

Towards a Neurobiology of Creativity in Nonhuman Animals

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We propose a cognitive and neurobiological framework for creativity in nonhuman animals based on the framework previously proposed by Kaufman and Kaufman (2004), with additional insight from recent animal behavior research, behavioral neuroscience, and creativity theories. The additional information has led to three major changes in the 2004 model—the addition of novelty seeking as a subcategory of novelty recognition, the addition of specific neurological processing sites that correspond to each of the processes, and the transformation of the model into a spectrum in which all three levels represent different degrees of the creative process (emphasis on process) and the top level, dubbed innovation, is defined by the creative product. The framework remains a three-level model of creativity. The first level is composed of both the cognitive ability to recognize novelty, a process linked to hippocampal function, and the seeking out of novelty, which is linked to dopamine systems. The next level is observational learning, which can range in complexity from imitation to the cultural transmission of creative behavior. Observational learning may critically depend on the cerebellum, in addition to cortical regions. At the peak of the model is innovative behavior, which can include creating a tool or exhibiting a behavior with the specific understanding that it is new and different. Innovative behavior may be especially dependent upon the prefrontal cortex and/or the balance between left and right hemisphere functions.

Keywords: novelty, creativity, innovation, observational learning, animal cognition

Creativity in humans is defined in a variety of ways. The most prevalent definition (and the one used here) is that a creative act represents something that is different or new and also appropriate to the task at hand (Plucker, Beghetto, & Dow, 2004; Sternberg, 1999; Sternberg, Kaufman, & Pretz, 2002). Traditionally, the creative product should be considered new by experts in a given area (see, e.g., Kaufman, Baer, & Cole, 2009; Kaufman, Baer, Cole, & Sexton, 2008); however, more recent theorists have questioned whether a product's novelty to the creators may also be of importance (Kaufman & Beghetto, 2009). A recent survey of over 90 papers about human creativity offered the following synthesized definition: "Creativity is the interaction among aptitude,

process, and environment by which an individual or group produces a perceptible product that is both novel and useful as defined within a social context" (Plucker et al., 2004, p. 90). The question of "how new must a behavior be to be considered novel" is a currently debated issue in the study of human creativity. One model proposes eight different ways in which a creative contribution can propel a field (Sternberg et al., 2002). These range from the basic level of replicating past work to the extreme of completely redefining how a field is conceptualized. Working within the context of these definitions of creativity in humans for the purposes of building our animal model provides a bridge between literature on human creativity and research on innovation in animals. In addition, we have chosen this unique approach because it circumvents many of the questions in the literature on innovation in animals that still remain unanswered (e.g., Ramsey, Bastian, & van Schaik., 2007); these basic questions have largely been answered in the human literature. For example, the question of who is qualified to judge novel or creative behavior—a current issue raised by Ramsey et al. in animal research—has been extensively discussed, tested, and addressed in the human creativity literature (e.g., Amabile, 1982, 1996; Baer, Kaufman, & Gentile, 2004; Kaufman et al., 2009; Kaufman, Gentile, & Baer, 2005; Kaufman, Lee, Baer, & Lee, 2007). While we do not argue that all of human creativity theory is exactly applicable to animals on a point-for-point basis, we do argue that better use can be made of what has already been established in the area. In using this approach we can eliminate parts of human creativity theory that do not apply to animals and keep what does, as opposed to rebuilding the entire theory from the ground up.

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Our discussion of the neurological basis of creativity in animals is based on structures present in the primate brain. Several of the species discussed (e.g., birds, dolphins) do not possess these exact structures. In these cases, we ask the reader to assume we are referring to the appropriate analog in the specific species, even though the underlying circuitry may be quite different. We also hypothesize that distance along the spectrum (proposed below) may be linked to brain complexity, such that animals lacking certain structures or their analogs (e.g., insects or fish), may be limited in their ability to move along the spectrum.

Kaufman and Kaufman (2004) have proposed a three-part model of animal creativity in nonhuman animals (henceforth referred to as “animals”) that includes recognition of novelty (the realization that an object or experience is novel), observational learning (the additional of a novel behavior to an animal’s repertoire via the observation of another animal, regardless of the cognitive process involved), and innovation (highest level of creativity, with emphasis on the product of the creative process) as components of behavior that contribute to the production of creative acts (see Figure 1). Here we describe an extension of the original model of animal creativity that is based on a synthesis of available research on creativity in both animals and humans and on the addition of neurobiological information.

The first modification to the original model is one of structure. In this paper, we have altered the appearance of the model to create a spectrum (see Figure 2). We argue that the “levels” in the original model (novelty recognition, observational learning, innovation) represent degrees on a spectrum; all are to some degree creativity, with the differentiating variable being the amount of correlated cognitive capacity (note that this causes “innovation” to be characterized as a subset of the general creative process; more on this later). This also allows for the idea that exhibiting behavior at each level of the model does not necessarily require mastering the previous level—that is, each level is, by itself, necessary and sufficient for creative behavior (see Figure 3 for examples of behaviors at each level of the model). For example, one does not necessarily have to master observational learning to be innovative, though we believe this situation to be the rare exception (we will use the term “level” throughout the course of this paper to describe the three divisions along the spectrum, as, despite the fact that the model is not a hierarchy, “level” still appears to be the most appropriate term).

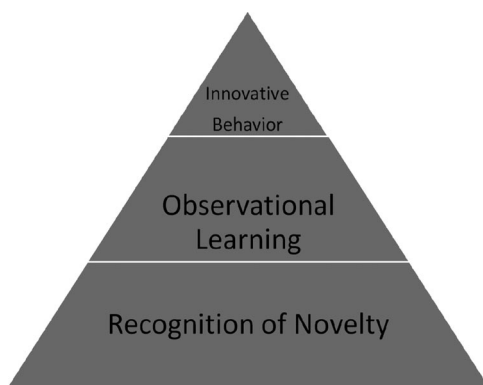


Figure 1. Original Kaufman and Kaufman (2004) model of animal creativity.

The second major change to the Kaufman and Kaufman (2004) model is the additional of correlating neurobiological data. We have compiled information on the specific behavioral and neurobiological correlates of each of the model’s three levels. One direct result of this is the addition of the *novelty seeking* classification to recognition of novelty (see below). It is also our goal to incorporate specific brain structures and processes into the model with hopes of encouraging collaboration between neuroscientists and creativity researchers. Such collaboration would allow work that is more theory-driven on creativity and the brain (e.g., Andreasen, 2005; Ardena, Chavez, Grazioplene, & Jung, 2010; Dietrich & Kalso, 2010; Heilman, 2005; Kaufman, Kornilov, Bristol, Tan, & Grigorenko, 2010) to be examined at structural and mechanical levels.

Lastly, the updated model formally incorporates the above mentioned novelty seeking as a subset of novelty recognition. Our neurobiological research provided evidence that the neurological location for the processing of novelty seeking is separate from that of the realization that an item or experience is novel, confirming previous suspicions based solely on behavior. Thus, it seemed appropriate to create a formal distinction defining novelty seeking as the act of looking for an object or experience that is novel (independent of the ability to determine if it is or is not actually novel). We do not wish to completely remove the act of novelty seeking from the overall category of novelty recognition; we merely intend to create a distinction for the purposes of discussion of behavior and neurological processes. Novelty seeking remains within the scope of novelty recognition. In addition, this allows the exploration of specific situations such as risk taking behavior, seeking novelty but failing to recognize it, and recognizing novelty without having sought it.

The goal of the original model and our work here is to integrate existing ideas on creativity in animals. There is an abundance of papers concerned solely with a particular aspect of creativity, but little research on the broader perspective offered by our model, which describes novelty recognition, observational learning, and innovation as different aspects or varying degrees of creativity. Reader and Laland (2003a) provide an excellent overview of the issues and problems integral to the study of creativity in animals. The extensive level of detail in this volume makes it vital for anyone conducting research in these specific areas. However, its breadth, for good reason, makes it impossible to provide an overarching perspective. By using a broad comparative perspective, including a comparison to humans, we hope to enhance the literature.

