10 Finding Minds: Evidence from Behavior

We now have a reasonable grasp of where in the living world nervous systems of varying complexity can be found. And this distribution of nervous systems, when viewed in the light of evolutionary relationships among animal groups, can tell us something about how replicable brains might be. This is not sufficient, however, to determine the distribution and replicability of animal *minds*. To better interpret the neuroanatomical data, we need outwardly observable signatures of the cognitive functions that are closely linked to our intuitive notion of what it is to be a thinking being in a meaningful world. For this, we must look to behavior.

Our search for the behavioral signatures of mind will focus on invertebrates, for it is only here, in the deepest phylogenetic depths of animal evolution, that the replicability of Umweltian cognition and consciousness can be established. Because brain-bearing invertebrate lineages, like arthropods and cephalopod mollusks, are likely to share a brainless common ancestor both with vertebrates and with one another (as argued in chapter 9), any minds that are found to exist in these invertebrate animals would by implication have separate evolutionary origins. Although there is substantial evidence of convergent cognitive evolution both within mammals and between mammals and birds (discussed in the coda to part II), such intraphyletic patterns of convergence are built on a homologous vertebrate brain and Umweltian platform—and thus they fail to evince the levels of projectibility that could support a cosmic biology of mind.

Reasoning about invertebrate minds is trickier than reasoning about vertebrate minds, because invertebrates, as we have seen, lack homologous brain structures (such as the cortex and midbrain) that are associated with conscious states in vertebrates. The absence of vertebrate-specific brain structures obviously does not preclude other, independently evolved brain structures from giving rise to mentality in invertebrates. Though we can make tentative analogical-style inferences about animal minds based on convergent functional

neuroanatomy,[1] discerning the functions of unfamiliar brain regions requires additional corroboration. Let us therefore consider the behavioral evidence for minds without spines.

1.   Cephalopod Smarts

We saw in the previous chapter that coleoid cephalopod mollusks have complex brains that rival those of mammals, possessing a vertical lobe that serves as a center of higher-order information processing, signal integration, and executive control. What sorts of cognitive capacities do these brain structures give rise to and how are they manifested in coleoid behavior?

1.1   Measuring an Alien Mind

Experimental research on coleoid cognition and behavior is sparse. Unlike the wide-ranging, systematic, and carefully controlled work on arthropods (which will consume the bulk of our discussion), much of the evidence for cephalopod intelligence is anecdotal or gleaned from field observations that are open to multiple interpretations. For instance, there are reports of octopuses breaking out of their laboratory tanks during the night to steal a crustacean from an adjacent aquarium, only to return to their assigned tank before experimenters arrive in the morning. A cursory scouring of aquarium hobbyist blogs reveals similar reports of octopod antics with varying levels of hyperbole and credibility.

Such cheeky activities, even if they were empirically verified, are not far removed from the octopus's natural behavioral repertoire. Octopuses are central place foragers that often hunt in tide pools at night; this requires that they navigate obstacles and occasionally exit the water, only to return safely to their den with (or having already consumed) their bounty. Aquarium escape, foraging, and return behaviors are indicative of important types of cognition (more on these below), but they may not demonstrate the kind of flexibility that is indicative of "thinking" or "insight," let alone a brazen attempt to pull a fast one on experimenters and hobbyists. We might say the same for other octopod anecdotes, such as one recounted in a recent book by Peter Godfrey-Smith, in which a scuba enthusiast is led by an octopus, hand-in-tentacle, back to its den "as if he were being led across the sea floor by a very small eight-legged child."[2] It is tempting to see such a formative event (at least for the diver) as a veritable alien encounter—a communing of kindred intellect spirits across the chasms of evolutionary time. But procuring shiny new objects and transporting them back to their den is what octopuses do in the ordinary course of things.

A hallmark of sophisticated cognition and, perhaps, of the richness of mind, is the ability to produce flexible rather than stereotyped responses to challenges that animals do not ordinarily encounter in their natural habitat.[3] Cognition research on octopuses, and to a lesser extent on cuttlefish (very little has been done with squid), shows coleoids to be domain-general problem solvers and possibly even tool users. For instance, octopuses have a strong penchant for pulling, a behavior that may to some extent be incorporated into the autonomous neural routines of their arms. And yet they can learn in the laboratory to maneuver an L-shaped box through a square-sized hole by performing a subtle combination of pushing and pulling movements that is far removed from any standard behaviors they have to carry out.[4] They can also famously learn to unscrew jars and bottles to retrieve a prey item inside,[5] and to unscrew containers from the inside to escape their own confinement—complex motor sequences that have no natural analog.

There is also work that suggests octopuses may be capable of causal reasoning and tool use, though this work is based on field observation and not subject to experimental controls. For instance, researchers diving with octopuses near Bali have observed numerous cases of octopuses awkwardly carrying around coconut shell halves which they assemble as a defensive shelter only when needed, deploying an unnatural "stilting" gait to move across the sea floor with their makeshift shelter (see figure 10.1).[6]

This behavior differs in its underlying flexibility from instinctual defensive behaviors, such as the occupation of empty gastropod shells by hermit crabs or pom pom crabs carrying stinging anemones on their claws for defense, in several key respects: (1) the causal properties of the coconut shell and its utility in defense against predation are presumably learned; (2) the item is carried around in a cumbersome and unnatural manner, which entails incurring a short-term cost (reduced locomotion and increased energy expenditure) for a long-term benefit (predation avoidance); (3) the tool is deployed only in situations that call for it; and perhaps most important, (4) the octopus behavior smacks of insight, foresight (prospection), and perhaps even causal reasoning. The fact that multiple individuals were observed carrying around coconut shells in this way also raises the prospect of observational learning, although the researchers did not speculate as such.

Coleoids also exhibit spatial memory that they use in navigation. Octopuses, for instance, become familiar with the topography surrounding their den and negotiate complex foraging excursions. In the laboratory, this takes the form of successful maze learning and detour-taking, both by aid of visual landmarks and by remembering the location of a place or object despite temporarily losing visual contact with it.[7] This indicates that octopuses have goal and object
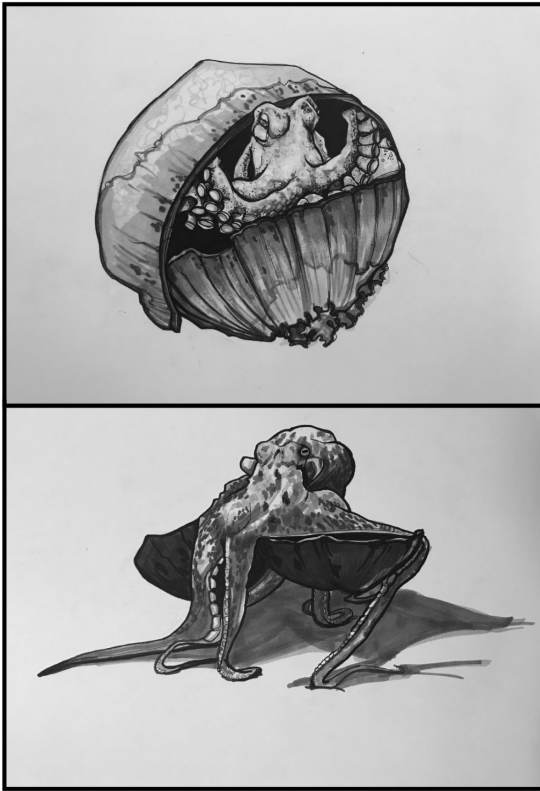
Figure 10.1
Veined octopus using coconut shell-half assembly as a shelter (*top*), and engaging in cumbersome stilt-walking with the tool, ready to deploy as needed (*bottom*)—a learned behavior that smacks of insight, planning, and causal reasoning. Redrawn from J. K. Finn, T. Tregenza, and M. D. Norman, "Defensive Tool Use in a Coconut-Carrying Octopus," *Current Biology* 19, no. 23 (2009): R1069–R1070.

permanence. They are also capable of conditional discrimination, and have long-term memory capacities that retain discrimination rules for weeks after the initial training period has ended. There is also recent evidence for episodic-like ("what/where/when") memory in cuttlefish (*Sepia*),[8] similar to the cognitive capacities that psychologists Nicola Clayton and Anthony Dickinson famously demonstrated in scrub jays.[9] More generally, octopuses are known to have an exploratory disposition that includes an affinity for novel objects, and they have been observed using their jet streams to "play" with unfamiliar objects in their aquarium.[10]

Cephalopod cognition researcher Jennifer Mather argues that coleoids demonstrate "imagination" by dangling a tentacle to lure a prey item, "causal reasoning" by using dynamic skin color displays to confuse their prey,[11] and

"behavioral flexibility" by using human trash to adorn their dens. However, these behaviors have innate analogs in other animals to which we do not normally attribute proper imagination, causal reasoning, or unusually flexible behavior (such as anglerfish, sailfish, and bower birds, respectively). Experimental challenges that place cephalopods outside of their depth, so to speak, are more telling in these regards. Debate over the nature of coleoid consciousness continues. Some researchers, such as Sidney Carls-Diamante, argue that given the autonomy of its arms, the octopus may be comprised of several cognitive systems and multiple loci of consciousness.

