A cognitive model’s view of animal cognition

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Abstract Although it is a relatively new field of study, the animal cognition literature is quite extensive and difficult to synthesize. This paper explores the contributions a comprehensive, computational, cognitive model can make toward organizing and assimilating this literature, as well as toward identifying important concepts and their interrelations. Using the LIDA model as an example, a framework is described within which to integrate the diverse research in animal cognition. Such a framework can provide both an ontology of concepts and their relations, and a working model of an animal’s cognitive processes that can compliment active empirical research. In addition to helping to account for a broad range of cognitive processes, such a model can help to comparatively assess the cognitive capabilities of different animal species. After deriving an ontology for animal cognition from the LIDA model, we apply it to develop the beginnings of a database that maps the cognitive facilities of a variety of animal species. We conclude by discussing future avenues of research, particularly the use of computational models of animal cognition as valuable tools for hypotheses generation and testing [Current Zoology 57 (4): 499–513, 2011].

Keywords Cognitive models, Computational models, LIDA, Ontology, Taxonomy

1 Introduction

Animal cognition can be viewed as the study of how animals convert sensory data into internal representations of their current situation, and go on to select an appropriate action in response to the situation. The life of each individual animal consists of a continual iteration of such sense, comprehend, and act cycles. Action selection is what cognition is about (Franklin, 1995).

The animal kingdom is vast. Though the number of extant animal species is quite controversial, it likely numbers in the tens of millions. The variety of cognitive processes found across species is also vast. At one end of the range we find the sessile sponge that has no need for cognition (Philippe et al., 2009), and the sea squirt (Tunicata) after whose chordate larva attaches itself permanently to a rock and no longer has any need to select actions, largely absorbs its nervous system (Llinás, 2002). At the other end reside a host of sophisticated cognizers including elephants, cetaceans, primates, and we humans. In between, for example in insects or arachnids, we can find instances of such cognitive processes as learning, attention, planning, and cognitive maps (Bleeker et al., 2006; Kaiser, 2003; Menzel and Giurfa, 2001; Wilcox et al., 1996).

Though animal cognition is a relatively new field of study, there is already an immense amount of data, information, and knowledge to be organized and assimilated. As with any developing scientific field, identifying the concepts that are important for study, and specifying how they are interrelated is a significant challenge. For example, in Bekoff, Allen, and Burghardt’s (2002) impressive edited volume of interdisciplinary essays on animal cognition, the term “cognitive” itself is used with different meanings by different authors in different contexts (Bekoff et al., 2002). It is important to note that a lack of agreement on the definition of a broad term such as “cognition” is not a death knell for the field of animal cognition. The scientific study of human emotions has faced a similar conundrum because the term “emotion” has notoriously resisted a widely accepted scientific definition (Izard, 2010). Yet, the field has actively progressed for over a century since Darwin’s seminal volume on the subject (Darwin, 1872).

A lack of agreement for basic terminology does, however, limit cross-species conclusions, and offers an easy point of attack for those who are skeptical about the cognitive facilities of non-human animals. Hence, in order to develop cross fertilizations among researchers studying similar phenomenon in different species, a set of operational definitions for critical terms that can be
applied to a reasonably broad set of species is needed. Together, these accepted concepts and their relations would form an ontology for animal cognition (Franklin and Ferkin, 2006). In this context, an ontology is a set of concept definitions with relations between them. This use of the term “ontology” is consistent with its use by information scientists but is very different from how it is used by philosophers.

While ontologies represent a useful starting point from which to systematically organize empirical discoveries into animal cognition, their value is limited because they are primarily static representations instead of active entities. What is needed are working models of an animal’s cognitive processes (cognitive models) that can be used to assimilate known findings and make predictions that can be empirically tested. Cognitive models are important because they offer assimilation frameworks that complement active empirical research. For example, one could incorporate a dozen known effects of human memory, such as fan effect, interference, retrieval-induced forgetting, priming, and recency (Tulving and Craik, 2000) into a conceptual memory model that simultaneously accounts for these effects. Such models offer a mechanistic account of memory as is the case of Anderson’s Human Associative Memory (Anderson and Bower, 1980), Kanerva’s sparse distributed memory (Kanerva, 1988), or a recent neural network model of retrieval-induced forgetting (Norman et al., 2007) (i.e., during retrieval a memory can impair the subsequent retrieval of associated memories). In addition to offering a unified framework to assimilate known findings, the true merit of a model lies in its ability to further research by generating testable predictions. Failure to empirically validate these predictions is a signal that aspects of the model need to be revised or reconceptualized.

