



An Inconvenient Truth: Some Neglected Issues in Invertebrate Learning

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Abstract

The burgeoning field of invertebrate behavior is moving into what was the realm of human psychology concepts. This invites comparative studies not only between invertebrate and vertebrate species but also among the diverse taxa within the invertebrates, diverse even when considering only the insects. In order to make lasting progress two issues must be addressed. The first is inconsistent use of fundamental terms defining learning. The second is a focus on similarities, giving little attention to dissimilarities. In addition, much work is needed on whether behavioral similarities are grounded in the same neuronal architecture when considering disparate phyla. These concerns identify are “inconvenient truths” that weaken comparative behavioral analysis.

Keywords Intelligence · Cognition · Learning · Behaviorism · Invertebrate

Over the past decade there has been a resurgence of interest in invertebrate learning, including several recent articles that review various aspects of invertebrate cognitive abilities (Giurfa & Sandoz, 2012; Menzel & Benjamin, 2013; Perry, Barron, & Cheng, 2013; Rankin, 2004). Key insect model species show abilities that seem remarkable given the relative complexity of the insect central nervous system. On a comparative level, however, there are some central unifying issues largely unconsidered. The issues fall into two broad categories: 1) inconsistencies and scientifically weak definitions of learning phenomena, and 2) a need to focus on behavioral inability as well as abilities, and whether abilities are grounded in the same neurological basis. We hope that by bringing these issues to light that some consensus can be reached both in terms of definitions and a broader research focus, making their way into sources where scientists

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will be conscious of these “inconvenient truths” and a stronger interdisciplinary approach to invertebrate learning will emerge, as suggested by Abramson (Abramson, 1994, 1997; Abramson & Chicas-Mosier, 2016; Abramson & Calvo, 2018). The importance is more than just semantics because it very much affects the quality of science in a Popperian sense (Popper, 1957). However, despite the philosophical confusion, neural explanations of complex behavioral phenomena are advancing at a remarkable rate in part because they have been able to bypass some of the issues discussed here (Perisse et al., 2013; Dickinson & Muijres, 2016; Sun et al., 2017; Namiki, Dickinson, Wong, Korff, & Card, 2018).

Inconsistencies in Defining Learning Phenomena

The study of insect behavior has roots not only in biology with works such as Maeterlink (1901) and Turner (see Abramson, 2009), but also at about the same time with separate roots in psychology where comparative psychology was born (Morgan, 1894). This duality has led to more recent periods of exciting cross infusions of ideas such as evolutionary psychology (Cosmides, 1989; Cosmides & Tooby, 1987; Symons, 1990) and cognitive ecology (see Hutchins, 2010). Nevertheless, it has also led to inconsistencies, one of which is the striking lack of a consistent definition of basic terminology related to animal behavior.

Behavior?

The inconsistency in defining “behavior” can be seen at the most basic level. For example, few of the glossaries of 138 introductory textbooks in psychology, animal behavior, and biology sampled contained a definition of “behavior.” Moreover, when students in these introductory courses were sampled their definition depended upon the field (Abramson & Place, 2005). Although the inconsistency across disciplines might not be surprising, there was also a lack of consistency within disciplines.

A case in point is that within the biological sciences there is also no consistent definition of behavior (Cvrčková, Žárský, & Markos, 2016). In fact, even “behavioural biologists don’t agree on what constitutes behaviour” (Levitis, Lidicker, & Freund, 2009). With as many as 25 different definitions of behavior (Levitis et al., 2009), Cvrčková et al. (2016) go on to suggest that an analysis of plant behavior might contribute to a reconceptualization of how to define animal behavior.

The lack of a consistent definition of behavior can also be seen in the definitions of conditioning phenomena (Abramson, 1994, 1997). Despite appearances, it is not true that there are universally accepted definitions of what is classical and operant conditioning. For example, Gormezano and Kehoe (1975) identifies several classical conditioning procedures and Woods (1974) identifies over a dozen operant procedures. These authors explicitly point out that what might be classical and operant conditioning on the surface are not measuring the same neurological processes. *How can one accurately study the behavior of invertebrates if there is no consistent definition of what it is?*

Intelligence?

As with the definition of behavior, there is “a collection of definitions of intelligence” (Legg & Hutter, 2007). In fact, there are over 70 distinctive definitions (Legg & Hutter, 2007). This later work confirmed an earlier investigation by Sternberg and Detterman (1986) who queried 24 behavioral theorists for their definitions of intelligence—they received 12 different responses. Even a cursory knowledge of the human intelligence literature reveals the many problems in measuring and interpreting intelligence (Abramson & Lack, 2014). Schlinger (2003) points out many of the problems with the term. These include no consistent definitions, definitions that change over time, circular reasoning, and errors of reification. The term intelligence has even been used to describe aspects of a plant’s behavior without understanding the considerable issues related to the term (Abramson & Chicas-Mosier, 2016).

As a result of this lack of consistency, researchers can now study naturalistic intelligence, musical intelligence, emotional intelligence, interpersonal intelligence, spatial intelligence, analytical intelligence, creative intelligence, and practical intelligence, among others (Gardner, 2006; Sternberg, 1984). In addition to the term’s application to living organisms, it is now being widely used with a sense of certainty in robotics under the umbrella “AI” (artificial intelligence; Nilsson, 2009). *How can one accurately study the intelligence of invertebrates, “brainless systems” or even a machine, if one has no consistent definition of what it is?*

Cognition?