From the perspective of many people who have spent time observing them in the ocean and in aquariums, octopuses show an inquisitiveness that seems to be lacking in most other creatures of the sea. Time will tell whether this common intuition can be translated into empirically tractable hypotheses. Meanwhile, research on cephalopod minds has begun to filter down into philosophy and public policy, with cephalopods even being included in some jurisdictions (such as the European Union) as an "honorary vertebrate" for the purposes of research ethics protocols. It may seem odd that an organism like the octopus, which has a relatively short lifespan and moves rapidly through developmental stages, would spend its brief lifetime learning so much about its world. This cognition-life-history conundrum will now be inflated to steroidal levels as we consider the stunning cognitive abilities of bees.

2. The Tiny Brain Revolution

In an episode of the American television series *The Twilight Zone* called "The Intruders" (1961), a lone woman in a rustic cabin hears a bang on her roof; shortly thereafter, she finds herself battling two miniature humanoid figures (each only a few inches tall) wearing pressure suits and wielding small radiation weapons. Terrified, she parries with them around the home until she manages to crush one of the creatures and toss it into the fireplace. She chases the second figure to the roof, where she finds a small spaceship and proceeds to destroy it with a hatchet. For the entire episode, there is no speaking at all, only shrieks of fear and pain, until the very end—when the tiny figure who had retreated to the small craft, with a now visible label "US Air Force Space Probe" blazoned on its side, frantically radios back to Earth that they have encountered a race of hostile giant humanoids and that the planet should be avoided at all costs. It becomes clear that the diminutive space aliens are in fact human astronauts visiting another planet.

Is it possible that *we* could be the backward, ignorant giants fearfully and gratuitously crushing intelligent aliens around us with nary a thought or care? Arthropods are the descendants of the very first lineage of life on Earth to evolve

eyes, brains, and able bodies. Although arthropod cognition and behavior has been far more systematically investigated than that of cephalopods, this work has yet to make its way into mainstream philosophical thought and science policy. Indeed, the latter remain in the grips of traditional stereotypes about insects, such as the supposedly reflexive, instinctual, and inflexible nature of their behavior; and many continue to assume that tiny, pinhead-sized brains cannot possibly support sophisticated cognition or consciousness.

However, there is now a sizable body of experimental work documenting flexible learning capabilities in insects that, in some cases, rival those found in mammals and birds. These cognitive abilities range from conditional discrimination and concept formation to spatial cognition, planning, causal reasoning, and social learning. Indeed, a review of the insect cognition literature leaves one with the impression that bees are likely to outperform birds and mammals on many quintessential cognitive tasks, such as matching-to-sample discriminations and the cross-modal transfer of learned concepts—often necessitating fewer trials for success than is necessary to train up similar abilities in mammals (including primates!).[12]

Why has this rich and important body of comparative cognition research had little influence on philosophical thinking about the nature, evolution, and ethical significance of animal minds? Many have assumed that such absolutely small-brained animals could not be loci of sophisticated visual processing, learning, memory, consciousness, and emotion. However, this is an empirical question, not an a priori truth, and the empirical tide is now turning. As far as cutting-edge work on invertebrate cognition goes, arthropods are where the action is.

2.1   What Do Insects See?

One way to approach the question of arthropod minds is from the angle of image-forming perception. What do compound-eyed arthropods, such as insects, see? We might presume, given extensive homology in the vertebrate visual system, that the way humans see the world is unlikely to be fundamentally different from the way that other vertebrates see, at least in very broad strokes. Visual perception in invertebrates with convergent head/eye/brain complexes is another matter entirely. What is the world like, if anything, through the eyes and brain of a bee?

"Bug goggles" are a children's novelty toy that claim to simulate the visual world of arthropods. In effect, they break up the human visual field into numerous mini-fields that are supposed to represent ommatidia (or units) of the compound eye, each rendering a miniaturized panorama with human-typic levels of spatial resolution. In actuality, to simulate arthropod vision, bug goggles need to generate a single, unified, lower-resolution visual field that is

assembled from light entering each individual ommatidium, broadcast across the retinal array, and then stitched together into a scene that is perceived without phenomenological gaps. Of course, one cannot blame the manufacturers of a plastic children's toy for not accurately simulating arthropod vision; indeed, creating a viable model of insect vision turns out to be exceedingly difficult and requires that we make certain theoretical commitments. Even if we fully understood arthropod optics, this does not tells us how visual information is processed and packaged in the animal's brain.

2.1.1 Holism versus Localism. How are certain animals, such as insects, capable of discriminating between objects? Do they perceive objects more or less as we do—with identifiable boundaries, motions, colors, and identities—or do they merely detect low-level features of objects and use these features as the basis of navigation, discrimination, and action? This is not simply an academic debate about the nature of visual representation—it is critical to questions about the convergent evolution of the Umwelt, and it goes to the very heart of what the world is like for these animals, if it is like anything at all.

Debates over "holism" that were prominent in early discussions of Gestalt psychology now play out in the form of a debate between "global perception" and "local feature detection." Some researchers have argued that visual information in insects is not assembled into complex representations, and thus is not "seen" in any meaningful way, at all. Instead, they claim, a cluster of unbound local features (such as edges, colors, etc.) are detected in visual processing streams that are confined to each ommatidium or to a small cluster of ommatidia.[13] If this is right, then low-level cues are never integrated into a single, seamless visual scene populated by meaningful objects, and thus there is no arthropod Umwelt. On this deflationary view, the behavioral feats of arthropods, no matter how sophisticated they appear, are merely reflexive responses to low-level cues; they do not involve holistic representations of objects in the world or of the organism's body within that object field.

If one subscribes to this deflationary view, then the answer to the question "What does the insect represent?" is something like "Local, unbound features of objects, not objects in their own right." And if this is true of arthropod visual representation, then the answer to the question "What does an insect see?" may very well be "Nothing at all," insofar as seeing implies a see-er, and the absence of stimulus and semantic binding implies the lack of Umweltian cognition and consciousness. What remains is a real-life zombie: an organism that can get around in a complex world in surprisingly sophisticated ways, even though it does not form complex representations or harbor an embodied subject of consciousness. This deflationary view of arthropod visual perception is complemented by a similarly deflationary interpretation of insect learning studies,

according to which combinations of low-level cues in a scene, pattern, or object are learned and used to guide incentivized behavior, even though the insect never represents stimuli as patterns or objects in the way that vertebrates do.

As we will see, these deflationary interpretations do not hold up to empirical scrutiny. Before examining the behavioral evidence for global visual processing in bees, however, it is useful to consider the ecological tasks to which these animals are adaptively suited. In the wild, bees and wasps are faced with complex, visually guided, central-place foraging tasks. They must learn and remember the types of flowers that are likely to be nectar-rewarding and their locations relative to the hive. This is challenging, because flower resources are ephemeral, patchily distributed, variably visited by competitors, and often distantly located (frequently many miles away from the hive). Generalist wasps that colonize new locales must learn which insects are appropriate prey items; and properly exploiting other food sources like carrion and flower patches requires active navigational search and memory so as to support multiple trips to and from the nest. Visual information is crucial to solving these tasks; olfactory cues, which diffuse rapidly in air, are insufficiently precise to support the high-flying navigational feats and real-time target selections that are involved in bee and wasp foraging.

On the face of things, it would seem that simple visual cues—such as unbound edges, colors, or other local features proposed by the deflationary view as the explanation for arthropod visual discrimination—would hardly suffice for these complex, high-octane activities. Holistic representation would seem to be crucial for active visual foraging on the wing, for which object recognition needs to be stable across visual angles and motion disturbances. One might think that comparably low-resolution visual systems, such as that of arthropods, would be more likely to rely on elemental cues than on holistic representations; but as bee cognition researcher Aurore Avarguès-Weber and colleagues point out, low-resolution visual systems may actually lend themselves to global over localized information processing. This is because global processing provides more useful total information than does feature detection, and it allows the animal to glean ecologically relevant signatures without being swamped by noisy detail.