In this fashion, model building is much like the theorize→predict→experiment→theorize cycle of experimental science. A theory is built, predictions made from the theory are tested by experimentation, and the theory is revised in light of empirical findings, tested again, etc. (Beveridge, 1957; Losee, 1993; Salmon, 2006). A cognitive model of a cognitive phenomenon in humans or animals also “lives” through a similar cycle. A model is designed and implemented, but experimentation shows that it does not perform as desired. Therefore, its underlying mechanisms are redesigned and rebuilt. More experimentation takes place yielding more revision and redesigning of the model and reconceptualization of the underlying theory. Science progresses by the perpetual iteration of these two cycles.

There has been some work on biorobot models of behavior of a variety of organisms such as lobsters (Grasso et al., 2000), cockroach kinematics (Quinn and Ritzmann, 1998), rat hippocampus (Burgess et al., 1998), and others (Beer et al., 1998; Webb, 2001). However, cognitive models have yet to play a significant role in the study of animal cognition, despite being indispensable tools in the study of human cognition (McClelland, 2009; Sun, 2008). The prominent cognitive models include computational models of human cognition such as connectionist models (Rumelhart et al., 1986; Sun, 2008), rational and Bayesian models (Chater et al., 2006; Tenenbaum et al., 2006), dynamical systems (Beer, 2000; Holden et al., 2009; Kello et al., 2008; Van Orden et al., 2003; Ward, 2002), symbolic systems (Bringsjord and Ferrucci, 1998; Fodor and Pylyshyn, 1988), and cognitive architectures (Anderson and Lebiere, 1998; Helie and Sun, 2010; Laird et al., 1987; Meyer and Kieras, 1997a; Meyer and Kieras, 1997b; Sun et al., 2005).

Many of these model some psychological theory of a particular aspect of cognition, attempting to account for experimental data. Others aspire to be general computational models of cognition. These models are usually designed around some unified theory of cognition (Newell, 1994). They include SOAR (Laird et al., 1987), ACT-R (Anderson and Lebiere, 1998), CAPS (Just and Carpenter, 1992; Just and Carpenter, 1987), CLARION (Helie and Sun, 2010; Sun et al., 2005), EPAM (Feigenbaum and Simon, 1984), EPIC (Meyer and Kieras, 1997a; Meyer and Kieras, 1997b), Icarus (Langley et al., 1991), and the LIDA model (Baars and Franklin, 2007; Negatu et al., 2007; Wallach et al., 2010).

In our view, these general cognitive architectures are of primary relevance to the study of animal cognition for three reasons. First, they aspire to account for a broad range of cognitive phenomena such as sensation, perception, categorization, memory, planning, action selection, and several others. This affords an understanding of the cognitive facilities of the entire animal, instead of a narrow focus on one or two cognitive abilities. Such a comprehensive understanding is critical, since the various processes in this broad range are so highly interconnected and interdependent. Second, a cognitive model inherently brings along its own ontology of cognitive modules and processes. This ontology can serve as a common framework to comparatively assess the cognitive capabilities of different animal species. In particular, we can avoid the
problem of ascertaining what it means to have an “episodic-like memory” for two distinctively different species such as meadow voles Microtus pennsylvanicus et al., 2008 or scrub-jays Aphelocoma coerulescens (Clayton and Dickinson, 1998), if we agree on the adopted model’s conceptualization of episodic-like memory. The third advantage of (computational) cognitive models is that they provide mechanistic accounts of cognitive phenomenon, thereby affording the ability to simulate experiments on a number of different animals as well as generate hypotheses that can be empirically tested in future experiments.

The present paper focuses on the first two advantages of broad cognitive models towards the study of animal cognition. We derive an ontology for animal cognition from the LIDA model of human cognition (Baars and Franklin, 2007; Negatu et al., 2007; Wallach et al., 2010) and apply this ontology to develop the beginnings of a database that maps the cognitive facilities of a variety of animal species (invertebrates, insects, avians, rodents, canids, and nonhuman primates). We conclude by discussing future avenues of research, particularly the use of computational models of animal cognition as valuable tools for hypotheses testing and generation.

2 Core and Higher-level Cognitive Processes in the LIDA model

The LIDA model is a comprehensive, conceptual and computational model covering a large portion of cognition in humans and other animals. It is largely based on Baars’ Global Workspace Theory (GWT) (Baars, 1988), a conceptual theory of the role of consciousness1 in cognition. Besides GWT, the LIDA model implements and fleshes out a number of psychological and neuro-psychological theories including situated and grounded cognition (Barsalou, 2008; Varela et al., 1991), perceptual symbol systems (Barsalou, 1999), working memory (Baddeley and Hitch, 1974), memory by affordances (Glenberg, 1997), long-term working memory (Ericsson and Kintsch, 1995), and Sloman’s H-CogAff cognitive framework (Sloman, 1999).