More recently, Ramsey et al. (2007) attempted to define and operationalize innovation in animals; but they did not include a comparison to research on creativity in humans, which has focused extensively on defining and operationalizing creativity. Because of this, the authors are unaware of the “appropriateness” characterization used in nearly all definitions of creativity in recent literature (Kaufman, 2009; Sternberg et al., 2002). For us, this is a particularly vital distinction when dealing with animals because an inappropriate innovation is likely to have a serious impact on survival. Lastly, we hope to add to the discussion begun by several of Ramsey et al.’s (2007) commentators who feel that their dismissal of novelty recognition and observational learning as forms of creativity is a serious flaw in

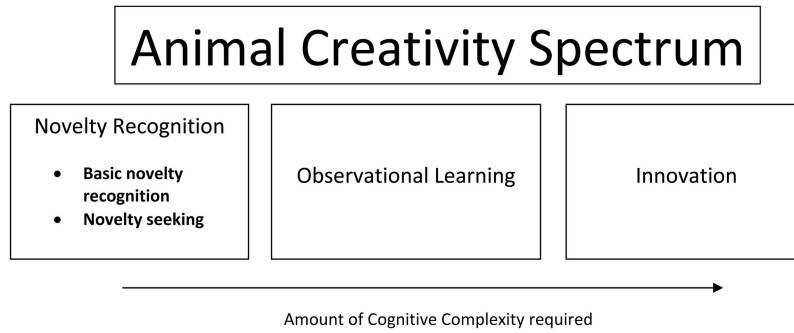


Figure 2. Newly conceptualized model of animal creativity.

their model (Logan & Pepper, 2007; Mettke-Hofmann, 2007; Viciano & Claidiere, 2007).

Novelty Recognition and Novelty Seeking

The ability to detect novelty has been argued to be a fundamental characteristic of the mammalian nervous system (Sokolov, 1963) and has been studied at length in both humans and other mammals. For example, both chimpanzees (*Pan troglodytes*; Menzel, Davenport, & Rogers, 1961) and free-ranging Japanese ma-

caques (*Macaca fuscata*; Menzel, 1966) have been found to spend more time manipulating unfamiliar objects than familiar ones, indicating an acknowledgment of the new stimulus cues being presented.

Novelty seeking and novelty recognition can be displayed independently of each other. For example, an individual can realize something in an environment is new without actually seeking it out—this may be evidenced by the startle response in which an individual (human or animal) is surprised by an unexpected event

Type	Definition	Example
Recognition of Novelty		
Basic novelty recognition	The ability to tell that something in the environment is different than it was previously. This ability to assess one’s environment is, at a very fundamental level, a form of the creative process.	While the cognitive faculty in and of itself cannot be observed, it often results in observable behaviors such as neophobia or neophilia.
Novelty seeking	This process may range from basic neophilia to risk taking behaviors and the personality trait “openness to experience”; all highly correlated with creativity. Some risk taking may not be thought of as “appropriate”, and therefore would not be a part of the creative process. The idea of novelty seeking is also more concerned with the process of finding novel items/experiences than with the attraction to said item or experience.	The creation of novel courtship displays by bowerbirds, a process in which males seek to create a novel courtship dance. While novelty generally has a positive effect on mating success, it is also risky because too much novelty may deter a female (Patricelli, Coleman, & Borgia, 2006), making the risk inappropriate.
Observational Learning	The addition of a novel behavior to an individual’s repertoire via the observation of another.	Transmission of tool use (such as use of hammer stones to break open nuts) within a population of capuchin monkeys (Biro et al., 2003; Ottoni, Resende, & Izar, 2005).
Innovation	The pinnacle of the creative process; focuses specifically on the result of this process, or the creative <i>product</i> .	Creation or modification of a tool for a specific purpose, such as bending a straight wire to “hook” food or unbending and re-bending an inappropriately shaped wire (Weir & Kacelnik, 2006).

Figure 3. Levels, definitions, and examples of the creativity spectrum.

(in other words, one novel to the situation). Likewise, it is possible to explore a familiar environment, looking for something that might be different, but fail to recognize differences when they do occur. For example, amnesiac humans with damage to the medial temporal lobe do not show normal enhancement of memory for novel objects or events, suggesting a failure to recognize their novelty (Kishiyama, Yonelinas, & Lazzara, 2004).

Highlighting novelty seeking in this manner also allows us to explore risk taking, which can be seen as an extreme form of novelty seeking. It is here that there is neurological divergence as well: novelty seeking is based in the dopamine system, while recognition critically depends on the hippocampus. Additionally, extensive research has been done on the dopaminergic activity associated with high and low risk taking, and there are interesting implications for the creative process.

Novelty Recognition

In this section we will expand on two traits vital to novelty recognition—neophobia/neophilia, and the acquisition of knowledge. Recent theories on creativity in humans are expanding the scope of what can be considered creativity. The definition of mini-c creativity in Kaufman and Beghetto's (2009; Beghetto & Kaufman, 2007) Four-C model of creativity over the life span stresses the importance of personal (or subjective) judgment of novelty and meaningfulness. This focus on subjective judgment distinguishes mini-c creativity from more objective expressions of creativity in which the novelty and meaningfulness of the outcome require external judgment. Therefore, even such basic components as seeking out new things or having a keen awareness of what is new or old are part of mini-c. In animals, these very individualized judgments of novelty can be expressed as neophobia or neophilia. Greenberg (2003) defines neophilia as an animal being spontaneously attracted to novel foods, objects or places, and neophobia as an animal displaying some aversion to approaching novel foods, objects, or places.

While the ideas of neophobia and neophilia might appear to be at opposite ends of a spectrum, they can coexist and, in the animal world, the ability to balance the two will lead to higher chances for survival in difficult situations. According to Greenberg and Mettke-Hoffman's (2001) model, when ecological pressures exist where exploration is key to survival (e.g., variable resources, island colonizers), but where said exploration is also associated with greater risks (e.g., increased competition or predation), species do best to have high levels of both neophilia and neophobia. For example, when Russel, McMorland, and MacKay (2010) fitted rats (*Rattus norvegicus*) with radiotransmitters and introduced them to a mammal-free island, the greatest recorded time of exploratory travel occurred during the first week postrelease, indicating a recognition of the environment's novelty. This behavior is neophilic, despite the fact that it occurs under ecological pressures which evoke neophobic responses. In addition, neophilia is linked to both the tendency to engage in problem solving (Greenberg, 2003), and problem solving abilities in and of themselves (that can lead to innovative behavior, as, e.g., Köhler's, 1925, insight work with chimpanzees). Explorations into neophobia and neophilia may well be accomplished via play behaviors, which in turn would encourage familiarity with items that might be used to develop tools (Burghardt, 2005).

Novelty detection is also linked to knowledge acquisition; that is, knowledge grows with exposure to novel stimuli or events. Knowledge is a component of most theories of creativity and has been identified as one of six basic requirements for creativity by Sternberg and Lubart (1996).¹ In addition, knowledge is required to be creative in a specific area, and to gain knowledge it is necessary to be able to recognize what is new and what is not. In fact, empirical analysis of creative genius shows that it takes an average of 10 years of experience in a field to amass sufficient knowledge to make creative contributions to that field (Hayes, 1989; Simonton, 2000). Lastly, there is, the concept of "problem finding" that been proposed as a key precursor to creative problem solving in humans (Carson & Runco, 1999; Runco & Nemiro, 1994).

Creative problem-solving is often conceptualized as a five-stage model (Wallas, 1926). First is *preparation*, in which the initial work commences. Next is *incubation*, in which the mind may focus on other tasks but continues to consider the task at hand. In *intimation*, one anticipates the coming breakthrough (this stage was dismissed by Hadamard, 1954). Next is the key insight in the *illumination* phase and the empirical testing in the *verification* stage.

Experts spend more time in the preparation (or planning) phase of a task than do novices (Gobet & Simon, 1996). This trend has also been evident in the completion of the creative work itself (Redmond, Mumford, & Teach, 1993). Caughron and Mumford (2008), in studying how planning impacts creative performance, found evidence for the importance of problem finding. Participants showed higher problem solving creativity when asked to focus on possible problems that might arise rather than when asked to plan the tasks that needed to be performed. The idea of problem finding is a direct application of the ability to recognize a novel situation and gather knowledge about it.

