University of Memphis

University of Memphis Digital Commons

CCRG Papers

Cognitive Computing Research Group

2008

Using Broad Cognitive Models and Cognitive Robotics to Apply Computational Intelligence to Animal Cognition

S. Franklin

M. Ferkin

Follow this and additional works at: https://digitalcommons.memphis.edu/ccrg_papers

Recommended Citation

Franklin, S., & Ferkin, M. (2008). Using Broad Cognitive Models and Cognitive Robotics to Apply Computational Intelligence to Animal Cognition. Retrieved from https://digitalcommons.memphis.edu/ ccrg_papers/80

This Document is brought to you for free and open access by the Cognitive Computing Research Group at University of Memphis Digital Commons. It has been accepted for inclusion in CCRG Papers by an authorized administrator of University of Memphis Digital Commons. For more information, please contact khggerty@memphis.edu.

For Applications of Computational Intelligence in Biology: Current Trends and Open Problems, Tomasz G. Smolinski, Mariofanna M. Milanova, Aboul-Ella Hassanien, editors

To be published by Springer-Verlag in the series "Studies in Computational Intelligence"

Using broad cognitive models to apply computational intelligence to animal cognition

Stan Franklin¹ and Michael H. Ferkin² The University of Memphis, Institute of Intelligent Systems, Fed Ex Institute of Technology¹ and Department of Biology², Ellington Hall, Memphis, TN 38152 USA

Abstract

The field of animal cognition (comparative cognition, cognitive ethology), the study of cognitive modules and processes in the domain of ecologically relevant animal behaviors, has become mainstream in biology. The field has its own journals, books, organization and conferences. As do other scientists, cognitive ethologists employ conceptual models, mathematical models and sometime computational models. Most of these models, of all three types, are narrow in scope, modeling only one or a few cognitive processes. This position chapter advocates, as an additional strategy, studying animal cognition by means of computational control architectures based on biologically and psychologically inspired, broad, integrative, hybrid models of cognition. The LIDA model is one such model. In particular, the LIDA model fleshes out a theory of animal cognition, and underlies a proposed ontology for its study. Using the LIDA model, animal experiments can be replicated in artificial environments by means of virtual software agents controlled by such architectures. Given sufficiently capable sensors and effectors, such experiments could be replicated in real environments using cognitive robots. Here we explore the possibility of such experiments using a virtual or a robotic vole to replicate, and to predict, the behavior of live voles, thus applying computational intelligence to cognitive ethology.

Introduction

The analysis of animal behavior cannot be complete without an understanding of *how* behaviors are selected, that is, without the study of animal cognition (Allen 1997; Kamil 1998; Boysen and Himes 1999; Byrne and Bates 2006). The study of cognitive modules and processes in the domain of ecologically relevant animal behaviors (cognitive ethology) has become an exciting research area in biology. The field has its own journals (e.g., *Animal Cognition*), books (e.g., Bekoff *et al.*,

2002), organization (Comparative Cognition Society) and conferences (e.g., 2006 Comparative Cognition Society Annual Meeting, Melbourne, FL).

As do other scientists, cognitive ethologists employ conceptual models (e.g., Allen 1997), mathematical models (e.g., Alsop 1998; Kruschke 2001) and sometime computational models (e.g., Saksida 1999). Most of these models, of any of the three types, are narrow in scope, modeling only one or a few cognitive processes. In contrast to these models, empirical studies of how animal behaviors are selected should be guided by comprehensive theories and integrated conceptual models. While grounded in the underlying neuroscience and consistent with it, these theories and models must be conceptually at a higher level of abstraction, dealing with higher-level entities and processes.

This position chapter advocates studying animal cognition by means of computational control architectures based on biologically and psychologicallyinspired, broad, integrative, hybrid models of cognition. Using such a model, experiments with animals could be replicated in artificial environments with virtual software agents controlled by such architectures. Given sufficiently capable sensors and effectors, such experiments could be replicated in real environments using cognitive robots. The LIDA (Learning Intelligent Distribution Agent) model provides just the kind of broad, integrated, comprehensive, biologically and psychologically inspired theory that is needed. In particular, the LIDA model can model animal cognition, and underlies a proposed ontology for its study (Franklin and Ferkin 2006).

Software agents in robotic simulators as virtual animals

Autonomous agents (Franklin and Graesser 1997) are systems embedded in, and part of, an environment that sense their environment and act on it, over time, in pursuit of their own agenda. In addition, they must act so as to potentially influence their future sensing, that is, they must be structurally coupled to their environment (Maturana 1975; Maturana and Varela 1980). Biological autonomous agents include humans, other animals and viruses. As well as computer viruses and some robots, artificial autonomous agents include *software agents*, that is, agents that "live" in computer systems, in databases, or in networks. The "bots" that autonomously explore the internet indexing web pages for Google are examples of software agents. Artificial autonomous agents also include cognitive robots (Clark and Grush 1999; Asada *et al* 2001; Franklin 2005b).

Robotic simulators are software tools offering often 3D modeling, simulation and animation of any physical system. They are particularly designed as virtual environments for simulations of robots, hence the name. Examples include ARS MAGNA, RoboWorks, Rossum's Playhouse, Khepera Simulator, and very many others. Within such an abstract, virtual world with its own physics, a simulated robot can both sense and act so that it becomes an autonomous software agent. Such a simulated robot typically has a simulated body within the robot simulator.

Modeling such a simulated robot "living" within a robotic simulator after an animal, say a meadow vole, creates an *artificial animal* software agent. The simulator, thought of as the artificial animal's environment, can be made to

contain objects of various sorts, including other agents. Such objects can have simulated weight, rigidity and other realistic physical properties. Such other agents can be made to behave in a relatively realistic manner, as for example do the various agents that occur in video games. An artificial animal (AA) can sense this environment via artificial sights, sounds, odors, touches, tastes, etc., corresponding to the senses available to the animal (robot). AA's artificial effectors can manipulate artificial objects, including itself, in rather realistic ways as compared to a real robot, and in a more or less realistic manner as compared to an animal.

Behavioral experiments with animals typically may involve some sort of structure, such as a runway with two chambers at its end, or a maze. This structure can be simulated within the artificial environment, the robotic simulator. AA's "body" can then be placed appropriately within the simulated structure, an artificial run of the experiment carried out, and data gathered as to how AA responded to the experimental situation in terms of location, action, timing, etc. Repeated artificial runs will allow the virtual replication of the experiment and its dataset. Or, the virtual experiment can be run first. Its data would then predict the results of carrying out the experiment *in vivo*.

As any autonomous agent must, AA has a control structure that interprets its sensory input, selects an action according to its own agenda, and guides its actions on its environment. The computational architecture of any such AA control structure gives rise to a conceptual cognitive model, that is, a theory of how AA and the animal it simulates interprets its sensory data, and chooses and guides its actions. Conversely, any cognitive model can be implemented in a computational architecture that can be used to control AA. Thus, in principle, any scientific hypothesis that arises from the cognitive model can be tested using both a virtual experiment and an *in vivo* experiment.

Using such an experimental paradigm insures that the conceptual cognitive model that gives rise to the computational architecture of AA's control system will be broad and comprehensive. It must involve perception, which makes sense of sensory input. It must contain motivational elements and procedural memory with which to make action selections. Finally, it must include sensory-motor automatisms with which to execute actions. Such comprehensive cognitive models allow for the testing of a broader range of hypotheses than do more constrained models. They also enable more complete, and therefore more satisfactory, explanations of the cognitive processes responsible for the observed behavior. We contend that the adoption of such an experimental paradigm will result in significant advances in the way biological theory guides experimentation in animal behavior.

But there's more to the story. Computational architectures derived from integrated, comprehensive cognitive models are sure to be rife with internal parameters whose values must be tuned (discovered) before the system can perform properly as a control structure for AA. It is well known that a model with sufficiently many free parameters can be tuned so as to reproduce essentially any specific dataset. What is wanted is a tuned set of internal parameters whose values remain constant while a number of disparate datasets are reproduced. Such a tuned parameter set offers reassurance as to the accuracy and usefulness of the model. An inability to find such a tuned parameter set should warn its designers that something is amiss with the model, and that it needs revision. The particular parameters that resist such tuning point researchers to modules and process within the model that are likely to require revision.

But how are such parameters in a computational architecture to be tuned. The problem is essentially a search problem. Given the dataset from one previous in vivo experiment that the model should predict and explain, one searches for a set of parameter values that, when implemented, will allow AA to replicate this existing dataset. If found, this search procedure is iterated on the dataset of a second previously performed in vivo experiment resulting, hopefully, in a tuned parameter set that will allow the replication of both datasets. Further iteration of this procedure should, if the model is correct, yield a stable set of values for the internal parameters of the computational architecture that should work for replicating a number of different existing in vivo experiments. Thus, the replication of existing data sets from previously performed experiments will allow the tuning of internal parameters in the theoretical model. Parameters that resist such tuning over several different data sets indicate flaws in the model that must be repaired. This parameter tuning provides something like a metric for assessing the quality of a cognitive model as a basis for understanding the cognitive processes responsible for the behavior of AA.

In summary, a tuned version of the computational model will allow AA to successfully replicate essentially any simulatable experiment with the animal in question. Successfully accomplishing this goal will provide substantial evidence of the accuracy and usefulness of the conceptual cognitive model. Cognitive hypotheses from the model can then be tested by *in vivo* experiments with real animals to see if their data is predicted by running AA in the same experimental situations. If so, we will have shown the ability of the theoretical model to predict as well as to explain.

