segments, each segment demarcated by a landmark that triggers some associated motor instruction (Collett and Collett, 2002). Chained sensorimotor vectors can generate sophisticated route following behavior.

**Map-based navigation:** Ethologists agree that honeybees deploy dead reckoning and route following. Collett and Collett (2002) argue that we can explain honeybee navigation solely through such navigational capacities. Other researchers disagree, insisting that we must also posit a “cognitive map” of the environment. More specifically, they argue that the honeybee exploits an *allocentric* cognitive map, anchored to the external environment rather than to the bee’s own body (as an *egocentric* map would be). One reason this controversy has proved so recalcitrant is that scientists employ conflicting, and sometimes obscure, notions of “cognitive map.” To a first

approximation, a cognitive map is a unified mental item whose properties reliably correlate with the spatial distribution of objects and properties.

A related issue is whether honeybees can fly novel shortcuts in a familiar environment. Historically, many scientists have held that such an ability would indicate a “map-like” spatial memory. Yet certain shortcuts are explicable through a sophisticated route-following model that includes appropriate operations on sensorimotor vectors. For instance, a honeybee that learns routes from two distinct feeders back to the hive can, in certain circumstances, home directly to the hive when released from a novel site intermediate between the two feeders (Menzel, et al. 1998). We can explain this behavior as resulting from a weighted average over sensorimotor vectors correlated with the two learned routes (Giurfa and Capaldi, 1999). On the proposed model, the honeybee “interpolates” between its two learned routes, without deploying an integrated cognitive map.

For a period, most researchers concluded that the evidence did not warrant attributing cognitive maps to honeybees. Recently, however, improvements in technology and experimental design have transformed the debate, lending renewed support to the cognitive map hypothesis (De Marco and Menzel, 2008).

Through modern radar technology, we can track flight paths of individual bees over large distances. Menzel and colleagues allowed bees to perform orientation flights in a new environment, so that bees could familiarize themselves with their surroundings. Researchers then divided bees into three test groups: VF bees, trained to a feeder placed at varying locations within 10 meters of the hive; SF bees, trained to a stationary feeder 200 meters from the hive; and R bees, recruited through the waggle dance by foragers trained to the stationary feeder. Researchers trapped bees en route to the feeder or en route to the hive, displacing them to various

locations. Flight paths of displaced SF and R bees divided into three stages: (i) an initial straight vector that would have carried the bee back to the hive (or feeder) had the bee not been displaced; (ii) a circuitous search of the local environment; (iii) a relatively straight path towards the hive (or sometimes first to the feeder and *then* to the hive). VF bees did not exhibit stage (i), since they had not learned any routes in their training. SF, R, and VF bees performed equally well during stage (iii), even when displaced to locations too far from the hive for beaconing.

These results show that honeybees can navigate from arbitrary locations within the range of initial orientation flights. Since VF and SF bees performed equally well, this navigational ability must reflect persisting mental changes induced during orientation flights. Menzel and Giurfa (2006) conclude that orientation flight provide bees with a flexible “landscape memory,” which correlates hive-centric vectors either with distal landmarks or else with patterns of proximal stimulation. Dead reckoning must play a dominant role in forming these correlations, since dead reckoning provides the bee’s only initial source of spatial coordinates. Once the bee has formed its map, it can localize itself with respect to the map’s hive-centric coordinate system, in the sense that it can compute a hive-centric vector corresponding to its own position in space. It can then perform vector addition to compute a course to the feeder. In this sense, the honeybee has a “cognitive map.”

Navigation with respect to the cognitive map differs in several respects from route following. First, it does not consist in a correlation between stimuli and motor commands. VF bees have not mastered the sensorimotor vectors emphasized by Collett and Collett (2002), because they are not trained to specific routes. Their orientation flights do not include sensorimotor routines corresponding to elements in the cognitive map. Second, the map supports computations, such as addition of arbitrary vectors, that outstrip mere motor response to stimuli.

In these two respects, landscape memory is more “cognitive” than route following. Its links to sensory stimuli and motor output are complex, indirect, and flexible.<sup>1</sup>

When route following is available, it dominates the cognitive map, as manifested by stage (i) flights of displaced SF and R bees. The cognitive map apparently serves as a “backup system” that guides behavior only when route-following becomes inapplicable.

How does the honeybee form and update the cognitive map based on experience? How does the cognitive map interact with other navigational capacities, such as dead reckoning and route following? How does the cognitive map figure in the honeybee’s path-planning? So far, these questions remain unanswered.

## §2.2 The waggle dance

Under certain circumstances, a foraging bee returning to the hive from a desirable resource performs a *waggle dance* inside the hive. Paradigmatic resources include food, water, and potential new hive sites. I focus on food as illustrative.

To a first approximation, the dancing honeybee repeatedly traverses a figure-8 pattern whose two circles meet in a straight line. While traversing the straight line, the bee repeatedly waggles its abdomen. The average orientation of the bee’s waggle run with respect to gravity reliably correlates with the food source’s solar bearing (i.e. the angle one must fly relative to the sun to reach the food source from the hive). The average duration of the waggle run reliably correlates with distance from the hive to the food source. The dance recruits various bees, who

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<sup>1</sup> Cheng objects to Menzel by correctly noting that the bee need not possess “an overall map plotting the geometrical relations of all significant locations” (2006, p. 204). Yet Cheng acknowledges that the honeybee must master a large collection of hive-centered vectors, each vector correlated either with distal landmarks or else with patterns of proximal stimulation. He also acknowledges that the honeybee must subsume the vectors under operations such as averaging and addition. He misleadingly assimilates these vectors to the sensorimotor vectors emphasized by Collett and Collett. He thereby elides the fact that VF bees have not mastered sensorimotor routines. The “landscape memory” acquired during orientation flights is not “route learning,” because it does not consist in a correlation between sensory stimulations and motor routines.

promptly fly towards the vicinity of the food source. Upon arriving in the vicinity, recruits search for the food source. This search exploits various cues, including odor. However, the initial flight towards the food's vicinity does not exploit odor, as shown by carefully controlled radar tracking experiments (Riley, et al., 2005). In some sense, the bee dance must “encode information” that correlates with location of the food source, information which recruits can “decode.”