Moreover, the brains of flying insects (like bees and wasps) engaged in active navigation and foraging must compute and update their relative positions with respect to landmarks, reference points, and targets; some of these points of interest are not accessible at any given moment to the senses and hence must be retained in memory. They must also solve "reafference" problems, or confusions due to inputs generated by their own motion, in order to

perform the navigation and discrimination feats that they accomplish on the wing every day of their short but productive lives. For these purposes, generating a single, panoramic, internal simulation (an idealized, dynamic, updating representation) of one's body in space that integrates all available sensory inputs may be more computationally efficient than deploying a battery of nonintegrated sensory modules, each of which must be linked up to action in the right way.[14] The Umwelt may be a computationally parsimonious way— perhaps *the* most parsimonious way—of rapidly navigating an informationally complex world where spatial representation is at a premium. Perhaps that explains its convergent evolution in distant branches of the tree of life.

2.1.2 Inverted Faces and Abstract Paintings. There is now strong evidence that some insects, especially those with hypertrophied mushroom bodies, are capable of binding visual and semantic properties to objects that retain their identity over space and time, as well as integrating information from olfactory, mechanosensory, and gustatory senses into what appears to be a unified, dynamic simulation of the surrounding world.[15] Evidence for global perception in arthropods comes first and foremost from pattern recognition studies that aim to control for local feature detection. The upshot of this work is that bee brains can generate learning rules based on the holistic configuration of low-level elements of a scene, bind affective valences to these global categorizations, and then apply these rules to novel stimuli.[16]

One such type of study tests whether insects can recognize faces even when experimenters control for local features. Paper wasps have been shown to recognize the faces of conspecifics,[17] and honeybees can learn to recognize human faces even when they are confronted with face recognition tasks that are designed to be challenging for human subjects.[18] More tellingly, when the images of human faces are turned 180 degrees, the ability of honeybees to recognize them markedly drops off, just as it does for humans. This "inversion effect," as it is called—wherein inverting the images in face recognition tasks results in far lower accuracy and longer reaction times—is generally taken to be diagnostic of "configural" (global or Gestalt-like) rather than featural processing. The logic is that because bees are subject to the inversion and scrambling effects in the very same way that humans are, this indicates that bees represent the stimuli in a similar way to humans: namely, as a Gestalt or holistic representation that "pops out" of the visual scene. Likewise, when pictures of real faces that contain all relevant low-level cues are presented in a scrambled arrangement, bees do not recognize them as the training stimulus.[19] Low-level cues, such as visual centers of gravity (empty regions of space), color, edges, and visual angles, have all been excluded as the basis of discrimination by

manipulating highly schematized faces that control for these variables. These results cannot be explained in any obvious way by feature detection.

Even if bees represent *faces* holistically, one might wonder whether this ability is produced by a specialized subsystem that does not extend to object perception in general because it is designed specifically to attend to the faces or heads of conspecifics or predators. The data suggest otherwise. Gestalt-like perception in bees has been shown not only for faces, flower morphologies, and forest scenes,[20] but also for paintings and even artistic traditions—a surprising competency that has also been demonstrated in birds.[21] For instance, bees can learn to distinguish specific Monet paintings from specific Picasso paintings, an ability that is perhaps not too far removed from their vaunted pattern-recognition abilities. More impressively, however, they are capable of learning *artistic styles*, such as impressionism and cubism, and they can apply these style discrimination rules to novel paintings in the same tradition—even controlling for color, brightness, and other low-level features.[22]

Bees succeed at this task even controlling for elemental cues such as brightness, color, feature orientation, salience of edges, spatial frequency, and other properties that might subtly differ between artistic traditions. For example, because it is possible that bees could use complex color combinations as low-level cues for discriminations between paintings and painting styles, researchers tested whether the learned discrimination rules would transfer across greyscale images of the paintings. Not only did they successfully transfer, but greyscale discriminations of novel paintings were more successful, possibly because color patterns were interfering with holistic style judgments.

It is unlikely that simple elemental cues could account for these discriminations, given the extraordinary complexity of the individual paintings and the control of confounders. As with complex forested landscapes and visual landmarks, paintings are more effectively detected and remembered by virtue of Gestalt-like representations than by disarticulated low-level cues. Precisely how bees and birds, or humans for that matter, detect structural regularities across artistic traditions is not fully understood. Nevertheless, these results suggest that bees can represent very complex and ecologically alien patterns and apply those learning rules to novel tasks.

This raises the question of how readily insects, such as bees, take to global visual processing? Is the holistic representation of patterns and objects the predominant mode of arthropod visual perception, or must attention be modulated in the right ways to achieve these Gestalt-like effects? We know from experimental work that humans are disposed toward global information processing. That is, we tend to see the forest before the trees (which is presumably why the devil is always buried in the details). In contrast, it was long

thought that insects would prefer local to global processing, even if they could be taught to discriminate using holistic representations. The idea was that local feature processing is a faster and more frugal cognitive strategy, and hence an evolutionarily preferable one for animals working with more limited computational power.

However, this view of insect visual perception is also being overhauled. Recent discrimination experiments that manipulate local and global variables in stimulus patterns (such as global shapes made up of smaller shapes) show that given an option, bees prefer global processing over local featural processing unless they are specifically trained to attend to local features.[23] It is unclear to what extent these observations extend to other arthropods with homologous or convergent visual systems. Regardless, what this work suggests is that whether lineages rely on local or global information processing hinges less on their absolute brain size or the acuity of their vison and more on the ecological design problems they need to solve.

2.1.3 Mimicry as a Natural Experiment in Visual Perception. There is another, overlooked source of evidence for holistic perception that has yet to be mined: patterns of signaling in nature. The evolution of mimicry and other forms of visual signaling constitutes a "natural experiment" in comparative cognition that can provide insights into the perception of the "intended" receivers of those signals. If there are forms of mimicry that are striking in their holistic content to humans, then it seems likely that the coevolving lineages at which these signals are aimed also perceive their world in a Gestalt-like way. Determining precisely which lineages are the intended receivers of mimicry signals is a difficult problem that we will bracket for the time being. Animals mimicking bees, ants, beetles, and millipedes routinely pass to naïve human observers as authentic individuals of their model, at least until closer inspection. Mimetic complexes are thought to evolve in a stepwise fashion, with each incremental modification conveying a slightly stronger signal until the entire suite is produced. This can involve many dozens of modifications to numerous aspects of the organism from morphology and behavior to olfactory and tactile elements.

Some remarkable cases of mimicry appear, at least on their face, to provide evidence for holistic visual perception in the receivers of those signals. For instance, several lepidopteran caterpillars have evolved to resemble venomous snakes. Henry Walter Bates described one such hawkmoth caterpillar as "the most extraordinary instance of imitation" he had ever seen—so startling in its physical and behavioral resemblance to a snake that it had reportedly frightened people in a local village. Caterpillars that mimic venomous snakes are equipped with a suite of features that include (inter alia) faux eyes on a triangular "head," "scales," a forked "tongue," and a rearing up and striking behavior (see figure 10.2).

Figure 10.2
Caterpillar snake mimic, *Hemeroplanes triptolemus*, indicating holistic signal perception. Photo courtesy of Andreas Kay.

Ant mimicry is among the most iterated forms of complex mimicry, involving numerous modifications that include (inter alia): forelimbs altered to mimic antennae (which are waved in ant-like fashion in the air), faux compound eyes (in the case of camera-eyed jumping spider ant mimics), the loss or reduction of wings (if the mimic originally had them), constricted abdominal regions, narrowing of the thorax to create an ant-like waist, an upward-angled rear segment, a large horizontally positioned head with illusorily large mandibles, elbowed and clubbed antennae, microstructural modifications to match the coloring, reflectance, and texture of ant bodies, and behavioral modifications such as engaging in a zig-zag/ stop-and-start running gate and foregoing non-ant-like motions like jumping and flying.[24]

This rich set of multimodal modifications presumably generates an "ant" percept in the receiver—a categorization that has some desirable effect from the mimic's standpoint, either in deterring a would-be predator (such as a bird or wasp) or allowing the sender to gain access to ants themselves or their resources. Ant mimicry is common in predatory terrestrial arthropods, such as spiders and mantids, though the target of this signaling is unclear and may involve a mix of defensive and aggressive motivations. In defensive cases, ant mimics capitalize on the toxicity and stinging reputations of true ants; in aggressive "wolf in sheep's clothing" scenarios, ant mimicry may act to deceive ants themselves in order to prey directly on ants, their larvae, or their vigilantly tended "domesticated" subjects, such as aphids.