Moore (2013a, 2013b) notes that cognitive psychology represents a group of theoretical positions that incorporate mentalism, which is a philosophy that stretches back to the ideas Plato and Descartes (Brennan, 1998). That is, mental processes originate from the brain of humans. That paradigm evolved only recently into studies focusing on how to influence human responses through stimuli or thought-process modification (e.g., Piaget, 1936, 1953), morphing into the field of cognitive psychology in the 1960’s (Neisser, 1967). As with the definition of behavior, there is no consensus across researchers defining cognition. A recent study surveying introductory psychology and cognitive textbooks found no consistent definitions. Not only were there no consistent definitions, but similar to the terms intelligence there were many types of cognition. Cognition now includes analytical cognition, cultural cognition, and holistic cognition (Abramson, 2013). If this trend goes unchecked one can easily imagine studies examining “unconscious cognition” in invertebrates and “brainless” preparations. Information about the use of the term cognition and its history can be found in Whissell, Abramson, and Barber (2013) and Chaney (2013), respectively.

More concerning than the variability in definitions of cognition is that it is typically so broadly defined that it encompasses almost any behavior and refers to all processes where sensory input is eventually used, even in the absence of relevant stimulation (Neisser, 1967). In fact, there is no criterion to evaluate whether a behavior can be considered cognitive (Adams, 2010; Adams & Aizawa, 2008), which violates the fundamental properties of science (Popper, 1957). When asked to define cognition, the founding editor of the journal *Cognitive Psychology* replied that it is “What I like”

(Amsel, 1989). This sort of reply is typical and has even led to questioning psychology as a science (i.e., as defined by Popper, 1957).

Although cognition was originally the realm of human psychology, it is now firmly entrenched in behavioral ecology as the evolution of “cognitive architecture” of species (Real, 1991), and in sociology as cognitive sociology (DiMaggio, 1997). Nevertheless, a recent study published in *Science* attempted to replicate 100 studies in the areas of cognitive and social psychology. The results were disappointing if not alarming. Of 100 published experiments appearing in three highly ranked journals, 65% of which included 50% of the cognitive experiments could not be replicated and of those that were replicated many had reduced effect sizes (Open Science Collaboration, 2015). A major problem hindering replication was that many of the terms used by psychologists are not clearly defined and it is precisely these terms that have been uncritically accepted in other disciplines. In discussing definitional issues related to cognitive science Cvrčková et al. (2016) note that like the terms “behavior” and “intelligence,” “Similarly, cognitive sciences apparently *can* live without clear-cut formal definitions of cognition,” but that creates issues in science.

It has also been suggested that the cognitive perspective constricts research (Overskeid, 2008). This concern is supported by Cromwell and Panksepp (2011) who further emphasize how the overuse and misuse of the term “cognition” is slowing progress in behavioral neuroscience. In addition, the “cognitive” revolution has created a generation of followers who have little formal knowledge about traditional learning methodologies, proper control procedures, and alternative viewpoints (Abramson, 2013).

In reading the invertebrate learning literature there seems to be an uncritical acceptance of the interpretation of behavior in terms of cognition—however defined. If there are not objective criteria to establish whether a behavior is “cognitive,” how can an invertebrate researcher or those interested in “brainless” systems, claim that cognition exists in these organisms (Aizawa, 2014)? *How can one accurately study the cognition of invertebrates or “brainless systems” if one has no consistent definition of what it is?*

Invertebrate Inabilities: Striking “Nonsimilarities” to Vertebrates

Morphologic and physiologic comparison of phyla is based both on similarities and upon differences, and so should behavioral comparisons. In the last half-century work has claimed that invertebrates, at least the model insect organisms (e.g., Giurfa & Sandoz, 2012), possess many more of the behavioral abilities once only ascribed to the more advanced vertebrate organisms.

Indeed, there are important similarities even on neuron level. The classic model of learning and memory involves changes in changes in neuron dendritic networks and the strength of particular dendritic connections, which has supporting evidence from mammal to insect model organisms (e.g., Withers, Fahrbach, & Robinson, 1993; Roberts, Tschida, Klein, & Mooney, 2010; Yang et al., 2014; Waddell, 2016; Felsenberg, Barnstedt, Cognigni, Lin, & Waddell, 2017; Cognigni, Felsenberg, & Waddell, 2018). This experience-related neuro-networking is associated with anatomical changes in brain structure such as that seen in the mushroom bodies of honey bees (Muenz et al., 2015). In fact, an inverse correlation exists between the number of

synaptic boutons in mushroom bodies and ability of honey bee reversal learning (Cabirol, Cope, Barron, & Devaud, 2018). The potential for making new dendritic connects apparently potentiates learning to some degree.

Without diminishing the importance of that body of work, it is as important to focus on the limitations that result from the simple nervous systems, and the dissimilarities among taxa that result.