Despite intensive research, this “encoding” and “decoding” remain mysterious. For instance, we do not know precisely which sensory stimulations caused by the waggle dance allow recruits to decode the dance. Sound, touch, and comb vibration apparently all play a role (Dyer, 2002). Nor do we know exactly how dead reckoning, route following, and the cognitive map inform dance production and reception.

Despite these gaps in our knowledge, we know that considerable cognitive complexity underlies the waggle dance. A forager's evaluation of whether to perform a waggle dance and how vigorously to perform it depends on various factors, including quality of the food source, uncertainty of reward, distance from the hive, risk of predator attack at the food source, and the colony's current nutritional need (Abbott, and Dukas, 2009), (De Marco, 2006), (Seefeldt and De Marco, 2008). Specific properties of the waggle dance depend on the forager's past experience. In particular, the dancing bee relies in complex and poorly understood ways upon dead reckoning and past exposure to landmarks (De Marco and Menzel, 2008). How recruits react to the waggle dance depends on their own history. The dance induces novice foragers to locate new food sources, whereas its main effect on experienced foragers is to reactivate interest in a previously visited site (Biesmeijer and Seeley, 2005). A striking illustration occurs when a dancer carries the scent of a flower species previous encountered by a prospective recruit with extensive foraging experience. If the dancer indicates an unfamiliar location, then the prospective

recruit typically ignores the dance, instead relying on its own past foraging experience (Grüter, Sol Balbuena, and Farina, 2008).

In sum, the waggle dance is embedded in a rich context of memories and motivational states. The surrounding cognitive context heavily informs dance production and reception.<sup>2</sup>

For a vivid example, consider the *solar ephemeris function*. As the sun moves through the sky, its compass direction changes. Dead reckoning with respect to a sun-compass requires mastery of the solar ephemeris function, which yields the sun's compass direction as a function of time. The solar ephemeris function varies according to season and latitude, but honeybees learn it quickly from a few environmental observations (Gallistel and King, 2009, pp. 220-226). They exploit it during the waggle dance, as illustrated by the following fact: if recruited foragers are trapped for several hours when leaving the hive, then upon release they fly in the approximate compass direction of the food source, not its current direction relative to the sun. In other words, they compensate for the delay, rather than choosing the solar bearing they would have chosen had they left the hive immediately. Apparently, the waggle dance is integrated into mental computations that draw crucially on the solar ephemeris function.

### **§3. Representation and truth-conditions**

I now want to examine the foregoing results for their philosophical import, with an emphasis on Millikan's work. I first offer some background remarks concerning the explanatory status of intentional content.

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<sup>2</sup> The controversial "Lake Experiment" purported to demonstrate a particularly sophisticated cognitive structure underlying dance reception. Gould and Gould (1982) trained foraging bees to visit a feeder gradually moved further into a lake. Foragers successfully recruited other bees to the feeder when it was on land but not once it was located well into the lake. A natural interpretation, endorsed by Gallistel (2009), is that potential recruits evaluate a dance for "plausibility" by comparing it with a preexisting cognitive map. However, a recent experiment by (Wray, et al., 2008) using modern radar tracking casts the Lake Experiment into doubt.

Folk psychology assigns a central role to *intentional explanations*, which individuate mental states and linguistic performances through their *truth-conditions*, i.e. conditions for correct or accurate representation of the world. Should scientific psychology likewise individuate mental states and linguistic performances truth-conditionally? Fodor (1987) and many others hold that it should, while Stich (1983), Field (2001) and others hold that it should not. I know of no convincing argument for the latter position. I also think that many impressive scientific theories already assign truth-conditions a central explanatory role. Two examples:

(a) *Vision science* studies how the visual system estimates features of the distal environment (Knill and Richards, 1996). The science explains diverse phenomena, including perceptual constancies and illusions.<sup>3</sup> As Burge (2010) notes, its explanatory generalizations routinely cite truth-conditions.<sup>4</sup> For instance, vision science explains how the human visual system deploys various cues --- including binocular disparity and monocular linear perspective --- to estimate *that* a perceived object has a certain depth. Any two cues may yield conflicting depth estimates. The science delineates algorithms, grounded in Bayesian decision theory, through which the visual system fuses conflicting estimates into a unified estimate *that* the object has a certain depth (Knill, 2007). Explanatory generalizations of vision science share a crucial feature with folk psychology: they routinely individuate mental states through their truth-conditions.

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<sup>3</sup> Millikan writes that explaining perceptual constancies is “a problem of nearly unimaginable complexity that is still largely unsolved” (2005, p. 67). Perceptual constancies are indeed complex. However, vision scientists have made substantial progress in illuminating them (Knill and Richards, 1996).

<sup>4</sup> Burge speaks of “veridicality” rather than “truth.” I use “truth” in a broad sense equivalent to Burge’s “veridicality.” Another wrinkle is that vision science individuates mental states not through their truth-conditions but through state-types that set truth-conditions *relative to context*. Truth-conditions vary depending on the context (e.g. which of two qualitatively indistinguishable objects the perceiver is currently perceiving). For discussion, see (Burge, 2010, pp. 384-396). This wrinkle does not affect my argument, so I ignore it.