One might want to infer from the iterated evolution of holistic mimetic complexes that the coevolutionary receivers of those signals are perceiving the world holistically. However, holistic-style mimicry could evolve even if the receivers do not perceive objects at all. For example, it could be that the more cues that are present in a given case of mimicry, the more likely it is that a receiver engaging in local feature processing, or some multitude of such receivers for whom different features are salient, will detect the signal. For some receivers, colors may be salient, whereas for others edges are more likely to be picked up. Perhaps, then, mimicry complexes evolve not because receivers form holistic representations but because the mimicry complexes contain salient and redundant low-level cues for a large variety of receivers. Of course, striking mimicry complexes can also be explained by the receivers perceiving objects in a gestalt-like fashion. The holism versus localism question thus seems to be underdetermined with respect to the mimicry data.

In addition, there is an apparent problem with patterns of mimicry that the holism view would have to satisfactorily resolve. If the strength of the signal (whether true or false) is directly correlated to its adaptiveness, and if better mimics send stronger signals, then mimics should tend toward suites or complexes that increase their resemblance to the model. But if this is true, then how can we account for the ubiquity of inferior mimetic signals that could be picked up merely through elemental feature detection, such as the simple eye spots on fish? The lack of a strong resemblance between many mimics and their models could support the deflationary view, insofar as it suggests that apparently weak signals are sufficient to fool the low-level feature detection mechanisms of the evolutionarily relevant receivers, be they vertebrates or arthropods.

However, the fact that mimicry is frequently imprecise can be attributed to a number of factors that have nothing to do with the perceptual representational capacities of the receivers. These include (1) the noxiousness of the model and the existence of alternative prey items (which affect the predator's foraging risk management), (2) the presence of other mimics (causing a breakdown in the mimetic signal), (3) the attempt to mimic multiple models simultaneously (with the result that no mimetic complex represents an adaptive peak), (4) the fact that a lineage is in the early phases of an adaptive optimization trajectory, (5) internal constraints or trade-offs that limit the moldability of the mimic, and (6) strategic evolutionary countermoves by the model away from the mimic, as the model suffers an evolutionary cost from the ubiquity of false signals (which creates an incentive for predators to unlearn or fail to learn the true signal).[25]

Taken together, these aspects of the evolution of mimicry can explain why, despite holistic representation on the part of their receivers, mimicry complexes are often less than striking. In addition, we should not take mimicry data in isolation. We have already seen experimental evidence that some visual discriminations in bees cannot be accounted for by local feature detection, and in addition that bees tend to prefer global over local processing. If the hymenopteran visual imaging systems studied thus far are representative of those possessed by the likely receivers of mimetic signals, then the existence of multifeature, multimodal mimetic signaling is likely to be the coevolutionary result of gestalt-like perception in the arthropod receivers of those signals (if there are any).

This brings us to the receiver problem. As noted earlier, to make any inferences about the representational capacities of the receivers of mimetic signals, we first need to determine who the receivers of the signals are; and identifying the receivers of mimetic signals requires, in turn, that we document the effects of a given case of mimicry on the foraging behaviors of potential predators or prey with which the senders coevolved. This turns out to be surprisingly difficult in practice, and investigations of this sort are sparse. It has long been presumed that many cases of mimetic signaling are aimed at thwarting visual predation by birds—an assumption that has driven much of the experimental work on the evolution of mimicry. The finding that birds are representing objects holistically is important but not all that surprising, given extensive homology in the vertebrate visual system. Gestalt-like mimetic signals aimed at fish and lizard receivers is somewhat more telling, though it, too, speaks to the basal nature of holistic visual perception in vertebrates.

Unfortunately, very little work has explored the extent to which mimetic signals are aimed specifically at *invertebrate* visual predators, such as dragonflies, wasps, mantids, and coleoid mollusks. There is evidence that dragonflies avoid dipteran (fly) bee mimics, and that mantids avoid mimics of toxic insects. The hoverfly bumblebee mimic not only avoids predatory attack by resembling a bee (see figure 10.3), but it also reportedly gains entry into bumblebee nests wherein it lays its eggs. Likewise, rove beetles have repeatedly evolved a complex suite of ant-like morphological and behavioral modifications that give them access to the nests of aggressive army ants; the mimics even join their army ant hosts on raids, foraging expeditions, and emigrations—when, that is, they are not busy consuming the army ant's brood.[26] The extent to which invertebrates are the receivers of mimetic signals is a question in need of further research and could prove important to the investigation of animal minds.

Figure 10.3
Hoverfly bumblebee mimic, *Volucella bombylans plumata*, photo by Charles Sharp, from Wiki Commons.

2.2 What Do Insects Think?

The Umweltian platform is the groundwork for a mental life upon which other cognitive mechanisms have been laid down. The high trainability of bees, using techniques pioneered by Nobel Prize-winning ethologist Karl von Frisch, allows researchers not only to design experiments that probe the ways that bees visually represent their world, but also to test for sophisticated cognitive abilities associated with intelligence, such as learning and problem solving. Cognitive competences like categorization, concept formation, planning, causal reasoning, and social learning offer flexible tools that can be applied to a wide range of life problems, including some that are far removed from a lineage's evolutionary history and encoded epistemic ecology. As we shall see in section 3, these generic tools of mind significantly enhance the goal-directed character of animal behavior.

2.2.1 Causal Reasoning and Social Learning. Like honeybees, bumblebees have proven adept at becoming competent with the ecologically foreign tasks that have been put to them in the laboratory. For instance, Lars Chittka's prolific bee cognition laboratory recently trained bumblebees to pull on a string to get a sucrose reward that was placed just out of reach under a transparent Plexiglas table. Although the videos of bumblebees performing this complex,

spooling motor sequence are striking, the feat is somewhat less impressive than it may at first seem. Only two creative (or lucky!) bees out of nearly 300 spontaneously and without training figured out the solution; all other bees that learned to solve the task were trained in a stepwise fashion, with artificial flower rewards attached to a string placed at progressively more distant locations under the table until the full pulling sequence was learned.

It is unclear whether the bees came to understand the causal structure of the string-pulling solution. It is perhaps more likely that, like primates and birds that have learned to perform similar tasks, the bees solved the problem using perceptual or proprioceptive feedback and trial and error techniques, rather than employing causal reasoning. That said, the results should not be undersold: they demonstrate a degree of behavioral plasticity on a par with that observed in mammals and birds. Perhaps more noteworthy than the learning of the behavior itself is that this unnatural string-pulling skill was socially transmitted at high rates to other members of the colony who were able to view a demonstration of the behavioral innovation through a Plexiglas window.[27] After observing a demonstrator bee pull the string to obtain the reward, a whopping 60 percent of observers solved the string-pulling task without training and on the first try (recall that only two out of nearly 300 bees figured out the solution without training or demonstration).

The mechanisms that underwrite social learning and cultural transmission in bees may be fairly low level or even "hard wired," including some combination of local enhancement (attraction to specific locations that demonstrators have visited), stimulus enhancement (a learned association between flowers that conspecifics have recently visited and the extraction of a reward), and trial-and-error learning as enhanced location and stimuli are thoroughly explored. Social learning in bees may not, therefore, involve the sort of high-level cognitive mechanisms that underpin human-like cultural transmission, such as a theory of mind, causal reasoning, or even the deliberate copying of a complex sequence of behaviors with a specific end-goal in mind. Cultural learning in bees—as with more explicit "teaching" that has been observed in tandem-running ants[28] and socially learned mate choice in drosophila[29]— shows that social learning is a robust, multiply realizable phenomenon that is not limited to creatures capable of metacognition (i.e., reflecting on one's mental states or those of others).

Having said that, the underlying mechanisms of social transmission in bees are poorly understood, and there are two reasons to think that low-level cognitive mechanisms may not be the whole story. First, there is evidence that bees can reflect on their own epistemic states (such as their relative levels of certainty),[30] and thus metacognitive contributions to social learning in arthropods,

though unlikely, are not definitively ruled out. Second, other recent experiments that have controlled for local and stimulus enhancement have found that bees may indeed be capable of causal reasoning and observational learning.

For instance, in an ingenious recent study, the Chittka laboratory taught bumblebees to bring a small yellow ball to a designated location on a blue platform in order to obtain a sucrose reward.[31] Experimenters used a plastic model bee to demonstrate how to successfully complete this unnatural task, and the vast majority of bees were able to solve it upon demonstration by the model. Next, to test the effects of social learning on skill acquisition, researchers trained bees on a similar task, except that three yellow balls were placed at varying distances from the target. In training the demonstrator bees, the researchers glued down the two yellow balls that were closest to the target so that the demonstrators learned to move only the furthest ball to the target in order to get the reward. Next, observer bees were placed in three conditions. In the first condition, a live demonstrator bee performed the task, moving the farthest yellow ball to the target whereupon a reward was produced; in the second "ghost" condition, a magnet moved the ball "magically" to the target and a reward was produced; and in the third condition, no demonstration of the task was provided. Observer bees in the first condition solved the task an impressive 99 percent of the time; observers in the second condition solved it 78 percent of the time; and observers in the last condition solved it only 7 percent of the time. More importantly, most of the successful observers moved the *closest* ball to the target, rather than the furthest one as shown by the demonstrator (the trained demonstrator had learned to ignore closer balls to the target because they were deliberately glued down in the training phase); this was true even when the closest ball was of a different color than the furthest ball used by the demonstrator.