Time Perception: Implications for Invertebrate Behavioral Ecology

Interval timing is a key element of foraging theory, models of predator avoidance, and concepts of competitive interactions (Bateson, 2003; Hills, 2003), and fundamentally differs from circadian timing (Hills, 2003). Further, investigating circadian rhythms, which appear to be ubiquitous across the animal kingdom (Bass, 2012; Edgar et al., 2012), does not necessarily assess arbitrary time-interval adaptability or learning in an individual organism. Although interval timing is well documented in the advanced vertebrate (i.e., birds and mammals) species (Lejeune & Richelle, 1982; Lejeune & Wearden, 1991), it is virtually unstudied in invertebrates and so models of animal behavior involving time perception may only superficially apply to invertebrates.

A basic form of interval timing experimental design in psychology is a fixed-interval schedule of reward in operant conditioning. Here a response is rewarded only after a specified duration of time has elapsed. If no response is required such a schedule is called a fixed time schedule (FT). When a species' time-perception includes interval-timing then the probability of its response increases dramatically as the end of the time interval approaches (e.g., Skinner, 1938). Thus, fixed-interval schedules are one of the most basic assessments of arbitrary interval timing and have traditionally been observed to produce qualitative "scalloped" or "break-and-run" cumulative response curves in organisms as well as lower time-interval response rates when compared to responding to continuous reinforcement (Ambler, 1976; Dews, 1969, 1978; Ferster & Skinner, 1957; Schneider, 1969; Skinner, 1938).

In contrast to circadian rhythms, interval timing is far from being ubiquitous in vertebrates, and thus appears to be a more difficult task (Eskin & Bitterman, 1960; Kleniginna & Currie, 1979; Laurent & Lejeune, 1985; Lejeune & Wearden, 1991). For example, fixed-interval tests using species as diverse as *Tilapia*, kingsnakes, and freshwater turtles produced negative results (Grossmann, 1973; Kleniginna & Currie, 1979; Laurent & Lejeune, 1985; Lejeune & Wearden, 1991). Indeed, the existence of interval timing then may be rare in invertebrate species given the differences in central nervous system complexity.

Honey bees have been a model organism to explore animal time-perception abilities as foraging behaviors likely necessitate some estimation of elapsed time (Boisvert & Sherry, 2006; Skorupski & Chittka, 2006). Nevertheless, even the circadian-timing of honey bees may be far less precise than once believed. The en masse arrival of foragers when floral resources become periodically productive each day (e.g., Butler, 1945; Visscher & Seeley, 1982) was thought to be a result solely of circadian rhythms (e.g., Bogdany, 1978). However, a limited number of bees monitor a site at any time; when the foraging site becomes productive the monitoring bees alert the colony via the nectar's odor (Farina, Grüter, & Diaz, 2005; Wenner, Wells, & Johnson, 1969). Indeed, simply injecting a puff of the scent associated with the nectar into the hive elicits

substantial rerecruitment of foragers to the flower patch in what Reinhard, Srinivasan, and Zhang (2004) call “scent-triggered navigation” (Johnson & Wenner, 1966; Wells & Rathore, 1995). Furthermore, monitoring occurs all day long for a site offering nectar rewards for a specific 2-h period in the afternoon (Wagner, Van Nest, Hobbs, & Moore, 2013). This finding contradicts what is expected from precision circadian-rhythm triggered foraging even with behavior influenced by “expectation” of reward. This is not to say that circadian rhythms are not present in honey bees; these rhythms are ubiquitous among both animals and plants, and are even present in cell cultures (e.g., Tanenbaum, 2005). In fact, among the first organisms shown to exhibit circadian rhythms was the honey bee (Beling, 1929; Wahl, 1932). Wahl (1932) provided more rigorous experimental controls to the earlier work of Beling (1929) by conducting some of the experiments in a salt mine. The results were much the same with many of the bees showing a sense of timing by arriving at the feeding station around the hour of prior feeding (Ribbands, 1953). Nevertheless, at least half the bees arrived in the several *hours* before the specified feeding hour, and no attempts were made to limit bees from exploratory visits throughout the day. In light of modern work, the data also exhibit characteristics of foragers monitoring the feeding station. There were other peculiarities with the early body of work, and Ribbands (1953) concluded that it “requires conformation.” Social activity under constant light or dark regimes also exhibit circadian rhythms, but activity initiation and cessation again are far from punctual, forming a normal distribution spanning many hours (Frisch & Koeniger, 1994). The presence of circadian rhythms is unquestioned, but the precision remains a fruitful area of research. Considering these studies on honey bee use of circadian timing it therefore may not be surprising that they fail in interval timing experiments.

A classic study of interval timing utilized free-flying honey bees trained to enter a hole in an automated artificial flower (Craig, Vamon, Sokolowski, Wells, & Abramson, 2014); there they received a 5 μ l nectar reward once each time a bee entered the hole, with only one bee tested at a time. The test subject was continuously reinforced prior to the experiment, and readily learned to reenter the hole repeated until full, at which time it left to return to the hive. The honey bee was then subjected to a fixed-interval reward schedule (15-s, 30-s, 60-s, or 120-s). No traditional evidence of temporal perception was found, and the longer fixed-interval schedules caused all subjects to cease returning to the operant chamber. This study was unique in that 6 measures of timing were investigated (Craig et al., 2014). These results suggest that arbitrary “long-interval” timing (e.g., hours) as examined by Beling (1929) and Wahl (1932) should also be reexamined in a Popperian (Popper, 1957) rigorous experimental approach with competing theories, although monitoring of sites suggests bees do not have this timing ability well developed.