The authors propose that their LIDA cognitive model, to be described next, is an appropriate example of a broad, integrated, comprehensive model of the kind we are advocating. We have proposed this model previously as the source of a useful ontology for the study of animal cognition (Franklin and Ferkin 2006).

The LIDA cognitive model and its architecture

The LIDA model is a conceptual (and partially computational) model covering large portions of human and animal cognition. Based primarily on global workspace theory (Baars 1988), the model implements and fleshes out a number of psychological and neuropsychological theories including situated cognition (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 (1999) cognitive architecture. Viewed abstractly, the LIDA model offers a coherent ontology for animal cognition (Franklin and Ferkin 2006), and provides a framework in the sense of Crick and Koch (2003) that can serve to guide experimental research. Viewed computationally, the model suggests computational mechanisms that can underlie and explain neural circuitry.

The LIDA computational architecture, derived from the LIDA cognitive model, employs several modules motivated by computational mechanisms drawn from the "new AI." These include the Copycat Architecture (Hofstadter and Mitchell 1995), Sparse Distributed Memory (Kanerva 1988), the Schema Mechanism (Drescher 1991), the Behavior Net (Maes 1989), and the Subsumption Architecture (Brooks 1991).

The LIDA model and its ensuing architecture are grounded in the LIDA cognitive cycle. Every autonomous agent (Franklin and Graesser 1997), be it human, animal, or artificial, must frequently sample (sense) its environment, process (make sense of) this input, and select an appropriate response (action). Every agent's "life" can be viewed as pursuing a continual sequence of these cognitive cycles. Each cycle constitutes a unit of sensing, attending and acting. A cognitive cycle can be thought of as a moment of cognition, a cognitive "moment." Higher-level cognitive processes are composed of many of these cognitive cycles, each a cognitive "atom."

During each cognitive cycle (Baars and Franklin 2003; Franklin *et al.* 2005) the LIDA agent, be it animal or artificial, first makes sense of its current situation as best as it can. It then decides what portion of this situation is most in need of attention. Broadcasting this portion enables the agent to finally choose an appropriate action and execute it. Please note, that consciousness in the LIDA model refers to functional consciousness, which is the functional role of the mechanism as specified by Baars' (1988) global workspace theory. The LIDA model takes no position on the issue of phenomenal consciousness in animals.

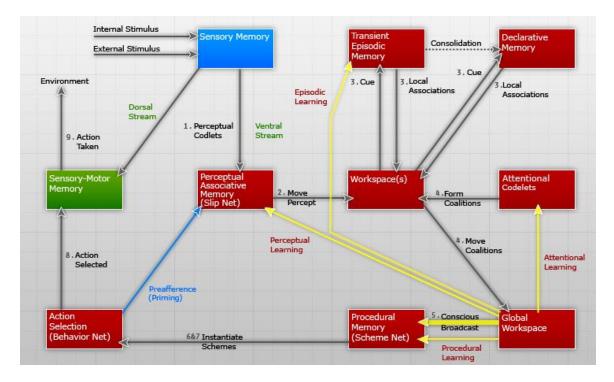


Figure 1. The LIDA Cognitive Cycle

The cycle begins with sensory stimuli from the agent's environment, both an external and an internal environment. Low-level feature detectors in sensory memory begin the process of making sense of the incoming stimuli. These lowlevel features are passed to perceptual memory where higher-level features, objects, categories, relations, situations, etc. are recognized. These recognized entities, comprising the percept, are passed to the workspace, where a model of the agent's current situation is continually being assembled and updated. The percept serves as a cue to two forms of episodic memory, transitive and declarative. The response to the cue consists of local associations, that is, remembered events from these two memories that were associated with elements of the cue. In addition to the current percept, the workspace contains recently previous percepts and the structures assembled from them that haven't yet decayed away. The model of the agent's current situation is assembled from the percept, the associations and the remaining previous models. This assembling process will typically require looking back to perceptual memory and even to sensory memory, to enable the understanding of relations and situations. This assembled new model constitutes the agent's understanding of its current situation within its world. It has made sense of the incoming stimuli.

For an agent "living" in a complex, dynamically changing environment, this current model may well be much too much for the agent to deal with at once. It needs to decide what portion of the model should be attended to. Which are the most relevant, important, urgent or insistent structures within the model? Portions of the model compete for attention. These competing portions take the form of coalitions of structures from the model. Such coalitions are formed by attention codelets, small, special purpose processors, each of which has some particular type of structure it wants to bring to consciousness. One such coalition wins the competition. The agent has decided on what to attend.

But, the purpose of all this processing is to help the agent decide what to do next. To this end, the winning coalition passes to the global workspace, the namesake of global workspace theory, from which its contents are broadcast globally. Though the contents of this conscious broadcast are available globally, the primary recipient is procedural memory, which stores templates of possible actions including their contexts and possible results. It also stores an activation value for each such template that attempts to measure the likelihood of an action taken within its context producing the expected result. Templates whose contexts intersect sufficiently with the contents of the conscious broadcast instantiate copies of themselves with their variables specified to the current situation. These instantiations are passed to the action selection mechanism, which chooses a single action from these instantiations and those remaining from previous cycles. The chosen action then goes to sensory-motor memory, where it picks up the appropriate algorithm (sensory-motor automatism) by which it is then executed. The action taken affects the environment, and the cycle is complete.

There are neural correlates for each of the modules and processes included in the LIDA cognitive cycle. For each such module or process, there is experimental data supporting these correlations. The LIDA model hypothesizes that in all animals, including humans, cognitive processing is via a continuing iteration of such cognitive cycles. These cycles occur asynchronously, with each cognitive cycle taking roughly 200 ms in humans and closely related primates. The cycles cascade, that is, several cycles may have different processes running simultaneously in parallel. This cascading must, however respect the serial order of consciousness in order to maintain the stable, coherent image of the world with which consciousness endows us (Franklin 2005a; Merker 2005). This cascading, together with the asynchrony, allows a rate of cycling in humans of five to ten cycles per second. A cognitive "moment" is quite short! There is considerable empirical evidence from neuroscience suggestive of such cognitive cycling in humans and closely related primates (Massimini *et al.* 2005; Sigman and Dehaene 2006; Uchida *et al.* 2006; Willis and Todorov 2006). None of this evidence is conclusive.

Global workspace theory postulates that learning requires only attention (Baars 1988). In the LIDA model this implies that learning must occur with each cognitive cycle. More specifically, learning occurs with the conscious broadcast from the global workspace during each cycle. Learning in the LIDA model follows the established artificial intelligence principle of 'generate and test (Winston 1992; Kaelbling 1994). New representations are learned in a profligate manner during each cognitive cycle (the generation). Those that are not sufficiently reinforced during subsequent cycles (the test) decay away. Three modes of learning, perceptual, episodic and procedural, employing distinct mechanisms (Nadel 1992, Franklin *et al.* 2005) have been designed and are in various stages of implementation. A fourth mode of learning is attentional learning, which has been contemplated but not designed.

Perceptual learning enables an agent to recognize features, objects, categories relations, situations, etc. It seems to be ubiquitous in animals. Episodic learning refers to the memory of events, the what, the where and the when (Tulving 1983, Baddeley *et al.*2001). In the LIDA model such learning is stored in transient episodic memory (Conway 2002; Franklin *et al.* 2005) and in the longer-term declarative memory (Franklin *et al.* 2005). At least episodic-like memory, that is episodic memory with no assumption of consciousness, has been demonstrated in many animal species (Dere *et al.* 2006) including meadow voles (Ferkin *et al. in press*). Procedural learning refers to the learning of new tasks and the improvement of old tasks. In the LIDA model such learning is accomplished in procedural memory (D'Mello *et al.* 2006b). Such procedural learning is widely observed in animal species (e.g., Foote *et al.* 2006).

Every autonomous agent must be equipped with primitive motivators, sometimes called drives that motivate its selection of actions. In humans, in animals, and in the LIDA model, these drives are implemented by feelings (Franklin and Ramamurthy 2006). Such feelings implicitly give rise to values that serve to motivate action selection. Feelings also act as modulators to learning.

The LIDA theoretical model traverses several levels of biological complexity within the overall rubric of animal cognition. At the highest level it models entire organisms by means of software agents such as a virtual vole. At one step lower, it models various higher-level cognitive processes such as deliberation (Franklin 2000), volition (Franklin 2000), metacognition (Zhang *et al.* 1998), automization, and non-routine problem solving (D'Mello *et al.* 2006b). Yet another step lower one finds cognitive modules and processes that operate within a single cognitive cycle, that is within a few hundred milliseconds. These lower-level processes include perception (Franklin 2005), various forms of memory (Franklin *et al.* 2005), attention (Baars and Franklin 2003), learning (D'Mello *et al.* 2006a), and action selection (Negatu and Franklin 2002). At yet a lower level, the nodes and links from LIDA's perceptual memory, implemented via a slipnet (Hofstadter and Mitchell 1995), provide the common representational currency throughout the model a la Barsalou's (1999) perceptual symbol system. Taking a dynamical systems point of view, each such node may be thought of as representing a basin of attraction in the state space of some underlying cell assembly (Skarda and Freeman 1987). By spanning these various levels of theoretical complexity, the LIDA model can be expected to contribute to our understanding of several levels of the dynamics of living systems.

The natural history of the meadow vole, Microtus pennsylvanicus

Meadow voles are small secretive rodents that inhabit ephemeral grasslands in the northern and eastern portions of the United States and Canada. Much is known about their life history. Meadow voles also display striking seasonal differences in behavior. That is, they do most of their breeding during the spring and summer, when the photoperiod or day length is relatively long, about 14 hours of light per 24-hour period. At this time of year, female meadow voles become sexually receptive to males, producing odors that are attractive to males as well as displaying behaviors directed towards males (Ferkin and Seamon 1987; Ferkin *et al.* 2001; 2004a, b).