This "shortcut" is striking for several reasons. One, it shows rather convincingly that observer bees were not mindlessly copying behaviors performed by the demonstrators or carrying out learned motor sequences in a blind, associative way. Instead, the causal shortcuts taken suggest that the bees understood the goal-oriented structure of the task before them and improved upon the demonstrator's tactics in light of the causal relations they observed. Such behavioral innovations even smack of means-end rationality. Two, unlike the string-pulling task, which required facing the target and acting on obstacles in its way, in the ball-rolling task the bees had to move *away* from the target stimulus in order to procure an object and transport it to the designated location to obtain a reward. This involved turning their backs to the target in order to drag the ball to the designated area, which suggests that the goal was not out of mind even when it was out of sight, hinting at planning, prospection,

or imagination. Three, the ball-rolling experiment ruled out location enhancement and stimulus enhancement as the bases of social learning. Trained demonstrator bees interacted with balls located farthest from the target, whereas observers chose to perform the sequence with balls located in the area closest to target, showing that observers were not attracted to the location that the demonstrator conspecific had visited. Further, observer bees chose the ball closest to the target even if the ball was a different color than the demonstrator's ball, which suggests that the stimulus was not enhanced in a way that made success through trial and error more likely.

2.2.2 Abstract Concepts. Concept formation is another hallmark of "thinking." As we have already seen, bees are capable of categorizing natural objects in their environment, such as flowers, trees, forest landscapes and faces, as well as highly unnatural objects like contrived patterns and paintings.[32] This could be taken to imply that bees have conceptual ontologies, though these data are based largely on "matching-to-sample" discrimination tasks that are potentially vulnerable to deflationary "low-level" interpretations that deny insects perceive any objects or form any concepts at all. Discriminations based on *abstract* concepts, such as relations, more decisively rule out deflationary interpretations. Abstract relations between stimuli hold irrespective of the physical properties of the related objects, and so discriminations based on abstract *relata* cannot in any obvious way be explained in terms of local feature detection.[33]

Thus far, bees have been shown to master relational concepts that include above/below,[34] same/difference,[35] greater than/less than,[36] and bigger than/smaller than,[37] and they are capable of deploying several of these relational rules simultaneously.[38] Even more impressively, bees can transfer relational concepts across sensory modalities, so that, for example, the sameness/difference rules that are learned for visual patterns can be transferred to olfactory stimuli and vice versa. Cross-modal transfer is especially telling because there is no conceivable physical cue that could support the transfer of a relational rule between, say, visual and olfactory stimuli—sensory modalities that exploit entirely different energetic and representational bases.

For instance, in a standard matching-to-sample setup, free-flying bees enter a Y-maze from an opening in the middle of a sample pattern or color; they are then presented with a choice between two arms of the maze, one bearing a stimulus that matches the one displayed on the entrance to the maze, and one bearing a different stimulus. Bees are trained to choose the arm of the maze with either the same or different pattern or color (see figure 10.4).

If successful, the bees are rewarded with a sucrose solution (simulating nectar). Once they have mastered the sameness/difference rule, the bees are then tested to see if they can apply that abstract relational concept to visual stimuli they have never before encountered, such as novel patterns for the color-trained
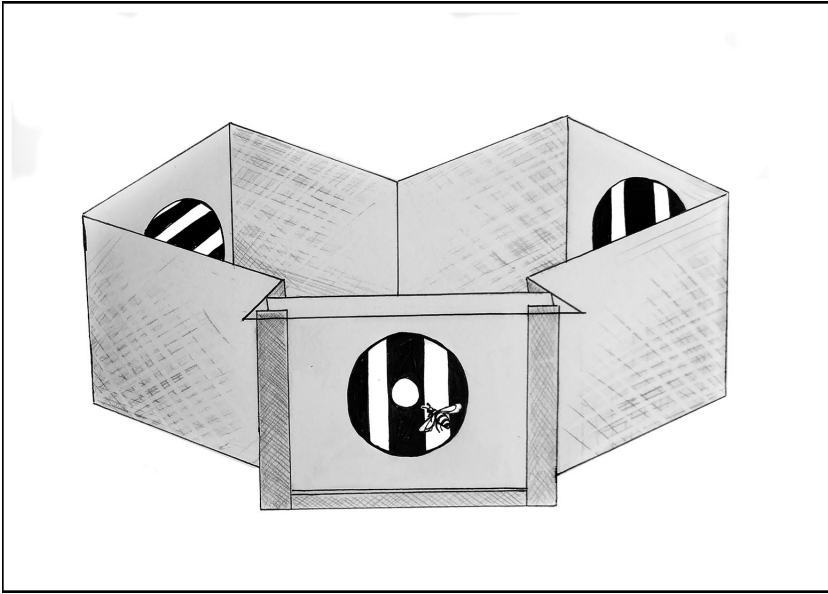
Figure 10.4
Y-maze training setup. Redrawn from A. Avarguès-Weber and M. Giurfa, "Conceptual Learning by Miniature Brains," *Proceedings of the Royal Society B 280*, no. 1772 (2013): 20131907.

bees and novel colors for the pattern-trained bees. Not only do bees succeed at this visual transfer task, but they are also capable of transferring these relational rules across sensory modalities—such as from visual to olfactory stimuli—even though these modalities share no common physical or representational cues.[39] More recently, Elizabeth Tibbetts and colleagues showed that paper wasps can master the logical operation of transitive inference, an ability associated with social dominance hierarchies. It bears stressing, once again, that these advanced, vertebrate-grade cognitive abilities are found in an animal with a brain no larger than a pinhead.

Do these results prove that bees can master abstract concepts, such as sameness/difference and above/below, in the higher-order cognitive sense that humans can? Although association-based explanations of these behaviors have not been ruled out,[40] the evidence is building that abstract concepts, as with holistic representation, is within the ken of animals with absolutely tiny brains. Even if deflationary models turn out to accurately describe the cognitive structure of abstract concept acquisition in insects, this would at a minimum show that bees have extraordinary learning capacities that more or less match higher cognitive learning in terms of identifying and exploiting complex causal structures in the world.

2.2.3 Numerosity, Time, and Planning for the Future.   Bees have also demonstrated numerosity competences, including the capacity to make greater than/less than judgments up to the number four, as well as a concept of zero or none[41]—cognitive abilities that were long thought limited to primates and parrots but now demonstrated more widely in the animal world. Dyer and colleagues have recently trained bees to employ add and subtract rules using colored symbols that represent addition and subtraction, and to apply these learned arithmetical operations to new sample sizes and shapes.[42] Chittka's research group has recently produced a simple biologically realistic model, involving only four virtual neural units, that can replicate some of the insect counting results, including the empty set response, thus offering a potential deflationary explanation of invertebrate counting behaviors.[43] It is unclear whether this model could account for bees learning arithmetic operations and using them to solve basic math problems across different kinds of objects, as just discussed, though it of course raises the specter that an alternative deflationary explanation could. But the fact that a deflationary explanation of an animal behavior can be devised does not mean that it is epistemically privileged over higher-cognitive explanations, whether taken individually or in light of the totality of the evidence.[44]

Numerosity abilities are linked to the perception of time, which requires some form of internal counting. We saw in previous chapters that noncognitive counting/memory systems are widespread the living world, including in plants and unicellular organisms. We also saw that the implicit (cognitively encapsulated) ability to bind objects in time is a critical component of object perception. An *explicit* sense of time, on the other hand, is much rarer, though it too has been shown in insects: bees, for instance, are capable of attending to the future.[45]

Jumping spiders (salticids), another prominent model for arthropod cognition, have also been shown to count in discrete numbers up to three,[46] and it would not be surprising if they could also explicitly sense the passage of time. Salticids have been shown to plan routes that include elaborate detours,[47] they exhibit highly flexible and prey-specific hunting behaviors, and they are capable of reverse learning.[48] For instance, in a recent route-planning experiment designed by leading arachnid cognition researchers Fiona Cross and Robert Jackson, jumping spiders were placed on a platform from which they could see two walkways, only one of which led to a box with a desirable prey item.[49] Recall that jumping spiders have excellent vision—in fact, the best vision of any spider, courtesy of two powerful, forward-facing, camera-type eyes. To reach the prey, the spider had to leave the tower and take a detour away from the prey item to access the correct walkway, which by design goes out of view during the journey. After a period of surveying the situation from the tower, most of the spiders, without prompting, took the detour, chose the correct

walkway, and retrieved the prey—even though none had any experience with the experimental setup or apparatus and indeed could have leapt out of it at any time. This complex navigational feat—one that is surely oversimplified compared to the actual spatial problems that jumping spiders face in the real world micro jungles they stalk—suggests a degree of planning and spatial cognition that meets our intuitive expectations about what minds are in the business of doing.

