EEB 122: Ecology, Evolution, and Behavior
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By submitting this essay, I attest that it is my own work, completed in accordance with University regulations.—Dakota E. McCoy

Research Proposal
Do Octopuses Think Like Vertebrates?
A New Comparative Test

by Dakota E. McCoy

Introduction

Octopuses[1] are non-social, short-lived invertebrates that are genetically and physically distant from the accepted cadre of intelligent animals: the social and long-lived primates, birds, dolphins, and elephants (Mather 1995). Yet a growing body of research suggests that octopuses have many higher-level cognitive abilities once thought to be unique to those few vertebrates. Since octopuses are so distantly related to the intelligent vertebrates, this implies that octopuses represent an example of convergent evolution of advanced cognition. Additionally, octopuses lack the characteristics that have often been correlated with intelligence, such as a complex social structure and longevity. For those two reasons, octopuses represent a unique opportunity to better understand the development of intelligence. Are the cognitive processes of the octopus completely analogous to those of vertebrates, or has its alien physiology and lifestyle produced a different "version" of intelligence? Studying the extent and nature of octopus cognition offers a new angle by which we can examine the evolution of intelligence and begin to answer this question. Previous studies of octopus intelligence have focused mainly on learning capabilities

[1] The plural of the word "octopus" is the subject of much controversy. The traditional plural, octopi, is in fact linguistically incorrect; since the word derives from the Greek, the correct plural form is actually "octopods" (Lidell and Scott 2011). However, since this word has not yet become an accepted part of the language, the author settles for the now widely-used, and less obviously incorrect, English plural "octopuses."

through classical conditioning techniques (for review, see Boal 1996), whereas the research proposed herein will use the methodology of past studies of octopus cognition (e.g. Bierens de Haan 1949, Walker et al. 1970, Boal 1996) to study two inter-related characteristic markers of higher cognition. Specifically, the proposed study will seek to determine whether octopuses have the capacity for delay of gratification, and whether octopuses will use play as an effective self-distracting coping mechanism.

Delay of gratification is the postponement of immediate reward to obtain a greater, delayed reward; in other words, it represents an exercise of self-control. Mischel (1974) defined the classic paradigm of delay of gratification as a two-step process. First, the subject chooses between the delayed versus immediate reward; second, the subject "bridges" the timed delay interval, often employing coping mechanisms such as self-distracting play (Mischel 1974). Delay of gratification is a hallmark of higher cognition, since it implies foresight, future planning, and goal-oriented behavior (Mischel 1974, Beran et. al 1998). Further, animals of high cognition employ sophisticated coping techniques to bridge the delay interval – the second part of the Mischel paradigm—most notably by playing with toys available to them to distract themselves while waiting for the reward (Evans and Beran 2010).

Most prior research of octopus intelligence has focused on examining learning ability through classical conditioning, demonstrating that octopuses learn quickly and in a manner akin to vertebrates (e.g., Fiorito et al. 1990). However, little work has been done examining less well-understood aspects of cognition, such as play and delay of gratification. Play has been observed in a wide variety of animals (e.g., Burghardt 1998, Heinrcih and Smolker 1998, Watson 1998) but the functional purposes of play are not well understood, particularly in object play by adult animals (Hall 1998). The capacity for delay of gratification implies complex abilities to link sequential actions, plan for the future, and predict future events (Mischel 1974). I propose to test octopuses' ability to delay gratification as an indication of foresight and future planning. Furthermore, I will test octopuses' ability to use object play as a coping mechanism to extend the time for which they are willing to wait for a reward. This framework of study will examine those two characteristics in a rigorous manner to better understand octopus cognition, shed light upon the development of foresight and the functionality of adult object play behavior, and thus provide a basis for comparison between octopuses and intelligent vertebrates.

Background

Octopus Intelligence

Previous research of octopus intelligence has made it clear that octopuses are on a similar cognitive level to highly developed vertebrates, with brains of similar relative size and complexity (Budelmann 1994, Ikeda 2009, Packard 1972, Young 1971,). Octopuses have displayed significant ability to learn visually and tactually and have demonstrated remarkable memories (Wells 1966, Wells 1978, Young 1991, Boal 1991, Fiorito and Scotto 1992, Alves et al. 2007). For example, octopuses have on a number of occasions demonstrated long-term memory and spatial learning capabilities related to den location and foraging experiments (e.g., Walker et al. 1970, Mather 1991, Papini and Bitterman 1991, Mather and Anderson 1999). One neurobiological study revealed that certain areas of the octopus brain show a "vertebrate-like potential for long-term learning and memory (Hochner et al. 2003). The observed behavior and cognition of octopuses to date suggests that they could well have the capacity to exhibit the self-control and forethought necessary for delay of gratification. The extensive research documenting octopus memory lends particularly compelling support to this hypothesis, since memory capabilities are a correlate of forethought.