The LIDA model includes a broad array of modules, processes, and computational mechanisms, and detailed descriptions of these components is beyond the scope of this paper. We do not see this as a serious concern because the goal of the present paper is not to apply LIDA to systematically model the cognitive system of one specific animal (e.g., as in the case of the virtual vole described in Franklin and Ferkin, 2008). A detailed description of the nuts and bolts of the model would be essential for such an endeavor. Instead, our main focus is on applying LIDA’s ontology as one approach to start organizing the animal cognition literature. As such, brief descriptions of the critical modules and processes are described. We begin by describing the core cognitive processes of the model, followed by a specification derived from the LIDA model on how these processes interact in a cycle that spans a few hundred milliseconds, and across multiple cycles that span several seconds (higher level cognitive processes).

2.1 Core cognitive processes

The core cognitive processes are likely to be shared with most cognitive architectures. These processes are described in the most general terms, instead of LIDA-specific jargon, in order to facilitate accessibility to a wide interdisciplinary audience. Details on how these core processes are implemented in LIDA are available in previous publications (Baars and Franklin, 2007; Negatu et al., 2007; Wallach et al., 2010).

Sensation The process by which input is received from the environment by sensory receptors and stored in short term sensory memory such as iconic memory (for vision) (Coltheart, 1980).

Perception and Perceptual Memory An integrated perceptual system is essential for any animal in order for it to recognize, categorize, understand, and integrate information about its world. Perception is the ability to interpret incoming stimuli by recognizing individuals or events, by categorizing them, and by noting relationships between such individuals, events and categories. Perception is ubiquitous among animal species, as is the learning of these facilities (Bitterman, 1965). As we interact with our worlds, or perceptual knowledge bases (perceptual memory) need to be updated in order to facilitate the future recognition of new entities (i.e., a new face or a new object). Perceptual learning is learning to recognize new objects, categorizations, relationships, and events, and to more effectively recognize old ones.

Declarative memories: episodic & semantic memory Episodic memory is a potentially long-term memory for the what, when, and where of events. Episodic memories in humans are considered to be consciously experienced and “relived” from a first-person perspective (Tulving and Craik, 2000). In the animal cognition

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1 We focus on “attention” instead of “consciousness” in order to avoid a (sometimes nonproductive) debate on animal consciousness.
While episodic memory is associated with remembering, semantic memory is concerned with knowing (Wilson and Keil, 1999). Semantic memory is long term storage of world knowledge and, unlike episodic memory, the content of semantic memory is considered to be independent of personal experience or of any specific event. For example, a territorial animal may have semantic knowledge of the boundaries of its territory. There is also expected to be considerable overlap between information stored in the perceptual and semantic memory systems.

**Working Memory (or Workspace)** Working memory is the manipulable scratchpad of the mind (Miyake and Shah, 1999). It holds sensory data, both endogenous (for example, imagined visual images and inner speech in humans) and exogenous (sensory), together with their interpretations. Its decay rate is measured in tens of seconds. Separate working memory components are associated with the different senses. Working memory in humans is believed to consist of (a) a visiospatial sketchpad for visual information, (b) a phonological loop for auditory information, (c) a central executive for binding, coordination, attention (see below), and task-sharing, and (d) an episodic buffer for the integration and short-term storage of verbal, visual, spatial, and temporal information (Baddeley, 2000; Baddeley and Hitch, 1974). Also, there are long-term processing components of working memory (Ericsson and Kintsch, 1995). It has been suggested that conscious input, rehearsal, and retrieval are necessary for the normal functions of working memory in humans (Baars and Franklin, 2003); we make no such claim for the present analysis of animal cognition.

**Selective attention** Humans and many animals gain evolutionary advantages from multiple sensory systems. These systems can sometimes burden efficient action selection due to vast amounts of data produced during interactions in their complex, dynamical environments. There is often too much information to attend to at once. In these situations, selective attention provides access to appropriately useful internal resources, thereby solving the relevance problem, that is, the problem of identifying those internal resources that are relevant to action selection in the current situation (Baars, 1988; 1997).

**Action selection and procedural memory** Deciding “what to do next” is essential for any animal or human (Franklin, 1995). An animal must utilize the information it perceives in order to select an effective action in service of its goals or drives. This is accomplished via action selection, where the attentional contents are used to select an appropriate action in service of goals, drives, and environmental opportunities. Procedural memory is the memory system that tracks what actions can be expected to achieve what results in a particular context. It also organizes actions into parallel groups for simultaneous action (e.g., clenching a fist) and ordered sequences for sequential processing (e.g., a mating ritual).

**Action Execution** A chosen action is executed by an appropriate mechanism. This process involves (mostly unconscious in humans) rapid sensory-motor coordination.