(b) *Empirical semantics* models linguistic comprehension as a speaker's attempt to pair an utterance with its truth-condition. Truth-conditional semantics, usually credited to Frege, illuminates numerous linguistic phenomena, including fine-grained inference patterns featuring quantifiers and other locutions. Recent integration with generative linguistics has substantially increased its explanatory power (Heim and Kratzer, 1998).

Thus, vision science and empirical semantics illustrate the explanatory benefits of truth-conditional individuation.

To what the extent does the truth-conditional explanatory paradigm generalize beyond human vision and linguistic comprehension? Does it fruitfully apply to non-human creatures? We must exercise caution here. As Dennett observes (1987, p. 23), we can provide an intentional "explanation" for why a lectern remains stationary: it believes that it has the optimal location in the universe, and it wants to remain at the optimal location. Virtually all philosophers regard this description as a mere *façon de parler*. But why? Partly, I submit, because it yields no explanatory benefits. Truth-conditional attribution plays no role in explanatory generalizations that subsume the lectern, so we have no reason to attribute truth-conditions to the lectern. Truth-conditions play a crucial role in our best theories of human vision and linguistic understanding, so we should attribute truth-conditions to visual states and linguistic performances.

Truth-conditions must earn their explanatory keep. We should attribute them only if they yield explanatory dividends. Before applying the truth-conditional paradigm to non-human creatures, we should confirm that the paradigm offers genuine explanatory advantages.

With this background in mind, let us examine Millikan's account.

### §3.1 Millikan's teleosemantics

Millikan offers a “teleosemantic” theory, whose goal is to isolate naturalistically specifiable facts by virtue of which a state or event has truth-conditions. The basic idea is that a state has a certain truth-condition if that condition's being satisfied is required for the state to fulfill its “proper function,” in a sense of “proper function” determined partly by evolutionary history. Her actual theory is quite complicated, but not in ways that my affect my discussion. Millikan repeatedly illustrates her theory by citing the honeybee dance. For instance, she writes that the “interpreter mechanisms in the watching bees... will not perform their full proper functions of aiding the process of nectar collection in accordance with a normal explanation unless the location of nectar corresponds correctly to the dance” (1993, p. 91). She concludes that bee dances “display the characteristic trait of the intentional; namely, then can be wrong or false. They can fail to correspond to a place where there is nectar. Should anything disturb the normal mapping between the shape of the dance and the location of nectar, this misalignment will, quite literally, lead the workers astray” (2004b, p. 97).

Millikan also illustrates her theory by discussing *bacterial magnetotaxis*. Magnetotactic bacteria contain inner magnets, *magnetosomes*, that cause the entire cell to orient along geomagnetic field lines. Thus, the bacteria “behave like tiny, self-propelled magnetic compass needles” (Bazyliniski and Frankel, 2004). As a result, the bacterium moves downwards towards less oxygenated regions of its habitat, which are also the regions in which it prospers.<sup>5</sup> Millikan concludes that the “proper function” of the magnetosomes is “to effect that the bacterium moves into oxygen-free water” (1993, p. 93). From her teleosemantics, she infers that bacterial states have truth-conditions: a given magnetosome orientation accurately represents the world just in case oxygen-poor water is located in the appropriate direction (2000, p. 400).

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<sup>5</sup> See (Bazyliniski and Frankel, 2004, pp. 218-220) for a more accurate description.

A natural objection to Millikan's analysis is that truth-conditions do not "earn their explanatory keep" in scientific theories of magnetotaxis. As Burge notes (2010, p. 300), we can offer a detailed biochemical theory of magnetotaxis (Bazyliński and Frankel, 2004). Our theory may mention the "biological function" of heading towards oxygen-poor areas. But it does not require that bacterial states are *accurate* or *inaccurate*, depending on distal conditions. Truth-conditional attribution contributes no explanatory force to a purely biochemical explanation. For instance, we gain no explanatory power by saying that magnetosome orientation is *inaccurate* in those cases where the reliable correlation with oxygen-poverty fails. Thus, the bacterium seems closer to Dennett's lectern than to humans. As applied to magnetotaxis, truth-conditional locutions are an expository flourish, not a serious contribution to good explanation.

Initially, Millikan seems on firmer ground regarding honeybee navigation and communication. It is tempting to say that a honeybee dance is *correct* or *accurate* just in case nectar is present at the appropriate location. It is tempting to describe a honeybee as communicating *that* nectar is present at some location (Tetzlaff and Rey, 2009). But I agree with Burge that we must tread carefully here (2010, pp. 509-514). I do not *deny* that honeybee navigational states and dance performances have truth-conditions. I say only that, given current scientific knowledge, we have scant reason to believe that they do.

Consider dead reckoning. We can easily build a machine that dead reckons (Gallistel and King, 2009, pp. 198-203). Our hypothetical machine has three components: a speedometer; a compass; and a central processor that performs iterated vector addition. Nothing about a speedometer *in itself* or a compass *in itself* generates truth-conditions. *We* can use such devices so as to confer truth-conditions upon them, but the devices do not have "original intentionality." Nor do truth-conditions seem to emerge from coupling a speedometer and a compass to a

processor that executes vector addition. We can offer a complete scientific account of vector addition without even mentioning distal conditions. The dead reckoning machine's computations yield states that reliably correlate with distal conditions (until enough noise accumulates to break the reliable correlation). The reliable distal correlations help explain why the machine facilitates successful navigation. Yet the machine's computations do not *in themselves* seem to involve truth-conditional content in any essential way. Nothing about dead reckoning *in itself* secures an explanatory role for truth-conditional individuation. (Cf. Burge, 2010, pp. 502-507.)