Some groups of salticids specialize in hunting other venomous spiders, including other salticids. These "Omar Littles" of the spider world (in reference to a character in the TV series *The Wire* who specialized in robbing drug dealers) exhibit extreme flexibility in their predation strategies.[50] They learn on the fly how to hunt dangerous prey that they have never encountered before, such as venomous web spiders and mantids, adapting to unfamiliar defenses, which they appear to probe for weaknesses.

Some salticid hunting techniques are eerily reminiscent of the stalking behavior of predatory cats like lions: they track down prey, carry out maneuvers to remain outside of the prey's field of view so as to not betray their position, and then pounce at the optimal time, often from behind or above after detouring to avoid detection.[51] Once a prey item with high escape ability or dangerous defenses is detected, the spiders orient and direct their attention toward the target, which they will typically approach from a flanking, rather than frontal, trajectory, often taking significant detours to do so. Their approach starts out in fast bursts, but slows to a crawl and finally to slow motion as they get close to the target. At this point they tuck away their pedipalps—fluttering chemosensory organs in the front of their head whose motion could give the game away. Various "movement masking" mechanisms are deployed, such as halting the approach when the prey item stops feeding or grooming or turns to face its stalker, then continuing the approach once the prey resumes feeding, grooming, or turns away.[52]

Jumping spiders have also been observed delaying the strike in favor of a closer approach if they are sufficiently camouflaged against their current background, thereby increasing the success rate of their attack.[53] In the case of dangerous prey, numerous venomous strikes are sometimes made, and the attacker waits (much like wolves, great white sharks, or komodo dragons) until the prey is sufficiently disabled so that it can safely be subdued.

We should not infer from these quintessential stalking behaviors that salticids have a theory of mind, or that they attribute belief states to prey, or that they can mentally simulate what other animals are seeing. If such metacognitive abilities are not necessary to explain the stalking behavior of predatory cats, then it would be gratuitous to impute them to spiders. Nor is anyone claiming that jumping spiders sit around ruminating on what kind of insect

they might want to have for lunch. But this is not a deflationary conclusion of any sort. Much like the findings for bees, as discussed earlier, many of the flexible behaviors found in jumping spiders implicate working memory, attention, object permanency, spatial cognition, the crafting of complex behavior through learned experiences, and the ability to form representations that are indicative of planning, "model-based" thinking or even mental simulation.

2.2.4 Mental Maps and Spatial Awareness. Given the kinds of tasks that bees accomplish on a day-to-day basis, it would not be surprising if they were capable of complex spatial representations that include mental simulations of three-dimensional space. However, the evidence for so-called cognitive maps in insects is mixed, in part because theoretical work suggests that surprisingly complex navigational feats (such as shortcuts) can be achieved by "lower level" memory-based guidance systems that do not rise to the level of a mental map.[54]

These are not trivial cognitive capacities by any means, and some of them necessitate a basic awareness of the body in space (such as orientations vis-à-vis landmarks and targets). The Umwelt itself is essentially a spatial map, even if it is restricted at the lower limit to immediately perceptible objects in the enveloping phenomenal field. The point, however, is that none of these mechanisms require that the organism consult a proper mental map of their surrounds. Yet even if bees only learn spatially disconnected "route maps" to targets and do not integrate these into a single mental map of their surrounding world,[55] such abilities still require complex spatial representations and cannot be explained in purely associational terms.

Nevertheless, some research does provide tantalizing evidence of mental maps in bees, though some of this work has not been adequately replicated. It is well known that foraging bees that have located a productive food source engage in a "waggle dance" in the hive that specifies the coordinates (distance and direction) of the bounty in order to recruit other foragers to the site. In a brilliant series of studies, bee cognition researcher James Gould trained the same bee foragers to visit two feeding stations of equal distance and reward magnitudes, one positioned along the shore of a lake (a natural source) and one positioned in the center of the lake (an unnatural source).[56] The same dancers gave the coordinates of both sites, but attending foragers were not recruited to the ostensibly implausible lake site whereas they were vigorously recruited to the shore site. This could indicate that the bees attending the dance situated the instructed location in their own mental map of the surrounding world, realized the location was in the center of the lake, and wrote it off as an error.

In a follow-up study, researchers moved the hive and feeding stations overnight to a similar-looking location, except that it was a tree-lined field of grass rather than a tree-lined lake. Bees that had yet to be out of the hive since it

had been relocated ignored the dance that instructed it to the feeding station that would, were the hive still in its original location, put the food source in the middle of the lake.[57] If these experiments could be replicated, they would suggest that the attending bee had a mental map of its surrounds in light of which it judged the instructed location to be implausible.

2.2.5 Metacognition.   We have already noted evidence that bees can effectively "report" on their epistemic state of uncertainty. Given the furious pace of arthropod cognition research, additional meta-cognitive surprises are likely in store. Indeed, there is now at least one study showing that ants pass the mirror self-recognition test.[58]

In this experimental paradigm, developed by psychologist Gordon Gallup, an animal placed under anesthesia is marked on a part of the body that is not visible to it, often on top of its head. Upon regaining consciousness, the animal is placed in front of a mirror and observed. If it inspects the spot using the image in the mirror, then it is deemed to pass the test, ostensibly recognizing the image in the mirror as itself. After being marked with a visible blue dot on the top of their head by experimenters, ants placed in front of a mirror inspected the mark and attempted to remove it, whereas ants with a brown dot that matched their body color did not, providing the first evidence of self-recognition in an arthropod.

Animals can widely distinguish their own body movements, vocalizations, or scents from those of conspecifics; and even more basally, animal and plant immune systems distinguish endogenous elements from intruders. Indeed, the self-world boundary is arguably a fundamental property of life itself. But "self-recognition" in the mirror experiments is noteworthy because it indicates *psychological* self-representation.

If replicated, the ability of ants to pass the mark test raises three possibilities: (1) the mark test is an inadequate test for self-recognition; (2) ants are capable of self-recognition but do not have "self-awareness" in a thick narrativistic sense; or (3) ants are self-aware in the thick sense just noted. Option 3 seems rather unlikely, given the totality of ant behavior, whereas option 1 amounts to ad hoc goalpost moving, motivated by empirically undefended assumptions about the types of cognition that absolutely small-brained animals are capable of.[59] Option 2, by contrast, is not inherently implausible. It should not be assumed that forming a basic representation of the self is evolutionarily difficult to achieve, nor that it is has no ecological utility for "simpler" animals. One could easily imagine scenarios in which mirrored reflections are an informationally significant feature of the ant Umwelt. Self-representation could be useful, say, to diagnose and treat parasites that are otherwise out of view.

The extent to which the sophisticated cognitive abilities found in insect and arachnid test subjects can be projected to arthropods writ large is unknown.

Nevertheless, the ability of some invertebrates to replicate many of the complex tasks that "advanced" vertebrates are capable of learning calls into question prevailing assumptions about the relation between mind and brain. Lars Chittka and Jeremy Niven distill two key questions from insect cognition research: "How do insects generate such diversity and flexibility of behavior with so few neurons?" and "If so much can be achieved with relatively little neuronal hardware, what advantages are obtained with bigger brains?"[60] Both of these questions remain at the foreground of invertebrate cognition research.

2.3   What Do Insects Feel?

Thus far, we have been framing arthropod minds in wholly cognitive terms, such as memory, representation, association, and the like. Let us now switch gears to consider the second major way of thinking about the Umwelt: in terms of phenomenology. Consciousness is a more fraught investigation, of course, and some readers will, quite understandably, prefer to remain safely ensconced in the cognitive realm. Yet consciousness, which we will use synonymously with "sentience" and "subjectivity," is closely linked to, if not constituted by, cognitive structures which are themselves measurable. These include (*inter alia*) stimulus and semantic integration, attention, emotion, the open-ended capacity to form associations,[61] and other causal structures that are epistemically accessible to science.