### 2.2 The cognitive cycle

A model based on several specialized mechanisms, each implementing various facets of cognition, requires an iterative process to bring about the functional interaction among the various components. In LIDA, this is accomplished with the cognitive cycle. Every autonomous agent (Franklin and Graesser, 1997), human, animal, or artificial, must frequently sample (sense) its environment and select an appropriate response (action). Animals, such as humans and very likely many other species, process (make sense of) the input from such sampling in order to facilitate their action selection and make it more effective. The animal’s life can be viewed as consisting of a continually iterated sequence of these cognitive cycles. Each cycle consists of three phases, an understanding phase (sensation, perception, working memory), an attending phase (working memory and attention), and an action phase (action selection and execution). This cycle is commonly referred to as the action-perception cycle (Freeman, 2002; Schoner et al., 1998). As will be described below, higher-level cognitive processes are composed of many of these cognitive cycles.

**Understanding** The cycle begins with sensory stimuli from sources in the animal’s external and internal environment being intercepted in sensory memory. Low-level feature detectors in sensory memory begin the process of making sense of the incoming stimuli; for example, detecting spatial frequencies in the striate cortex (Hubel and Wiesel, 1959; Silverman, Grosorof et al., 1989). These low-level features are passed on to per-
ceptual memory where higher-level features, such as objects, categories, relations, events, etc., are recognized. These recognized entities, the percepts, are passed to working memory, where a model of the animal’s current situation is assembled.

This percepts serves as a cue to episodic memories. Responses to the cue consist of local associations, that is, remembered events from these two memory systems that were associated with the various elements of the cue. A new model of the animal’s current situation is assembled from the percepts (from perception) and associations (from episodic memory). The newly assembled model constitutes the animal’s understanding of its current situation within its world. For example, a male meadow vole might sniff a scent mark (sensation), categorize it as a female in postpartum estrus (Ferkin and Johnston, 1995), a highly sexually receptive state (perception), and retrieve a memory of a previous violent encounter with this particular female (episodic-like memory) (Ferkin et al., 2008).

**Attending** For an animal operating within a complex, dynamically changing environment, this current model may well be much too rich for the animal to consider all at once in deciding what to do next. It needs to selectively attend to a portion of its current situational model. Portions of the model compete for attention. These competing portions take the form of coalitions of structures from the model. One of the coalitions wins the competition. In effect, the animal has decided on what to attend. The contents of the winning coalition are then broadcast globally, completing the attending phase of the cycle. Continuing with our example of the meadow vole, it might choose to attend to the fact that the female is in postpartum estrus, which would suggest approaching this female or the retrieved memory of the aggressive encounter with this female, which might suggest avoidance.

**Action** The purpose of all this processing is to help the animal choose what to do next. Though the contents of this attentional broadcast are available, and used, globally, the primary recipient is procedural memory, which stores templates of possible actions including their contexts and possible results. Templates whose contexts intersect sufficiently with the contents of the attentional broadcast are instantiated and passed to the action selection mechanism, which chooses a single action from one of these instantiations. The chosen action is then executed. The action taken affects the environment, outer or inner, and the cycle is complete.

### 2.3 Higher-level cognitive processes

The LIDA model hypothesizes that all human, as well as much of animal, cognitive processing is via a continual iteration of such cognitive cycles. These cycles occur asynchronously; with each cognitive cycle taking roughly 300 ms. The cycles can cascade, that is, several cycles may have different processes running simultaneously. This cascading, together with the asynchrony, allows a rate of cycling in humans of five to ten cycles per second. A cognitive “moment,” that is a single cycle, is thus quite short! There is considerable empirical evidence from neuroscience suggestive of, and consistent with, such cognitive cycling in humans (Doesburg et al., 2009; Freeman, 2002; Fuster, 2004; Massimini et al., 2005; Sigman and Dehaene, 2006; Uchida et al., 2006; Willis and Todorov, 2006).

Higher-level cognitive processing in humans includes categorization, deliberation, volition, metacognition, reasoning, planning, problem solving, language comprehension, and language production. Many of these also occur in other animals as will be described in the next section. In the LIDA model cognitive cycles are the atoms out of which higher-level cognitive processes are built. Each of the higher-level cognitive process is a multi-cyclic process that can be implemented over multiple cognitive cycles. Some of these processes are described below.

**Deliberation** Deliberation refers to such activities as planning, deciding, scheduling, etc., that require one to volitionally attend to an issue (Franklin, 2000). Suppose one wants to drive from a new location in a city one is familiar with to the airport. This is a new route so one might imagine landmarks along the way, which turns to take and so, deliberate about how best to get there. In a deliberative process, options may be constructed and evaluated, and plans created. This process can be thought of as using an internal simulation of interaction with the environment, in the service of decision making, problem solving or planning.