Honeybee navigation is much more sophisticated than our hypothetical dead reckoning machine. Even the honeybee "sky compass" involves impressive computations grounded in the solar ephemeris function. Moreover, honeybee navigation deploys route following and cognitive maps, so it is vastly more sophisticated than any kind of dead reckoning. But do these increases in sophistication suffice to generate truth-conditions?

Consider the experimental results collected by Menzel and colleagues concerning VF, SF, and R bees. To explain those results, we can posit a "cognitive map," subject to certain mental operations, whose properties reliably correlate with the spatial distribution of distal objects and properties. What further explanatory power do gain by attributing truth-conditions to the cognitive map? A key point here is that, on *any* plausible view, reliable correlation does not suffice for truth-conditions. Black clouds correlate with rain, and a high temperature correlates with illness, but neither phenomenon is truth-conditional (Millikan, 2004, p. 31). So the mere fact that a honeybee cognitive map reliably correlates with distal states is not enough to show that the map is truth-apt. Truth-conditional attribution requires additional backing beyond mere reliable correlation. Where does one find such backing in the current scientific literature?

A similar worry applies to the waggle dance. As I emphasized, the mechanisms underlying dance production and reception remain mysterious. Perhaps our best theory of those mechanisms will ultimately treat the honeybee as pairing dances and truth-conditions, just as empirical semantics treats a human speaker as pairing sentences and truth-conditions. At present, this is mere speculation. We lack a developed theory of the mechanisms underlying dance production and reception, let alone a developed theory that assigns an essential role to truth-conditions. For instance, suppose a honeybee dance “represents” location  $x$  but that nectar is not located at  $x$ . Then the dance leads recruits astray, in that they fly towards a location that holds no value for them. Perhaps, following Millikan, we should say that the waggle dance does not achieve the function for which it was evolutionarily selected: guiding other bees towards desirable locations. Yet why should we say that the waggle dance is *inaccurate*? Truth-conditional attribution is an expository flourish, not a serious contribution to good explanation.

We humans can confer truth-conditions upon the waggle dance. We can recognize that the dance is “inaccurate” *for us*, just as we recognize that a faulty speedometer is inaccurate *for us* or that magnetosome orientation is inaccurate *for us*. But the question is whether something about the bees themselves, as opposed to our own activity, renders the dance truth-apt. Do honeybees confer truth-conditions on their dances? Millikan’s teleosemantics answers affirmatively. My question is whether we have any independent reason, aside from Millikan’s own theory, for endorsing that conclusion. In particular, are there any explanatory generalizations that individuate honeybee mental states and performances truth-conditionally?

The current scientific literature features no such generalizations. The literature emphasizes that map and waggle dance properties reliably correlate with distal properties. It emphasizes that the correlation serves an important biological function. It nowhere requires that

the map or waggle dance is *inaccurate* in those cases where the reliable correlations fails, any more than current science requires that magnetosome orientation is *inaccurate* in those cases where the reliable correlation with oxygen-poverty fails.

Broadly representational language does play a significant role in the scientific literature on honeybee navigation and communication. Ethologists frequently write that the waggle dance “encodes spatial information,” that aspects of the dance “represent” location, that the honeybee navigates by deploying mental “symbols,” and so on. As Burge notes (2010, pp. 492-518), however, we can easily paraphrase this representational talk by citing reliable correlations, biological functions, and the like.

Gallistel’s (1990, 1998) treatment of representation, which Millikan (2004b) cites sympathetically, illustrates the point. On Gallistel’s theory, “[t]he brain is said to represent an aspect of the environment when there is a functioning isomorphism between some aspect of the environment and a brain process that adapts the animal’s behavior to it” (1990, p. 15). The isomorphism obtains between the representing system (e.g. mental representations exploited during dead reckoning) and the represented system (e.g. velocity and displacement in physical space). The isomorphism is *structure-preserving*, since relations in the represented system (e.g. the relation between velocity and displacement in physical space) correspond to operations within the representing system (e.g. integration or vector summation). The isomorphism is *functioning* because it is “used by the representing system in coping with --- surviving and reproducing in --- the represented system” (1998, p. 15).

Gallistel argues that dead reckoning and map-following involve “representation,” in his proprietary sense. For instance, the honeybee exploits a systematic structure-preserving correspondence between its cognitive map and physical space. Similarly, Gallistel argues that the

honeybee dance represents the distance and direction of relevant food sources: “[t]he correspondence between elements of the dance and the geometry of the terrain outside the hive is used to control the food-seeking flight of the recruited bees” (1998, p. 22).

Let us grant that Gallistel’s theory isolates one legitimate sense in which honeybees “represent” their environment. The fact remains that Gallistel does not assign truth-conditions a significant role. Nothing in Gallistel’s treatment requires that honeybee states and performances are prone to *error* if the world does not cooperate. Explanatory weight resides solely in the “functioning isomorphism” between mind and world. There is no obvious reason why “functioning isomorphisms” must have truth-conditional content. For instance, magnetotaxis exploits an isomorphism between magnetosome orientation and direction of oxygen-poor water. So Gallistel’s theory of representation, like Millikan’s, entails that magnetosome orientation “represents” oxygen-poverty. Yet there is no clear reason, independent of Millikan’s teleosemantics, for saying that magnetotaxis involves truth-conditions. The burden of proof lies with those who claim that functioning isomorphism suffices for truth-conditions.<sup>6</sup>

