THE SELECTION AND ADAPTIVE USE OF MATERIALS IN NUT-CRACKING BY WILD BEARED CAPUCHINS (CEBUS LIBIDINOSUS):

A PERCEPTION-ACTION PERSPECTIVE

by

QING LIU

(Under the Direction of DOROTHY M. FRAGASZY)

ABSTRACT

Nut-cracking is a complex tool use behavior that has only been discovered in wild chimpanzees and capuchin monkeys. The study of animal tool use has long emphasized the cognitive processes such as reasoning and representation in tool use but has largely ignored the act of too use itself.

This research employs a Perception-Action perspective derived from the Gibsonian Ecological Psychology framework to study the selection and adaptive use of materials in nut-cracking by wild capuchin monkeys in Brazil. I first reviewed the background literature on the study of animal tool use and compared the traditional representational approach and the proposed Perception-Action perspective (Chapter 1). Next I presented the first study in which capuchin monkeys selectively used effective novel pits on anvils, using exploratory behaviors to detect affordances (Chapter 2) and the second study in which the capuchin monkeys adaptively and effectively used hammer stones of different weights to crack nuts by modulating forces and lifting height (Chapter 3). Chapter 4 summarized the findings and discussed the significance of the Perception-Action perspective in the study of animal tool use and problem solving.

INDEX WORDS: perception-action coupling; nut-cracking; anvil; hammer stone; tool use; affordance detection; motor control; accommodation; adaptive use; regulation; bearded capuchins; *Cebus libidinosus*.

THE SELECTION AND ADAPTIVE USE OF MATERIALS IN NUT-CRACKING BY WILD BEARED CAPUCHINS (CEBUS LIBIDINOSUS):

A PERCEPTION-ACTION PERSPECTIVE

by

QING LIU

B.S., Peking University, China, 2004

M.S., University of Georgia, Athens, GA, 2007

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2011

THE SELECTION AND ADAPTIVE USE OF MATERIALS IN NUT-CRACKING BY WILD BEARED CAPUCHINS (CEBUS LIBIDINOSUS):

A PERCEPTION-ACTION PERSPECTIVE

by

QING LIU

Major Professor:	Dorothy M. Fragaszy
Committee:	Irwin Bernstein Kathy Simpson

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
August 2011

Dedicated to my dearest dad.

ACKNOWLEDGEMENTS

I would like to express my heartfelt thanks to my mentor and advisor, Dr. Dorothy Fragaszy, for teaching me how to become a scientist and guiding me with great patience through my graduate career at UGA. Her passion for her devoted field has always been one of the biggest inspirations for me. Her compassionate support and friendship has been so very touching and unimaginable among usual advisor-student dyads. I can only say that I have been very fortunate to have her as my major professor. I would also like to deeply thank my committee members, Dr. Irwin Bernstein and Dr. Kathy Simpson for their support and helpful suggestions and comments on my research and manuscripts. Though not on my committee, Dr. Elisabetta Visalberghi has also been my research mentor on the nut-cracking project. Thank you for all your guidance and encouraging words!

`I would like to thank all my dearest friends who have supported me through all these years with your love, encouragement and caring friendship: Rui Hu, Miaomiao Chi, Rachel Han, Jessi Crast, Summer Zu, Erica Kennedy, Carrie Rosengart, Tephilla Jeyaraj, Brian Stone, Allison Foote, Wenyi Zhou, Dongshu Xu, Li Bin, Zhang Yuan, Feng Bo and everyone else whose names got stuck inside my head for now.

Qingyang, love of my life, without you, I would not have gotten here. Until the day the ocean doesn’t touch the sand, I will always love you!