During the breeding season, female meadow voles are also territorial (Madison 1980). They defend their nests and territories often by behaving aggressively towards intruders. However, fighting is costly and not frequent (Ferkin and Seamon 1987). Female meadow voles use other means to defend their territory. Specifically, females scent mark along the borders of their territories and near their nests, and over-mark the scent marks of male and female conspecifics that they encounter. By scent marking and over-marking, female meadow voles are able to delineate boundaries of their territories and also announce their residency in an area.

Male meadow voles are not territorial. Instead, they wander through large home ranges that encompass the territories of one or more females. Males often do not display overt behaviors against male conspecifics. They seldom fight with other males and they do not target the scent marks of other males and over-mark them (Ferkin and Seamon 1987; Ferkin *et al.* 2001, 2004a). However, males scent mark and over-mark in areas containing the marks of female meadow voles (Ferkin *et al.* 2004a, b). This does not mean that male voles do not compete with one another, they do. However, male-male competition is more subtle; males compete with one another in two ways. First, males recall the location and reproductive condition of females that they encounter during their daily wanderings. That is, they display a memory for what, when, and where (Ferkin et al. in press). Second, once they locate females that are willing to mate with them, males will assess the risk and intensity of sperm competition. They do so, by determining whether the female has recently encountered other males. Male meadow voles investigate the area near the female, attempting to determine if other males have left their scent marks nearby. If so, the male, when he mates with the female, will increase his sperm investment 116% relative to his investment if he does not encounter fresh scent marks of other males nearby (del-Barco-Trillo and Ferkin 2004, 2006, 2007b).

Although many males may mate with females, the variance in reproductive success among males is highly skewed, so that only a relatively small number of males actually sire offspring (Sheridan and Tamarin 1988; Boonstra *et al.*1993). What it is that makes these males more successful is not known. However, studies suggest that the more successful males 1) produce odors that are more attractive than those of other males to females (Ferkin and Seamon 1987), 2) have higher titers of prolactin and gonadal steroids relative to those of other males, which makes the former more attractive and interesting than the latter to females (Leonard and Ferkin 2005), 3) display more behaviors directed at attracting and showing their interest in females (Ferkin *et al.* 1996, 2004, 2005); 4) have more copulatory interactions with females (delBarco-Trillo and Ferkin 2004, 2007a), 5) are better fed than less successful males (Pierce and Ferkin 2005; Pierce *et al.* 2005), and 6) are older and more experienced than other male meadow voles (Ferkin and Leonard *in press*).

As we mentioned above, meadow voles are seasonal breeders. They generally do not breed during the late fall and winter, when the day length is short and the daily photoperiod is less than 10 hours of light per 24-hour period. During the non-breeding season, females meadow voles relax their territorial borders, produce odors that are no longer attractive to males, but are attractive to females, display behaviors that are directed more at females than at males, and form communal nests with neighboring females and their last litters. Aggressive behavior between females is reduced and is replaced with affiliative and amicable acts (Madison 1980; Ferkin and Seamon 1987). At this time of year, males generally produce odors that are no longer attractive to females. Few males direct behaviors towards females as potential mates. Males appear to be solitary during the winter (Madison 1980). During the winter, scent marking and over-marking behavior is no longer directed at opposite-sex conspecifics and with self-grooming behavior serve a role in maintaining the cohesiveness of members of that communal nest (Leonard and Ferkin 2005; Ferkin and Leonard in press).

Meadow voles and cognition – Some case studies

In this section, we summarize the results of some experiments on voles that imply a strong cognitive component to their behavior. For example, meadow voles can distinguish between unfamiliar and familiar conspecifics, littermates and non-littermates, and between sexually receptive and sexually quiescent opposite-sex conspecifics. Meadow voles respond preferentially to the odors of littermates relative to non-littermates by spending more time investigating the odors of the former as compared to those of the latter (Ferkin 1989; Ferkin *et al.* 1992). Adult female voles behave amicably towards familiar females but not towards unfamiliar females, whereas adult male voles behave agonistically towards familiar males but not unfamiliar males (Ferkin 1988). Male voles overmark the scent marks of females in heightened sexual receptivity, during postpartum estrous, as compared to those of females that in other states of sexual receptivity (Ferkin *et al.* 2004a, b)

Depending on the social context, the perceptual memory of voles may last several hours to several days (Ferkin *et al.* 2005, *in press*). Perceptual memory can be fleeting or long term. For instance, a new person met briefly at a party may not be recognized a few weeks later, while a friend from childhood who hasn't been seen for decades may be recognized in spite of the changes brought by age. Perceptual and episodic memory (what, when, and where) depend to some extent, and in different ways, on association. In perceptual memory and object is associated with its features, a category with its members. Recall from episodic memory is accomplished in animals (and in at least some artificial agents) by means of associations with a cue. Improvement of performance during procedural learning is accomplished in animals by associating particular actions with desired results. Thus association plays different roles in the various memory systems and their various forms of learning, and can be expected to require distinct mechanisms.

First, we asked the question, is it possible for voles to have a sense of number? To address this question, we determined whether voles discriminate between two different scent-marking individuals and identify the individual whose scent marks was on top more often than the other individual (Ferkin *et al.* 2005). We tested whether voles show a preference for the individual whose scent marks was on top most often. If so, the simplest explanation was that voles can make a relative size judgment, such as distinguishing an area containing more of one individual's over-marks as compared to less of another individual's over-marks. We found that voles respond preferentially to the donor that provided the greater number of over-marks as compared to the donor that provided the fewer number of over-marks. Thus, we concluded that voles might display the capacity for relative numerousness. Interestingly, female voles were better able than male voles in distinguishing between small differences in the relative number of over-marks by the two scent donors.

Next, we conducted a series of experiments to determine whether reproductive condition of female meadow voles affects their scent marking behavior as well as the scent marking behavior of male conspecifics (Ferkin *et al.* 2004b). We did so because, during the breeding season, the reproductive condition of female mammals changes. Females may or may not be sexually receptive. In experiment 1, females in postpartum estrus deposited more scent marks than females that were neither pregnant nor lactating, reference females or ovariectomized females (OVX females). In experiment 2, male voles scent marked more and deposited more over-marks in areas marked by postpartum estrus females than by reference and OVX females. In experiment 3, postpartum estrus females deposited more scent marks and over-marks in areas marked by males than did females in the other reproductive states. The results of these experiments showed that male and female voles may vary the number, type, and location of scent marks they deposit in areas scented by particular conspecifics.

We also tested the hypothesis that male meadow voles posses the capacity to recall the what, where, and when of a single past event associated with mate selection in two experiments (Ferkin et al. in press). Briefly, male voles were allowed to explore an apparatus that contained two chambers. One chamber contained a day-20 pregnant female (24 hours prepartum). The other chamber contained a reference female. Twenty-four hours after the exposure, the males were placed in the same apparatus, which was empty and clean. At this time, the pregnant female would have entered postpartum estrus, a period of heightened sexual receptivity. Males initially chose and spent significantly more time investigating the chamber that originally housed the pregnant female (now a postpartum estrus female) than the chamber that originally housed the reference female. Male voles also explored an apparatus containing a chamber with a postpartum estrus female and one chamber containing a reference female. Twenty-four hours later, males were placed into an empty and clean apparatus. The males did not display an initial choice and they spent similar amounts of time investigating the chamber that originally housed the postpartum estrus female (now a lactating female) and the chamber that originally housed the reference female. The results of these and additional experiments suggest that male voles may have the capacity to recall the what, where, and when of a single past event, which may allow males to remember the location of females who would currently be in heightened states of sexual receptivity.

We also examined the effects of winning and losing on over-marking behavior of mammals, a behavior associated with intrasexual aggression and competition (Ferkin 2007). We tested the hypothesis that meadow voles adjust their overmarking behavior according to aggressive interactions they had experienced with a same-sex conspecific. The hypothesis was partially supported. That is, female voles that won their encounter over-marked a greater proportion of their opponent's over-marks than did females that either lost their encounter or females that were evenly matched in their encounter. Females that lost their encounter and females that were evenly matched over-marked a similar proportion of their opponent's over-marks. Male voles, however, independent of whether they won, lost, or were evenly matched, over-marked a similar proportion of their opponent's scent marks. The present findings suggest overmarking may not play a major role in male-male competition, but likely plays a large role in female-female competition among meadow voles.

We also determined to what degree meadow voles display self-cognizance and use self-referent phenotype matching for self recognition (Ferkin *et al. unpubl. data*). We tested animals using habituation/dishabituation tasks in which they were exposed to their own current urine scent marks and those of either 1) unfamiliar same-sex conspecifics, 2) same-sex siblings, 3) their past selves (post gonadectomy with no steroid-hormone replacement), 4) their past selves (post gonadectomy with steroid-hormone replacement), and 5) their past selves (intact gonads). Briefly, we discovered that voles behaved as if the scent marks of their past and present selves were the same if the reproductive condition of the voles was not changed and from the same donor. If, however, the voles were gonadectomized and their reproductive condition changed, they behaved as if the scent marks of their past and present selves were the different donors.