This phenomenon is evident in animal studies as well. Russon (2003) asserts that innovation in orangutans (*Pongo pygmaeus*) is a product of the combination of previously learned behavior. Kummer and Goodall (1985) also include basic skills in their discussion of conditions necessary for innovation, and very early in the study of animal innovation, combinations of established behaviors were evident in classic experiments like those of Köhler (1925). Lastly, experimental evidence in callitrichid monkeys shows a correlation between exploration/innovation and age, but not neophilia; the variability in amount of innovation is age and experience, not interest in new things (Kendal, Coe, & Laland, 2005).

Novelty Recognition and the Hippocampus

Our efforts to identify potential neural substrates of creativity in animals begin with a discussion of hippocampal involvement in novelty detection and recognition. The ability to detect novel events or stimuli has been linked to the broader class of memory known as declarative memory, or memory for both autobiographical experience and for knowledge about the world. In mammals, the formation and storage of declarative memory depends on medial temporal lobe

¹ Traditionally meant to mean acquired knowledge, not congenital knowledge.

structures including the hippocampus and the adjacent entorhinal, perirhinal, and parahippocampal cortices (Zola-Morgan & Squire, 1993). Recognition memory or the ability to recognize objects or events as novel appears to involve the same neural structures as those that mediate declarative memory (Aggleton & Shaw, 1996).

Several brain regions have been implicated in novelty processing, and it has been suggested that these regions represent a distributed network for novelty detection (Knight & Nakada, 1998). This network includes areas in the lateral and orbital prefrontal cortex, anterior insular and anterior temporal cortex, temporoparietal cortex, cingulate gyrus, amygdala, parahippocampal gyrus, and the hippocampal formation itself (Ranganath & Rainer, 2003). Of these, the hippocampus and surrounding hippocampal cortices appear to show the clearest relationship to novelty detection in animals (see Squire, Wixted, & Clark, 2007). For example, selective hippocampal lesions have been reported to impair recognition memory performance in humans (Manns, Hopkins, Reed, Kitchener, & Squire, 2003), nonhuman primates (Nemanic, Alvarado, & Bachevalier, 2004; Zola et al., 2000), and rodents (Clark, West, Zola, & Squire, 2001; Clark, Zola, & Squire, 2000; Gould et al., 2002; Zola et al., 2000). The hippocampus also shows changes in regional blood oxygenation in response to the presentation of novel stimuli in humans (Yamaguchi, Hale, D'Esposito, & Knight, 2004). Furthermore, functional MRI (fMRI) studies in the hippocampus and in the surrounding parahippocampal region have demonstrated novelty responses for objects and for relationships among objects (e.g., Kohler, Danckert, Gati, & Menon, 2005; see also Pihlajamaki et al., 2005).

Kohler et al. (2005) provided evidence that several regions of the hippocampal formation in humans show selective novelty responses depending upon whether the stimuli presented were novel in terms of stimulus relationships or in terms of the identity of single objects themselves. A region in the right medial hippocampus, for example, responded to the novelty of spatial and nonspatial relationships, but not to the novelty of individual objects. In contrast, a region in the right perirhinal cortex responded to the novelty of individual objects, but not to relationships among those objects.

Nonhuman primates with hippocampal damage are significantly impaired in delayed nonmatching to sample tasks that depend on recognition memory (Zola et al., 2000). The rat hippocampus is similarly involved in novelty detection. For example, infusions of the cholinergic antagonist scopolamine into dorsal CA3 cause deficits for both spatial and nonspatial novelty detection for visual objects. Conversely, the cholinergic agonist physostigmine enhances both spatial and nonspatial visual object novelty detection (Hunsaker, Rogers, & Kesner, 2007). These results show that cholinergic modulation in the hippocampus significantly contributes to novelty detection. The perirhinal cortex, which interacts directly with hippocampus, similarly plays an essential role in rats' ability to discriminate the familiarity of objects (Mumby, Glenn, Nesbitt, & Kyriazis, 2002).

Novelty Seeking

In addition to novelty recognition per se, novelty seeking can play a role in the emergence of innovative behavior in animals. Neophilic animals, by definition, encounter more novelty than their normal conspecifics. Research in humans has shown a distinct correlation between innovation and experience with novelty (Amabile, 1996). It is likely that novelty seeking is similarly

related to innovative behavior in animals, and that it could be considered a trait that is indicative of an animal that is more likely to engage in innovative behavior, just as it is indicative of an animal more likely to engage in problem solving (Greenberg, 2003). Studies of creative people indicate that not only do they crave a variety of stimulation, but they also require high amounts of exploration (Pufal-Struzik, 1996).

The connection between novelty seeking and creativity can be observed when studying creative personalities (Feist, 2010). In humans, personality is most often measured via the "Big Five" personality factors: emotional stability, extraversion, openness to experience (sometimes just called openness), conscientiousness, and agreeableness (Goldberg, 1990; McCrae & Costa, 1997). Although there is extensive research on how all five factors relate to creativity (e.g., Feist, 1998), the strongest and most-studied association is with openness to experience. The openness to experience factor is split into several subcomponents, one of which is *actions*, the idea of trying new things and having many interests (McCrae, 1987). This actions subcomponent can almost be seen as a direct parallel to neophilia in animals, because these animals are, quite literally, acting on their interest in new environmental conditions or objects. Other direct comparisons between human and animal personality traits include the comparison of the factors *affiliative*, *hostile*, and *fearful* (Chamove, Eysenck, & Harlow, 1972) to Eysenck and Eysenck's (1985) *extraversion*, *psychoticism*, and *neuroticism* (Dellu, Mayo, Piazza, Le Moal, & Simon, 1993), as well as several behavioral characteristics that appear to be comparable in rats and humans (Dellu et al., 1993; Garcia-Sevilla, 1984).

Mice have been shown (both genetically and behaviorally) to possess two very stable personality factors—activity and anxiety (Ramos & Mormède, 1998). However, more recent experiments, which added an exploratory component to testing, uncovered a third factor that was dubbed novelty seeking, providing empirical support for the personality trait parallel (Ibáñez, Ávila, Ruipérez, Moro, & Ortet, 2007; Ibáñez, Moya, Ávila, Moro, & Ortet, 2009). One of the more common ways of defining creativity in humans is the aforementioned "novel and appropriate" characterization (Sternberg et al., 2002). We suggest that although novelty seeking is *one* component of creative behavior, it may not always be considered actually creative. For a behavior to be creative it must also be appropriate to the situation. If novelty seeking can be likened to risk taking (that we believe it can, particularly when investigating a novel situation may get one killed), then appropriateness can be likened to sensibility, and a risky idea or act can only be called innovative if it is sensible. Indeed, Garamszegi, Eens, Török, and Tregenza (2008) believed they may have provided evidence of this scenario in the field, showing correlations between risk taking behavior in exploration, aggression, and choice of singing perch; birds who risked predation by singing from perches lower to the ground also established pair-bonds faster than their conspecifics. Their work has also empirically supported the idea that novelty seeking and risk taking are intimately related to both each other and to an individual's well being (Garamszegi, Eens, & Török, 2009).

We propose that risk-taking and sensible risk-taking fall in different areas of the model and require different cognitive capabilities (see Sternberg, Kaufman, & Grigorenko, 2008). For example, the Japanese dish fugu is a particular cut of blowfish that, if

prepared incorrectly, can be deadly. Deciding to use a novel method to prepare fugu (that would be novelty seeking as defined by the lowest level of the model) can only really be considered innovative (as defined by the top of the model) if it is sensible, or appropriate to the task—that is, the task of eating and not dying. Zuckerman (1994) has proposed a sensation seeking trait that would highly correlate with this openness to experience factor. There are four dimensions of sensation seeking: *boredom susceptibility*, *disinhibition*, *experience seeking*, and *thrill and adventure seeking*. While experience seeking is the dimension seemingly most related to creativity in a traditional sense, it is not hard to see how thrill and adventure seeking and boredom susceptibility are related to risk taking behavior.