Last but not least, I would like to thank all the amazing capuchins at Boa Vista. Without your participation, I would not have collected so much data and great memories at BV. Jatoba, I wish you the longest and most peaceful reign ever at BV. You will always have a special place in my heart.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Animal tool use and the representational perspective

Tool use appears in the paleoarchaeological record as early as 2.6 million years ago (Semaw et al. 2003) and is a ubiquitous feature of all human cultures. Therefore, tool use has received considerable attention from comparative psychologists. One widely known series of experiments on tool use was conducted by Wolfgang Köhler, in which he tested captive chimpanzees (*Pan troglodytes*) in various tool use situations and concluded "insight" led to effective problem-solving in some individuals (Köhler 1925). In the mid-20th century, Jane Goodall's discovery of flexible termite fishing by wild chimpanzees suggested complex tool use and tool making were not uniquely human. Since then, interest in animal tool use and problem-solving increased dramatically both in the wild and in laboratory settings.

Early comparative psychologists believed that there is a psychological continuity among species ("continuity hypothesis") and that if animals show behaviors similar to humans, it is because there are also similar psychological processes at work ("analogy hypothesis", as reviewed by Osiurak et al. 2010). It is these ideas that attracted several generations of researchers to study problem-solving and tool use in animals, in the hope of identifying the cognitive origins of human tool use. In this quest, comparative psychologists have employed Piagetian theory to study the cognitive abilities of animals in tool use and problem-solving. For example, in a thorough review of primate cognition Tomasello and Call (1997) pointed out that one "defining characteristics of cognitive processes is some form of mental representation" (p10). This means that in the decision making process, the organism must use information from sources (such as memory, categorization, inference, insight etc.) other than information directly perceived (Tomasello and Call 1997). Piaget (1952) called this "mental trial-and-error", meaning that the organism must mentally test alternative scenarios in its mind. In other words, they believe that cognition in tool use and problem-solving is reflected in the ability to "think it through". Therefore studies following this view focus on testing animals' ability to think it through when faced with a problem. Pulling in objects on a continuous surface (with a painted area as a fake trap) versus a discontinuous (with a real trap) surface is an example of such tasks (e.g. Povinelli 2000). In such studies, researchers were interested to see if the animals were able to mentally test different scenarios (food reward falls into the real trap vs. not fall into the fake trap) and make the correct choice before acting on the objects.

Such studies take a representationalist point of view about cognition. Fodor is a philosopher and cognitive scientist best known for his "language of thought" hypothesis. He believes thought is represented in a mental "language". Fodor argued in his book *Language of Thought* (which is a theoretical landmark for computational psychology) that "the only psychological models of cognitive processes that seem even remotely plausible represent such processes as computational (processes)" and that "computation presupposes a medium of computation: a representational system" (Fodor 1975, p27). Fodor and Phylyshyn further wrote in 1988 (p7) on major traditions in modern theories about the mind, "representationalists hold that postulating representational states is essential to the theory of cognition; according to representationlists, there are states of the mind which function to encode states of the world".

Most studies on animal tool use and problem-solving follow this representational approach and ask how animals represent tools/objects in tool use and problem-solving tasks (as reviewed in Call 2010; Emery and Clayton 2009; Tomasello and Call 1997; Povinelli 2000). However, a review of this literature yields two common types of results. One is negative results that animals did not successfully solve the problem leading to the conclusion that they did not have such cognitive abilities. The other type is that animals did successfully solve some problems and failed the others suggesting they only learned some associative rule that the task itself could not rule out (e.g. learning to associate continuous surface with successful retrieval of reward, instead of understanding what a trap does). Only a very limited number of studies were confident to report that causal reasoning was demonstrated and alternative explanations ruled out (e.g. one rook *Corvus frugilegus* in Seed et al. 2006; and three new Caledonian crows *Corvus moneduloides* in Taylor et al. 2009).

Considering this body of work as a whole, one major limitation is that it heavily emphasized "higher-level" cognitive abilities such as causal reasoning and understanding (computation with mental representations) only while largely ignoring the act of tool use. This happened mainly because researchers in this line of work assumed actions and cognitive abilities can be separated and because researchers mainly hoped to uncover the cognitive mechanisms responsible for tool use and problem-solving. The focus on cognitive mechanisms has led to the widely shared (though not necessarily correct) view that tool use concerns not what the organism does in the tool use act, but concerns the way the organism conceives tools and problems (to be solved) in its mind. To many comparative psychologists, tool use equals a cognitive means-ends problem for the organism. The representational approach fundamentally posits that the mind encodes the outside world via mental representations and cognition is the computation process during which mental representations are being manipulated. Therefore for representationalists, cognition is “mental gymnastics” (Chemero 2009) and is divorced from the rest of the body (bodily actions and action capabilities). Studies derived from this approach usually focus on testing a judgment about a tool but not the tool use process itself.