2.3.1 Sentience.   Biologist-philosopher duo Andrew Barron and Colin Klein propose,[62] following neuroscientist Bjorn Merker,[63] that the egocentric representation of the mobile animal in three-dimensional space is sufficient for subjectivity. We might fold in a fourth dimension that seems to be implicit in the Barron-Klein model, namely the integration of time—which, as we saw in chapter 8, is crucial for object identity, spatial navigation, and Umweltian cognition more broadly. Even the simple pursuit of a visual object involves the implicit perception of time, such as comparing current three-dimensional states of the world to previous ones in order to determine motion relative to the object and hence progress toward the goal.

Barron and Klein maintain that the egocentric representation of the body in space is achieved through the construction of a "unified model" or "integrated simulation" that is run in the organism's brain. By this, Barron and Klein mean something like a dynamic, updating model of the surrounding world: the organism's best guess about ecologically relevant states of the external environment and its own body within it. Their contention is that sentience is either equivalent to this simulation or arises out of it (their stance on the cognition-consciousness relation is unclear).

If this is right, then we can infer that arthropods represent an independently evolved locus (or loci, depending on how cognitively sophisticated the last common arthropod ancestor was) of sentience, given that (1) some insects and arachnids appear to form Umweltian representations, including a spatiotemporal awareness of the self (or body) in a field of affectively valenced objects, and (2) on the most plausible phylogeny of bilaterian brains, arthropods and vertebrates share a brainless and hence non-conscious (at least in the Umweltian sense) common ancestor (as discussed in chapter 9). Some annelids, such as the camera-eyed bristle worms (alciopids), are actively swimming visual predators that may also meet the conditions for Umwelt-like subjectivity and perhaps constitute a separate origin of consciousness—though to date little work has been done on bristle worm nervous systems, cognitive capacities, and behaviors.

The Umweltian ability to actively navigate and search a three-dimensional space implicates another cognitive process that is linked to animal sentience: attention. "Attention" refers to the selective focus of perceptual resources on some features of a scene rather than others. Attention is crucial for many search tasks, given the overwhelming amount of information that is available in the environment at any given moment, much of which amounts to ecological noise. Given constraints on information processing, we might expect attention-like mechanisms, which make some features of the environment more salient than others, to be a universal feature of minds wherever they evolve.

It is hard to make sense of the flexible learning and complex foraging behaviors of bees and other insects without the guidance of attentional processes. In a visual search, animals deploy a search image that focuses on certain salient characteristics, such as those associated with suitable prey items, foraging locations, competitors, or predators. Not surprisingly, both honeybees and bumblebees have been shown to use attentional mechanisms in foraging, navigation, and discrimination. As we saw earlier, bees can be trained to direct their attention to local rather than global features of objects, and vice versa. Studies of attention in honeybees show that visual search by these animals is comparatively slow and serial and thus more easily encumbered by distracting information (such as environmental clutter). To compensate for a lack of robust parallel processing, honeybees engage in a behavior called "peering," which involves a side-to-side scanning of a visual scene to obtain better spatial resolution. By contrast, in bumblebees, visual search is more mammal-like in that it is faster and carried out using parallel processes. Even the less-distractible bumblebees, however, are not capable of making complex scene discriminations on primate-level timescales, suggesting that there may be computational limits that come with absolutely small brains.[64]

There is no reason to think that attentional mechanisms are unique to bees among arthropods. The neural signatures of attentional tracking are found in the mushroom bodies of insects more broadly, such as in drosophila and cockroaches.[65] As for arachnids, it is difficult to imagine how jumping spiders are capable of stalking their prey, planning routes, and subduing deadly spiders in flexible ways without the filter of attentional mechanisms. The same is true of visual search in cephalopod mollusks. Octopuses, for instance, scan for, detect, navigate to, and remember rewarding foraging patches, they take an interest in novel objects, and they learn to make fine-grained prey discriminations—none of which could be accomplished without attention.

2.3.2 Emotional Intelligence.   Normally when we talk about "emotional intelligence" in humans, we are referring to the ability to interpret the emotional states of oneself and others and to modulate one's affect in order to manage personal relationships and achieve one's goals. However, emotional capacity is a foundational type of intelligence in its own right. Emotions are central to adaptive action and an important part of what makes the world meaningful—what gives an organism a welfare of its own.

In short, emotions are action-tendencies that include a cognitive appraisal of some internally modeled state of affairs in the world and an accompanying somatic state or "feeling," which together generate appropriate action (such as approach or avoidance). Actions like visual search would arguably be impossible without affective valences being attached to perceived objects and outcomes. Neuroscientist Antonio Damasio argues that action is often guided by the "fainter image of an 'emotional' body state, without having to reenact it in the body proper."[66] Damasio conjectures that these affective markers, or "as-if" emotional simulations, are trained up over the course of ontogeny and permit rapid decision-making by bypassing the slow and energetically costly experience of a full-blown emotional state. These "as-if" feelings occur outside of attention or conscious awareness.

If Damasio is right about the causal relation between action, cognition, and emotion, then it would seem that the sophisticated learning, navigation, and discrimination behaviors exhibited by arthropods and cephalopods must involve affective capacities. Although emotion research on arthropods is still in its infancy, some recent work suggests that insects have full-blown emotion-like states, including positive and negative affect, that are mediated by dopamine—the same hormone that regulates emotion in humans and other vertebrates. For instance, Clint Perry and collaborators demonstrated that bumblebees, just like humans, tend to interpret ambiguous stimuli more optimistically after exposure to a pleasant stimulus, whereas they display pessimistic behaviors after exposure to a negatively valenced stimulus.[67]

Although the totality of the research discussed in this chapter indicates that insects are likely to experience some states as positive and others as aversive, relatively little is known about pain perception in invertebrates. Insects often do not respond to bodily damage in the same way that, say, mammals and birds do (such as by grooming the injured body parts). This should not be taken to imply that the world is not affectively meaningful to insects, however, or that they do not have a welfare of their own.[68] If the aversiveness of pain is an adaptive mechanism that motivates animals to avoid particular situations, then we might expect that any animal capable of instrumental learning through selective exposure to punishment or other negative stimuli—an ability amply demonstrated in insects—will also be capable of experiencing pain.

Having said all this, we are not yet in a position to definitively rule out the possibility, discussed earlier, that many or all arthropods are high-functioning philosophical zombies—that no subjective states accompany insect behaviors regardless of how sophisticated they might appear.[69] The same might be said for many nonhuman vertebrate animals. Although it is true that some surprisingly complex forms of information processing can take place outside of full conscious awareness, such as during sleepwalking and to a much lesser extent under general anesthesia, we do not see unconscious or even semiconscious downhill skiers or baseball outfielders—and yet comparably complex activities are expertly carried out by insects every day.

There are, moreover, no recognized cases of unconscious learning that involve attending to novel stimuli, observing the behavior of conspecifics, forming abstract concepts, and acquiring intricate motor sequences that have yet to be routinized and are far removed from a lineage's evolutionary history. Insofar as very low-level explanations of these documented behaviors have plausibly been excluded, the evidence supports an "inference to the best explanation" that some invertebrates have a mental life.[70] In light of the foregoing discussion, the burden of proof should shift to those who want to argue that arthropods are a diverse troupe of jointed-legged zombies—and this burden has not, in my view, been met.

In sum, when neuroanatomy, behavior, and evolution are taken together as mutually reinforcing lines of evidence, they set forth a powerful case for the presence of invertebrate minds.[71] The fact that sophisticated forms of cognition, and perhaps even consciousness, can be realized in animals with pinhead-sized brains—arthropods being proof of concept—should only increase our confidence in the cosmic character of mind and its evolution.

3.   Umweltian Teleology and Macroevolutionary Ecology

Whatever one thinks of the relation between Umweltian cognition and consciousness, the capacity to situate the body in a three-dimensional field of objects is critical for the sophisticated goal-oriented behavior that marks intelligent life, be it on Earth or anywhere else.

3.1   Goal-Direction in an Umweltian Informational Space

A central if not defining feature of living things is that they are goal directed. Unlike inanimate physical systems, organisms are "teleologically" organized in that they appear to "aim" at certain ends, such as self-maintenance, reproduction, homeostasis, and so forth. The seminal account of goal-directedness in biology is due to the philosopher of science Ernst Nagel, who describes three features of goal-directed systems.[72] First is *plasticity*: the goal can be reached by the system following alternative paths or starting from different initial positions. Second is *persistence*: the system is maintained in its goal-directed behavior by compensating for disturbances that would otherwise prevent realization of the goal (provided these disturbances are not too great). And third is *orthogonality*: the variables coordinated must be independent of one another, in the sense that the value of either linked variable at any given moment must be nomically (read: physically) compatible with any value of the other variable (so as to rule out goal-directed behavior in purely physical systems, like candles and tornadoes).