Additionally, octopuses continue to surpass cognitive expectations, particularly in their variety of learning capabilities. A large body of work provides evidence for the neurobiological basis of advanced learning capabilities in octopuses (for reviews, see Boycott and Young 1950, Boycott 1954, Young 1961, Wells 1962, Young 1964, Sanders 1975, Young 1977, Wells 1978, Chichery 1992, Boal 1996, Mather 1995), and a recent group of studies have showed further experimental confirmation for learning abilities in octopuses (for review, see Ikeda 2009). In a particularly striking example of unexpected learning abilities in octopuses, Fiorito and Scotto (1992) showed that the common octopus could swiftly learn to select one of two options by watching another octopus undergo trial and error. This particular characteristic of intelligence, social learning, is not one that would have been predicted to be evident in a non-social animal such as octopuses. Evidence of octopus ability to learn socially draws into question our longstanding connection between advanced cognition and complex sociality, and prompts further research of other potential cognitive abilities of octopuses, such as the study proposed herein.

Octopuses are also able to solve complex problems. Problem solving abilities have mostly been studied through the use of mazes, and several studies show octopuses navigating mazes more swiftly over time (Buytendijk 1933, Bierens de Haan 1949, Boycott 1954). Further, careful statistical analysis in one study showed that the octopuses were solving a maze through sequentially linked actions, rather than through simple associative trial and error (Fiorito et al. 1990). Therefore, octopuses may be able to understand the framework of a delay-of-gratification test, which requires a step beyond the simple association between choosing an option and receiving food. In order to succeed at delay of gratification, the octopus must be able to link its actions to delayed results over a long period of time, a cognitive task of which it appears to be capable based on the maze studies.

While anecdotal evidence has suggested for years that octopuses are very curious and will play with novel objects (e.g., Forister 2002), two recent studies provide scientific basis for this claim. Two of eight octopuses studied by Mather and Anderson (1999) showed exploratory play of a new object—a flexible funnel—by aiming jets of water to regularly transport it back and forth, a process analogous to bouncing a ball. Additionally, Kuba et al. (2006) introduced Legos to fourteen octopuses, nine of which demonstrated exploratory play behavior with the Legos. Kuba et al. (2006) also investigated the timing and development of their behavior, concluding that play followed a period of exploratory behavior in a manner similar to that of vertebrates, suggesting an analogous origin of this cognitive characteristic. It appears that both octopuses and intelligent vertebrates use play as a mechanism to examine and explore new situations and objects, so it appears that this functional cognitive purpose of play is common to octopuses and vertebrates. The research proposed herein will determine whether octopuses share with vertebrates another functional purpose of play; specifically, will octopuses use play as a coping mechanism for self-distraction during a delay interval? Further, will the availability of toys allow octopuses to cope with longer delay intervals?

Previous Studies on Delayed Gratification and Play Behavior

The commonly accepted Mischel paradigm describes delay of gratification as a two-step process (Mischel 1974). The first stage is choosing whether to wait or to receive the immediate reward, and the second stage consists of bridging the time during the delay. Bridging consists of any thoughts and actions the subject takes while waiting during the delay (Beran et al. 1998, Mischel 1974). In studies done with children, the conditions of the bridging interval greatly affect the length of time a child will endure delay of gratification: if the reward is present during the bridging interval, the child cannot wait as long (Mischel and Ebbeson 1970, Mischel and

Moore 1973, Mischel 1981,), but if photographs of the reward are present, the child is able to wait longer (Mischel and Moore 1973). There is thus some evidence that presence of the actual reward impedes cognitive ability, while the presence of symbols may help with self-control. Further, it is clear that conditions during the bridging interval have an impact on performance in delay of gratification tests. Beran et al. (1998) conducted a study with chimpanzees via the Mischel paradigm, in which (i) the chimpanzees were taught that they had a choice between an immediate reward and a delayed, more-preferred reward, and (ii) chimpanzees that had been language trained with lexigrams were offered symbols of the reward to help bridge the gap interval. All chimpanzees delayed gratification when the food reward was present, and one of three chimpanzees displayed the greatest capacity for delay of gratification when lexigrams were present during the bridging interval (Beran et al. 1998).