**Problem solving** Procedural Memory consists of templates for actions that can be selected under the appropriate conditions. For example, an animal might choose to drink water from a puddle if (a) it is thirsty, (b) water is nearby, (c) there are no predators in sight, etc. However, when confronted with novel situations, for example, a barrier is preventing access to the puddle there might not be any templates or procedures that can be utilized. An impasse is reached (Laird, Newell and Rosenbloom, 1987) and (non-routine) problem solving would be required to construct a plan to resolve the im-
not of metacognition. Volitional decision making Suppose that, being thirsty one morning, one consciously considered the possibilities of coffee, tea, and orange juice, weighing the advantages and disadvantages of each, in a form of internal dialogue that does not have to involve language. Eventually deciding to drink coffee is a volitional decision.

Metacognition Defined as thinking about thinking, metacognition, is a complex high-level cognitive process. For example, one might reflect on one’s actions and decisions and choose alternate action sequences. Knowing what one knows, a metamemory, is another metacognitive facility, that might be present in some species such as tufted capuchin monkeys (Basile et al., 2009; Fujita, 2009). It should be noted that self-consciousness is sometimes, erroneously we think, said to be a form of metacognition. Going back to at least the work of Gallup (1970), the study of self-consciousness in animals rests largely on the mirror test, which is a question of perception or recognition, not of metacognition.

3 Towards A Common Framework to Integrate Diverse Research in Animal Cognition

Having provided a high-level description of the LIDA model, we now focus on providing the beginning stages of a mapping between the core and high-level processes, and the animal cognition literature. Table 1 lists a number of studies that provide evidence for some of the core cognitive processes in a number of diverse animal species. A similar table, but with an emphasis on higher-level cognitive facilities, is presented as Table 2. In both tables, the animal kingdom is divided into mammals and non-mammals. Within the non-mammals, we consider insects, other invertebrates like cephalopods, and avians, while rodents, canids, and non-human primates represent the mammals. These tables were constructed by cursorily surveying the recent literature on animal cognition. Our survey primarily focused on recent (within three years) articles from the journal Animal Cognition, although less recent articles from this and other journals are included as well.

It is important to highlight four important points with respect to these tables. First, the tables are not intended to serve as a comprehensive review of the animal cognition literature, but mainly as an initial step towards highlighting similarities among different species within the framework of one cognitive model (i.e., LIDA). Alternate tables can be constructed by utilizing alternate cognitive models as reference points and/or by expanding the list of animal species. Second, both tables are intentionally incomplete. Empty cells do not indicate that there is no evidence that a particular species does not possess a certain cognitive ability. Instead, empty cells simply indicate that we have not provided any evidentiary examples. Importantly, some facets of animal cognition, such as spatial cognition, navigation, tool use, and social relationships, have received considerable attention in the literature and are not covered here. Third, in constructing these tables, we have not attempted to critique the authors’ experimental protocols or reinterpret their conclusions. A critical examination of the literature might be more appropriate for a review or survey paper, and is beyond the intention and scope of this brief overview of some of the recent animal cognition literature. Fourth, each table is intended to give a glimpse of how a cognitive model like LIDA could be used to organize an ongoing, comprehensive database of the animal cognition literature. A record in such a database would have the form (cognitive process, species, and references) where the references would speak to how that species is known to exhibit that cognitive process or not.

3.1 Core cognitive processes

Table 1 does not include any citations for sensation and action execution because it is assumed that most animals can sense and act on their environments. Any animal that would fall into the reactive category (described in the higher-level cognitive processing section below) would have the capacity to sense and act, irrespective of how impoverished or limited their sensory and action capabilities might be.

Considerable evidence also indicates that most animals can perceive and categorize objects in their environment. Animals of all sorts can identify food sources, potential mates, potential predators, etc. Pigeons have been taught to categorize using such concepts as tree, fish, and human, some well outside of their evolutionary background (Herrnstein and Perrett, 1985). Honey bees have been taught to identify human letters independently of size, color, position or font (Gould, 1990). An African grey parrot can identify such features as size, number, color, and material of objects or sets of objects that it has never been seen before (Pepperberg, 1990).

On the basis of the examples listed in Table 1, it is reasonable to conclude that most animals do have some form of perceptual or recognition memory system.

As behavior complexity increases, an animal must...
construct, maintain, and manipulate an internal representation of its world. Simply put, it needs a working memory. As Table 1 indicates, there is evidence that suggests that several animal species have some form of working memory. For example, the ability to perform an immediate serial recall (ISR) task, where a participant is presented with a list of items and is required to recall them after encoding, is a hallmark of human working memory. Recent evidence indicates that rhesus macaque’s were able to perform a spatial ISR task (Botvinick et al., 2009), thereby providing some evidence for a short-term memory system that resembles human working memory. Another source of evidence in support of a working memory emerges from research on target tracking in dogs (Kundey et al., 2010). Here, dogs are required to track a moving object, which involves creating a representation of the object in (working) memory and generating predictions about its future position, a feat that would be difficult without some sort of working memory.