In recent years, researchers in and outside this line of work have become increasingly aware of the limitations stemming from the traditional representational approach (Call 2010; Chemero 2009; de Waal and Farrari 2010; Lockman 2000; Osiurak et al. 2010). The mixed (at best) results (that most animals failed to show these mental processes) suggest that perhaps a new theoretical approach, one that does not rely on mental representations as explanatory concepts about tool use but rather does afford systematic exploration of these behaviors, would be useful.

A perception-action perspective to tool use

As Lockman (2000) suggested, if we believe that tool use requires advanced level of representation and abstract reasoning abilities, this implies that tool use must be a discontinuous developmental phenomenon that depends on the emergence of representational reasoning. This view also leads researcher to interpret ineffective actions before reaching success as evidence for "cognitive gaps or deficiencies". As an alternative, Lockman (2000) proposed the Perception-Action framework derived from Gibson’s ecological psychology for studying tool use behavior and its development in human children.

The Perception-Action framework emphasizes the coupling of perception and action in behavior (Gibson, 1979; Gibson and Pick, 2000; Lockman, 2000). It views common activities as exploratory actions from which individuals gain more knowledge about the environment. From this framework, the development of tool use can be viewed as the process during which the actor learns about the relationship between objects and surfaces in relation to him/herself through actions and learns how to modify the objects or environment through action. The focus here is the tool-using act or pre-tool-using act, and the consequence of certain actions on subsequent actions (perception of the environment and the actor's ability to act in that environment).

A key concept in this framework is termed “affordance”, representing the action possibility for the individual actor in relation to the environment (Gibson, 1979). Affordance is essentially the “currency” or the “medium” in the environment-actor system, in which the actor perceives the affordance of the environment based on his or her own capabilities, executes action in the environment and gains new perceptual information from that action, leading to better detection of affordances and effective goal directed action. For example, studies show human adults efficiently detect affordances of surfaces or objects in activities such as walking on surfaces, sitting on chairs, climbing stairs, or passing apertures (as reviewed by Young et al.

2000). It was also shown that humans detect affordances of objects using exploratory routines. For example, Lederman and Klatzky (1996) showed that people maintained limited and consistent patterns of finger movements when manipulating objects for information (e.g. hefting to know about weight). Developmentally, detection of affordances appears early in life. Studies showed that infants in their second half-year already modify their manual exploratory actions according to different properties of various objects and surfaces (Bourgeois et al. 2005). As Lockman (2000) suggested, applying the Perception-Action framework to tool use development in young children, we can think of tool use as a problem of "detecting affordances" and relating affordances of different objects/surfaces through actions.

From the Perception-Action perspective, tool use is understood as a continuous phenomenon, both ontogenetically and phylogenetically. Thus, we can study how individuals of any species or age detect affordances of objects or surfaces using species-typical exploratory routines and how they detect affordances of actions combined with surfaces, as occurs in tool use, and how they manage the multiple and mobile frames of references inherent in tool use (as when one object is brought into a particular spatial relation with a surface or another object – Lockman 2000). In the case of tool use, affordances involve physical and spatial interrelations of objects and surfaces rather than a property of any single object or surface, and thus they depend upon the actors' use of objects. For example, a stone may be used effectively to crack a nut when held in one position but not another, and on one surface but not another.

Applying the Perception-Action framework to tool use in nonhuman animals leads to the following hypotheses:

1) Animals detect affordances of objects and of object/ surface/ action combinations using species-typical exploratory actions.