The results of Craig et al. (2014) are in accordance with both prior fixed-interval time-perception investigations in invertebrates, even though Grossmann (1973) and Boisvert and Sherry (2006) reported seemingly contrasting findings with each other. Grossmann (1973) did not find any evidence of temporal control in honey bees using a qualitative analysis of cumulative curves; post-reinforcement pauses were not identifiable, and no increase in response rate within the interval was reported. Although Boisvert and Sherry (2006) reported group-average differences in post-reinforcement pause, their analysis was based on group data not individual performance, and may be due to an unrepresentative, abstract aggregate analysis.

Abramson, Nolf, Mixson, and Wells (2010a) suggest that although honey bees show many of the behavioral abilities of vertebrates, honey bees may not be using the same neural architecture as vertebrates as observed in responses to aversive stimuli and stimulus removal (Abramson, 1986; Abramson & Buckbee, 1995; Abramson, Armstrong, Feinman, & Feinman, 1988). Indeed, Skorupski and Chittka (2006) point out that interval timing could be accomplished via several different approaches, and along these lines molecular studies have linked interval timing to elements of circadian rhythms; however, these elements appear to be distinct cellular mechanisms (Agostino, Golombek, & Meck, 2011). Thus, circadian rhythms may be an indicator of rudimentary interval timing in insects in general, and point to more likely candidates for tests of interval timing than the honey bee. Bumble bees may be such a candidate based on known foraging difference from honey bees (Gegeer & Lavery, 2004; Lihoreau, Chittka, & Raine, 2010; Lihoreau et al., 2012; Raine & Chittka, 2007).

In addition to the experiment described above, our laboratory has also conducted Pavlovian experiments using the proboscis extension reflex in restrained honey bees. In yet unpublished experiments honey bees were given 48 presentations of food in an automated training situation (Abramson & Boyd, 2001). The food presentations were separated by 10-min intervals, and thus the experiment lasted 8 h. Of 20 honey bees, proboscis extension responses occurring prior to the food presentation appeared in only 8 cases out of a possible 960 opportunities (i.e., 20×48). There was no evidence of Pavlovian temporal conditioning. A similar experiment was performed with green crabs in which harnessed crabs (Abramson et al., 1988) received a brief air-puff to the eye over the course of 14 days, with 30 presentations per day. The intertrial intervals were, for separate groups of 10 crabs each, 2.5, 5, and 10 min. Again, no evidence of temporal control in restrained crabs was found. The longer the crabs were receiving air-puffs to one of the eyes, the greater the probability that the eye would remain retracted. This experiment was replicated in a fixed-interval situation where crabs press a lever to receive food (Abramson & Feinman, 1990). Thirty daily operant conditioning sessions revealed no evidence of temporal control. On the contrary, like honey bees, the response was greatest after receipt of the reward. These unsuccessful efforts to find timing in crabs mirrored the observations of Balci (2015). We note that without rigorous experimental controls negative results, whether using a PER type approach or with free roaming subjects, are questionable and that even with good controls there is a need for replication under a variety of scenarios.

If interval timing were well developed in invertebrates there would be an obvious methodological flaw in classical conditioning studies of these organisms. Classical conditioning studies of invertebrates almost universally have used a fixed time between presentations of the conditioned stimulus, known as the intertrial interval. Obviously, if the invertebrate model under investigation showed interval timing, any classical conditioning study using a fixed intertrial interval would have an inherent confounding effect between the passage of time as a conditioned stimulus and the explicit conditioned stimulus used in training. What should be done to control for temporal conditioning (as is done in vertebrate studies) is to use a variable intertrial interval.

At least for honey bees in PER experimental designs, use of a fixed intertrial interval is experimentally sound because harnessed bees in such a situation do not exhibit temporal conditioning (Abramson, Sokolowski, & Wells, 2011). The inability to find

successful interval timing in invertebrates such as the honey bee is seldom mentioned in the literature. Rather, the honey bee is pictured as an organism that has a precise timing mechanism, and this now seems not to be true. What should be a research focus are the striking dissimilarities between invertebrates and vertebrates, as well as the similarities. Understanding system limitations has always been key for insights into any device or operation, whether it be mechanical, electric circuit/logic, or business orientated. Doing so for insects open the door to ask fundamental evolutionary and behavioral ecology questions regarding how insects get around having CNSs with 1/50 to 1/2000 the neurons of rodents, birds and nonhuman primates such as monkeys (Herculano-Houzel et al., 2011; Herculano-Houzel & Kaas, 2011; Menzel & Giurfa, 2001; Olkowicz et al., 2016) when that information is used in concert with studying similarities.

Intentionality and Causality Models

Neuroscience models based on causality have been championed in the age of computers. A particular response is the result of a specific event, which makes perfect sense in the age of robotics. Excluding random events, causality asserts that every physical response can be traced to a set of provoking causal chain of in the past. In reality, often the causal events cannot be identified, but faith in the causality model is restored by assuming numerous small random events have made it impossible to follow the causality chain of event. Intentionality models start at a different point, the mental intent leading to actions (Dennett, 1987; Turner, 2017), and as Turner (2017) points out, causality and intentionality models need not be mutually exclusive. The types of intent possible may very well define basic species-level mental differences, and deserves more scrutiny. Object permanence has been a classic experimental approach to test of intentionality in vertebrate model systems.