Novelty Seeking, Risk Taking, and the Dopamine System

Risk taking can be seen as an extreme form of novelty seeking, which is linked to high dopamine levels and activation of the reward pathway, particularly in the basal ganglia, including the nucleus accumbens (Bardo, Donohew, & Harrington, 1996; Flaherty, 2005). In rats, novelty seeking behavior can be attenuated pharmacologically by blocking dopamine receptors, demonstrating the dopaminergic control of novelty seeking (Self, 2004). In particular, the mesolimbic dopamine system has been implicated in mediating novelty seeking behavior. Specifically, dopamine antagonists injected into the nucleus accumbens in rats decreased novelty-induced locomotor activity in an open field test (Hooks & Kalivas, 1995).

The role of the dopamine system is further demonstrated in experiments where dopamine antagonist drug treatment disrupted novelty seeking behavior in rodents by blocking the positive incentive value of novelty (Bardo et al., 1996), without affecting locomotor activity (Bardo et al., 1993; Misslin, Ropartz, & Jung, 1984). Damage to the mesolimbic dopamine system also disrupts novelty seeking behavior. For example, excitotoxic damage to the dopamine system causes a reduction in locomotor and rearing behavior in novel environments (Fink & Smith, 1979a). Dopamine system lesions also disrupt exploration of novel objects in rats (Fink & Smith, 1979b). Among the many subtypes of dopamine receptors, dopamine D1 receptors are critical for the expression of novelty seeking behavior. Studies have found that the D1 antagonist SCH 23390 blocks novelty seeking behavior in rats without affecting locomotor activity (Bardo et al., 1993). Dopamine receptor activation appears to influence novelty seeking behavior by mediating the positive incentive or rewarding properties of novelty itself (Bardo et al., 1996). Indeed, dopamine activity has been linked to the process of reinforcement in several studies (Delgado, 2007; Schultz, 1997). In addition to dopamine's role in novelty seeking, the reinforcing properties of dopamine are implicated in both drug-seeking and risk-seeking behavior.

Observational Learning

As discussed in our original model of animal creativity, observational learning is the addition of a novel behavior to an individual's behavioral repertoire via watching another, irrespective of the cognitive processes used in the learning of this behavior (Kaufman & Kaufman, 2004). While this ability may not be strictly required

to produce an innovative product (the top level of the model), we argue that it is part of the creative process. As previously mentioned, studies of professional trajectories show that approximately 10 years is required from the time a person enters a field to amass the knowledge required to make any kind of substantial contribution (Bloom, 1985; Hayes, 1989). According to this "ten year rule," these years are spent learning the mechanics of the field, discovering all of the practical issues that cannot be taught in a book, and extensively plying one's trade. These 10 years do not represent a basic "how to" apprenticeship; rather, these are years of active experimentation and new ideas (Gardner, 1993). They are years spent engaging in observational learning. An individual (human or nonhuman) completely isolated from others could eventually gain enough information to innovate through trial and error (an innovation that would, indeed, "count" as innovation on a small, individual scale); however, the process can be greatly expedited by observing another, more experienced individual.²

In humans, observational learning studies have demonstrated the potent effect of modeling on creativity. For example, Bandura's (1986) Social Cognitive Theory discusses learning via both behavioral and cognitive modeling, and hypothesizes that people are likely to engage in a behavior after either method of modeling—the important factor is that the behavior is modeled at all. Studies have shown an increased likelihood of creative behavior following individuals' observation of creative role models (Simonton, 1975, 1984), junior scientists' observation of senior scientist mentors (Hooker, Nakamura, & Csikszentmihalyi, 2003), as well as individuals' observations of modeled creative techniques or solutions in rater-judged creativity situations (Anderson & Yates, 1999; Belcher, 1975; Harris & Evans, 1974; Shalley & Perry-Smith, 2001; Zimmerman & Dialessi, 1973). Belcher (1975) compared groups of children who either saw a video demonstrating creative behavior, saw a video talking about creative behavior, or read a book designed to promote creative ideas. The children who saw the video demonstrating creative behavior scored higher on tests of creativity than both of the other groups of children (the test for creativity was in no way related to the creative activities the children saw or read about). Because of studies such as these we feel comfortable hypothesizing that observation of creative acts promotes creativity in animals, just as it does in people. In addition, this phenomenon was noted by Reader (1999). This jump is necessary—albeit large—for the time being, as we found only a single study addressing this issue in animals. That study, concerned with stimulus enhancement, supports our theory that observation of creativity causes an increase in creativity of conspecifics. Specifically, object manipulation by naïve long tailed macaques (*Macaca fascicularis*) increased as they watched another engage in tool use. Interestingly, in this study, the naïve

² It is important to note that the level of creative eminence is directly related to the importance of novelty. Kaufman and Beghetto (2009) proposed a 4-C development model that discusses mini-c (personal creativity), little-c (everyday creativity), Proc (expert creativity), and Big-C (legendary creativity). At the mini-c level, an idea only needs to be new to the person having that idea. It does not need to be objectively novel. At higher levels, a creative idea typically needs to be new to the field to be considered creativity. Simonton (2008) has noted some exceptions, such as *zeitgeist* and chance, in which different people arrive at the same idea nearly simultaneously.

animals' manipulations were novel as compared to those of the tool user (Zuberbühler, Gyax, Harley, & Kummer, 1996).

Observational learning in animals can be differentiated from imitation because learning is not necessarily specific to an exact behavior. Learning is more environment- or process-oriented (Heyes, 1993; Tomasello, 1999). For this reason, observational learning is appropriate in a creativity spectrum, in contrast to the more product oriented imitation replication of a behavior as a means toward a very specific end (Kuczaj, Paulos, & Ramos, 2005). However, imitation in animals is an extremely complicated and much debated topic, and the distinction between mimicry and imitation with intent is particularly hard to discern (Tomasello, 1996; Whiten & Ham, 1992). According to Kuczaj and Yeater (2006):

[While] it is clear that many species can learn via observational learning, there is a lack of consensus concerning both what sorts of things can be learned by watching others and what types of observational learning should "count" as imitation. These disputes have led to disagreements about the extent to which various nonhuman species engage in imitation, based in large part of different definitions of imitation (p. 413).

In animals, the term "observational learning" represents a broad construct referring to the observation-dependent acquisition of behaviors ranging from comparatively simple contextual fear conditioning (see Guzmán et al., 2009), to more complex spatial learning (see Petrosini et al., 2003), to the observational learning of highly complex tool use (see Mitchell, Thompson, & Miles, 1997; Price, Lambeth, Schapiro, & Whiten, 2009). For the purpose of this paper (and for simplicity's sake), we will use the term observational learning to mean simply the addition of a novel behavior to an individual's behavioral repertoire via watching another, irrespective of the cognitive processes used in the learning of this behavior (see Kuczaj, Makecha, Trone, Paulos, & Ramos, 2007; Kuczaj & Yeater, 2006).

The importance of members of a species demonstrating observational learning is great, as observational learning usually implies heightened levels of cognition and the possibility for the development of traditions or "culture" within a group (Whiten & Van Schaik, 2007). Sargeant and Mann (2009) supported these notions with their long-term study on wild bottlenose dolphins' (*Tursiops* sp.) foraging behavior. As predicted, individual females used diverse, specific foraging types of behavior that were observed and more likely to be adopted by offspring. This type of observational learning was hypothesized by Sargeant and Mann to be important in the development of traditions or culture in the group, and thus indirect evidence for higher cognition.

In apes, monkeys, and dolphins (e.g., Inoue-Nakamura & Matsuzawa, 1997; Ottoni, Resende, & Izar, 2005; Yeater & Kuczaj, 2010), observational learning of skilled tool users by novices suggests a directed motivation to learn from more proficient members of the group. Ottoni et al. (2005) demonstrated this with provisioned wild capuchins (*Cebus apella*) by showing that novices preferred to observe a more skilled conspecific 76% of the time during tool use events (in this case nutcracking). This is presumably indicative of an attempt to learn via observation. Additionally, observational learning of tool use is not limited to the young or even inexperienced; it is consistent instead with cognitive development and continues into early adulthood (Russon, 2006).

Beck (1980) provides a detailed review of tool use by the above, as well as numerous other species. Because of the taxonomic diversity featured in his review, and because tool use appears to spread within a population via observational learning, it is logical that observational learning arose analogously in these species, as opposed to from a common ancestor.