It appears that lexigrams improve primate ability to cope with delay of gratification, but this is not particularly relevant to studying octopus cognition because octopuses have not been language trained with lexigrams, as have chimpanzees. A more relevant coping mechanism, self-distracting play, has been observed in delay of gratification studies of children (e.g., Mischel et al. 1972, Miller and Karniol 1976, Toner and Smith 1977, Cournoyer and Trudel 1991) and, only recently, of chimpanzees (Evans and Beran 2007). Evans and Beran (2007) found that chimpanzees employed play to distract themselves during the bridging interval of a delay of gratification study using food rewards. Chimpanzees played significantly more with toys during the bridging interval than not, and their performance on delay of gratification tests improved when the coping mechanism of play was available to them (Evans and Beran 2007). In other words, the chimpanzees were able to wait longer for a reward when toys were present. A similar result, an improvement in capacity to delay gratification, was found in several studies of children

(Mischel et al. 1972, Miller and Karniol 1976, Toner and Smith 1977, Cournoyer and Trudel 1991). Since octopuses have been shown to display play behavior (e.g., Mather and Anderson 1999, Kuba et al. 2006), it is reasonable to hypothesize that octopuses may be able to use play as a coping mechanism, similarly to chimpanzees.

Delay of gratification has mostly been observed in chimpanzees and humans. However, other animals have occasionally exhibited impulse control for a short amount of time. For example, pigeons characteristically choose the immediate, but smaller, reward (e.g. Fantino 1966, Mazur and Logue 197,8 Logue et al. 1984), but Ainslie (1974) and Grosch and Neuringer (1981) successfully rained pigeons to forego an immediate reward to receive a larger reward. Similar research has been done with rats (see Killeen et al. 1981). Therefore, there is some precedent for delay of gratification in animals that are not usually characterized as highly intelligent. However, studies of delay of gratification in non-primates often utilize extensive training techniques and only teach a subject to consistently choose a greater, delayed reward over a less, immediate reward (Grosch and Neuringer 1981). In that situation, it may be that the animal has simply been trained to exhibit patience for a greater reward; it may or may not understand the situation given to it. The study proposed herein will provide a set of control trials to allow to octopus to choose a delayed or immediate reward in several different situations, thus providing a baseline for comparison in order to better understand the cognitive implications of the octopus' performance. This setup requires a more complex cognitive task than that asked of non-primates in previous studies, since it offers an actual choice to the subject. Additionally, to differentiate between octopus performance and the performance of non-primates on previous studies, the proposed research will determine to what extent octopuses possess the capacity to delay gratification. That is, I will determine what time interval is the maximum that octopuses will tolerate to receive a food reward twice as large as the immediate reward.

Hypotheses

1. **Delay of Gratification:** The octopus will choose to forego an immediate reward in order to obtain a greater, but delayed, reward. That is, octopuses will display delay of gratification, similarly to primates.
    i. I will determine the maximum time delay an octopus will consistently endure (i.e., over 75% of the time) to receive a reward double that of the immediate option.
2. **Self-Distraction A:** The octopus will play significantly more with toys when undergoing time delay for a reward than during non-testing times. That is, octopuses will employ self-distraction, similarly to primates, during delayed gratification trials.
    i. Toys will be made available to the octopuses at all times. I will record the amount of time each octopus spends playing with the toys during the delay interval and compare this figure to the amount of time it spends playing with the toys at other times.
3. **Self-Distraction B:** The presence of toys will enable the octopus to endure significantly longer delay periods for the doubled food reward than in trials where no toys are present.
    i. We will determine the maximum delay time an octopus will consistently (over 75% of trials) endure—in the presence of toys—to receive a reward double that of the immediate option.

Methods

Participants

Four common octopuses (*Octopus vulgaris)* will be used in this study, all of approximately the same age, between 3 and 6 months old. The octopus will be cared for and fed following Walker et al.'s (1970) guidelines for octopus experimentation. They will be housed individually in four identical tanks, outfitted with movable sliders to provide cover and isolation during testing. Diet will be constant throughout experimentation. Because of the octopus's propensity to attack and grasp things presented to it, and the underwater environment, the procedure described here differs slightly from what has been previously used with studies of delay of gratification in primates.