Intentionality, as revealed in object permanence tasks, has been demonstrated in a wide range of advanced vertebrates including birds (Hoffmann, Rüttler, & Nieder, 2011; Pepperberg & Funk, 1990), bottlenose dolphins (*Tursiops truncatus*), and California sea lions (*Zalophus californianus*; Singer & Henderson, 2015), cats (Dumas, 1992), dogs (Fiset & LeBlanc, 2007), human infants (Baillargeon & DeVos, 1991), and nonhuman primates (Call, 2001). Basic object permanence, as described at the invertebrate level (Etienne, 1984) has been observed in the dragonfly larva's (*Aeschna cyanea*) fixed position in response to the visual obstruction of a prey item (Etienne, 1984). Also, Cross and Jackson (2014) recently demonstrated that salticids (*Portia africana*) not only fixate, but also represent prey type independent of changes in prey orientation. These anticipatory behaviors are likened to the second stage of Piagetian object permanence (Anderson, 1990; Piaget, 1954).

Operant conditioning presents an approach that can ask questions related to object permanence, and honey bees have long been a model organism for studying insect neuroscience. However, the techniques used to explore psychological phenomena in honey bees have been limited to only a few primary methodologies such as the proboscis extension reflex (PER), sting extension reflex (SER), and free-flying target discrimination-tasks. Methods to explore operant conditioning in bees and other invertebrates are not as varied as with vertebrates, which may be due to the availability of a suitable response requirement. Operant conditioning centers on learning from the consequences of behavioral choices (Abramson, 1994), and is less well-studied in

invertebrates than is classical conditioning when compared to the vertebrate counterparts (Abramson, 1994; Brembs, 2003).

Like classical conditioning, operant conditioning has been a dominant element in the analysis of learning across the animal kingdom (Jenkins, 1979), not only for the insight provided in basic animal cognition but also as a means to explore how environmental factors affects behavioral responses. Illustrative examples of the latter include alcohol in primates (Field, Schoenmakers, & Wiers, 2008), pesticide ingestion by insects (Abramson, Squire, Sheridan, & Mulder, 2004), and the broad field of “cognitive ecology” (Dukas & Ratcliffe, 2009). Various forms of operant conditioning provide the determinants for advanced cognitive processes (Menzel, 2012; Menzel & Giurfa, 2001) and capacities for conceptual learning even in organisms with neuronal systems as relatively simple as the honey bee (Avarguès-Weber & Giurfa, 2013). *Drosophila*, *Aplysia*, and *Lymnaea* have been important invertebrate models that have provided insights into the cellular and molecular basis of operant learning beyond what can be gleaned from their vertebrate counterparts (Brembs, 2003), and *Apis mellifera* is now proving as valuable due to its rich behavioral repertoire associated with foraging and social interactions (Agarwal et al., 2011; Giray et al., 2015).

Abramson, Dinges, and Wells (2016) developed a new method to explore operant conditioning in honey bees: the cap pushing response (CPR). The CPR protocol requires bees to exhibit a novel behavior by pushing a cap to uncover a food source. The experiment showed that they need explicit training in pushing objects before they can solve the task (Abramson et al., 2016). Moreover, an analysis of the errors was most revealing in terms of intent. If bees are trained using a dome shaped cap over the food source and that cap was subsequently replaced with a circular cap, with the dome shaped cap moved to the outer rim of the dish, the bees would not go to the center and push the circular cap out of the way to reveal the food source; instead the bees pushed the dome cap. The bees clearly did not associate the cap with what is underneath. Here we see that a model of intentionality tells us much more about the neuronal processes of the honey bee forager than a simple causality model. It tells us that learning is highly specific in bees. It also tells us that bees are not as plastic as some of the research suggests and that researchers must be careful in ascribing complex problem-solving behavior to them. The purpose of the shaping was to teach the bees that moving an object (whether it was a cap or a cross) will uncover a food source that they had experience with. Much of the current learning literature suggests that there are striking “cognitive” similarities with vertebrate organisms. Based on these “cognitive” studies it should not make a difference what object the bee pushes. What should be important was that pushing reveals a food source *at a fixed spatial position* that the bee had previous experience with. The results observed are in concert with PER bees could not respond to the absence of the CS if the absence served as the conditioning stimulus (Abramson et al., 2010a).

These results suggest the strategies to access concealed food sources exist naturally, but experience can hasten the bee’s mastery of such strategies. Not only must bees solve complex discrimination problems, they must also solve mechanically challenging tasks in their daily routine (Cakmak et al., 2009; Raine & Chittka, 2007). Indeed, honey bees have been observed exploiting flowers with unsuitable morphologies for pollinator resource collection such as plants with anemophilous characteristics (Giovanetti & Aronne, 2011). Honey bees have also been observed manipulating papilionate flowers,

such as *Robinia pseudoacacia*. These flowers have pollen release mechanisms for which the honey bee is often too physically weak to activate (Córdoba & Cocucci, 2011). However, honey bees appear to learn to favor *R. pseudoacacia* flowers that are easier to trip and in many cases were able to trip the pollen release mechanism while accessing the nectar or finding a suitable foothold (Córdoba & Cocucci, 2011; Giovanetti & Aronne, 2011). Learning to manipulate flowers to access a nectar and pollen reward may be the natural foundations for motor-task operant behavior in honey bees.