Observational Learning and the Cerebellum

Evidence suggests that the cerebellum is involved in the link between seeing and doing—or processing movements and behavior that have been observed, for the individual to produce them later. The cerebellum is also critically involved in the internal representation of action, an ability used to understand and learn the skills of others by observation (Petrosini et al., 2003). The critical role in observational learning played by the cerebellum is suggested by a number of experiments on spatial learning. Lesion studies in rats show that an intact cerebellum is necessary for observational learning in spatial tasks. Leggio and colleagues (2000) allowed normal rats to observe another rat perform several spatial navigation trials in the Morris water maze. This procedure is known to result in significant "savings" in the observer animal, such that subsequent performance is far superior to that seen in naïve rats. The rats then received lesions of the cerebellum, and upon recovery, were tested for the first time in the Morris water maze. These rats displayed no defects in spatial learning or in exploration, and, importantly, benefited from the prelesion observation as much as controls. However, when the cerebellar lesion preceded observation training, rats showed a complete lack of spatial observational learning. Thus, just as these researchers previously found that the acquisition of spatial procedures through experience depends on cerebellar circuits (Petrosini et al., 2003; Petrosini, Molinari, & Dell'Anna, 1996), results from this experiment suggest that these same circuits play a critical role in the acquisition of spatial procedures through observation. Based on these findings, Leggio et al. concluded in this study that cerebellar circuitry provides a common neural basis for the observation of actions that are to be reproduced and for the actual production of those actions.

In addition to subserving both experience-based learning and observational learning in spatial navigation, the cerebellum is similarly involved in learning to use tools. Indeed, the tendency for tool use varies along with the morphology of the cerebellum across a number of different species. Iwaniuk, Lefebvre, and Wylie (2009) note that although previous research found no reliable correlation between overall cerebellar volume and tool use, they have discovered a strong correlation between tool use and the overall length of cerebellar foliation or lobules created by the folding of cerebellar cortex in birds and mammals. As with the cerebral cortex, greater degrees of infolding of the cerebellar cortex provide more surface area and consequently greater potential for information processing. Iwaniuk et al. argued that if the evolution of tool use is correlated with relative cerebellar cortex length, then species that use tools often will have greater levels of cerebellar foliation than species that rarely or never use tools. When they compared the degree of cerebellar foliation in a large number of different types of birds, they found that the degree of cerebellar foliation was greatest in parrots, corvids, and gulls, birds that are renowned for their intelligence. Moreover, they reported a direct

evolutionarily correlation between cerebellar foliation in different bird taxa and tool use itself.

Neuroscience studies in monkeys and humans provide additional evidence that the cerebellum is critically involved in tool use. For example, there is a significant increase in cerebellar activity during tool use in monkeys (Obayski et al., 2001) and humans (Imamizu, Kuroda, Miyauchi, Yoshioka, & Kawato, 2003). Given the role of the cerebellum in tool use, it is reasonable to expect that this brain structure is also involved in observational learning of tool use. Consistent with this position, positron emission tomography (PET) scans of the brains of monkeys made during a novel tool use task revealed increased activity in the right cerebellum, in addition to activation in the prefrontal cortex, intraparietal sulcus, and early visual cortices (Obayski et al., 2001). Based partly on these findings, the authors suggested that effective, appropriate use and modification of tools depends on interactions between the fronto-cerebellar and fronto-parietal circuits.

While the cerebellum is essential to the motor requirements of tool use, other brain structures have been directly implicated in the ability to learn to use tools through observation of others. In particular, a special class of visuomotor neurons, neurons termed “tool-responding mirror neurons,” has been identified in the lateral sector of monkey ventral premotor area F5 (see Ferrari, Rozzi, & Fogassi, 2005). Broadly, mirror neurons are believed to be involved in understanding the behavioral actions made by others by matching the visual description of an action with the internal motor representation of the same action in the observer (Arbib, 2005; Mitchell, 2007; Rizzolatti, Fogassi, & Gallese, 2001). Tool-responding mirror neurons became active when a monkey observed actions performed by a human experimenter using a tool (e.g., stick or pliers). This neuronal response exceeded that recorded when the monkey observed a similar action made with the hand (or the mouth) but without the tool. These neurons responded also when the monkey itself executes the action. These findings suggest that tool-responding mirror neurons afford the observing monkey with the ability to represent the movements of others and, in turn, to use those representations to guide their own actions. Furthermore, this ability to translate others’ movements into their own movements extends beyond the motor representations of their body to include representations of tools used by others as they relate to their own movements. The existence of these highly specialized neurons illustrates the critical role that the motor cortex plays in understanding action goals (Ferrari et al., 2005).

Innovation

In this part of the model, we use the term “innovation” to denote product or outcome, as opposed to the more process-oriented term “creativity,” which we use to characterize the spectrum of behavior addressed by the three-level model described herein. This distinction between creative processes and creative product is common in human creativity research (e.g., Kaufman & Baer, 2006), and is also discussed in reference to animals by Reader and Laland (2003b).

One early attempt to characterize innovation in animals was provided by Mitchell (1987), who published a framework describing imitation in animals. Mitchell’s model focused on imitation and therefore described the creative product, as opposed to the

creative process or behavior. One reason why the creative product is a more appealing basis for a model is that it is much easier to measure a creative product, whereas techniques to code or assess the creative process are still rudimentary and require a high level of communication with the creator (Kaufman, Plucker, & Baer, 2008). Mitchell described five levels of imitation: mimicry (such as what is seen in the coral snake and kingsnake, where the nonvenomous kingsnake is nearly indistinguishable from the venomous coral snake); recreation of a model, recreation of a model and subsequent modification upon comparison to the original model, copying to achieve the same goal with a slightly different method; and planned imitation (Mitchell, 1987). The second level of our model encompasses these classifications, and benefits from Mitchell’s earlier work. For example, we see parallels in both models such as the consideration of the required degree of cognitive functioning at each level, the integration of modeling, the recognition of learning and evaluation processes, and the acknowledgment of the existence of spontaneous or self-motivated imitation.

More recently, Russon, Kuncoro, Ferisa, and Handayani (2010), in a paper aimed at cataloging innovations involving water by orangutans, have provided what we see as an extremely promising methodology for defining innovation using four categories—the application of old means to new ends, accidental innovation, independent problem solving, and social problem solving (“cross fertilization”). These categories were developed using literature from both human and animal worlds.

In both humans and animals, innovation can be goal-directed. Arguably one of the most famous examples in animals is Köhler’s (1925) work on insight in chimpanzees. In these experiments, chimpanzees were placed in a room in which a banana was suspended from the ceiling just out of reach. Also in the room were a number of boxes. Köhler observed the subjects “studying” the situation for several minutes and then suddenly executing a sequence of behaviors. The chimpanzees pushed the boxes under the banana, stacked them, and then climbed up and reached for the banana. This study in and of itself may be doubted for lack of appropriate experimental controls; however, its conclusions were supported by the experimental work of Schiller (1957). Additionally, when Epstein, Kirshnit, Lanza, and Rubin (1984) (dedicated Skinnerians) repeated the procedure with pigeons (*Columba* sp.), they drew similar conclusions about creative problem solving abilities.

Innovation has since been observed in other situations. A variety of species have shown a diverse range of foraging innovation (Borsari & Ottoni, 2005; Fitzpatrick, 1979; Grieg, 1979; Lefebvre, 1995; Stewart, Gordon, Wich, Schroor, & Meijaard, 2008; Vos, Quakenbush, & Mahoney, 2006); tool innovation (Waga, Dacier, Pinha, & Tavares, 2006; Weir & Kacelnik, 2006); innovative defense tactics (Boinski, 1988; Moura, 2007); innovation in mate choice (Orrell & Jenssen, 2002); innovative pilfering techniques by ravens (*Corvus corvus*) in response to situational changes (Bugnyar & Heinrich, 2006); as well as innovative pretend play, such as Koko, a captive gorilla (*Gorilla gorilla*), holding a toy alligator to her nipple and signing “drink” (Matevia, Patterson, & Hillix, 2002). Very recently, tool use was documented for the first time in an invertebrate, the veined octopus (*Amphioctopus marginatus*), of which several individuals were observed (independently of each

other) purposefully transporting coconut shells to build shelters and/or places to hide (Finn, Tregenza, & Norman, 2009).