Apparatus

The tanks will rest upon a broad table with 2 feet of clear table surface in front of each tank. Two large identical clear food tubes, one of which will contain the immediate reward and the other the delayed reward, will be placed on the table in sight of the octopus being tested, one on either end of the tank. This setup of visual food rewards behind glass has been used successfully in many pervious experiments studying octopus memory and cognition (e.g., Buytendijk 1933, Bierens de Haan 1949, Schiller 1949, Boycott 1954, Wells 1964, Wells 1967, Wells 1970). The larger reward will fill the tube twice as high as will the small reward, so that the larger reward can easily be visually distinguished by the octopus. The two choices presented to the octopuses will be a red spherical block and a blue cubical block, each attached identically to single-hinged wooden poles. Previous studies of octopuses have successfully used such simultaneous visual discrimination tactics to train octopuses (for review, see Boal 1996). The poles will be hinged in such a way that the blocks can be submerged near the octopus underwater while the pole is operated by the experimenter. When the octopus grasps one of the blocks, the block that was not chosen will be retracted out of the water, and the selected food reward will be dispensed.

Procedure

Preliminary training:

Purposes: The purposes of the preliminary training are (i) to ensure that the octopus links the reward signal, a the two second audio tone, with food reward; (ii) to ensure that it understands that the clear tubes in front of the tank contain its food; and (iii) to habituate the octopus to the presence and actions of the experimenter.

The octopuses will be fed in the following manner each day for two weeks: the experimenter will place a clear tube filled with food in front of the tank, play a two second tone, and immediately give the food to the octopus.

***Training 1*:**

Purposes: The purposes of Training 1 are (i) to train the octopus to link its action of grabbing one of two wood blocks to the result of receiving a food reward, (ii) to train the octopus to understand that the food blocks on either side correspond to the tube reward in front of that food block, and (iii) to train the octopus to associate one block with an immediate reward and the other block with a delayed reward.

The tubes will be placed in front of the octopus tank upon the table, with the immediate reward tube on the left and the delayed reward tube on the right.[2] The blocks will be presented to the octopuses on the same side as their corresponding reward. To counterbalance bias towards one block or color, the red sphere will correspond with immediate reward for octopuses 1 and 2

[2] It is possible that the octopuses will exhibit side bias, which is a tendency of some animals to adopt a strategy of always selecting the same side choice in a testing situation. There is no precedent which would lead me to expect that octopuses will display side bias, particularly since octopuses have 8 manipulator limbs instead of 2. The data from this phase will be analyzed and, if side bias is present, additional control trials will be added in which the sides will be switched (see "Training 2").

and delayed reward for octopuses 3 and 4. Similarly, the blue cube will correspond with the delayed reward for octopuses 1 and 2 and the immediate reward for octopuses 3 and 4. The time delay in this phase will be 15 seconds before the food reward is given.

Each octopus will undergo 10 trials per day. During each trial, one of the two tubes, left or right, will be filled with food reward and the other will be left empty. The tubes will be placed in clear sight of the octopus, then the blocks will be simultaneously presented to the octopus in the tank. When the octopus grasps a block, the untouched block will be removed from the water and the corresponding unselected tube will be moved backwards, away from the tank. If the octopus grasps the incorrect block, corresponding to the empty tube, the empty tube will be lifted and presented towards the octopus, and a 30 second delay will begin before the next trial commences. This 30 second delay serves as negative reinforcement of an incorrect choice, so that the octopuses cannot simply adopt the strategy of swiftly selecting both choices without figuring out which choice corresponds to the food reward. If the octopus grasps the correct block, corresponding to the food reward, a two second tone will play and the octopus will be given the food reward from the tube. If the correct block is the delayed reward block, the two second tone will indicate the start of the 15 second delay. At the conclusion of the delay, a one half second tone will sound and the experimenter will give the food reward to the octopus. By only providing one desirable choice to the octopuses and one empty choice, I will train the octopuses to understand the correlation between block side and reward side. Additionally, the octopuses will learn that the left block is the immediate reward and the right block is the delayed reward.