The utilization of strategies to gain access to a concealed food source suggests honey bees are capable of utilizing knowledge of representation in regard to working memory tasks (Baddeley, 2012) which provides supporting evidence for “aboutness” or “intentionality,” a form of mental representation (Dennett & Haugeland, 1987; Turner, 2017). Indeed, evidence to date does suggest that the basic neural mechanisms are similar and simple across vastly different animals. Nevertheless, there are also emergent properties which are manifested as different degrees in representation of intentionality in animal species, but still grounded in a simple neuronal basis. For example, in avoidance behavior, the main question is, how can the absence of an event be reinforcing? The answer is that it must be expected. Further manifestation of intentionality is seen in honey bee solutions to complex problems in that variation exists among the population of foragers; some bees make choices based solely on reward, some only on effort required, and some simply on flower color ignoring both changes in reward and work involved. Individuality in choice arises when the foraging problem becomes more difficult because of increased complexity of the problem (Cakmak et al., 2009; Giray et al., 2015). Representation in arthropods is an important point to consider in the discussion of consciousness (Barron & Klein, 2016). However, when considering consciousness from different zoological levels, interpretations of behavior must consider the natural history of the animal (Etienne, 1984; Gómez, 2005; Nagel, 1974).

The waggle-dance behavior itself is of enormous potential value as a tool for studying the neurologic mechanisms underlying a complex insect behavior, regardless of whether its value lies as an abstract “language,” simply supplying olfactory information, or somewhere in between (e.g., Frisch, 1967; Gould, 1975; Wenner & Wells, 1990; Grüter & Farina, 2009). Similar behavior is observed in other *hymenoptera* including stingless bees, wasps, bumblebees, and ants (Grüter & Farina, 2009), but even proponents believe that its use by honey bees is less efficient than once thought and that honey bees rarely make use of the information (Dornhaus & Chittka, 2004; Grüter, Balbuena, & Farina, 2008). These latter points speak to the idea that the neurologic basis may provide valuable information on neuro-systems across the *hymenoptera* and even insects in general rather than for just the honey bee.

In closing, even operant conditioning in an invertebrate is open to question. There has been no study that has ever demonstrated that an invertebrate can be trained to modify some aspect of the operant response such as its duration and/or direction. For example, a rat can be trained to press a lever up or down, left or right, and with various degrees of force and delays. There has been no study of performance of invertebrates under schedules such as the differential reinforcement of high or low rates of response (DRH and DRL schedules), respectively. This suggests that a distinction be made between behavior controlled by its consequences, which would be called instrumental behavior, and arbitrary behavior controlled by its consequences which would be called

operant conditioning (Abramson, 1994, 1997). Although many consider instrumental and operant behavior to be synonymous in that both represent behavior controlled by its consequence, comparative analysis has revealed that they are not the same (Abramson, 1994, 1997). Operant conditioning is more advanced than instrumental conditioning in that it creates “arbitrary” behavior. This distinction is important for those interested in invertebrate learning. For true operant conditioning to be demonstrated, an invertebrate must not only show that it can manipulate a device but also show that it knows how to use it (Abramson, 1997). Running a maze uses a natural behavior (walking) and does not show that the bee can use its natural behavior in novel ways. The development of arbitrary behavior is the hall mark of operant conditioning, and thus maze learning is not considered operant learning in the comparative psychology literature.

Stimulus Omission and Presentation

Insects as diverse as flies and bees are able to readily learn to associate an odor with specific appetitive or aversive events (Smith, Abramson, & Tobin, 1991; Vergoz, Roussel, Sandoz, & Giurfa, 2007). Further, the CNS abilities of honey bees are suggested to enter the realm of that were originally thought to be limited to the more complex vertebrates (Giurfa, Zhang, Jenett, Menzel, & Srinivasan, 2001). This includes the ability to categorize stimuli (Srinivasan, Zhang, & Zhu, 1998; Zhang, Lehrer, & Srinivasan, 1999), solve delayed matching-to-sample and non-matching-to-sample problems, master sameness and difference interrelationships of spatial objects (Giurfa et al., 2001), learn contextual information (Collett & Baron, 1995; Collett, Fauria, Dale, & Baron, 1997), and categorize visual information (Giurfa, Eichmann, & Menzel, 1996; van Hateren, Srinivasan, & Wait, 1990; Hill, Wells, & Wells, 1997; Horridge & Zhang, 1995). In fact, bees have even been reported to learn concurrently to extend their sting to one odor and their proboscis to another because aversive and appetitive learning occur via different amines in insects (Beggs et al., 2007; Vergoz, Roussel et al., 2007; Vergoz, Schreurs, & Mercer, 2007). These seeming similarities, however, hide some basic differences.