Finally, we examined sperm competition in male meadow voles (delBarco-Trillo and Ferkin 2004, 2006, 2007b), Sperm competition occurs when a female copulates with two or more males and the sperm of those males compete within the female's reproductive tract to fertilize her eggs. The frequent occurrence of sperm competition has forced males of many species to develop different strategies to overcome the sperm of competing males. A prevalent strategy is for males to increase their sperm investment (total number of sperm allocated by a male to a particular female) after detecting a risk of sperm competition. It has been shown that the proportion of sperm that one male contributes to the sperm pool of a female is correlated with the proportion of offspring sired by that male. Therefore, by increasing his sperm investment a male may bias a potential sperm competition in his favor.

We showed that male meadow voles increase their sperm investment when they mate in the presence of another male's odors. Such an increase in sperm investment does not occur by augmenting the frequency of ejaculations, but by increasing the amount of sperm in a similar number of ejaculations. We also found that sperm investment of males exposed to the scent marks of five male conspecifics was intermediate between that of males exposed to the scent marks of one male and that of males exposed to no scent marks of conspecific males (delBarco-Trillo and Ferkin 2006). We have recently discovered that males do not increase their sperm investment if the donors of the scent marks are males that are in poorer condition than the male subject, but do so if the male donors are in similar or better condition than the subject male (Vaughn et al. unpubl. data). Thus, males can distinguish between different male donors and adjust their sperm investment accordingly. How they do so and what cognitive processes are involved in regulating the physiological response of the vas deferens in the male's testes is under investigation (delBarco-Trillo and Ferkin 2007b).

Hypotheses

A previous ontology provides a conceptual framework within which to conduct empirical research and fashion hypotheses (Franklin and Ferkin 2006). Formulating hypotheses is one of the functions of mathematical, computational, and conceptual models. Thus, it's reasonable to formulate potentially testable hypotheses for the LIDA model. By doing so, we hope to encourage empirical testing of our hypotheses. Here we present a few selected testable hypotheses that may be tested with the current LIDA technology.

1. The Cognitive Cycle: The very existence of the cognitive cycle in various species, along with its timing (asynchronously cascading at a rate of roughly 5-10 hz) is a major hypotheses. Neuroscientists have

provided suggestive evidence for this hypothesis (Lehmann et al. 1998; Halgren *et al.* 2002; Freeman 2003).

- 2. Perceptual Memory: A perceptual memory, distinct from semantic memory but storing some of the same contents, exists in humans (Nadel 1992; Franklin *et al.* 2005), and in many, perhaps most, animal species.
- 3. Transient Episodic-Like Memory: Humans have a contentaddressable, associative, transient episodic memory with a decay rate measured in hours (Conway 2001). While perceptual memory seems to be almost ubiquitous across animal species, we hypothesize that this transient episodic memory is evolutionary younger, and occurs in many fewer species (Franklin *et al.* 2005). We refer here to episodic-like memory instead of to episodic memory, as in humans, to avoid the controversy over phenomenal consciousness in animals, about which the LIDA model takes no position (Ferkin *et al. in press*). Further reference to episodic memory in non-human animals should be read as episodic-like.
- 4. Consolidation. A corollary to the previous hypothesis says that events can only be encoded (consolidated) in long-term declarative memory via transient episodic memory. This issue of memory consolidation is still controversial among both psychologists and neuroscientists (e.g. Lisman and Fallon 1999). However, the LIDA model advocates such consolidation.
- Consciousness: Functional consciousness is implemented computationally by way of a broadcast of contents from a global workspace, which receives input from the senses and from memory (Baars 1988, 2002).
- 6. Conscious Learning: Significant learning takes place via the interaction of functional consciousness with the various memory systems (e.g. Standing 1973; Baddeley 1993). The effect size of subliminal learning is quite small compared to conscious learning. Note that significant implicit learning can occur by way of unconscious inferences based on conscious patterns of input (Reber *et al.* 1991). All memory systems rely on attention for their updating, either in the course of a single cycle or over multiple cycles. (Franklin *et al.* 2005).
- 7. Voluntary and Automatic Memory Retrievals: Associations from transient episodic and declarative memory are retrieved automatically and unconsciously during each cognitive cycle. Voluntary retrieval from these memory systems may occur over multiple cycles using volitional goals.
- 8. **Deliberative, volitional decision making:** Such functionally conscious decisions that deliberatively choose between alternatives are, following Global Workspace Theory (Baars 1988 Chapter 9), are hypothesized in the LIDA model (Franklin 2000) to follow William James' ideomotor theory (James 1890). Thus a decision is reached in favor of a proposed

alternative when no objection to it is raised. Volitional decision making is inherently a multi-cyclic, higher-order cognitive process.

Connecting the LIDA Model and the behavior of a meadow vole

In what follows we will describe each of the steps in LIDA's cognitive cycle, stated in *italicized text* as if applying to a human, while also carrying along their application in the mind of a hypothetical male vole.

Imagine a male vole has turned a corner, and encountered scent marks from different conspecifics (Ferkin and Johnston 1995). Some of these scent marks are old and some are fresh, some are overlapping and some are not. This male vole detects these marks, identifies the donors that deposited the marks, and spends more time investigating the most numerous and the freshest marks (Ferkin et al. 1999, 2001, 2004a, b, 2005). The male vole distinguishes between the different scent donors and responds preferentially to the donors that are of most interest to him. The most interesting donor may likely be a sexually receptive female with whom he would attempt to copulate (delBarco-Trillo and Ferkin 2004). The mechanism that the male voles used to discriminate between the different scent donors would likely have involved perceptual learning (Franklin and Ferkin 2006) Keep in mind that the cognitive cycle to be described takes, in total, only a fifth of a second or so to complete.

Here are the nine steps of the LIDA cognitive cycle together with an example interpretation in the mind of our assumed male vole.

1. **Perception**. Sensory stimuli, external or internal, are received and interpreted by perception producing meaning. Note that this step is preconscious.

In its perceptual memory the male vole categorizes the scent marks as being from males or females (a category), as known (an individual), and as sexually receptive (a feature) (Ferkin and Johnston 1995a, b). During this step our vole scans its perceptual memory and makes associations between scent marks and scent donors, assessing the identity, sex, and reproductive condition of the scent donors (Ferkin et al. 1999, 2004a, b, 2005)

This perceptual memory system identifies pertinent feeling/emotions along with objects, categories and their relations.

In the male vole, feeling nodes for interest and for sexual arousal are somewhat activated. If this is a sexually receptive female, for example, all of these activated nodes are over threshold and become part of the percept.

2. Percept to Preconscious Buffer. The percept, including some of the data plus the meaning, is stored in preconscious buffers of LIDA's working memory. In humans, these buffers may involve visuo-spatial, phonological, and other kinds of information. Feelings/emotions are part of the preconscious percept.

For the male vole, the percept has identified the freshest scent marks coming from a female in postpartum estrus, a highly sexually receptive female. These females readily mate when they encounter males. However, females are only receptive to males for 12 hours after they deliver pups (Ferkin *et al.* 2004a).

 Local Associations. Using the incoming percept and the residual contents of the preconscious buffers (content from precious cycles not yet decayed away), including emotional content, as cues, local associations are automatically retrieved from transient episodic memory (TEM) and from declarative memory.

The contents of the preconscious buffers, together with the retrieved local associations from TEM and declarative memory, roughly correspond to Ericsson and Kintsch's (1995) long-term working memory and to Baddeley's (2000) episodic buffer. These local associations include records of the agent's past feelings/emotions, and actions, in associated situations.

Assuming that our male vole possesses declarative memory, the retrieved local associations may include the memory of a previous sexual encounter with this particular female and his reaction to her, a memory for what, when, and where (Ferkin et al. in press) For example, our male vole may have a memory of this female, when she was not in postpartum estrus, but simply pregnant and not sexually receptive (Ferkin and Johnston 1995a, b), which allows our male vole to anticipate that this female will only be in postpartum estrus for a few hours, and then she becomes not interested in mating. Although such expectation may come from either perceptual memory or semantic memory, anticipating the what (a female is highly sexually receptive for a relatively narrow window), the when (a female may no longer be highly sexually receptive), and the where (the location of that female relative to other female voles in the area), suggest that such processing may involve an episodic–like memory (Ferkin et al. in press)

4. Competition for Attention. Coalitions of perceptual and memory structures in the workspace compete to bring relevant, important, urgent, or insistent situations to consciousness. (Consciousness here is required only in the functional sense as defined in global workspace theory and as defined by its role in the middle steps of this cognitive cycle. Phenomenal (subjective) consciousness is not assumed.) The competition may also include such coalitions from a recently previous cognitive cycle. Present and past feelings/emotions influence this competition for consciousness. Strong affective content strengthens a coalition's chances of being attended to (Franklin and McCauley 2004).

In the male vole, one coalition that is on the lookout for sexual opportunities will carry the other vole's identity, her reproductive status and readiness to mate, some details of the previous encounter, and the feelings associated with the current percept and the previous encounter. This coalition will compete with other such coalitions for "consciousness," but may not win the competition. Suppose our male's first encounter with that female's odor indicated that she has also attracted the attention of a predator, (fresh weasel scent marks are present), which has also become part of the percept, along

with a strong fear. In this case, another coalition on the lookout for danger may well win the competition, and the male vole may not respond by seeking out this female.

 Broadcast of Conscious Contents. A coalition carrying content gains access to the global workspace. Then, its contents are broadcast throughout the system.

In humans, this broadcast is hypothesized to correspond to phenomenal consciousness. No such assumption is made here. The conscious broadcast contains the entire content of consciousness including the affective portions.

Now imagine that the male vole did not detect a predator's odor and that the coalition about the female vole was attended to, that is, it came to his "consciousness."