In order to have "passed" the first phase of training, the octopus must grasp the correct block—i.e., the block on the same side as the tube containing a food reward— on its first try 7 out of 10 times for 3 days in a row.

Training 2 (if necessary to correct for side bias):

Purposes: The purpose of Training 2 will be to correct for side bias, if side bias was observed in training one. That is, if an octopus is observed to be consistently choosing one side 75% of the time, regardless of the positioning of the food reward, Training 2 will be enacted.

The procedure will be identical in every way to that of Training 1, except that the side positioning of the immediate reward tube and block and delayed reward tube and block will no longer be constant, but will be randomly determined, switching from side to side. In order to advance to the testing stage, the octopus must still choose the correct block, corresponding to the tube with the food reward, 7 out of 10 times for 3 days in a row.

Testing 1: 20 second delay

Purposes: The purposes of the Testing 1 phase are (i) to ensure that the octopuses understand the testing situation and do not demonstrate unexpected biases; that is, if reward sizes are equal (or larger) for the immediate option, the octopus should choose the immediate option, and (ii) to determine whether or not octopuses are capable of consciously deciding to delay gratification for 20 seconds in order to receive a larger food reward.

Each octopus will undergo five days of testing at this level, where each day consists of up to 10 reminder trials and 8 testing trials. In the reminder trials, food will only be placed in one of the two tubes, immediate or delayed, (randomly chosen); the octopus must correctly grasp the corresponding block 5 times in a row before beginning the test trials. This will ensure that the octopus knows the outcome of choosing each block and is not just randomly selecting.

The 8 test trials will consist of 4 “delay” trials in which the larger reward corresponds to the delayed reward choice, 2 “equal” trials in which the rewards are small and equal for delayed and immediate, and 2 “immediate” trials in which there is a small reward for the immediate choice and no reward for the delayed choice. The “immediate” and “equal” trials serve to demonstrate whether or not the octopus truly understands the testing situation; if it does, it should select the immediate choice for all 4 of these trials, since the reward is either equal or greater for selecting the immediate. Thus, the “immediate” and “equal” trials provide a baseline with which to compare the “delay” trials. The “delay” trials, thus, will determine whether the octopus is able to consciously make a choice to delay gratification for 20 seconds in order to receive a larger reward. The larger reward will only be present for the “delay” trials and will only be associated with the delayed gratification option. The “equal” and “immediate” trials are necessary to establish a baseline, but only the small reward option will be present in these trials to prevent to octopus from getting confused and associating the larger reward with the immediate option. These 8 trials will be randomly ordered, to control for any bias based on order of presentation.

In each trial, the octopus will be presented with two clear tubes of food; the larger reward will be visually filled twice as high with food as the smaller reward. Right after the tubes are placed on the table right in front of the tank, the wooden blocks will be presented to the octopus. Once the octopus grasps a block, the 2-second tone will be played to signal to the octopus that it will receive a food reward, the unselected block will be retracted, and the unselected tube will be pulled back from the tank. If the octopus grasps the immediate reward block (red for octopuses 1 and 2, blue for octopuses 3 and 4), the experimenter will instantly give the food within the selected tube to the octopus. If the octopus grasps the delayed reward block, the experimenter will begin the 20 second delay as soon as the octopus grasps the block. Once the delay is over, a one-half second tone will sound, and the experimenter will give the food reward to the octopus. Once the food has been given, the experimenter will reset the conditions and begin the next trial.

In order to move on to the next phase of testing, the octopus must choose to delay gratification for a larger reward at least 3 out of 4 times 3 days in a row.

Testing 1 b: 40 second delay

The procedure will be identical to that used in Testing 1 a, except that the delay for the delayed reward choice will be 40 seconds instead of 20 seconds. In order to move on to the next phase of testing, the octopus must choose to delay gratification for a larger reward at least 3 out of 4 times 3 days in a row.

Testing 1 c: 60 second delay

See above.

Testing 1 d: 120 second delay

See above.

Testing 2: Self-distracting Play

Purposes: The purposes of this phase are (i) to examine whether the octopuses use self-distracting play to cope with the delayed reward condition, and (ii) to determine if the presence of toys will allow them to wait longer for the reward. Will the octopuses play significantly more with toys during testing delays than at other times? Additionally, will the octopuses improve their performance—i.e., become more patient—when toys are present?