Ernst Mayr defended an account of goal-direction according to which teleological (or what he preferred to call "teleonomic") behavior is behavior that results from the operations of an internal genetic program, which provides instructions for how to achieve the goal and how to respond to disturbances.[73] Rather than thinking of Mayr's proposal as an *account* of goal-directed behavior, it is probably better to think of it as an *explanation* of goal-directed behavior as defined in accordance with Nagel's property-systems criteria (or something in their vicinity). This allows us to remain neutral to the proximate mechanisms that realize goal-directed behavior, of which genetic programs, if they exist, may be simply one type. Belief-desire psychology, if *it* exists, may be another realizer of goal-direction.

Focusing on internal genetic programs also risks glossing over the structure of goal-directed systems. Hierarchical approaches to goal-direction, such as that proposed by theoretical biologist Daniel McShea, are more promising in this regard.[74] McShea understands goal-directed behavior as the movement of some entity within a larger "field" that contains and directs but does not rigidly determine the behavior of that entity. It is this wiggle room within a larger structure

that makes plasticity and persistence possible, and the enveloping field ensures that the organism's behavior can be continually directed from any location within the field. Goal-directed systems, from torpedoes to tortoises, have this "upper-directed" structure. Like Nagel's account, McShea's theory of goal-directed behavior is agnostic to underlying mechanisms—the response properties of the enveloped entity could be caused by internal genetic programs, by the information-processing functions of sensory modalities, by agentic psychological capacities, or by some combination of these things—but the deep hierarchical structure of the system remains the same across all cases of goal-direction.

The potential payoff of McShea's account is broad, but its most natural application is in thinking about the structure of teleological systems in which physical relations are important. In physics, "fields" are physical quantities that assume different values at different locations in space. It is easy to see how chemical or light fields can envelop and guide but not rigidly determine behavior. In contrast, understanding internal homeostatic mechanisms as upper directed is somewhat belabored and requires postulating an abstract "phase space" (an issue we will not address here). Thinking of the organism as embedded within spatially enveloping information fields is helpful for understanding how basic goal-directed behavior was transformed by the evolution of the Umwelt.

Although McShea does not gloss fields in informational terms, for fields to do what they need to do on the hierarchical account—that is, to direct (but not determine) the behavior of the enveloped system—they must provide goal-relevant information to the organism. If they are to provide goal-relevant information, fields must be defined in relation to an organism's sensory, representational, and response capacities. Simple goal-directed behavior, such as that exhibited by bacteria, protists, plants, and animals with very rudimentary nervous systems, is guided by low-dimensional stimulus fields like basic chemical or light gradients. In contrast, sophisticated goal-oriented behavior is only achieved by integrating information from a wide range of spatiotemporally extended stimulus fields, increasing the persistence, plasticity, and sophistication of animal behavior.

The Umwelt is a nesting of the body (or subject) within a spatially extended field of objects bundled with physical properties and affective valences (see chapter 8). It is populated with meaningful entities, including things to be avoided (e.g., predators and obstacles), sought out (e.g., mates, conspecifics, and food), used in navigation (e.g., landmarks), and ignored (e.g., noise), enabling organisms to respond to fluctuations in their enveloping sensory fields with a degree of rapidity, flexibility, and precision that more diffuse, lower-dimensional stimulus fields do not support. With the aid of perceptual filters, attentional

mechanisms, categorization abilities, and motivational states (drives or wants), the Umwelt generates goals and identifies ways of realizing these goals from a wide range of initial conditions and perturbations. It does this, for instance, by generating a stable visual field that can be used to direct foraging and navigation; by keeping a representation of a target in mind even when it is not immediately present to the senses; and by learning new associative and causal structures in the world that can be brought to bear on future problems.

The unity of the Umwelt is explanatorily crucial here. It entails the conjoined experience of numerous bound objects strewn over space and time, which are themselves integrated representations of multiple stimulus fields, such as shape, color, motion, identity, and valence. Detecting the motion of an object allows an organism to track it for pursuit or avoidance. Object permanency allows an animal to continue tracking an object even when it is partially occluded or temporarily out of view, as well as to project the object's future states, all of which may prove crucial to survival. Holistic forms of representation speed up detection, categorization, and affective appraisal, and with them goal-directed response. Some lineages have evolved the ability to act not only on concrete features of the bio-physical environment but also on abstract relations in the world, which further increases behavioral plasticity and persistence. Likewise, information about mental states adds yet another "informational field" that can direct and redirect an organism toward its ends. By enabling organisms to act on richer sources of information, Umweltian cognition and the cognitive bells and whistles that have been folded into it have greatly enhanced goal-directed behavior.

3.2   Active Predation and the Modern Evolutionary Arms Race

It is no accident that lineages boasting the greatest visual acuity—vertebrates, cephalopods, and arthropods—have independently evolved the most sophisticated nervous systems, motor capacities, and goal-directed behaviors in the living world.[75] Minds helped to construct the complex informational ecologies that image-forming eyes allowed. This, in turn, drove further expansions in cognitive-behavioral repertoires, which created additional problems and opportunities, which were solved and exploited through new cognitive, perceptual, proprioceptive, and motor innovations, and so on, resulting in a convergent complexification trend in at least three lineages of life.

Paleobiologists Mark McMenamin and Andrew Parker both have hypothesized that the evolution of eyes in the Cambrian seas kick-started the modern era of active predation (macroheterotrophy), spurring the rapid evolution of defensive countermeasures and triggering an arms race that would dominate the future history of animal life to the present day.[76] The Ediacaran fauna (encountered

earlier in this book), which predated the true critters of the Cambrian, were soft-bodied, photoautotrophic animals that appear to have lacked any complex sensory apparatuses, heads, or swimming appendages that would be indicative of active lifeways. The Ediacaran world was, in essence, a two-dimensional world concentrated around microbial mats and occupied primarily with filter-feeding. Evidence for predation in the Ediacaran is virtually nonexistent, leading McMenamin to dub this period of multicellular evolution the "Garden of Ediacara." This is not to say that there was no heterotrophy at all—but to the extent that predation existed, it was limited to languidly following chemical gradients or fortuitously bumping into prey items.

Once eyes and, crucially, Umweltian cognition had coevolved in the base of the Cambrian, the listlessness of the primeval Garden was lost. As Dorian Sagan puts it in his forward to McMenamin's book, "the evil empire of carnophagy had begun … and sashimi was everywhere." The evolution of the first image-forming eye in arthropods enabled this clade to fill all active predatory niches during the early phases of animal evolution, as epitomized by the apex carnivore *Anomalocaris* whom we met near the outset of this book. The Earth's first major predators (such as the anomalocarids) are hard to come by in the fossil record, as they would not have had mineralized skeletons that are likely to be preserved. However, the signature of active predation is reflected in the near-simultaneous skeletonization of numerous animal groups (such as the elaborate spines of trilobites, wiwaxiids, and echinoderms, and the bore-resistant shells of brachiopods), as well as the emergence of complex aggressive and defensive behaviors (such as boring, burrowing, and masticating)—two key hallmarks of the Cambrian Explosion that are indicative of arms race escalations.[77] The emergence of active arthropod predators was rapidly followed by the evolution of the vertebrate camera eye and the rise of vertebrates to ecological prominence, and somewhat later by the mollusk eye and radiations of highly active ammonites and belemnoids in the Paleozoic seas.

Missing from Parker and McMenamin's "Light Switch" theory of the Cambrian explosion, however, is the crucial role of mind and meaning. As we saw in chapter 6, complex optical apparatuses exist in box jellyfish and even unicellular dinoflagellates to little or no neurocognitive effect. Image-forming organs thus seem to be a necessary, but not sufficient, condition for the evolution of brains and minds. As philosopher Michael Trestman rightly points out, Parker uses the term vision in a way that implies more than merely an image-forming optical apparatus, but he does so without acknowledging the critical role of cognition in the Cambrian story.[78] According to Trestman, the key was "cognitive embodiment," which allowed for coordinated control over active animal bodies. Therefore, it was not the image-forming eye per se but the eye

combined with *Umwelt-grade cognition* that gave predators the search-and-destroy capabilities that likely precipitated a major ecological transition from the soft-bodied, inactive fauna of the Ediacaran to the great diversity of able-bodied and formidably defended bilaterian body plans that we see today.

Because of its contributions to goal-direction, the Umwelt is likely to be of great significance to the morphology, behavior, and relational structure of all complex living worlds.

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