### §3.2 Differences in explanatory structure

Millikan might turn my argumentative strategy against me. She might deny that truth-conditions play a central explanatory role even in vision science or empirical semantics. She might propose that we can replace any intentional explanations offered by scientific psychology

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<sup>6</sup> Gallistel classifies beaconing as “nominal representation,” i.e. “something that technically satisfies the definition of a numerical representation, but is not ‘really’ such” (1990, p. 27). Non-nominal representation requires a “rich formal correspondence between processes and relations in the environment and operations the brain performs” (1990, p. 27), whereas the only relation preserved by nominal representation is identity. Presumably, Gallistel would also classify magnetotaxis as nominal representation. In contrast, honeybee navigation “non-nominally represents,” because it supports structure-preserving operations such as vector addition. Thus, one might propose that “non-nominal representation” (in Gallistel’s sense) suffices for truth-conditions even though “nominal representation” does not. This proposal would avoid the magnetosome counter-example. But it faces other hurdles. For instance, a simple dead reckoning machine “non-nominally represents,” but I see no reason why it must generate truth-conditions.

with explanations that cite reliable correlations, biological functions, functioning isomorphisms, or other non-truth-conditional notions.

I see little prospect for successfully developing this proposal. Vision science features numerous explanatory generalizations that type-identify mental states truth-conditionally. The generalizations derive from ordinary belief-desire explanation, by way of Bayesian decision theory. A typical model (Knill, 2007) explains how the visual system estimates *that* an object has depth  $d$  by fusing an estimate *that* it has depth  $d'$  (based on binocular cues) with a possibly conflicting estimate *that* it has depth  $d''$  (based on monocular cues). There is no obvious way to preserve the benefits of such a model while eschewing truth-conditions. Eliminating truth-conditions would require wholesale reconstruction of the science. Similarly, truth-conditions occupy a seemingly indispensable role within empirical semantics. In contrast, nothing like proper functions or functioning isomorphisms plays an explicit role within vision science or empirical semantics. For instance, a perceptual state studied by vision science may well *have* a biological function. But the explanatory generalizations of vision science do not mention that function. The generalizations type-identify mental states through their truth-conditions (e.g. estimating *that* an object has a certain depth), without any explicit mention of biological fitness, natural selection, functioning isomorphism, and so on.

As Burge (2010) emphasizes, we must distinguish two explanatory paradigms, subserved by distinct schemes for taxonomizing mental states. The first paradigm mentions reliable correlations, functioning isomorphisms, biological functions, and the like. The second paradigm mentions truth-conditions. One need only compare our current best science of magnetotaxis (Bazylinski, D., and Frankel, R. 2004) with our current best science of vision (Knill and Richards, 1996) to appreciate how profoundly the two explanatory paradigms differ. There is no

reason to think that we can reproduce the second paradigm's explanatory benefits within the first paradigm. There is no reason to think that we can gut vision science and empirical semantics of their core theoretical notions without explanatory loss. Philosophers who claim that we can owe us detailed reconstructions of the relevant scientific theories.

Millikan might respond that she uses "representation" and "truth-conditions" in a proprietary sense not answerable to pre-theoretic or traditional philosophical usage. If we grant that bacteria and honeybees satisfy the appropriate clauses in Millikan's teleosemantics, then it follows by stipulation that those states have truth-conditions *in Millikan's sense*.

This response does not address my underlying objection: that Millikan elides disparities between the two explanatory paradigms distinguished above. The first paradigm traffics in notions such as functioning isomorphism, proper function, and so on. The second paradigm traffics in truth-conditions. By attributing truth-conditions even to bacteria, Millikan blurs the difference between these two paradigms. She thereby obscures crucial differences between humans and bacteria. She also distracts attention from a crucial *empirical* question: which explanatory paradigm most appropriately applies to more difficult cases, such as the honeybee? We cannot overcome these worries by introducing a special stipulated usage on which bacteria have "truth-conditions." Such a usage merely reinforces the misleading impression that no significant difference separates the two explanatory paradigms.

Good terminology tracks underlying distinctions in explanatory structure. Well-chosen theoretical terms "carve nature its joints," rather than blurring important distinctions among explanatory paradigms. We should reserve truth-conditional locutions for those domains where they play a genuine explanatory role.

#### §4. Psychological structure

By questioning whether honeybee navigation and communication involve truth-conditional contents, I am not urging that we treat honeybees within an associationist or behaviorist framework. Any plausible view of honeybee cognition must recognize complex psychological structure that such frameworks do not accommodate.

As I have discussed, honeybee navigation and communication involve computation over mental states that “represent” (in Gallistel’s sense) various distal properties, such as displacement and solar bearing. To take a particularly compelling example, there is decisive evidence that honeybees execute dead reckoning. Dead reckoning is a very simple navigational capacity, but it already illustrates the limitations of a purely associationist approach. During dead reckoning, the animal records its current displacement from a home location. Even very simple invertebrates can store this record in memory for relatively long periods. No one has the slightest idea how to model such memory storage within a purely associationist model (Gallistel and King, 2009). The divergence from associationist psychology becomes particularly vivid when we consider the solar ephemeris function, which plays an integral role in the honeybee’s sky-compass. To compute compass direction from current solar bearing, the bee must consult a stored memory that encodes the solar ephemeris function. It must perform a trigonometric computation of a kind totally alien to associationist psychology.

As I also emphasized in §2, there is evidence that honeybees store cognitive maps in memory. The mere suggestion is anathema to behaviorism or associationism.

Thus, by questioning whether honeybee navigation and communication involve truth-apt mental states, I am not questioning the broadly “cognitive” nature of those phenomena. Honeybee mental activity has far more internal psychological structure than any behaviorist

would countenance. Indeed, as I will argue in the next section, there is an important respect in which Millikan underestimates the extent of this psychological structure.