2) Detecting affordances by direct contact with the body (that is, via one relation) should be easier than by indirect contact, because indirect contact adds at least one additional degree of freedom to the system. Evaluating or managing additional degrees of freedom increases the challenge of an activity.

3) Animals will modify their actions in response to varying affordances when they use tools.

Research aim

This dissertation research aimed to adopt the Perception-Action perspective in the study of tool use behavior in wild capuchin monkeys (*Cebus libidinosus*). Specifically, it set out to test the three general hypotheses stated above.

Wild bearded capuchin monkeys in Fazenda Boa Vista, Piauí, Brazil, routinely put a nut in a pit on an anvil and use hammer stones to crack open hard palm nuts (Fragaszy et al. 2004). Recent studies showed that the capuchin monkeys preferred heavier stones and nuts that are easier to crack in field experiments about choice (Fragaszy et al. 2010b; Visalberghi et al. 2009). These two studies demonstrated capuchin monkeys are selective about nuts and stones in nut-cracking prior to the cracking action. It would be necessary to investigate if they are selective about anvil sites (the one type of material in nut-cracking that they usually do not directly manipulate), and if and how they adjust the tool-using actions in real-time with different hammer stones and nuts of various sizes. Therefore, this research studied how capuchin monkeys selected anvil sites and how they adjusted and modified their actions when using stones of variable weights to crack nuts of variable sizes.

This dissertation research consists of two studies. The first study (Chapter 2, Liu et al. 2011) examined two aspects of affordances involving using anvils (and more specifically, pits in which they place the nut on anvils) used for nut-cracking (reactive force and stabilizing effect on the nut). The capuchins at Fazenda Boa Vista frequently reposition the nut in the same pit or move the nut to a different pit on the same anvil between strikes (Fragaszy et al. 2010a). These behaviors suggest that the capuchins might be evaluating the affordance of the pit. The capuchins also prefer some anvils to others (personal observation), which might reflect perception of differential effectiveness of the anvils as sites to crack nuts. Affordances of pits are interrelations of the pit, the nut and the stone upon striking the nut (and thus include the monkey's actions with the stone). Following the first two hypotheses stated earlier, in this study, I predicted the monkeys would generate exploratory actions to detect affordances of novel pits using their existing manipulative repertoire (namely positioning the nut and striking the nut with a stone) and that monkeys would switch between pits more frequently than they would switch between nuts and stones, because the affordances of nuts and stones could be evaluated by direct action on the object with the body, whereas the pits must be evaluated through indirect contact with nuts, stones, or both.

The second study (Chapter 3, Liu et al. to be submitted) tested the third hypothesis that animals would modify their actions in response to varying affordances for the same task. I predicted the monkeys would adjust/ adapt their actions when they use stones of different weights to crack nuts of different weights. Specifically, they would lift lighter stones higher than they would lift heavier stones. They would strike the stone downward faster with lighter stones than heavier stones and when they crack bigger nuts rather than smaller nuts of the same species. Motion of the stone was used to evaluate energetics and kinematics in these analyses.

References

Bourgeois, K. S., Khawar, A. W., Neal, A. S., & Lockman, J. J. (2005). Infant manual exploration of objects, surfaces, and their interrelations. *Infancy, 8*, 233–252.

Call, J. (2010). Trapping the mind of apes: Causal knowledge and inferential reasoning about object-object interactions. In E. V. Lonsdorf, S. R. Ross, and T. Matsuzawa (Eds.), *The mind of the chimpanzees: Ecological and experimental perspectives*. Chicago, IL: University of Chicago Press.

Chemero, A. (2009). *Radical embodied cognitive science*. Cambridge, MA: The MIT Press.

de Waal, F. B.M., & Ferrari, P. F. (2010). Towards a bottom-up perspective on animal and human cognition. *Trends in Cognitive Sciences*, *14*, 201-207.

Emery, N. J., & Clayton, N. S. (2009). Tool use and physical cognition in birds and mammals. *Current Opinion in Neurobiology, 19*, 27-33.

Fodor, J. A. (1975) *The Language of Thought*. New York, NY: Crowell.