Male Australian satin bowerbirds (*Ptilonorhynchus violaceus*) invest large amounts of energy and resources in creating elaborate nests to attract mates. After building these nests, the male birds spend time at the nest displaying patterns of behavior intended to further attract females. Studies have shown that novel behavioral displays, and novel or exotic objects and colors incorporated into the nests, significantly increase a male's chance of acquiring a mate (Borgia, 1985; Endler & Day, 2006). Not only is this a novel, goal-directed behavior, but it also incorporates an assessment of appropriate risk taking. For example, a behavioral display or nest that is too elaborate might attract unwanted predators in addition to female bowerbirds (Zahavi, 1975). Such excessive or elaborate behavior, while novel, would not be deemed innovative because it is ultimately not appropriate to the task of finding a mate.

Bowerbird studies have also shown that males will adapt their displays when females appear to be startled by enthusiasm or intensity. This finding demonstrates that the probability of modifying behavior can be influenced by situational occurrences (Patricelli, Coleman, & Borgia, 2006). As noted above, this ability to change behavior concurrently with the environment is also present in ravens (Bugnyar & Heinrich, 2006). Such innovation in mating behavior has only been reported in two other nonhuman species—chimpanzees and, recently, Amazon River dolphins (*Inia geoffrensis*). Both of these species use sticks and branches in courtship displays (Ingmanson, 1996; Martin, da Silva, & Rothery, 2008). Lastly, it appears that male bowerbirds with superior problem solving abilities are more likely to successfully mate (Keagy, Savard, & Borgia, 2009). Similar trends have been found in people; research indicates that creative people tend to have more sex than less-creative people (Nettle & Clegg, 2006).

Innovation by captive animals is also prevalent. Captive animals can be taught to innovate by being reinforced for “doing something new,” where the criteria for reinforcement is to exhibit an action that has not been displayed before (see Pryor, Haag, & O'Reilly, 1969). This training method has been used successfully in species such as marine mammals, dogs, cats, parrots, and horses (Pryor et al., 1969; Pryor, 1994, 1999, 2004). More recently, the “do something new” paradigm has been successfully used to foster production of novel vocalizations by captive walrus, *Odobenus rosmarus divergens* (Schusterman & Reichmuth, 2008).

In another captive study, dolphin calves were more likely to produce novel behaviors than adults, and although play complexity did increase as a function of age, these results still suggest that calves may be responsible for the quantity and spread of simple novel behavior within a community (Kuczaj et al., 2007). There is also a wonderful example in which a young dolphin watched an aquarium visitor blowing smoke rings, briefly returned to its mother to nurse, and then returned to the glass viewing window to blow identical rings of milk (Tayler & Saayman, 1973). Mitchell (1987), while relating this story, points out that this behavior not only entails the production of a novel behavior, but the realization that the people on the other side of the glass window would recognize the imitation.

Neurobiology of Innovation

In humans, there are several prominent theories on the neural mechanisms of innovation. Bogen and Bogen (1969) view innovation as a process dominated by the right hemisphere, which is associated with global and holistic processing. This view is consistent with the stereotype that left-handed (i.e., right hemisphere-dominant) people are more innovative than right-handed individuals. The argument is further supported by findings showing a positive correlation between figural and verbal creativity and cerebral blood flow in the right precentral gyrus (Chavez, Graff-Guerrero, Garcia-Reyna, Vaugier, & Cruz-Fuentes, 2004). Indeed, in this study of cerebral blood flow, most brain areas showing a correlation between level of activity and level of creativity were found in the right cerebral hemisphere. However, significant correlations were observed in both cerebral hemispheres, suggesting that innovative thinking may actually involve bilateral activation (Chavez et al., 2004).

Martindale (1999) put forth that innovation is a result of cognitive disinhibition in the frontal lobes. This theory asserts that one function of the frontal lobes is to inhibit creative behavior, and therefore lower levels of cortical activation in these areas would result in higher levels of innovation (Martindale, 1977). Bogoslavsky (2005) similarly emphasizes the notion that decreased activity in the frontal lobes can result in an enhanced output of creative behavior. On the other hand, Flaherty (2005) argues that creative drive and the generation of ideas depends on interactions between the temporal lobes, limbic system, and frontal lobes. Consistent with this argument, Razumnikova (2007) reports systematic changes in cortical EEG over the prefrontal cortex. These changes may reflect sustained attention involved in producing solution-related information retrieval and in the selection of verbal associates related to the intentional goal of creative thinking.

Dietrich (2004) provides a model (that we believe will translate easily to concepts in animal behavior) depicting the prefrontal cortex as having *processing* and *knowledge* modes. The processing modes are *deliberate* and *spontaneous*, while the knowledge domains are *emotional* and *cognitive*. These four categorizations provide four types of innovation (deliberate-emotional, deliberate-cognitive, spontaneous-emotional, and spontaneous-cognitive) when crossed. Dietrich also delegates the responsibility for integrating stimuli, determining appropriateness, and insight expression to the prefrontal cortex.

In addition to the more global “left hemisphere” hypotheses, and the general belief that the frontal cortices are especially involved in creative processes, some have made more specific arguments about underlying neurochemistry that may contribute to innovation. Flaherty (2005) suggests that dopamine may contribute to creativity partly by influencing novelty seeking behavior. However, others have reported no difference between subjects receiving placebo and those receiving the dopaminergic agonist bromocriptine when tested on a series of anagrams (Smyth & Beversdorf, 2007). These findings suggest that the dopaminergic system may not be critically involved in modulating cognitive flexibility, where such flexibility can be seen as a characteristic of creativity itself. The noradrenergic system, on the other hand, is strongly implicated in modulating cognitive flexibility. For example, administration of the beta-adrenergic antagonist propranolol, which reduces noradrenergic activity, has been found to facilitate

cognitive flexibility in a number of studies (e.g., Beversdorf, Hughes, Steinberg, Lewis, & Heilman, 1999; Beversdorf, White, Chever, Hughes, & Bornstein, 2002). Antagonism of the noradrenergic system appears to exert the greatest benefit when subjects must struggle to find a solution or when the cognitive task is otherwise highly challenging (Campbell, Tivarus, Hillier, & Beversdorf, 2008). The role that the dopaminergic, noradrenergic, and other neurotransmitter systems play in creativity will continue to unfold with further research using human subjects, where highly complex tests of creativity are possible.

In animals, specific research on the neurobiology of creative processing is expectedly more limited. There is, however, some data coming from the study of nonhuman primates that inform our understanding of how the brain might produce innovative behavior. Innovation rate and neocortical size have been found to be positively correlated in nonhuman primates (Reader & Laland, 2002). For example, capuchin monkeys, whose tool use has been extensively studied, have a proportionately large neocortex (relative to other structures). This proportionality is, in fact, similar to what is seen in the great apes (Rilling & Insel, 1999). The essential argument here is that neocortical development in these animals might provide the basis of innovative behavior in nonhuman primate species. Nonhuman primate innovation rate is also correlated with the variety of tool use reported for a given species, the frequency of social learning, and rates of individual learning (Reader & Laland, 2002). Such findings suggest that these cognitive capacities may have evolved together (Lefebvre, Reader, & Sol, 2004; Reader & Laland, 2002). It is important to note that the correlation between innovation and overall brain size has been identified nonprimate species as well, for example, birds (Lefebvre, Whittle, Lascaris, & Finklestein, 1997) and multiple species of bats (Ratcliffe, Fenton, & Shettleworth, 2006). Implications of such findings will be discussed below in the context of evolutionary adaptation.