From Clayton and colleagues landmark study on Western scrub-jays *Aphelocoma californica* (Clayton and Dickinson, 1998; Salwiczek et al., 2010) to Ferkin et al.’s. (2008) more recent study on meadow voles, considerable evidence suggests that several animal species do have the ability to encode and recall information about the what, where, and the when (episodic-like memory). While many insects might not need an episodic-like memory system, as behavioral complexity increases, there is an evolutionary advantage to remembering events from an animal’s past. For example, most non-human animals do not mate unless they are in a heightened state of sexual receptivity (Bronson, 1989), and in several cases, they live separately from their mates. Ferkin et al. (2008) argue that, when mating season arrives, males will benefit from an episodic-like memory in order to identify the females that are in a state of sexual receptivity (i.e., the what), their location (i.e., the where), and should also have some estimate of the length of time they expect the females to sustain that state (i.e., the when).

There is also evidence that suggests that some animal species are able to selectively attend to aspects of their environment. Chimpanzees, for example, can use tools, learn signs and symbols, and generally meet several criteria for intelligence. Attention is a necessary (but not sufficient) condition for these types of learning tasks (Baars and Franklin, 2003). Beyond non-human pri-

mates, emerging evidence also suggests that dogs are quite capable of attending to particular aspects of their environments (Horowitz, 2009). For example, Mongillo and colleagues demonstrate that dog’s focused visual attention (longer gaze periods and overall more attention) on their owners compared to strangers, an effect which was influenced by age (Mongillo et al., 2010). On the other side of the spectrum, octopi have been shown to engage in impressive learning tasks, such as observational learning (Fiorito and Scotto, 1992), which intrinsically requires selective attention.

Finally, as Table 1 indicates, with the exception of animals that simply react to stimuli without requiring any form of internal representations of their worlds, most animals select actions in service of drives and environmental opportunities. An excellent example of primitive action selection can be found in one of the most primitive species, the earthworm. In his extensive study of earthworms, described in his 1881/1885 book, and summarized by Crist (2002), Darwin concluded that earthworm behavior, particularly with respect to their ability to handle leaves while plugging burrows would require some form of action selection. This is because “grasping” actions were sensitive to the affordances of the leaves in remarkably sophisticated ways. Furthermore, these behaviors could not be readily explained by mere instinct because similar complexities of behavior were observed for non-native leaves (Darwin, 1881/1895). As succinctly stated by Crist (2002), “There was something more” (2002, pp.7).

### 3.2 Higher-level cognitive processes and levels of control

Table 2 lists several examples of higher-level cognitive processes. Rather than describing each process individually, it is useful to group these under the broad umbrella of levels of control. Sloman distinguishes three levels that can be implemented by an autonomous animal -- the reactive, the deliberative, and the metacognitive1 (Sloman, 1999). The first of these, the reactive, is the level we would typically expect of many insects, that is, a relatively direct connection between incoming sensory data and the outgoing actions of effectors. The key point is the relatively direct triggering of an action once the appropriate environmental situation occurs. Note that, though direct, such a connection can be almost arbitrarily intricate, requiring quite complex algorithms to implement in an artificial animal.

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1 Sloman speaks of meta-management rather than metacognition. We prefer the more common psychological term.
<table>
<thead>
<tr>
<th>Process</th>
<th>Non-mammals</th>
<th>Insects</th>
<th>Avians</th>
<th>Rodents</th>
<th>Canids</th>
<th>Non-human primates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sensation</td>
<td>–</td>
<td>–</td>
<td>–</td>
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</tr>
<tr>
<td>Perception</td>
<td>American lobster (Gherardi et al., 2010)</td>
<td>mosquito, honeybee (Avargues-Weber, et al., 2010; Gibson et al., 2010)</td>
<td>king penguin, Bengalese finche, tit (Lengagne et al., 2001; Suge and Okano, 2010; Tvardikova and Fuchs, 2010)</td>
<td>social rodent (Octodon degus), meadow vole (Fuchs et al., 2010; Vlautin et al., 2010)</td>
<td>domestic dog (Racca et al., 2010)</td>
<td>black tufted-ear marmoset, wild chimpanzee, rhesus macaque monkey (Emile and Barros, 2009; Girard et al., 2008; Slocombe et al., 2009)</td>
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<tr>
<td>Working Memory (excluding consciousness)</td>
<td>octopus (Mather, 2008)</td>
<td>honeybee (Menzel, 2009; Zhang et al. 2005)</td>
<td>Pigeon (Karakuyu et al., 2007)</td>
<td>rat, common voles, bank voles (de Saint Blanquat et al., 2010; Haupt et al., 2010)</td>
<td>domestic dog (Kundey et al., 2010)</td>
<td>rhesus macaque (Botvinick et al., 2009; Treichler and Raghanti, 2010)</td>
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<tr>
<td>Episodic-like Memory</td>
<td>octopus (Mather, 2008)</td>
<td>black-capped chickadee, scrub jay (Clayton and Dickinson, 1998; Feeney et al., 2009)</td>
<td>mice, meadow vole (Dere et al., 2005; Ferkin et al., 2008)</td>
<td>orangutan, bonobo (Martin-Ordas et al., 2010)</td>
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<tr>
<td>Attention</td>
<td>octopus (Mather, 2008)</td>
<td>bobwhite quail, pigeon (Jaime et al., 2009; Wilkinson and Kirkpatrick, 2009)</td>
<td>domestic dog (Horowitz, 2009; Mongillo et al., 2010)</td>
<td>Chimpanzee (Tomonaga and Imura, 2009)</td>
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<tr>
<td>Action Selection (Decision Making)</td>
<td>portia labiata, earthworms (Crist, 2002; Jackson, Pollard, Li and Fijn, 2002)</td>
<td>honeybee (Naug and Arathi, 2007; Zhang et al., 2005)</td>
<td>common cuckoo (Moskat and Hauber, 2007)</td>
<td>domestic dog (Gacsi et al., 2009)</td>
<td>Macaca tonkeana, Macaca mulatta (Sueur and Petit, 2010)</td>
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<tr>
<td>Action Execution</td>
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Table 2  Examples of higher-level cognitive processes across animal species