Fodor, J. A.,& Pylyshyn, Z. (1988). Connectionism and cognitive architecture: A critical analysis. *Cognition, 28*, 3-71.

Fragaszy, D. M., Izar, P., Visalberghi, E., Ottoni, E. B., & de Oliveria, M. G. (2004). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology, 64*, 359–366.

Fragaszy, D., Pickering, T., Liu, Q., Izar, P., Ottoni, E. B. & Visalberghi, E. (2010a). Bearded capuchin monkeys' and a human's efficiency at cracking palm nuts with stone tools: field experiments. *Animal Behaviour, 79*, 321-332.

Fragaszy, D., Greenberg, R., Visalberghi, E., Ottoni, E. B., Izar, P. & Liu, Q. (2010b). How wild bearded capuchin monkeys select stones and nuts to minimize the number of strikes per nut cracked. *Animal Behaviour,* 80, 205-214.

Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston, MA: Houghton Mifflin.

Gibson, E. J. & Pick, A. D. (2000). *An ecological approach to perceptual learning and development*. NY: Oxford University Press.

Köhler, W. (1925). *The mentality of apes.* London: Routledge and Kegan Paul.

Lederman, S. J., & Klatzky, R. L. (1996). Action for perception: manual exploratory movements for haptically processing objects and their features. In Wing, A., Haggard, P., & Flanagan, R. (Eds.), *Hand and Brain: The neurophysiology and psychology of hand movements* (pp. 431-446). San Diego: Academic Press.

Liu, Q., Fragaszy, D., Wright, B., Wright, K., Izar, P., & Visalberghi, E. (2011). Wild bearded capuchin monkeys (*Cebus libidinosus*) place nuts in anvils selectively. *Animal Behaviour, 81*, 297-305.

Liu, Q., Fragaszy, D., & Visalberghi, E. To be submitted. Wild bearded capuchin monkeys (*Cebus libidinosus*) adapt actions in response to varied hammer stones and nuts in nut-cracking.

Lockman, J. (2000). A perception–action perspective on tool use development. *Child Development, 71*, 137-144.

Osiurak, F., Jarry, C., & Le Gall, D. (2010). Grasping the affordances, understanding the reasoning: Toward a dialectical theory of human tool use. *Psychological Review, 117*, 517-540.

Piaget, J. (1952). *The origins of intelligence in children*. New York, NY: Norton.

Povinelli, D. J. (2000). *Folk physics for apes: The chimpanzee's theory of how the world works*. Oxford: Oxford University Press.

Semaw, S., Rogers, M. J., Quade, J., Renne, P. R., Butler, R. F., Dominguez-Rodrigo, M., Stout, D., Hart, W. S., Pickering T. & Simpson, S. W. (2003). 2.6-Million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *Journal of Human Evolution, 45*, 169-177.

Taylor A. H., Hunt, G. R., Medina, F. S., & Gray, R. D. (2009). Do New Caledonian crows solve physical problems through causal reasoning? *Proceedings of the Royal Society, 276*, 247–254.

Tomasello, M. & Call, J. (1997). *Primate cognition*. New York, NY: Oxford University Press.

Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P. & Fragaszy, D. (2009). Selection of effective stone tools by wild bearded capuchin monkeys. *Current Biology*, *19*, 213-217.

Young, M. F., Barab, S. A. & Garrett, S. (2000). Agent as detector: an ecological psychology perspective on learning by perceiving-acting systems. In: *Theoretical Foundations of Learning Environments* (Ed. by D. H. Jonassen). Mahwah, New Jersey: Lawrence Erlbaum Associates, Inc.

CHAPTER 2

WILD BEARDED CAPUCHIN MONKEYS (CEBUS LIBIDINOSUS) PLACE NUTS IN ANVILS SELECTIVELY[1]

---

[1] Liu, Q., Fragaszy, D., Wright, B., Wright, K., Izar, P., & Visalberghi, E. 2011. *Animal Behaviour, 81*, 297-305.