Research on bowerbirds has provided an interesting insight into the relationship between neural anatomy and innovation. Specifically, the volume of the brain has been positively correlated with bower complexity (Day, Westcott, & Olster, 2005; Madden, 2001), in addition to the following in other species: storage and retrieval of food (Sherry, Jacobs, & Gaulin, 1992); song complexity (Brenowitz, 1997); foraging innovation (Timmermans, Lefebvre, Boire, & Basu, 2000); and even degree of urbanization, where more urbanization is likely to produce more novel situations (Sasvari, 1979). As a general measure across species of birds, the size of the mesopallium and nipopallium, two structures believed to be equivalent to the mammal cortex, may be predictors of innovation rate (Timmermans et al., 2000) and tool use (Lefebvre, Nicolakakis, & Boire, 2002), respectively. However, Lefebvre and Sol (2008) do note that the predictive ability of these structures is not especially great and caution should be taken when considering them. It is also possible to use avian brain size to predict innovative ability. Overall brain size is positively correlated with a larger diversity of innovations (measured with reference to the innovative product), in addition to a larger number of technical-based (as opposed to food-based) innovations (Overington, Morand-Ferron, Boogert, & Lefebvre, 2009). For example, a relationship exists among zebra finches' (*Taeniopygia guttata*) song complexity, size of the high vocal center (nucleus responsible for learning and control of birdsong), and size of the telencephalon (avian fore-

brain), all three of which appear to be inherited characteristics (Airey, Castillo-Juarez, Casella, Pollak, & DeVoogd, 2000).

Other brain structures involved in innovation include the cerebellum in spatial tasks (Day et al., 2005) and the hippocampus in food storing and home-range size, both of which are thought to have a significant spatial component (Healy, Kort, & Clayton, 2005). Further, PET scans performed on macaques (*Macaca fasciata*) during a tool use task demonstrated activity in the cerebellum, basal ganglia, and various cortical areas (Obayski et al., 2001).

Evolutionary Advantages of Innovation

As with most behavior, innovative behavior is linked to a cost/benefit analysis. For innovation to occur, the costs of performing the behavior must be lower than the potential benefits of said behavior, and conditions such as these most often presents themselves in extremes of habitat or situation (Lee, 2003). Additionally, certain circumstances cater to innovative behavior. These include, but are not limited to, a complex social life, greater intelligence, and excess energy and free time (Kummer & Goodall, 1985).

Sol, Timmermans, and Lefebvre (2002) have proposed a "behavioral flexibility" hypothesis that posits a relationship between avian brain size and the ability to adapt to a novel environment, where higher brain volume is positively correlated with survival in non-native habitats (Reader & MacDonald, 2003; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005). Mammalian research has provided additional support for this hypothesis (Sol, Bacher, Reader, & Lefebvre, 2008). Conversely, researchers have also observed that resident bird species are more innovative than migratory birds and have speculated that this stems from a greater demand for novel uses of existing resources in an environment that does not change. Similarly, innovation rates may increase in the winter when resources become scarcer (Lefebvre et al., 2004). To provide a different methodology for the study of innovation in animals, Lefebvre, Whittle, Lascaris, and Finklestein (1997), performed an extensive search of the literature on terms such as "novel" or "innovative" and developed an empirical measure, which they termed "innovation rate," by tallying reported instances of foraging innovation in birds. Later, they were able to correlate the innovation rate with species forebrain size, providing support for a positive correlation between feeding innovation and forebrain size. This correlation has also been found in nonhuman primates (Reader & Laland, 2002).

Recently, Overington et al.'s (2009) meta-analysis of 76 avian species found a similar positive correlation between what they classify as "technical innovations" (e.g., novel parasitic behavior, novel true tool behavior, novel caching behavior) and residual brain size. Additional work examining innovation from an evolutionary perspective supported the conclusions that neocortical volume and innovation rates are correlated (for a review, see Deaner, van Schaik, & Johnson, 2006; Reader & Laland, 2002). In addition to the research in birds and nonhuman primates, this correlation between brain volume and behavioral flexibility/foraging innovation has even been found in scarab beetles, *Scarabaeidae* spp. (Farris, 2008); multiple species of predatory bats (Ratcliffe et al., 2006); and cichlid fish (Shumway, 2008).

The work of Wilson and colleagues takes a much broader, behavioral, perspective when it asserts that innovative behavior may have been one of the main driving forces behind the evolution of birds and placental mammals (Wyles, Kunkel, & Wilson, 1983). Wilson's work, and later Reader and Laland (2002), theorize that innovation and evolution work circuitously—innovation drives evolution, which in turn demands more innovation (Wilson, 1985).

There is also a small body of literature examining personality and individual differences from an evolutionary perspective. In survival theories such as Maynard Smith and Price's (1973) game theory, risky (or novel) behavior may directly affect an individual's survival (Gosling, 2001). Exploratory behavior can also be considered a personality trait and has been addressed as such in guppies (*Poecilia reticulata*) by Laland and colleagues (Laland & Reader, 1999; Laland & van Bergen, 2003). In addition, using the four categories previously detailed, Russon and colleagues (2010) were able to note variation in innovation (in orangutans) that was dependant on personality-like traits such as sociality, age/rank, and orphaning. Personality as a trait has been shown to be both individually variable and heritable within a population, however the mechanism by which this variation remains in a population is still unknown (Dingemans, Both, Drent, van Oers, & van Noordwijk, 2002). A balance between exploratory and nonexploratory behavior (or personality) appears to be important for survival. This can be seen at the individual level, such as the balance between neophilic and neophobic behavior in the rats introduced to the mammal-free island discussed above (Russell et al., 2010), or even at a population level as shown by simulations of ant colonies, which were most successful with a balance of uncreative workers and creative workers, who tended to range farther and to more novel areas when looking for food (Heck & Ghosh, 2002).

Lastly, several unique studies have examined evolutionary advantages of creative behavior in unusual species or settings. Heck and Ghosh (2002) modeled two types of foraging strategies in an ant colony: ants that only exploited known food sources by following established scent trails, and "creative" ants that searched for novel food sources and created new scent trails. They were able to quantitatively show (measured by foraging success) the result of manipulating the existence and extent of this creative trait in the colony, demonstrating the evolutionary advantage of having creative members of a group or society. Further, Sen and Gadagkar (2006) indirectly investigated the evolutionary advantage of creativity in Hymenopteran wasps by removing female wasps (who typically feed young) from the nest. This removal required and resulted in innovative caretaking behavior by male wasps to ensure the survival of young.

Possibilities for Empirical Studies

We are not the first to attempt to translate the measurement of human constructs to animals. McCrae and Costa's (1997; Goldberg, 1992) Five Factor model for personality has already been used to examine animal personalities and has had successful results in test studies (Kuczaj & Highfill, 2005), as have other measures of human personality models (Gosling, 2001; Uher, Asendorpf, & Call, 2008). As mentioned previously, these pioneering studies have shown promising parallels between personality traits such as openness to experience in humans and active or exploratory behavior in animals (see section on novelty seeking).

Mathematical models have also been developed to address the evolutionary advantages of personality in animals (Wolf, Doorn, Leimar, & Weissing, 2007).

We see the potential for other tests developed for humans, including tests of creativity, to provide insight into animal behavior. For example, one way that creativity is measured is by looking at divergent production. First proposed by Guilford (1950), divergent production is the ability to derive multiple response to an open-ended problem with no obvious, singular answer (a sample question might be, "What would happen if people no longer needed sleep?"). Guilford proposed four aspects to divergent production: fluency (the sheer number of answers produced in response to a question or problem), flexibility (the number of specific categories encompassed by the answers), originality (how novel the answers are), and elaboration (to what extent the answers are detailed). Currently, the most common divergent thinking test is the Torrance Tests of Creative Thinking (Torrance, 2008 version). In the most recent incarnation, flexibility was dropped from the Figural test because of its high correlation to fluency. Replacing flexibility were two new categories, abstractness of titles and resistance to premature closure (Torrance, 2008). If we apply this to an animal's behavior, such as chimpanzees' "termite fishing" (Suzuki, 1966), fluency might be measured by type of stick used (smooth stick, thorny stick, etc.), flexibility by the types of fishing tools used beyond sticks (vines, long leaves, etc.), originality by the number of times a particular tool was used (sticks are used very often, while long leaves may not be), and elaboration by the extent to which the animal went to make the tool operational (changes in length, removal of leaves from a stick, etc.). In addition, we see potential for the four constructs used by Dietrich (2004) to measure creativity to be adapted to constructs in animal behavior and used to examine creative behavior. Lastly, we believe that Amabile's (1982, 1996) Consensual Assessment Technique (CAT), used in the study of creativity in humans, may be of use to those attempting to define and study innovation in animals.