<table>
<thead>
<tr>
<th>Process</th>
<th>Other Invertebrates</th>
<th>Insects</th>
<th>Avians</th>
<th>Rodents</th>
<th>Canids</th>
<th>Mammals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deliberation</td>
<td>jumping spider</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>wild bearded capuchin monkey (Fragaszy et al., 2010)</td>
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<td></td>
<td>(Tarsitano, 2006; Wilcox et al., 1996)</td>
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<tr>
<td>Problem Solving</td>
<td>Octopus</td>
<td>leafcutting ant</td>
<td>blue-fronted parrot, neotropical parrots(^a) (de Mendonca-Furtado and Ottoni, 2008; Schuck-Paim et al., 2009)</td>
<td></td>
<td>dingo, wolves and dogs (Frank and Frank, 1982; Smith and Litchfield, 2010)</td>
<td>capuchin, gorilla(^b) (Martin-Ordas et al., 2008; Yocom and Boysen, 2010)</td>
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<td></td>
<td>(Moriyama and Gunji, 1997)</td>
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<tr>
<td>Planning</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>wild capuchin monkey, chimpanzee, orangutan (Janson, 2007; Osvath, 2010; Osvath and Osvath, 2008)</td>
</tr>
<tr>
<td>Numerosity</td>
<td>yellow mealworm beetle</td>
<td>Honeybee (Dacke and Srinivasan, 2008)</td>
<td>pigeons (Emmerton and Renner, 2009; Xia et al., 2001)</td>
<td></td>
<td></td>
<td>rhesus monkeys, chimpanzee (Beran, 2010; Livingstone et al., 2010)</td>
</tr>
<tr>
<td>Metacognition</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>tufted capuchin monkeys, rhesus monkey (Basile et al., 2009; Fujita, 2009; Smith et al., 2010)</td>
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<tr>
<td>Proto-self or Minimal-Self</td>
<td>sierra dome spider (Keil and Watson, 2010)</td>
<td>meadow vole (Vlautin et al., 2010)</td>
<td></td>
<td></td>
<td></td>
<td>chimps, cotton-top tamarins (Gallup, 1970; Hauser et al., 1995)</td>
</tr>
</tbody>
</table>

\(^{a}\)blue-fronted amazons, hyacinth and lear’s macaws. \(^{b}\)gorilla gorilla, pan troglodytes, pan paniscus, and pongo pygmaeus
The reactive level is perhaps best defined by what it’s not. “What a purely reactive system cannot do is explicitly construct representations of alternative possible actions, evaluate them and choose between them, all in advance of performing them” (Sloman, 1999). Reactive control alone is particularly suitable for animals occupying relatively simple niches in reasonably stable environments, that is, for animals requiring little flexibility in their action selection. Such purely reactive animals typically require relatively few higher-level, multi-cyclic cognitive processes, although this is not entirely outside of the realm of possibilities as documented by the complex navigation behavior of honey bees (Gould, 1990; Menzel and Giurfa, 2001).