Several types of learning occur. The contents of perceptual memory are updated in light of the current contents of consciousness, including feelings/emotions, as well as objects, categories, actions and relations. The stronger the affect, the stronger the encoding is in memory.

In the male vole, possibly along with others, representation in perceptual memory for the particular female vole, for the category of female voles, for readiness to mate, and for sexual interest would each be strengthened.

Transient episodic memory is also updated with the current contents of consciousness, *including feelings/emotions*, as events. *The stronger the affect, the stronger would be the encoding in memory.* (At recurring times not part of a cognitive cycle, the contents of transient episodic memory are *consolidated* into long-term declarative memory.)

If the male vole possesses a transient episodic memory, and studies suggest that he may (Ferkin et al. in press), the event of having again encountered this particular female vole, her condition, and his reaction to her would be encoded, taking information from the "conscious" broadcast.

Procedural memory (recent actions) is updated (reinforced) with the strength of the reinforcement influenced by the strength of the affect.

For the male vole, the prior acts of turning the corner and sniffing the encountered scent marks would be reinforced. In this case, both acts would have been learned and become familiar.

Thus, perceptual, episodic and procedural learning occur with the broadcast in each cycle.

 Recruitment of Resources. Relevant behavior representations respond to the conscious broadcast. These are typically representations whose variables can be bound from information in the conscious broadcast. The responding representations may be those that can help to deal with the current situation. Thus consciousness solves the relevancy problem in recruiting internal resources with which to deal with the current situation. The affective content (feelings/emotions), together with the cognitive content, helps to attract relevant behavioral resources.

For the male vole, possibly among others, behavior representations for turning the head, for turning the body, for sniffing the scent marks and for moving in the direction that the female vole was traveling, may respond to the information in the broadcast.

7. Setting Goal Context Hierarchy. The recruited behavior representations use the contents of consciousness, including feelings/emotions, to instantiate new goal context hierarchies, bind their variables, and increase their activation.

Goal contexts are potential goals, each consisting of a coalition of behaviors, which, together, could accomplish the goal. Goal context hierarchies can be thought of as high-level, partial plans of actions. It is here that feelings and emotions most directly implement motivations by helping to instantiate and activate goal contexts, and by determining which terminal goal contexts receive activation. Other, environmental, conditions determine which of the earlier goal contexts receive additional activation.

For the male vole, a goal context hierarchy to seek out the female vole would likely be instantiated in response to information from the broadcast.

8. Action Chosen. The action selection mechanism chooses a single behavior, perhaps from a just instantiated goal context or possibly from a previously active goal context.

This selection is heavily influenced by the various feelings/emotions. The choice is also affected by the current situation, external and internal conditions, by the relationship between the behaviors, and by the residual strengths of various behaviors.

In the male vole, there may have been a previously instantiated goal context for avoiding the weasel previously sensed. An appropriate behavior in avoiding the predator may be chosen in spite of the presence of the female vole. Alternatively, a beginning step in the goal context for approaching and exploring the female vole may win out.

9. Action Taken. The execution of a behavior results in its action being performed, which may have external or internal consequences, or both.

This is LIDA taking an action.

If this particular male that has few opportunities to copulate with a female, searching for the female would likely have been selected, resulting in behavior codelets acting to turn the male in the direction of the female, to sniff, and to begin his approach. If on the other hand, our vole has frequent opportunities to mate with females, he may stop his search for this female when he encounters the odor of a weasel or a male conspecific (delBarco-Trillo and Ferkin 2004).

Sample experiments for tuning a Virtual Vole

The computational LIDA architecture is composed of a number of closely interconnected modules with their associated processes. Their implementation is outlined in Table 1 below, which specifies the conceptual name of the module, the name of its implementation in the architecture, the source of inspiration for the data structure and algorithms employed, and references to detailed explanations.

Module	Implementation	Source	References
Perceptual Memory	Slipnet	Copycat Architecture	Hofstadter and Mitchell (1995); Franklin (2005b)
Transient Episodic Memory	Sparse Distributed Memory	Sparse Distributed Memory	Kanerva (1988); D'Mello <i>et al.</i> (2005)
Declarative Memory	Sparse Distributed Memory	Sparse Distributed Memory	Kanerva (1988); D'Mello <i>et al.</i> (2005)
Procedural Memory	Scheme Net	Schema Mechanism	Drescher (1991); D'Mello <i>et al.</i> (2006b)
Action Selection	Behavior Net	Behavior Net	Maes (1989);, Negatu and Franklin (2002)

Table 1. LIDA modules and their implementations

Each of the LIDA modules and their associated processes involve a number of internal parameters that must be specified before the model can be used to replicate experimental data. Such specification of parameters, the tuning of the model, is typically done by trial and error so as to induce the model to replicate the data from one specific experiment. This provisionally tuned model is then further tuned to replicate data from both the original experiment and a second experiment. The model is then considered tuned, and ready to try on other, prospective, experiments.

Some change in the model would be needed if it proves difficult or impossible to successfully tune some parameter. In that case, one must conclude that the data structure or something in one of its associated algorithms requires adjustment. Thus, the difficulty of tuning the model serves as a sort of implicit metric measuring the correctness of the model.

In the next subsections we describe experiments with voles that might be expected to serve to tune a Virtual Vole, software agent operating within a robotic simulator and simulating a live vole.

Odor preference tests for tuning the virtual vole

In a previous experiment, we quantified the olfactory response of reproductively active voles to the odors of reproductively active same- and opposite-sex conspecifics. The position of the male or female donor was varied on the left- or right-side of the Y-maze to prevent any side bias displayed by the subject (Ferkin and Seamon 1987). We recorded, continuously for 5 minutes, the amount of time male and female subjects investigated the baskets containing the donor voles. Thus, we showed that voles discriminate between and respond preferentially to opposite-sex conspecifics over same-sex conspecifics (Ferkin and Seamon 1987).

We also performed opposite-sex donor tests in which male subjects were exposed to scent marks of ovariectomized + blank treated females (not sexually receptive) and ovariectomized + estradiol treated females (sexually receptive), and female subjects were exposed to scent marks of gonadectomized + blank treated males (not sexually receptive) and gonadectomized + testosterone treated males (sexually receptive). Each male and female subject was exposed to a unique pair of opposite-sex odor donors. We found that male and female subjects spent more time investigating opposite-sex conspecifics given hormone replacement than opposite-sex conspecifics not given hormone replacement. Thus, voles prefer opposite-sex conspecifics that are sexually receptive to those that are not sexually receptive (Ferkin and Johnston 1993, 1995a, b).

The Y-maze apparatus used in Ferkin and Seamon (1987) can be simulated within a robotic simulator along with the various scent markings. This would allow a virtual vole to act as subject. Knowing ahead of time the desired range of results would allow the tuning of the various parameters in the several modules of the LIDA architecture as implemented in the virtual vole. As mentioned above, replication of these and other such experiments would allow the testing of the implementation of the LIDA model in control of the virtual vole.

Episodic-like memory tests for verifying the tuning of the virtual vole

As the initial tuning of the internal parameters of the virtual vole would have been done using odor preference tests, the question remains of whether these tunings are specific to only those tests. Or, is the tuning of parameters sufficiently general to make the virtual vole a good simulation of live meadow voles in a variety of experimental situations? We suggest testing for the generality of the parameter tuning by replicating other previously performed experiments with live meadow voles. One possibility would be the experiments on episodic-like memory.

Episodic-like memory, the memory for events, allows an animal to recollect the what, the where and the when of what happened. The LIDA model asserts that such episodic-like memory comes in two forms, transient episodic-like memory and declarative memory. Transient episodic-like memory lasts only a relatively short period of time, a few hours or a day in humans. In voles with their much shorter life span, it may be reasonable to assume an even more rapid decay in transient episodic-like memory. Declarative memory is long-term episodic-like memory that in humans may last for decades or a lifetime. This section describes

already completed experiments that may be replicated with virtual voles to further test and adjust the tuning of their parameters. They also serve as background for possible future experiments designed to tease out the distinction between transient episodic-like memory and declarative memory in voles, if the latter exists.

Despite the controversy swirling around the ability of animals to recollect specific aspects of past events (Clayton and Griffiths 1998; Tulving 2005), it is not difficult to imagine that some animals may use information from such past events to secure a mate. An important feature that often characterizes most nonhuman mammals is that females do not mate with males when they are not in a heightened state of sexually receptivity, such as estrus or postpartum estrus (Bronson 1989). Thus, for many species of mammals, and particularly the majority of whom in which opposite-sex conspecifics live separately during the breeding season, males should be able to discriminate among females in different states of sexual receptivity. They should be able to identify females that are in a heightened reproductive state, their location, and the amount of time that the females are in this heightened state. Such a capacity would benefit, for example, a male meadow vole, a microtine rodent.

Adult male and female meadow voles live separately during the breeding season. At this time of year, female voles tend to occupy territories that are fixed spatially, but are dispersed widely across the home range of several males (Madison 1980). Female voles are induced ovulators and do not undergo estrous cycles (Milligan 1982; Meek and Lee 1993). Thus, the reproductive condition and sexual receptivity varies among female voles during the breeding season. That is, female voles may be pregnant, lactating, both pregnant and lactating, neither pregnant nor lactating, or in a period of heightened sexual receptivity during postpartum estrus (Keller 1985). Postpartum estrus females are more likely to mate with a male than females that are not pregnant or lactating, or females that are pregnant, lactating or both (Ferkin et al. 2004; delBarco-Trillo and Ferkin 2007a).