### **§5. Pushmi-pullyu representations**

Does honeybee cognition exhibit anything like belief-desire structure, as enshrined in ordinary folk psychology? Carruthers (2004) answers affirmatively. He holds that bees can execute a practical inference schematized roughly as follows:

BEL [nectar is 200 meters north of hive]

BEL [here is at hive]

DES [nectar]

MOVE [200 meters north]

Millikan rejects any such suggestion (2004a, pp. 17-18):

Does the bee come to believe there is nectar at location *L*, desire to collect nectar, know that to collect nectar at *L* requires going to *L*, hence desire to go to *L*, and hence, no other desires being stronger at the moment, decide to go to *L*, and proceed accordingly? Surely not. The comprehending bee merely acquires an inner representation that is at the same time a picture, as it were, of the location of nectar (relative to its hive) and that guides the bees direction of flight. The very same representation tells in one breath what is the case and what to do about it.

On Millikan's picture, honeybee cognition does not divide neatly into "cognitive" and "conative," or "informational" and "motivational," states. Instead, it operates at a more primitive level that blends information and motivation together inextricably. In that respect, it differs profoundly from human cognition.

This picture of honeybee cognition recurs regularly in Millikan's work. In her later writings, she adopts the label *Pushmi-Pullyu Representation* (PPR). A PPR has both "descriptive" and "directive" content. It mediates directly between perception and behavior, so it is a more primitive form of representation than a purely descriptive representation (such as a belief) or a purely directive representation (such as a desire). As Millikan notes, a PPR resembles Gibsonian perception of an *affordance*, although Gibson himself was leery of "internal representations." Cognition defined entirely over PPRs is closely tied to perception and behavior, in a way that more sophisticated cognition is not: "[r]epresentations that are undifferentiated between indicative and imperative connect states of affairs directly to actions, to specific things to be done in the face of those states of affairs" (1984, p. 99). Thus, a PPR generates a "perception-action" cycle, in which sensory input "directly" causes action. Millikan suggests, without asserting, that primitive animals display only pushmi-pullyu representation (2004a, pp. 18-19): "[o]ne possibility is that the simplest animals, at the level of insect, for example, may be governed almost entirely by a set of perception-action cycles arranged in a hierarchy that determines which shall take precedence over which." She contrasts the "sort of inarticulate pushmi-pullyu comprehension the bee has" with "articulate, well-differentiated, and uncommitted human beliefs and desires" (2004a, pp. 22).

How does Millikan's analysis of honeybee cognition fare against Carruthers's, in light of §2? Carruthers's specific formulation strikes me as problematic, for two reasons: first, it assumes that relevant honeybee mental states have intentional content; second, it depicts nectar location and honeybee location as recorded by discrete belief-states, not integrated into a holistic map-like structure. I find no warrant for either suggestion in the current science. Nevertheless, I believe that current science favors Carruthers's general approach. Current science supports a

clean division between “informational” and “motivational” elements in honeybee cognition. Indeed, Menzel (2008) explicitly commends Carruthers’s belief-desire analysis as a framework for studying honeybee cognition. Menzel does not mention anything like PPRs. His discussion is unusual only in being so explicit. Honeybee researchers routinely assume a sharp demarcation between memories and motivational states.

Research by Menzel and colleagues illustrates the point. As noted in §2, displaced SF bees first flew the route they would have flown if not displaced, then explored the environment to orient themselves, and finally flew *either* directly to the hive *or* to the hive by way of the feeder. Besides supporting the existence of a cognitive map, this phenomenon indicates a motivational element that varies independently from the map. As Menzel and Giurfa put it (2006, p. 28), one operation at the bee’s disposal must be “a shift in motivation (fly toward the hive or toward the feeder).” The shift in motivation is independently manipulable from the cognitive map. Apparently, then, honeybee cognition features a primitive analogue to the separation between beliefs and desires.

Other results bolster this conclusion. As noted in §2, whether and how a forager dances depends in complex ways on various factors (such as profitability of the food source, danger of predation, hive nutritional status), as does the reaction of prospective recruits to the dance. How can we explain this complexity unless we posit honeybee spatial memories that influence behavior in conjunction with independently manipulable informational and motivational states?

Current science provides no indication of honeybee representations that blend descriptive and imperatival elements. Nothing in current science suggests that honeybee memories and motivational states are inextricably intermingled. Attributing imperatival force to honeybee dances or to honeybee cognitive maps adds no explanatory force to the theories canvassed in §2.

More seriously, Millikan's emphasis on PPRs obscures the complex psychological underpinnings of honeybee cognition. Her discussions suggest a fairly Gibsonian picture: honeybee navigation and communication involves perception-action cycles, rather than complex cognitive chains that connect to perception and action only at the peripheries. Millikan's picture conflicts with the results canvassed in §2. As she notes, a "purely pushmi-pullyu animal" --- a hypothetical animal whose only representations are PPRs --- "is certainly capable of learning, but this learning is what psychologists call 'procedural learning.' It learns what to do after what, completion of each link in the chain producing perception of a new affordance, which guides production of the next link" (2004b, p. 185). Route following is an example of procedural learning. Perhaps one can also regard dead reckoning as a kind of procedural learning. Yet honeybees do not navigate solely by dead reckoning and route following. They also navigate by employing cognitive maps. Map-based navigation requires formation and revision of a cognitive map based on dead reckoning and sensory stimulations. It requires path-planning with respect to the map, including vector addition. These mental computations are not reducible to direct links between perception and action. They are not purely procedural. Millikan's Gibsonian picture omits crucial cognitive activity underlying honeybee navigation and communication.