In theory, therefore, aversive conditioning such as escape should yield behavioral responses that are similar to the results obtained with positive rewards, and like that of advanced vertebrates (Mackintosh, 1983). In signaled avoidance, a signal or cue is presented shortly before the onset of an aversive stimulus such as electric shock. If a response is made to the signal, the signal typically terminates and the shock is omitted. This procedure was considered to represent a “cognitive” process because the central question of avoidance studies was: “How can the absence of an event be reinforcing?” The answer is that it must be expected (Mowrer, 1947), which is a fundamental component of cognitive models (Abramson, 1997; Amsel, 1989). Nevertheless, the results of avoidance experiments with bees (Abramson, 1986), crabs (Abramson et al., 1988), and earthworms (Abramson & Buckbee, 1995) revealed that the avoidance response was strengthened not by the *omission* of an expected aversive event (i.e., not getting shocked), but only by its presentation (i.e., receiving the shock).

These results on aversive conditioning open a larger and fundamental question about the learning process of invertebrates. Can the removal of a stimulus serve as a signal predicting any type of event for an invertebrate? Experimental comparison of addition and deletion tasks for any animal has been notably rare (reviewed in Hearst & Wolff,

1989), and this problem continues to be understudied (Abramson & Buckbee, 1995; Miranda, Jackson, Bentley, Gash, & Nallan, 1992). Most of the literature related to addition versus deletion problems has shown the *feature-positive effect*. In essence, discrimination problems in which the response was based on the presence of a feature (feature-positive) were learned rapidly, whereas discrimination problems where the response was based on the absence of a feature (feature-negative) were learned slowly and subjects reached poor performance levels. The feature-positive effect (superiority of feature-positive over feature-negative learning) has been found to occur with pigeons (Jenkins & Sainsbury, 1969), rats (Crowell & Bernhardt, 1979), monkeys (Pace, McCoy, & Nallan, 1980), and humans (Healy, 1981; Neisser, 1963; Newman, Wolff, & Hearst, 1980; Sainsbury, 1971). This also appears to be true in honey bees (Abramson et al., 2013).

Abramson, Nolf, Mixson, and Wells (2010) further explored the feature-positive/feature-negative question, and designed experiments investigating a Pavlovian conditioning situation where the presence and absence of the stimulus are reversed temporally with respect to the presentation of a reward. Instead of a conditioned stimulus (e.g., odor) signaling the presence of a reward, the stimulus (e.g., odor) is present in the environment except just prior to the presence of the reward. Thus, the absence of the stimulus, or offset of the stimulus (e.g., absence of odor), serves as a conditioned stimulus and is the reward cue. Using both simple Pavlovian conditioning and discrimination learning protocols, honey bees learned to associate the onset of an odor as conditioned stimuli when paired with a nectar reward. They could also learn to associate the onset of a puff of air with a nectar reward. However, bees could not associate the offset of an order stimulus with the presentation of a nectar reward in either a simple conditioning or a discrimination-learning situation (Abramson, Giray, et al., 2010). These results support the model that a different neural architecture and/or information filtering is used by invertebrates to deal with certain environmental situations, including signaled avoidance. Once again, data that appeared to show a “striking similarity” turned out to be a “striking dissimilarity.”

A case in point is well known to those using honey bees in free-flying situations. When the test site is moved a few meters, returning foragers have surprising difficulty finding/recognizing the reward site (Sanderson et al., 2013; see also crop attached bees in Wenner & Wells, 1990). When the table is moved (complete with, feeder bottles and the plastic tray that the bottles rest on) all the cues specifying food are indeed moved, but not far and clearly within sight, which vertebrates would go to rather than the bare ground at the original point. In fact, the phenomenon allows scientists to deal with just a few experimental subjects (bees) in an experiment although dozens have been trained to a feeding station. A similar observation is seen when training bees in a free-flying situation (Abramson, 1990) on a plain-gray target to visit a site for a drop of sucrose. When the plain-gray target is switched to the experimental target the bee may easily take 5 or 10 min before it lands on the training target. One would have thought that the switch in targets would be minimal for the bee, but is not the case.

These behaviors have important implications for free-flying studies of possible repellents. In a study designed to show that citronella was repellent for bees (Abramson, Giray, et al., 2006) it was subsequently demonstrated that the repellent effect (decrease of bees to a feeder treated with the repellent) was entirely due to the fact that the odor represented a new stimulus situation for the bee. This is the same

effect that we discussed earlier when the training target was replaced with the experimental target. It has theoretical significance in part because of the experimental design employed and the conclusions reached based on that design. What most view as a repellent (because bees decrease visits when it is first introduced) is shown to be due simply to a stimulus change that reduces the number of bees. Further, even odors that are considered repellents (e.g., DEET) will elicit feeding via conditioning (Abramson, Wanderley, Wanderley, Silva, & Michaluk, 2007; Abramson, Singleton, et al., 2006; Abramson, Wilson, et al., 2006; Abramson, Giray, et al., 2010).

The insect mushroom body appears to be the center of CNS learning and memory that associates olfactory cues with either aversive or appetitive behaviors. As well as network level feedback to consolidate learning, Kenyon cells are modeled as having multiple synaptic link areas, compartments, where Kenyon cells form synapses with mushroom-body output-neurons and dopaminergic neurons in complex feedback micro-circuits (Cognigni et al., 2018). Olfactory stimulated Kenyon cells have bidirectional interaction with dopaminergic neurons, which in turn stimulate Kenyon cells in presynaptic and mushroom-body output-neurons in postsynaptic contacts. These micro-feedback circuits appear critical for learning in both aversive and appetitive scenarios (Cervantes-Sandoval, Phan, Chakraborty, & Davis, 2017).