An identical set of three toys will be provided to octopuses 1 and 3. The toys will be in the cage at all times, including times when the octopus is not testing. Octopuses 2 and 4 will not be provided with toys, but will undergo identical testing to the others. This is to control for the possibility that the octopuses naturally become better at delaying reward receipt over time, so that there is a baseline with which to compare the effects, if any, of the presence of toys.

The testing procedure will be identical to that of *Testing 1*, with delay times of 20 seconds, 40 seconds, 60 seconds, and 120 seconds. Each trial will be videotaped, and the videotapes will each be coded by two independent observers for the amount of time the octopus spends interacting with the toys during the testing sessions. These times will be compared to the amount of time the octopus spends interacting with the toys during randomly selected sections of video-recorded time of equal length from non-testing portions of the day. Additionally, time spent interacting with the toys will be compared between trials in which the delayed option is the right choice and when the immediate option is chosen. Videos from the reminder trials, in which only one tube is filled with food, will also be examined and compared with non-testing videos.

Similarly to Testing 1, the octopus will advance to the greater delay time if it chooses to delay gratification at least 3 out of 4 times for 3 days in a row. The time delay level to which the octopuses advance, and their overall percentage of delay trials selected, will be compared to Testing 1 to see if the presence of toys improves their ability to delay gratification. Since two control octopuses will not undergo this phase of training, but will instead repeat Training 1, the progress in delay of gratification abilities can be compared to the natural progress of an octopus not exposed to the potential coping mechanism of toys.

Results/Interpretation

Hypothesis 1: Delay of Gratification

The results of this study will shed light on whether or not octopuses have the cognitive ability to wait, delaying immediate gratification, for a larger reward. This ability has only been found to a significant level in primates, which potentially developed intelligence through the same pathways as humans (Evans and Beran 2007). Whether or not mollusks display this cognitive ability, it will provide valuable information about the development of intelligence in an organism totally unrelated to humans. If octopuses can delay gratification, particularly if they employ self-distraction as a coping mechanism, it will suggest that mollusk cognition evolved in a parallel fashion to primate cognition; this result would encourage researchers to examine what evolutionary pressures produce such similar cognition in species as different as octopuses and chimpanzees. Further, it would be the first instance of a very short-lived creature demonstrating significant ability to understand the future and predict effects of their actions, thus challenging the traditional hypothesis that such capacities evolved coincidentally with longer lifespans.

Conversely, should octopuses prove unable to delay gratification, an important difference between invertebrate and vertebrate cognition will have been found. The implication of this result is either that octopus intelligence is, in fact, fundamentally different in certain ways than primate intelligence or that octopus intelligence is not as evolved as that of primates. We can then seek to understand the effects of differing environmental selection pressures on cognition by examining this alien intelligence. Regardless of the results of this portion of the study, it will allow us to better understand the evolution of higher cognition in animals.

Hypotheses 2 and 3: Self-Distracting Play

Additionally, this study will further examine play behavior in octopuses by studying whether or not octopuses play with available toys to distract themselves. Since octopuses are highly intelligent and short-lived, it makes sense that they would have a high innate propensity for play and exploration; evolutionarily, octopuses that investigated novel types of crabs, taking time to figure out how to pry open the shell, would have access to a new food source and would thus have a greater chance to survive than non-curious octopuses. Play is characteristic of intelligent life, since it provides an avenue to gather information and experiment (Siviy 1998). Instances of juvenile play have been well documented and examined, often with the conclusion that play provides an avenue for cognitive training (e.g., Biben 1998). However, a less well understood aspect of play is the purpose of object play in adult animals (Hall 1998). Adult object play has been characterized as "resistant to explanation" (Biben 1998) and has been the focus of far less studies than juvenile exploratory play. The results of the proposed study will provide further data to examine adult object play, and will further elucidate potential functional purposes of play in animals. Whether or not octopuses use play behavior to distract themselves remains to be seen, and will provide another interesting avenue to examine the development of higher cognition.

Literature Cited

Ainslie G. 1974. Impulse control in pigeons. Journal of the Experimental Analysis of Behavior 21: 485–489.

Alves, C., J.G. Boal, and L. Dickel. 2007. Short distance navigation in cephalopods: A review and synthesis. Cognitive Processing 9:239–247.

Biben, M. 1998. Squirrel monkey play fighting: Making the case for a cognitive training function for play. Pages 161-182 in Animal Play: Evolutionary, Comparative, and Ecological Perspectives (M. Bekoff and J.A. Byers, Eds.) Cambridge, USA.