On the other hand, deliberative control typically employs such higher-level cognitive processes as planning, scheduling, and problem solving. Such deliberative processes in humans, and perhaps in some other animals, are typically performed in an internally constructed virtual reality (i.e., a representation of aspects of the world might be needed). Such deliberative information processing and decision making allows an animal to function more flexibly within a complicated niche in a complex, dynamic environment. An internal virtual reality for deliberation requires a short-term working memory in which temporary structures can be constructed with which to “mentally” try out possible actions without actually executing them. In many cases, the action selected during almost all cognitive cycles consists of building or adding to some representational structures in working memory during the process of some sort of primitive deliberation. Sub-processes that create such structures modify or compare them, etc., are typically implemented as internal reactive processes. Deliberation builds on reaction. A likely animal example of deliberation is the jumping spider Portia fimbriata stalking its prey by making a lengthy detour around and above the prey, and losing sensory contact with the prey for a significant time period, before sighting the prey again and descending on it from above and behind (Wilcox et al., 1996).

As deliberation builds on reactions, metacognition typically builds on deliberation. Sometimes described as “thinking about thinking,” metacognition in humans and animals involves monitoring deliberative processes, allocating cognitive resources, and regulating cognitive strategies (Flavell, 1979; Smith and Washburn, 2005). Metacognitive control adds yet another level of flexibility to an animal’s decision making, allowing it to function effectively in an even more complex and dynamically changing environmental niche. Although there is reasonable skepticism about the possibility of metacognition in animals, Beran and colleagues make a compelling case for some form of metacognition via uncertainty monitoring in rhesus monkeys Macaca mulatta (Smith et al., 2010).

4 Conclusions

Cognitive models of human or animal cognition intrinsically need to traverse several levels of biological complexity. At the highest level one considers models of entire organisms and computer and robotic simulation of virtual animals (Webb, 2003). At one step lower, one encounters higher-level cognitive processes such as deliberation, volition, automization, non-routine problem solving, planning, and social cognition. These higher-level cognitive processes operate at temporal scales of a few seconds. Still lower one finds cognitive modules and processes that operate within a few hundred milliseconds. These lower-level processes include perception, categorization, various forms of memory, attention, learning, action selection, and action execution. At yet a lower level, one might consider modeling activities within a single low-level process. For example, one could consider modeling the process of recognition, how actions are selected in the service of motivations or drives, or how memories are encoded and retrieved, and so on. It is important to understand the dynamics of several levels of living systems by spanning these various levels of theoretical complexity.

The present paper focuses on two levels of processes: specifically core processes that span a few hundred milliseconds, such as perception, action selection, etc. and higher-level cognitive processes that arise from complex interactions between the core processes, such as planning, deliberation, and navigation. Furthermore, we focus on one cognitive model, namely LIDA, and a relatively coarse and restricted set of animal species. A useful next step would be to consider alternate models of cognition such as SOAR (Laird et al., 1987), ACT-R (Anderson and Lebiere, 1998), CAPS (Just and Carpenter, 1992; Just and Carpenter, 1987), CLARION (Helie and Sun, 2010; Sun et al., 2005), EPAM (Feigenbaum and Simon, 1984), EPIC (Meyer and Kieras, 1997a; Meyer and Kieras, 1997b), and Icarus (Langley et al., 1991). Using more refined taxonomies of the animal kingdom and expanding Tables 1 and 2 will ostensibly yield a sufficiently large ontology of animal cognition that will support generalizations both within and across species. They can be expanded still further into the kind
of searchable database of the animal cognition literature described above.

It is important to conclude this article by providing some thoughts on how computational models of animal cognition can be used to bridge the gap between the models of entire organisms micro-theories of core processes levels of biological complexity. In general, contemporary research on animal cognition is typically functional in nature and often mathematical (primary for models of human cognition). Functional models of animal cognition are intended to both explain cognitive processes and predict their functionality, that is, what can be expected to happen under various conditions. Although these functional models are useful, even essential, to understand animal cognition, they do not reliably yield insight into the underlying mechanisms of the cognitive processes. On the other hand, computational models of cognition are mechanistic in nature. That is, they provide a theory that specifies the mechanism, such as connectionism, Bayesian inference, dynamical systems, symbolic systems, and cognitive architectures, which underlies various cognitive phenomena. Such computational mechanisms can suggest possible biological mechanisms to be explored and, thus, guide research into animal cognition.

Hence, we advocate studying animal cognition by means of computational control architectures based on biologically and psychologically inspired, broad, integrative, hybrid models of cognition such as the LIDA model we described. Using such a model, experiments with animals can be replicated in artificial environments via computer simulations of virtual animals controlled by such cognitive architectures. The cognitive architecture of the virtual animal would functionally model the cognitive processes of the animal being experimented with. The computational architecture is essentially the same model acting through the underlying mechanisms. The computational architecture yields insight into the mechanisms underlying the cognitive process of the animal. The in vivo animal experiments together with the in silico virtual experiments serve to test both the functional model and the computational model. Both the high-level functional model and the underlying computational model can then be brought more in line with the results of these experiments. After alterations to the agent suggested by the new version of the architecture are made, new experiments can be designed and carried out to test the current version. The amalgamated theorize→experiment→theorize cycles of experimental science and computational modeling continues.

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