Sexual receptivity in female varies and they enter PPE asynchronously. To increase his fitness, male meadow voles should mate with as many females as possible (Boonstra *et al.* 1993), particularly those females that have entered postpartum estrus (Ferkin *et al.* 2004; delBarco-Trillo and Ferkin 2007a). Thus, we hypothesize that after a single visit to a female, male voles would later recollect her previous reproductive state (what); her location (where), and how long she would be in that reproductive state (when) (Ferkin *et al. in press*), thus demonstrating episodic-like memory. The experimental design of this experiment (Ferkin *et al. in press*) is described below.

All female voles were between 125-135 days of age when used in the tests. Female meadow voles do not undergo estrus cycles (Milligan 1982; Keller 1985). To represent different levels of female receptivity, we used females that were pregnant for 20 days (day 20 pregnant), in postpartum estrus, females that were not pregnant or lactating, termed reference females, and day 2 lactating females. Gestation lasts 21 days in voles, thus day 20 pregnant female voles deliver their litters within 24 hours (Keller 1985). Immediately after parturition, these females enter postpartum estrous (PPE), a period of heightened sexual receptivity, which lasts 8-12 hours (Keller 1985; Ferkin *et al.* 2004; delBarco-Trillo and Ferkin 2007a). The postpartum estrus females had delivered pups 4-6 hours prior to testing. Reference females were not currently pregnant or lactating (Ferkin and Johnston 1995). The reference females had previously delivered a litter about 3-4 weeks before being used in the experiment (see below); these females had lived singly for approximately 21 days before testing began.

In experimental conditions 4 and 5 (see below), we used females that were in their second day of lactation for each condition. Lactation is 14-16 days in duration, and pups are weaned when they are 16-18 days old (Keller 1985). The day 2 lactating females were no longer in postpartum estrus and thus were no longer in a heightened state of sexual receptivity (Ferkin and Johnston 1995). The postpartum estrus females and day 2 lactating females had not lived with their mate for 17 and 18 days, respectively, before the testing began.

It is important to note that postpartum estrus female voles are in a heightened state of reproductive receptivity and readily mate with males (Keller 1985; Ferkin and Johnston 1995; delBarco-Trillo and Ferkin 2007a). In contrast, reference females, day 20 females, and day 2 lactating females are not in a heightened state of sexual receptivity, but they may mate (Ferkin and Johnston 1995; delBarco-Trillo and Ferkin 2004, 2006). In addition, postpartum estrus females produce odors that are more attractive to males relative to those produced by females that are day 20 pregnant, day 2 lactating, or reference females, who produce odors that are similar in their attractiveness to males (Ferkin and Johnston 1995; Ferkin *et al.* 2004).

All behavioral observations were performed on voles placed in a T-shaped apparatus (Fig. 2). We used two opaque Plexiglas cages with wired tops for observation purposes. The large boxes served to house the female donors. There was a transparent divider with small holes between the females' living area and the area that males explored. This divider allowed males to investigate the female's living area without coming into direct contact with that female.

Test for Episodic-Like Memory

We conducted an experiment, with five experimental conditions, in which male subjects were exposed to unique female donors (Ferkin *et al. in press*). Each experimental condition contained two phases, an exposure phase and a test phase. In both phases of the five experimental conditions, a male meadow vole from one of the above treatment groups was placed into the starting box located at the base of the T-shaped arena (Fig. 2) for 30 seconds before the gate was lifted and the male was allowed to explore the entire apparatus. Each male underwent a single exposure and single test (see below).

Experimental Condition 1 –During the exposure phase, male voles were placed into an apparatus that housed a reference female in one box and a day 20 pregnant female in the other box (Fig. 2). During the exposure phase, we recorded continuously for 10 minutes, the total amount of time male voles spent in the arms of the apparatus that housed each female donor (Fig. 2). We also

noted the position of the home-boxes (left- or right-side of the apparatus) that housed each particular female donor. The position of a particular female's homebox in the left- or right-side of the apparatus was alternated for each male subject during the exposure phase. After the 10-minute exposure, the male was returned to its own cage. Then, we disconnected the two-female home-boxes from the apparatus, and cleaned and disinfected the apparatus.

The test phase took place 0.5 hour after the exposure phase. During the test phase, the male voles were re-introduced into the apparatus that now contained boxes that housed no female donors; the boxes contained only clean wood chip bedding. We recorded continuously for 10 minutes, the total amount of time that male voles spent investigating the arm of the apparatus that previously housed the reference female that they were exposed to and the arm that previously housed the day 20 pregnant female. During the test phase male voles spent similar amounts of time investigating the arm of the apparatus that would have housed the reference female (Ferkin *et al. in press*).

Experimental Condition 2 - Male voles were exposed to an arena containing a day 20 pregnant female and a postpartum estrus female. 0.5 hour later, male voles were allowed to investigate an empty arena. We recorded the initial choice of the male vole and the amount of time that he spends in both arms of the arena. During the test phase male voles spent more time investigating the arm of the apparatus that would have housed the postpartum estrus females than the arm of the apparatus that would have housed the day-20 pregnant female (Ferkin *et al. in press*).

Experimental Condition 3 - Male voles were exposed to an arena containing a day 2 lactating female and a reference female. 0.5 hour later, male voles were allowed to investigate an empty arena. We recorded the initial choice of the male vole and the amount of time that he spends in both arms of the arena. During the test phase male voles spent similar amounts of time investigating the arm of the apparatus that would have housed the day 2 lactating female and the arm of the apparatus that would have housed the reference female (Ferkin *et al. in press*).

Experimental Condition 4 - Male voles were exposed to an arena containing a day 20 pregnant female and a reference female. 24 hours later, male voles were allowed to investigate an empty arena. The test phase took place 24 hours after the exposure phase. At this time, the day 20 pregnant female had delivered pups and had entered into postpartum estrus. During the test phase, the male voles were re-introduced into the apparatus that now contained boxes that housed no female donors; the boxes contained only clean wood chip bedding (Fig. 2). During the test phase, which occurred 24 hours after the exposure phase, males spent more time investigating the arm of the apparatus that would have contained the postpartum estrus female than the arm of the apparatus that would contained the reference female (Ferkin *et al. in press*)

Experimental Condition 5 - Male voles were exposed to an arena containing a postpartum estrus female and a reference female. Twenty-four hours later, male voles were allowed to investigate an empty arena. We recorded the initial choice of the male vole and the amount of time that he spends in both arms of

the arena. During the test phase, which occurred 24 hours after the exposure phase, male voles spent similar amounts of time investigating the arm of the apparatus that would have housed the day 2 lactating female and the arm of the apparatus that would have housed the reference female (Ferkin *et al. in press*).

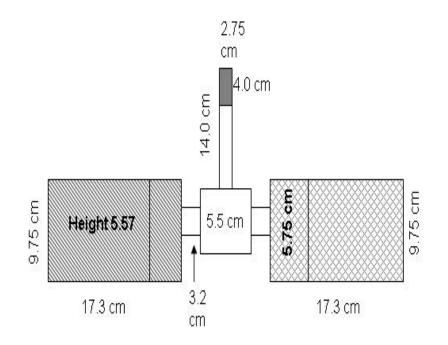
The results of these experiments suggest that male voles may have the capacity to recall the what, where, and when of a single past event, which may allow males to remember the location of females who would currently be in heightened states of sexual receptivity. Viewed from the LIDA model, the outcomes of Experimental conditions 1-3 indicate recollection of an event after a time interval of 0.5 hour between the exposure of a subject male vole to female odor and its later testing can be attributed to transient episodic-like memory (Ferkin *et al. in press*).

In that the life span of a meadow vole is only about four months in the wild and approximately 18 months in captivity (Sheridan and Tamarin 1988; Ferkin and Leonard *in press*), we suspect that the bottom end of the time span for testing for long-term episodic-like memory would be 24 hours or less. However, experiments can be repeated using a 48 hour time interval, which would correspond to long-term episodic in humans,

Replication of Episodic-Like Memory experiments using LIDA model virtual voles. These tests would involve placing a virtual vole in a virtual arena that simulates that described for real voles (Fig. 2) and following experimental methods for virtual voles identical to those of the episodic-like memory experiments described above. Specifically, we will use virtual voles and a virtual arena to replicate the tests described above for a live vole in experimental conditions 1-5. During the test trials with the virtual voles, we will identify the initial choice of the virtual male voles and the total amount of time that they spend investigating the arm of the apparatus that previously housed the virtual conspecific females. By doing so, we would be able to compare the response of the virtual male vole with those of the live male voles and test the efficacy of the LIDA model for predicting the behavior of voles.

Successful replication of these episodic-like memory experiments with a virtual vole would demonstrate the efficacy of one aspect of the LIDA model. Also, replication of these experiments, both in vivo and virtual, would allow the LIDA model to distinguish transient episodic memory in voles with its rapid decay rate from declarative (long-term episodic-like) memory, which can last a lifetime (See hypothesis 3 above).

Figure 2 – The testing arena for Episodic-like memory in voles



A Possible experiment for testing a LIDA hypothesis

With a properly tuned virtual vole in hand it becomes possible to test the various hypotheses listed above that are derived from the LIDA model. In this section we suggest one such possible experiment designed to test Hypothesis 8. The earlier hypotheses involve processes that are thought to operate within a time frame of a very few hundred milliseconds, making them difficult, though not impossible, to test using live animals. A test of Hypothesis 3 was described in the previous section.