Bierens de Haan, J. A. 1949. Animal psychology. Hutchinson, London, UK.

Boal, J. 1991. Complex learning in *Octopus bimaculoides*. American Malacological Bulletin 9:75–80.

Boal, J. G. 1996. A review of simultaneous visual discrimination as a method of training octopuses. Biological Reviews of the Cambridge Philosophical Society 71:157–190.

Boycott, B. B. 1954. Learning in *Octopus vulgaris* and other cephalopods. Pubblicazione della Stazione Zoologica di Napoli 25:67–93.

Boycott, B. B., and J.Z.Young. 1950. The comparative study of learning. Symposium of the Society for Experimental Biology 4: 432–453.

Budelmann, B. U. 1994. Cephalopod sense organs, nerves and the brain: Adaptations for high performance and life style. Marine and Freshwater Behaviour and Physiology 25: 13–33.

Burghardt, Gordon M. 1998. The evolutionary origins of play revisited: Lessons from turtles. Pages 1-26 in Animal Play: Evolutionary, Comparative, and Ecological Perspectives (M. Bekoff and J.A. Byers, Eds.) Cambridge, USA.

Buytendijk, F. J. J. 1933. Das Verhalten von Octopus Nach teilweiser Zerstorung des "Gehirns" [The behavior of Octopus after partial destruction (or removal) of its brain]. Archives Neerlandaises de Physiologie de l'Homme et des Animaux18: 24–70.

Chichery, R. 1992. L'apprentissage chez les mollusques [Learning in mollusks]. Psychologie Française 37:15–20.

Cournoyer, M., and M. Trudel.1991. Behavioral correlates of self-control at 33 months. Infant Behavior and Development 14:497–503.

Evans, T. A., and M.J. Beran. 2007. Chimpanzees use self-distraction to cope with impulsivity. Biology Letters 3: 599-602.

Fantino, E. 1966. Immediate reward followed by extinction vs. later reward without extinction. Psychonomic Science 6: 233-234.

Fiorito, G., and P. Scotto. 1992. Observational Learning in *Octopus Vulgaris*. Science:545-547.

Fiorito, G., C. Vonplanta, and P. Scotto. 1990. Problem-solving ability of *Octopus vulgaris* Lamarck (Mollusca, Cephalopoda). Behavioral and Neural Biology 53:217-230.

Forister, A. 2002. The octopus and the orangutan: More true tales of animal intrigue, intelligence, and ingenuity. Library Journal 127:136-136.

Grosch, J., and A. Neuringer. 1981. Self-control in pigeons under the Mischel paradigm. Journal of the Experimental Analysis of Behavior 35:3-21.

Hall, Sarah L. 1998. Object play by adult animals. Pages 45-60 in Animal Play: Evolutionary, Comparative, and Ecological Perspectives (M. Bekoff and J.A. Byers, Eds.) Cambridge, USA.

Heinrich, B., and R. Smolker. 1998. Play in common ravens (*Corvus corax*). Pages 27-44 in Animal Play: Evolutionary, Comparative, and Ecological Perspectives (M. Bekoff and J.A. Byers, Eds.) Cambridge, USA.

Hochner, B., E. R. Brown, M. Langella, T. Shomrat, and G. Fiorito. 2003. A learning and memory area in the octopus brain manifests a vertebrate-like long-term potentiation. Journal of Neurophysiology 90:3547–3554.

Ikeda, Y. 2009. A perspective on the study of cognition and socialityof cephalopod mollusks, a group of intelligent marine invertebrates. Japanese Psychological Research 51:146–153.

Killeen,P.R., J.P. Smith, and S.J. Hanson. 1981. Central place foraging in *Rattus norvegicus*. Aniimal Behavior 29:64–70.

Liddell, H.G. and R.Scott. 2011. A Greek-English Lexicon. AT: http://www.perseus.tufts.edu/, DOA 2 May 2011.

Logue, A. W., and T.E. Penia-Correal. 1984. Responding during reinforcement delay in a self-control paradigm. Journal of the Experimental Analysis of Behavior 41:267-277.

Mather, J.A. 2004. Cephalopod skin displays: From concealment to communication. Pages 193-214 in Evolution of Communication Systems: A Comparative Approach (D. K. Oller and U. Griebel, Eds) Cambridge, MA.