The CAT makes use of qualified experts to measure creativity. It is perhaps best summarized by a quote; in 1964, Supreme Court Justice Potter Stewart tried to explain "hard-core" pornography, or what is obscene, by remarking "I shall not today attempt further to define the kinds of material I understand to be . . . [hard-core pornography]; and perhaps I could never succeed in intelligibly doing so. But I know it when I see it." In the CAT, a creative product such as a story or a drawing is assessed by a group of expert raters. Past research on the results has concluded that these experts agree at a strikingly high rate as to how creative the story or poem is, with Cronbach's alpha values in the range of .7 to .95 (e.g., Amabile, 1996; Baer, 1998; Kaufman & Baer, in press). This idea could easily be used to rate innovation in animals using an appropriate group of experts on a particular species or type of behavior. The survey methodology described by Reader and Laland (2001) is an initial step in this direction—using an author's writing within an article to define a novel behavior. Rather than being a narrow definition composed of subjective judgments such as Ramsey et al.'s (2007) recently proposed dichotomous key, which was calculated to contain 55 steps (Giraldeau, Lefebvre, & Morand-Ferron, 2007; Kendal, Dean, & Laland, 2007), this technique provides both a necessarily flexible definition and an empirically sound methodology.

Most recently, two models, Russon et al. (2010), as discussed previously, and Lehner, Burkart, and van Schaik (2010) have proposed methods for measuring innovations in natural settings. Russon and colleague's methodology was based on a synthesis of human and animal literature. Lehner and colleague's methodology was developed based on captive animal behavior, and subsequently tested in wild populations; it uses geography to define the area in which an innovation can be considered shared or novel. We are excited about the prospect both of these methods of measuring innovation, and we look forward to further results.

As with all models, empirical testing is a critical part of verifying the accuracy and, more importantly, the usefulness, of a model—in particular, one which makes so much use of anecdotal evidence (for discussion, see Lefebvre & Sol, 2008). The most obvious method of verification of the model is to examine the brain structures of an assortment of animals and then make projections as to their creative abilities (or lack thereof). Lefebvre and Sol (2008) emphasize this technique in regard to general cognitive abilities such as the assumed relation that more complex lifestyles (e.g., sociality) require more complex brain structures. However, this may be difficult to accomplish with higher level creativity, as many studies have already been carried out with the small number of animals suspected to have the brain and cognitive complexities necessary for innovation. Ongoing research in these areas does, however, seem to occasionally yield new examples of animals capable of complex cognitive abilities, such as the relatively recent discovery of mirror self-recognition in Asian elephants, *Elephas maximus* (Plotnik, de Waal, & Reiss, 2006). Therefore, it may be worthwhile to further pursue studies of innovative abilities in species related to those in which innovation has already been identified such as carnivores (the large cats, dogs, and pinnipeds), cephalopods (octopi and kin), or other animals in the superorder Paenungulata (manatees and hyaxes).

It may be possible to correlate brain structure and innovative abilities in animals that have already been studied (and therefore disallow predictive hypotheses). This has been done with interesting results by Lefebvre and colleagues (1997), who showed evidence for a positive correlation between forebrain size and innovative or adaptive abilities in birds. Even further, it may be possible to use the brain structures and processes that have been identified as necessary and sufficient for the creative process to "build" (via computer model), and subsequently test, a brain that should be capable of creativity. An initial step toward this particular goal may have already been accomplished successfully by Heck and Ghosh's (2002) modeling of a synthetic colony of ants with creative characteristics discussed earlier.

Attention to novelty is not limited to mammals and birds, and has been documented in species such as turtles, lizards, and crocodiles (Glickman & Sroges, 1966). We believe that the development of our model from ideas that stem from multiple disciplines and a large variety of species will be an asset to comparative studies of creativity. In a similar vein, we believe new methodologies such as behavior analysis, examination of traits from a developmental perspective (evo-devo), and exact or signature DNA sequence analysis (Pollen & Hofmann, 2008) will lend new insight into studies of creativity in animal species.

Environmental enrichment programs, designed to provide cognitive activities for captive species, are increasingly becoming required at zoos and aquariums (Shepardson, Mellen, & Hutchins,

1998). However, there appear to be few studies providing quantitative analyses of the effectiveness of such enrichment. One of these studies found that marine mammals became desensitized to novel enrichment items that remained in their environment for continuous periods. However, more attention was given to the objects when they were removed and replaced after 3 days. When removed and returned after three weeks, subjects' attentiveness to the objects had returned to the same level as when the item was originally introduced (Kuczaj et al., 2002). A second study, which specifically examined time periods of novelty decline, showed novel devices to effectively provide enrichment for 2 days, and that a full 14-day period was required for the original magnitude of novelty reaction to be reattained (Green, 2003). As enrichment becomes required in facilities with captive animals, more time and resources must be allocated to it, and thus empirical evidence of its effectiveness will be vital.

Finally, much more research is necessary on cetaceans, which have a brain structure unlike humans and other primates. The cetacean brain has no frontal lobe and a dramatically reduced hippocampus. The area analogous to the frontal lobe is often referred to as the "orbital lobe" (Morgane, Jacobs, & McFarland, 1980), and despite its disproportionately small size, has shown extensive cellular variation and differentiation (Reuter et al., 2005). The cerebellum is also enlarged in many cetacean species relative to primates (Marino, 2005).

Because many of the structures that are absent or greatly reduced in cetaceans are ones associated with creativity in other species, a comparative approach specifically involving cetaceans has the potential to be very informative. Thus far, very little research has been done on these anatomical differences. One hypothesis is that the decrease in size of some brain structures is at least partially related to the decrease in olfactory needs that comes with a marine lifestyle. Likewise, the existence of a well-developed amygdala may indicate a corresponding increase in other sensory input (Marino, 2005). It is known that cetaceans have a very well-developed limbic system, entorhinal cortex, and degree of neurotransmitter connectivity. Additionally, cetaceans possess a "paralimbic region," not found in any other species, for which the function is still currently unknown (Morgane et al., 1980). Any or all of these structures may be connected with creativity and/or innovative behavior.

Conclusion

In the present work, we have taken a multidisciplinary approach to modeling creativity in animals. By beginning to integrate perspectives from biology, psychology, and behavioral neuroscience, we aim to encourage a dialogue across disciplines and to expand the current understanding of creativity in general. By integrating concepts from psychologists' study of human creativity with ideas coming from neuroscience and animal behavior, we have made an effort to provide a structure within which creativity in animals can be examined. This framework proposes a three-level model of creativity. The first level is composed of both the cognitive ability to recognize novelty, a process linked to hippocampal function, and the seeking out of novelty, which is linked to dopaminergic activity. The next level of the model is observational learning, ranging in complexity from imitation to the cultural transmission of creative behavior, where such observational learning has been

linked to cerebellar function. The highest level of the model is innovative behavior, which appears to be especially dependent upon the prefrontal cortex. We have offered a wide range of examples of the kinds of behavioral abilities that are argued to play an important role in creativity in animals. These behaviors include novelty recognition, novelty seeking, observational learning, including observational learning of tool use among conspecifics, and innovative behaviors ranging from male bower birds' construction of elaborate and unique nests with which to attract females, to fashioning and using new tools by chimpanzees. One of our key goals in the articulating this model is to stimulate conversation among scientists from a variety of disciplines, for example, ethology, biology, psychology, and neuroscience. Future research may focus on in-depth explorations in areas such as neuroplasticity, neuroanatomy in nonhuman animals, neurochemical changes during behavior and problem solving, and the evolution of these traits or mechanisms. By linking the elements of our model of creativity in animals to examples from these different domains, we hope to both engender excitement about these questions and to provide a common language for researchers from across multiple disciplines to discuss creativity in animals. Indeed, by integrating concepts from theories of human creativity with the available research on animal behavior and brain research, we believe that this model provides researchers with a useful synthesis of existing theory and research as it relates to creativity in animals.

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