Testing for Volitional Decision Making in Meadow Voles

Hypothesis 8 predicts that some animals are capable of deliberative, volitional decision making. Humans deliberate and make volitional decisions. Do other animals such as meadow voles have this ability? In many animal experiments the subject is faced with a forced choice of response to a stimulus, say push this lever or that. Such experimental situations almost always have involved learning on the part of the subject. In this case, the subject's action selection is likely to have resulted from perceptual recognition and learned action selection, all within a single cognitive cycle, rather than from deliberative decision making. On the contrary, studies of searching for live prey suggest that the jumping spider, Portia labiata, may engage in deliberate decision making. In the field studies (Wilcox and Jackson. 2002) these spiders were observed to spend a number of tens of minutes out of sensory contact, circling behind and above a prey spider, before lowering itself on a thread and ambushing the prey, which has appeared in a location that was "anticipated" by the spider. Such ambush behavior would seem to require deliberation, and even planning. This behavior on the part of these jumping spiders has also been tested experimentally by Tarsitano (2006). Here we suggest a version of Tarsitano's (2006) experiments, adapted to test the hypothesis that meadow voles are capable of making decisions deliberatively. This section will briefly describe such an experiment.

The experimental apparatus consists of a relatively simple maze together with a platform above the maze from which the entire maze can be viewed through a transparent floor. The maze has two disjoint zigzagged arms that interleave with one another in three dimensions in some complex way, with the ends of the two arms separated.

In the exposure phase of the experiment the subject male vole has the run of the platform from one end of which he can see and smell a postpartum estrus female vole positioned at the end of one of the arms of the maze. The subject male vole can sense but not approach the female vole, and can inspect the maze below the platform through its transparent floor. In the test phase of the experiment the subject male vole is positioned at the beginning of the maze where he is faced with a choice of the two entrances of the two arms, and where he is unable to detect the postpartum estrus female vole. Having no procedural learning on which to depend, but only the perceptual learning from his inspection of the maze from his earlier vantage point on the platform, the subject vole, faced with the entrances to the two arms, must carry out a deliberative selection of which of the two arms to explore to encounter the postpartum estrus female. Based on the preferences of male voles, for postpartum estrus females (Ferkin *et* *al.* 2005), a male would demonstrate deliberative decision making by initially choosing and exploring the arm that will bring him into contact with the postpartum estrus female. Such a response by the male voles would have been the result of prior deliberative planning and a prior volitional decision to seek the postpartum estrus female along the appropriate arm. Such a decision will have likely occurred while the subject vole was exploring the platform, and discovered that one arm of the maze led to the postpartum estrus female and the other arm did not lead to the postpartum estrus female. This choice cannot be successfully made with the sensory information available to the subject vole positioned at the beginning of the maze. The capacity to make the appropriate choice and choose the direct path to the female would provide support for the hypothesis that meadow voles make deliberative decisions.

Experimenting with a Cognitive Robot

In principle, it should be possible to perform real world experiments using an artificial animal, say an artificial vole, in the form of a cognitive robot controlled by some cognitive architecture based on, for example, the LIDA model. Using such a cognitive robot would retain all the benefits described above for the use of software agent simulations of animals, say virtual voles. In addition, the use of such artificial animals/cognitive robots might be expected to reveal real world issue or difficulties that could be obscured by the use of virtual animals in a simulated environment.

The major problem with designing cognitive robots for such a purpose would seem to be sensing. It is difficult to imagine an artificial vole with the acute sense of smell of a real vole. With the advent of nanotechnology and other new techniques, artificial olfaction is becoming a reality (Pearce *et al.* 2002). Replicating experiments using cognitive robots as artificial animals may someday become a reality.

Conclusion

We conclude that it is in principle possible to employ virtual animals in the form of software agent simulations to benefit biological theory. Controlled by cognitive architectures such as LIDA, such virtual animals allow biologists to test their theories directly by replicating experiments within a virtual environment. To do so requires that the controlling cognitive architecture, like LIDA, be sufficiently broad and comprehensive to serve to control a software agent. Thus broad, comprehensive theories of animal cognition should prove themselves of value to biologists.

References

- Allen C (1997): Animal cognition and animal minds. In Machamer P, Carrier M (eds), *Philosophy and the Sciences of the Mind*: Pittsburgh University Press and the Universitätsverlag Konstanz, pp 227-243.
- Alsop B (1998) Receiver operating characteristics from non-human animals: Some implications and directions for research with humans. *Psychonomic Bulletin & Review* 5:239-252.

Asada M, MacDorman KF, Ishiguro H, Kuniyoshi Y (2001) Cognitive developmental robotics as a new paradigm for the design of humanoid robots. *Robotics and Autonomous Systems* 37:185–193.

- Baars BJ (1988) A Cognitive Theory of Consciousness. Cambridge: Cambridge University Press.
- Baars BJ (2002) The conscious access hypothesis: origins and recent evidence. *Trends in Cognitive Science* 6:47–52.
- Baars BJ, Franklin S (2003) How conscious experience and working memory interact. *Trends in Cognitive Science* 7:166–172.
- Baddeley A, Conway M, Aggleton J (2001) *Episodic Memory*. Oxford: Oxford University Press.

Baddeley AD, Hitch GJ (1974) Working memory. In Bower GA (ed), *The Psychology of Learning and Motivation*. New York: Academic Press, pp 47– 89.

- Barsalou LW (1999) Perceptual symbol systems. *Behavioral and Brain Sciences* 22:577–609.
- Bekoff M, Allen C, Burghardt GM (2002) *The Cognitive Animal*. Cambridge, MA: MIT Press.
- Boonstra R, Xia X, Pavone L (1993) Mating system of the meadow vole, *Microtus* pennsylvanicus. Behavioral Ecology 4: 83-89.
- Boysen ST, Himes GT (1999) Current issues and emerging theories in animal cognition. *Ann. Rev. Psych.* 50:683–705.
- Brooks RA (1991) How to build complete creatures rather than isolated cognitive simulators. In VanLehn K (ed), *Architectures for Intelligence*. Hillsdale, NJ: Lawrence Erlbaum Associates, pp 225–239.
- Bronson FH (1989) *Mammalian Reproductive Biology*. University of Chicago Press, Chicago
- Byrne RW, Bates LA (2006) Why are animals cognitive? *Current Biology* 16:R445–R448.
- Clark A, Grush R (1999): Towards a cognitive robotics. *Adaptive Behavior* 7:5-16.
- Clayton NS, Griffiths, DP (1998). Episodic-like memory during cache recovery by scrub jays. *Nature* 395: 272-274
- Conway MA (2002): Sensory-perceptual episodic memory and its context: autobiographical memory. In Baddeley A, Conway M, Aggleton J (eds), *Episodic Memory*. Oxford: Oxford University Press, pp 53–70.
- Crick F, Koch C (2003) A framework for consciousness. *Nature Neuroscience* 6:119–126.
- D'Mello SK, Ramamurthy U, Franklin S (2005) Encoding and Retrieval Efficiency of Episodic Data in a Modified Sparse Distributed Memory System, *Proceedings of the 27th Annual Meeting of the Cognitive Science Society. Stresa, Italy.*
- D'Mello SK, Franklin S, Ramamurthy U, Baars BJ (2006a) A Cognitive Science Based Machine Learning Architecture, *AAAI 2006 Spring Symposium Series Sponsor: American Association for Artificial Intelligence.* Stanford University, Palo Alto, California, USA.

- D'Mello SK, Ramamurthy U, Negatu A, Franklin S (2006b) A Procedural Learning Mechanism for Novel Skill Acquisition. In Kovacs T, Marshall JAR (eds), *Proceeding of Adaptation in Artificial and Biological Systems, AISB'06*, Vol 1. Bristol, England: Society for the Study of Artificial Intelligence and the Simulation of Behaviour, pp 184–185.
- delBarco-Trillo, J. & Ferkin, M. H. (2004) Male mammals respond to a risk of sperm competition conveyed by odours of conspecific males. *Nature* 431: 446-449.
- delBarco-Trillo J, Ferkin MH (2006) Male meadow voles respond differently to risk and intensity of sperm competition. *Behavioral Ecology* 17: 581-585.
- delBarco-Trillo J, Ferkin MH (2007a) Female meadow voles, *Microtus pennsylvanicus*, experience a reduction in copulatory behavior during postpartum estrus. *Ethology* 113: 466-473.
- delBarco-Trillo J. Ferkin MH (2007b). Increased sperm numbers in the vas deferens of meadow voles, *Microtus pennsylvanicus,* in response to odors of conspecific males. *Behavioral Ecology and Sociobiology.* 61: 1759-1764.
- Dere E, Kart-Teke E, Huston JP, De Souza Silva MA (2006) The case for episodic memory in animals. *Neuroscience and Biobehavioral Reviews* 30:1206–1224.
- Drescher GL (1991) *Made-Up Minds: A Constructivist Approach to Artificial Intelligence*. Cambridge, MA: MIT Press.
- Ericsson KA, Kintsch W (1995) Long-term working memory. *Psychological Review* 102: 211–245.
- Ferkin MH (1988) The effect of familiarity on social interactions in meadow voles, *Microtus pennsylvanicus*: a laboratory and field study. *Animal Behaviour* 36: 1816-1822.
- Ferkin MH (1989) Adult-weanling recognition among captive meadow voles (*Microtus pennsylvanicus*). *Behaviour* 118: 114-124.
- Ferkin MH (2007) Effects of previous interactions and sex on overmarking in meadow voles. *Behaviour*. 144: 1297-1313.
- Ferkin MH, Johnston RE (1993) Roles of gonadal hormones on controlling sex-specific odors in meadow voles (*Microtus pennsylvanicus*). *Hormones and Behavior* 27: 523-538.
- Ferkin,MH, Johnston RE (1995a) Meadow voles, *Microtus pennsylvanicus*, use multiple sources of scent for sexual recognition. *Animal Behaviour* 49: 37-44.
- Ferkin MH, Johnston RE (1995b) Effects of pregnancy, lactation, and postpartum oestrous on odour signals and the attraction to odours in female meadow voles, *Microtus pennsylvanicus. Animal Behaviour.* 49: 1211-1217.
- Ferkin MH, Leonard ST (2005) Self-grooming by rodents in social and sexual contexts. *Acta Zool. Sinica*. 51: 772-779.
- Ferkin MH, Leonard ST Age of the subject and scent donor affects the amount of time that voles self-groom when they are exposed to odors of opposite-

sex conspecifics. in Beynon R, Hurst J, Roberts C, Wyatt T (eds), *Chemical Signals in Vertebrates 11*. Springer Press. in press.