To be fair, scientists such as Collett and Collett (2002) embrace something like a Gibsonian picture. They try to explain honeybee navigation solely in terms of "procedural learning," such as route following, rather than "declarative learning," such as mastery of a cognitive map. It seems to me, however, that this position does not accommodate the experimental results of Menzel and his colleagues, which reveal a "landscape memory" distinct from mastery of sensorimotor routines.<sup>7</sup>

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<sup>7</sup> Something close to Millikan's Gibsonian picture may apply to the navigation of some other insects, such as the Australian desert ant (Wehner *et al.*, 2006).

Millikan sometimes notes the developing scientific evidence for honeybee cognitive maps, but she does not substantially alter her approach (2005, p. 97): “there is evidence that bees carry neural maps in their heads, but we do not have to assume this is so to see that the dances are representational. It could be that the watching bees responded directly to the dances by pivoting about to a certain direction and flying that way for a certain time.” I find this passage misleading, because nothing resembling the honeybee dance could exist without the surrounding cognitive structure that Millikan dismisses as incidental. Honeybees make sophisticated use of dead reckoning, landmarks, the solar ephemeris function, and so on. They perform impressive computations, store memories for use at unknown future times, and exploit those memories during path-planning. It is doubtful that any navigation-communication system remotely similar to the honeybee’s could function as Millikan suggests: through “direct response” to dance signals. For instance, the hypothetical system proposed by Millikan would not incorporate computations involving a solar ephemeris function. Hence, it would not allow recruits to exploit a given waggle dance at a significantly later time of day (as honeybee recruits can do).

In another passage, Millikan tries to reconcile her PPR framework with the cognitive map hypothesis. She writes (2005, p. 174):

Actually, there is evidence that the bee has a map in its head of its environment and that the dance induces it, first, to mark the nectar location on this map (Gallistel, 1990). Still, assuming that the only use the bee ever makes of a mark for nectar on its inner map is flying to the marked position to collect the nectar, then the nectar on the bee’s inner map is itself a PPR. And it seems reasonable to count a representation whose only immediate proper function to produce an inner PPR as itself a PPR.

I see no reason for “assuming that the only use the bee ever makes of a mark for nectar on its inner map is flying to the marked position to collect the nectar.” I am not even sure that it makes sense to talk about the honeybee making use of a *particular* mark on the cognitive map. The bee makes use of the map *as a whole*. It uses the map to localize itself and to plan paths between arbitrary locations. As far as we know, the honeybee may also consult its map when deciding on a response to another bee’s waggle dance. What use the bee makes of its map depends on its motivational state, which is independently manipulable from the map itself, and probably on other memories as well. Thus, this passage understates relevant cognitive structure.<sup>8</sup>

I conclude that Millikan’s account downplays the cognitive complexity underlying honeybee navigation and communication. Those phenomena involve sophisticated patterns of mental computation, patterns that we are only beginning to understand. Calling the patterns “perception-action” cycles misleadingly suggests absence of intervening cognitive processes.

## **§6. Folk psychology as an explanatory paradigm**

To what extent should scientific theories of animal cognition replicate ordinary folk psychological practice? I have proposed two respects in which Millikan answers this question unconvincingly. On the one hand, she overextends the folk psychological practice of individuating mental states truth-conditionally. On the other hand, she understates the extent to which simple creatures instantiate something like the division between beliefs and desires. For these two reasons, Millikan provides a misleading picture of the overlap between human and

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<sup>8</sup> Also problematic is Millikan’s claim that the waggle dance induces recruits to revise their cognitive maps. The waggle dance surely induces *some* relevant change in spatial memories of recruits. But the change may not involve a change in the cognitive map. For all we currently know, the recruits may simply acquire a sensorimotor vector that is not integrated with the cognitive map.

non-human mental capacities. Needless to say, my two objections do not diminish the abundant insights into insect cognition offered by Millikan's work.

### Works Cited

Abbott, K., and Dukas, R. 2009. "Honeybees Consider Flower Danger in their Waggle Dance."

*Animal Behavior* 78: pp. 633-635.

Bazyliński, D., and Frankel, R. 2004. "Magnetosome Formation in Prokaryotes." *Nature Reviews*

*Microbiology* 2: pp. 217-230.

Biesmeijer, J., and Seeley, T. 2005. "The Use of Waggle Dance Information by Honey Bees

Throughout Their Foraging Careers." *Behavioral Ecology and Sociobiology* 59: pp.

133-142.

Burge, T. 2010. *Origins of Objectivity*. Oxford: Oxford University Press.

Carruthers, P., 2004. "On Being Simple Minded." *American Philosophical Quarterly* 41: pp.

205-220.

Cheng, K. 2006. "Arthropod Navigation: Ants, Bees, Crabs, Spiders Finding Their Way."

*Comparative Cognition: Experimental Explorations of Animal Intelligence*, eds. E.

Wasserman and T. Zentall. Oxford: Oxford University Press.

Collett, T.S., and Collett, M. 2002. "Memory Use in Insect Visual Navigation." *Nature Reviews*

*Neuroscience* 3: pp. 542-552.

De Marco, R. J. 2006. "How Bees Tune Their Dancing According to Their Colony's Nectar

Influx: Re-examining the Role of the Food-receivers' 'Eagerness'." *Journal of*

*Experimental Biology* 209: pp. 421-432.