The same odor can be used to elicit appetitive behavior in one context and aversive behavior in another. Further, learning in the second context does not erase the first learning scenario, which demonstrates separate locations. After learning to associate an odor with a reward, the mushroom body network appears to represent omission of the expected reward in a similar manner to aversive event learning (Felsenberg et al., 2017), which leads to extinction of the response behavior. Along those lines, familiarity to nonrewarding environmental odors seems to be a short-lived neuronal process (Hattori et al., 2017), which could be interpreted in terms of Abramson's findings (Abramson et al., 2010a) as a return to a state as if the odor did not exist in the environment. Removal of a stimulus thus would be no different than if it never existed. Overall modulation of a behavior seems to be the product of the corresponding Kenyon cell compartments along the length of arbors (Felsenberg et al., 2017).

In concluding this section, “striking differences” might be equally important to “striking similarities” when comparing invertebrate behavioral abilities to their vertebrate counterparts.

Concluding Thoughts

We hope that this article will encourage researchers to look at alternative models for the analysis of behavior of invertebrates and “brainless” systems. An unawareness or ignoring that there are a lack of generally accepted definitions of psychological phenomena whether it is associated with behavior, cognition, intelligence, or the procedures used to generate classical and operant conditioning. In terms of the philosophy of science, this creates fundamental issues because either the model testes is not scientific in the Popperian sense or altogether different models are being tested under the disguise of a test of the same model (Popper, 1957).

The experimental focus should be on the functional analysis of behavior where a researcher looks for observable relationships expected by rigorous models in the sense

of Popper (Moore, 1996, 2011, 2013a, 2013b). Rather than become bogged down in a sea of terms that have no consistent meaning, a functional analysis tests for relationships between independent and dependent variables that are defined by Popperian models (Lee, 1988; Goddard, 2012). When a relevant independent variable is initially discovered the effect is systematically replicated—replication is the foundation of a functional analysis (Sidman, 1960). Unfortunately, replication is apparently becoming rare in the behavioral sciences with devastating results not only regarding the lack of replication, but also to the way data is analyzed (Grice, 2011; Grice, Barrett, Schlimgen, & Abramson, 2012).

There is also the issue that behavioral scientists focusing on the “striking similarities” in the behavior of invertebrates and vertebrates, but not giving the same concentration on the “striking dissimilarities.” These dissimilarities are often overlooked in the literature. Research in invertebrate learning can benefit by testing behaviorist principles in the form of empirical ecological hypotheses subject to experimental scrutiny. Unfortunately, the typically view of the behaviorist perspective are those of perhaps Watson and B. F. Skinner (Todd & Morris, 1992). However, there are many forms of behaviorism. In addition to Watson’s version and Skinner’s “radical behaviorism” are the groups of behaviorists known as “Neobehaviorists.” Neobehaviorists such as Clark Hull, Edward C. Tolman, Abram Amsel, Neal E. Miller, O. H. Mowrer, and Kenneth W. Spence make use of intervening variables and represent some of the most significant figures in the history of psychology.

The use of intervening variables by the neobehaviorists shares many characteristics with the cognitivists. Denny (1986), for example, has shown that by altering the meaning of stimulus and response the cognitive and neobehaviorist position can be merged. Miller (1959) has shown that by modifying some neobehaviorist concepts, motivation and conflict can be better understood. One of the best efforts to reconcile the neobehaviorism of Hull with the cognitive behaviorism of Tolman was undertaken by MacCorquodale and Meehl (1953) who, using a mathematical model, united the views of Hull and Tolman. Stepanov and Abramson (2008) provide a review of early mathematical models associated with neobehaviorism. Leahey (1992) has suggested that as there is little difference between the neobehaviorist position and cognitive psychology, so that cognitive psychology is not so much so a revolutionary position rather than an extension of neobehaviorism.

Finally, the remarkable similarities in learning abilities seen between insect model species such as the honeybee and vertebrate counter parts such as rodents, birds, and primates, however, does not mean that the neuronal anatomy underpinning are the same. A case in point appears to be “sameness” and “difference” recognition abilities (Cope et al., 2018). This task has two distinct levels of ability. The first is simple match-to-sample or delayed-match-to-sample tasks. The second level centers upon concept learning of sameness or difference, and is much more difficult. For this it is necessary to show the concept can be applied in a new context. Although showing that honey bees can master the first level task is not too surprising based on their foraging ecology, honey bee’s ability to master the second level based on their CNS complexity is remarkable (Giurfa et al., 2001). In the advanced vertebrate models, “sameness” and “difference” appear to be true cognitive-model abilities (i.e., top-down), originating from the prefrontal cortex in mammals (Wallis, Anderson, & Miller, 2001), which insects have no counterpart to. Kenyon cells of insects may fulfill this computational

requirement for novelty detection (Szyszka, Galkin, & Menzel, 2008; Hattori et al., 2017) as shown by the computational model of Cope et al. (2018). Although the neurologic model proposed by Cope satisfies both the known anatomical and behavioral constraints of insects, rigorous scientific test of the model remain in the future. Nevertheless, considering the differences in neuroanatomy as well as behavioral abilities “gives us a clue that the cognitive architecture of insects may differ fundamentally from that of many vertebrates” (Abramson, Nolf, et al., 2010).

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