- Ferkin MH, Li HZ (2005) A battery of olfactory-based screens for phenotyping the social and sexual behaviors of mice. *Physiology and Behavior* 85: 489-499.
- Ferkin MH, Seamon JO (1987) Odor preferences and social behavior in meadow voles, *Microtus pennsylvanicus*: seasonal differences. *Canadian Journal of Zoology* 65: 2931-2937.
- Ferkin MH, Lee DN, Leonard ST (2004a) The reproductive state of female voles affects their scent marking behavior and the responses of male conspecifics to such marks. *Ethology* 110: 257-272.
- Ferkin MH, Li HZ, Leonard ST (2004b) Meadow voles and prairie voles differ in the percentage of conspecific marks that they over-mark. *Acta Ethologica* 7: 1-7.
- Ferkin MH, Mech SG, Paz-y-Mino C (2001). Scent marking in meadow voles and prairie voles: a test of three hypotheses. *Behaviour* 138: 1319-1336.
- Ferkin MH, Tamarin RH, Pugh SR (1992) Cryptic relatedness and the opportunity for kin recognition in microtine rodents. *Oikos* 63: 328-332.
- Ferkin MH, Combs A, delBarco-Trillo J, Pierce AA, Franklin S. Meadow voles display a capacity for what, where, and when. *Animal Cognition.* in press.
- Ferkin MH, Leonard ST, Bartos K, Schmick MK (2001a) Meadow voles and prairie voles differ in the length of time they prefer the top-scent donor of an over-mark. *Ethology* 107: 1099-1114.
- Ferkin MH, Pierce A A, Sealand RO, delBarco-Trillo J (2005) Meadow voles, *Microtus pennsylvanicus*, can distinguish more over-marks from fewer overmarks. *Animal Cognition* 8: 82-89.
- Foote AD, Griffin RM, Howitt D, Larsson L, Miller PJO, Hoelzel AR (2006) Killer whales are capable of vocal learning. *Biology Letters* 2:509–512.
- Franklin S (2000) Deliberation and Voluntary Action in 'Conscious' Software Agents. *Neural Network World* 10:505–521.
- Franklin S (2005) A "Consciousness" Based Architecture for a Functioning Mind. In Davis DN (ed), *Visions of Mind*. Hershey, PA: Information Science Publishing, pp 149–175.
- Franklin S (2005a) Evolutionary Pressures and a Stable World for Animals and Robots: A Commentary on Merker. *Consciousness and Cognition* 14:115– 118.
- Franklin S (2005b) Cognitive Robots: Perceptual associative memory and learning, *Proceedings of the 14th Annual International Workshop on Robot and Human Interactive Communication (RO-MAN 2005)*, pp 427-433.
- Franklin S, Baars BJ, Ramamurthy U, Ventura M (2005) The role of consciousness in Memory. *Brains, Minds and Media* 1:1–38.
- Franklin S, Ferkin MH (2006) An Ontology for Comparative Cognition: a Functional Approach. *Comparative Cognition & Behavior Reviews* 1:36–52.
- Franklin S, Graesser AC (1997) Is it an Agent, or just a Program? A Taxonomy for Autonomous Agents, *Intelligent Agents III*. Berlin: Springer Verlag, pp 21–35.

- Franklin S, Ramamurthy U (2006) Motivations, Values and Emotions: Three sides of the same coin, *Proceedings of the Sixth International Workshop on Epigenetic Robotics*, Vol 128. Paris, France: Lund University Cognitive Studies, pp 41–48.
- Gibson JJ (1979) *The Ecological Approach to Visual Perception*. Mahwah, New Jersey: Lawrence Erlbaum Associates.
- Glenberg AM (1997) What memory is for. *Behavioral and Brain Sciences* 20:1–19.
- Hofstadter DR, Mitchell M (1995) The Copycat Project: A model of mental fluidity and analogy-making. In Holyoak KJ, Barnden JAORoEe (eds), Advances in connectionist and neural computation theory, Vol. 2: logical connections. Norwood N.J.: Ablex, pp 205–267.
- James W (1890) *The Principles of Psychology*. Cambridge, MA: Harvard University Press.
- Kaelbling LP, Littman ML, Moore AW (1996) Reinforcement Learning: A Survey. Journal of Artificial Intelligence Research 4:237–285.
- Kamil AC (1998) On the proper definition of cognitive ethology. In Balda R, Pepperberg I, Kamil AO (eds), Animal cognition in nature: The convergence of psychology and biology in laboratory and field. New York: Academic Press, pp 1–28.

Kanerva P (1988) Sparse Distributed Memory. Cambridge MA: The MIT Press.

- Keller, B. L. (1985) Reproductive patterns. in Tamarin RH, (ed), Biology of new world *Microtus*. 8th edn. (American Society of Mammalogists, Special Publication, Lawrence, KS, pp 725-778.
- Kruschke JK (2001) Toward a unified model of attention in associative learning. Journal of Mathematical Psychology 45:812-863.
- Leonard ST, Ferkin MH (2005) Seasonal differences in self-grooming in meadow voles, *Microtus pennsylvanicus*. *Acta Ethologica*. 8: 86-91.
- Madison DM (1980) An integrated view of the social biology of meadow voles, *Microtus pennsylvanicus. The Biologist* 62:20-33.
- Maes P (1989) How to do the right thing. Connection Science 1:291–323.
- Maturana HR (1975) The Organization of the Living: A Theory of the Living Organization. *International Journal of Man-Machine Studies* 7:313–332.
- Maturana, H R, Varela FJ (1980) Autopoiesis and Cognition: The Realization of the Living, Dordrecht. Netherlands: Reidel.
- Meek LR, Lee TM (1993) Prediction of fertility by mating latency and photoperiod in nulliparous and primiparous meadow voles (*Microtus pennsylvanicus*). *Journal of Reproduction and Fertility* 97:353-357.
- Merker B (2005) The liabilities of mobility: A selection pressure for the transition to consciousness in animal evolution. *Consciousness and Cognition* 14:89–114.
- Milligan SR (1982) Induced ovulation in mammals. Oxford Reviews of Reproduction 4:1-46.
- Negatu A, Franklin S (2002) An action selection mechanism for 'conscious' software agents. *Cognitive Science Quarterly* 2:363–386.

Negatu A, McCauley TL, Franklin S (in review) Automatization for Software Agents.

- Pearce TC, Schiffman SS, Nagle HT, Gardner JW (2002) Handbook of Machine Olfaction: Electronic Nose Technology. Weinheim: Wiley-VCH.
- Pierce AA, Ferkin MH (2005) Re-feeding and restoration of odor attractivity, odor preference, and sexual receptivity in food-deprived female meadow voles. *Physiology and Behavior*. 84:553-561.
- Pierce AA, Ferkin MH, Williams TK (2005) Food-deprivation-induced changes in sexual behavior of meadow voles, *Microtus pennsylvanicus*. Animal Behaviour 70:339-348.
- Saksida LM (1999) Effects of similarity and experience on discrimination learning: A non associative connectionist model of perceptual learning. *Journal of Experimental Psychology: animal Behavior Processes* 25:308-323.
- Sheridan M,Tamarin RH (1988) Space use, longevity, and reproductive success in meadow voles. *Behavioral Ecology and Sociobiology* 22: 85-90.
- Skarda C, Freeman WJ (1987) How Brains Make Chaos in Order to Make Sense of the World. *Behavioral and Brain Sciences* 10:161–195.
- Sloman A (1999: What Sort of Architecture is Required for a Human-like Agent? In Wooldridge M, Rao AS (eds), *Foundations of Rational Agency*. Dordrecht, Netherlands: Kluwer Academic Publishers, pp 35–52.
- Tarsitano M (2006) Route selection by a jumping spider (*Portia labiata*) during the locomotory phase of a detour. *Animal Behavior* 72:1437–1442.
- Tulving E (1983) *Elements of episodic memory*. Oxford: Clarendon Press.
- Tulving E (2005) Episodic memory and autonoesis: uniquely human? in Terrace HS, Metcalfe J (eds), The missing link in cognition, New York, Oxford University Press, pp 3-56.
- Varela FJ, Thompson E, Rosch E (1991) *The Embodied Mind*. Cambridge, MA: MIT Press.
- Wilcox S, Jackson R (2002) Jumping Spider Tricksters: Deceit, Predation, and Cognition. In Bekoff M, Allen C, Burghardt GM (eds), *The Cognitive Animal*. Cambridge, MA: MIT Press, pp 27–33.
- Winston PH (1992): Artificial Intelligence, 3rd ed. Boston: Addison Wesley.
- Zhang Z, Dasgupta D, Franklin S (1998) Metacognition in Software Agents using Classifier Systems, *Proceedings of the Fifteenth National Conference on Artificial Intelligence*. Madison, Wisconsin: MIT Press, pp 83–88.