Mather, J. A. 1991. Navigation by spatial memory and use of visual landmarks in octopuses. Journal of Comparative Physiology 168:491–497.

Mather, J. A. 1995. Cognition in cephalopods. Advances in the Study of Behavior 24: 317–353.

Mather, J. A. 1994. Home choice and modification by juvenile *Octopus vulgaris* (Mollusca, Cephalopoda) – specialized intelligence and tool use. Journal of Zoology 233:359-368.

Mather, J. A. 2008. To boldly go where no mollusc has gone before: Personality, play, thinking, and consciousness in cephalopods. American Malacological Bulletin 24:51-58.

Mather, J. A., and R.C. Anderson. 1999. Exploration, play, and habituation in octopuses *(Octopus dofleini)*. Journal of Comparative Psychology 113:333–338.

Mazur, J. E., and A.W. Logue. 1978. Choice in a "selfcontrol" paradigm: Effects of a fading procedure. Journal of the Experimental Analysis of Behavior 30: 11-17.

Miller, D.T., and R. Karniol. 1976. Coping strategies and attentional mechanisms in self-imposed and externally imposed delay situations. Journal of Personality, Sociology, and Psychology 34:310–316.

Mischel, W. 1974. Processes in delay of gratification. Pages 249–292 in Advances in Experimental Social Psychology, Vol. 7 (L. Berkowitz, Ed.)Academic Press, New York, NY.

Packard, A. 1972. Cephalopods and fish: The limits of convergence. Biological Reviews 47:241–307.

Packard, A. 1963. The behaviour of *Octopus vulgaris*. Bulletin de l'Institut Oceanographique de Monaco 6:35-49.

Papini, M. R., and M.E. Bitterman. 1991. Appetitive conditioning in *Octopus cyanea*. Journal of Comparative Psychology 105:107–114.

Sanders, G. D. 1975. The cephalopods. Pages 1-101 in Invertebrate Learning (W. C. Corning, J. A. Dyal, and A. O. D. Willows, Eds). Plenum, New York, NY.

Schiller, P. H. 1949. Delayed detour response in the octopus. Journal of Comparative Physiology and Psychology 42: 220–225.

Siviy, S.M. 1998. Neurobiological substrates of play behavior: Glimpses into the structure and function of mammalian playfulness. Pages 221-242 in Animal Play: Evolutionary, Comparative, and Ecological Perspectives (M. Bekoff and J.A. Byers, Eds.) Cambridge, USA.

Thompson, K.V. 1998. Self assessment in juvenile play. Pages 183-204 in Animal Play: Evolutionary, Comparative, and Ecological Perspectives (M. Bekoff and J.A. Byers, Eds.) Cambridge, USA.

Toner, I.J., and R.A. Smith.1977. Age and overt verbalization in delay-maintenance behavior in children. Journal of Experimental Child Psychology 24:123–128.

Walker, J. J., N. Longo, and M.E. Bitterman. 1970. The octopus in the laboratory: Handling, maintenance, training. Behavior Research Methods and Instrumentation 2:15–18.

Watson, D.M. 1998. Kangaroos at play: Play behaviour in the Macropodoidea. Pages 61-95 in Animal Play: Evolutionary, Comparative, and Ecological Perspectives (M. Bekoff and J.A. Byers, Eds.) Cambridge, USA.

Wells, M. J. 1962. Brain and behaviour in cephalopods . London: Heinemann.

Wells, M. J. 1964. Detour experiments with octopuses. Journal of Experimental Biology 41:621–642.

Wells, M. J. 1966. Learning in the octopus. Symposia of the Society for Experimental Biology 20:477–507.

Wells, M. J. 1967. Short-term learning and interocular transfer in detour experiments with octopuses. Journal of Experimental Biology 47:383–408.

Wells, M. J. 1970. Detour experiments with split-brain octopuses. Journal of Experimental Biology 53:375–389.

Wells, M. J. 1978. Octopus: Physiology and behavior of an advanced invertebrate. London: Chapman and Hall.

Young, J. Z. 1971. The anatomy of the nervous system of *Octopus vulgaris*. Oxford: Clarendon Press.

Young, J. Z. 1983. The distributed tactile memory system of *Octopus vulgaris*. Proceedings of the Royal Society of London 218: 135-176.