- De Marco, R. J. and Menzel, R. 2008. "Learning and Memory in Communication and Navigation in Insects." *Learning and Memory: A Comprehensive Reference*, ed. R. Menzel and J. Byrne. New York: Elsevier.
- Dennett, D. 1987. *The Intentional Stance*. Cambridge: MIT Press.
- Dyer, F. 2002. "The Biology of the Dance Language." *Annual Review of Entomology* 47: pp. 917-949.
- Field, H. 2001. *Truth and the Absence of Fact*. Oxford: Clarendon Press.
- Fodor, J. 1987. *Psychosemantics*. Cambridge: MIT Press.
- Gallistel, C. R. 1990. *The Organization of Learning*. Cambridge: MIT Press.
- . 2008. "Insect Navigation: Brains as Symbol-Processing Organs." *Invitation to Cognitive Science*, vol. 4, eds. D. Osherson, D. Scarborough, and S. Sternberg. Cambridge: MIT Press.
- . 2009. "The Foundational Abstractions." *Of Minds and Language*, eds. M. Piattelli-Palmarini, J. Uriagereka, and P. Salaburu. Oxford: Oxford University Press.
- Gallistel, C. R., and King, A. 2009. *Memory and the Computational Brain*. Malden: Wiley-Blackwell.
- Giurfa, M., and Capaldi, E. 1999. "Vectors, Routes, and Maps: New Discoveries about Navigation in Insects." *Trends in Neuroscience* 22: pp. 237-242.
- Gould, J. L., and Gould, C. G. 1982. "The Insect Mind: Physics or Metaphysics?". In *Animal Mind-Human Mind*, ed. D. Griffin. Berlin: Springer-Verlag.
- Grüter, C., Sol Balbuena, M., and Farina, W. 2008. "Informational Conflicts Created by the Waggle Dance." *Proceedings of the royal Society B* 275: pp. 1321-1327.
- Heim, I., and Kratzer, A. 1998. *Semantics in Generative Grammar*. Malden: Blackwell.

- Knill, D. 2007. "Robust Cue Integration: A Bayesian Model and Evidence from Cue Conflict Studies with Stereoscopic and Figure Cues to Slant." *Journal of Vision* 7: pp. 1-24.
- Knill, D., and Richards, W. 1996. *Perception as Bayesian Inference*. Cambridge: Cambridge University Press.
- Menzel, R. 2008. "Insect Minds for Human Minds." *Human Learning*, eds. M. Guadagnoli, A. Benjamin, J. S. de Belle, B. Etnyre, and T. A. Polk. San Diego: Elsevier.
- Menzel, R., Geifer, K., Müller, U., Joerges, J., and Chittka, L. 1998. "Bees Travel Novel Homeward Routes by Integrating Separately Acquired Vector Memories." *Animal Behavior* 55: pp. 139-152.
- Menzel, R., and Giurfa, M. 2006. "Dimensions of Cognition in an Insect, the Honeybee." *Behavioral and Cognitive Neuroscience Reviews* 5: pp. 24-40.
- Millikan, R. 1984. *Language, Thought, and Other Biological Categories*. Cambridge: MIT Press.
- . 1993. *White Queen Psychology and Other Essays for Alice*. Cambridge: MIT Press.
- . 2000. "Biosemantics." *The Oxford Handbook of the Philosophy of Mind*, ed. B. McLaughlin. Oxford: Oxford University Press.
- . 2004a. "On Reading Signs: Some Differences Between Us and the Others." *Evolution of Communication Systems: A Comparative Approach*, eds. D. K. Oller and U. Griebel. Cambridge: MIT Press.
- . 2004b. *Varieties of Meaning*. Cambridge: MIT Press.
- . 2005. *Language: A Biological Model*. Oxford: Clarendon Press.
- Riley, J., Greggers, U., Smith, A. D., Reynolds, D. R., and Menzel, R. 2005. "The Flight Paths of Honeybees Recruited by the Waggle Dance." *Nature* 435: pp. 205-207.
- Seefeldt, S., and De Marco, R. J. 2008. "The Response of the Honeybee Dance to Uncertain

- Rewards.” *Journal of Experimental Biology* 211: pp. 3392-3400.
- Srinivasan, M. 2010. “Honey Bees as a Model for Vision, Perception, and Cognition.” *Annual Review of Entomology* 55: pp. 267-284.
- Srinivasan, M. V., Zhang, S. W., Lehrer, M., and Collett, T. S. “Honeybee Navigation *En Route* to the Goal : Visual Flight Control and Odometry.” *Journal of Experimental Biology* 199: pp. 237-244.
- Srinivasan, M. V., Zhang, S. W., and Bidwell, N. J. 1997. “Visually Mediated Odometry in Honeybees.” *Journal of Experimental Biology* 200: pp. 2513-2522.
- Stich, S. 1983. *From Folk Psychology to Cognitive Science*. Cambridge: MIT Press.
- Tetzlaff, M., and Rey, G. 2009. “Systematicity and Intentional Realism in Honeybee Navigation.” *The Philosophy of Animal Minds*, ed. R. Lurz. Cambridge: Cambridge University Press.
- von Frisch, K. 1967. *The Dance Language and Orientation of the Bees*. Cambridge: Harvard University Press.
- Wehner, R. 1994. “The Polarization-Vision Project: Championing Organismic Biology.” *Fortschritte der Zoologie* 39: pp. 103-143.
- Wehner, R., Boyer, M., Loertscher, F., Sommer, S., and Menzi, U. 2006. “Ant Navigation: One-Way Routes Rather than Maps.” *Current Biology* 16: pp. 75-79.
- Wray, M., Klein, B., Mattila, H., and Seeley, T. 2008. “Honeybees Do Not Reject Dances for ‘Implausible’ Locations: Reconsidering the Evidence for Cognitive Maps in Insects.” *Animal Behavior* 76: pp. 261-269.