Reprinted here with permission of publisher.

Abstract

Are wild bearded capuchin monkeys selective about where they place nuts on anvils, specifically the anvil pits, during nut cracking? In the present study, we examined (1) whether capuchins' preferences for particular pits are influenced by the effectiveness of the pit in cracking the nut and/or by the stability of the nut during striking, (2) how capuchins detect the affordances of novel pits and (3) the influence of social context on their selections. Anvil pits varied in horizontal dimension (small, medium and large) in experiment 1 and in depth (shallow, medium and deep) in experiment 2. In both experiments, three different pits were simultaneously presented, each on one anvil. We coded the capuchins' actions with the nut in each pit, and recorded the outcome of each strike. In both experiments, capuchins preferred the most effective pit, but not the most stabilizing pit, based on the number of first strikes, total strikes and nuts cracked. Their choice also reflected where the preceding individual had last struck. The capuchins explored the pits indirectly, placing nuts in them and striking nuts with a stone. The preference for pits was weaker than the preference for nuts and stones shown previously with the same monkeys. Our findings suggest that detecting affordances of pits through indirect action is less precise than through direct action, and that social context may also influence selection. We show that field experiments can demonstrate embodied cognition in species-typical activities in natural environments.

Keywords: affordance, anvil use, capuchin, Cebus libidinosus, embodied cognition, nut cracking, perception-action, selectivity, social influence, tool use

Introduction

Humans are selective when choosing a tool for the job at hand, as when seeking a hammer of the right weight or rake of the right length. This trait was present as early as 2.6 million years ago, when our ancestors selectively used particular materials for processing animal flesh and bones (Semaw et al. 2003). Nonhuman animals may also be selective. Darwin's (1881) work on how earthworms (*Lumbricus terrestris*) explore and select different leaves or paper triangles to pull into their burrows is a classic example illustrating how widespread selectivity is across the animal kingdom. Among others, chimpanzees (*Pan troglodytes*), New Caledonian crows (*Corvus moneduloides*) and capuchin monkeys (*Cebus libidinosus*) have been studied for their selectivity in tool use (Boesch and Boesch 1983; Chappell and Kacelnik 2002; Visalberghi et al. 2009). For example, recent studies have shown that wild bearded capuchin monkeys select hammer stones to crack nuts and seeds with respect to stone weight and friability (tendency to crumble) (Visalberghi et al. 2009; Ferreira et al. 2010). Fragaszy et al. (2010b) further report that wild bearded capuchin monkeys select heavier stones to crack larger, more resistant nuts, and prefer nuts that are easier to crack (i.e., of low resistance) over nuts that are harder (i.e., of high resistance). Thus bearded capuchin monkeys are selective about tools and the objects they process with tools.

Selectivity rests upon perception of affordances. In his ecological approach to perception and action, Gibson (1979) used the term 'affordance' to label properties of the relationship between actor and environment (here, objects and surfaces) that the actor needs to perceive in order to generate effective actions. Action is used to generate these perceptions which in turn will guide future actions. In other words, perception and action are inextricably linked. In tool use, actors need to detect the affordances of surfaces and objects and the relations between them.

Applying this framework to nut-cracking with a stone percussor, the tool user needs to detect affordances of the nut, stone and the anvil in combination with each other. Explicitly interpreted, the affordance of the nut is the ease of cracking on the anvil with the stone. The affordance of the hammer stone is its suitability to strike the nut open when the nut is placed on the anvil. Previous studies have shown that bearded capuchin monkeys attend to these affordances in their selection of nuts and stones (Visalberghi et al. 2009; Fragaszy et al. 2010b). Our concern in this report is the affordance of the anvil in its quality as a striking platform for the nut and stone. A good platform should 1) provide high reactive force (i.e., transmits the force of impact to the nut) so that the nut cracks in fewer strikes than on an anvil with low reactive force, 2) keep the nut in place following striking, and 3) provide easy accessibility to the capuchins and good stability.

The current study addresses the first two aspects of the affordance of anvils: their effectiveness for cracking the nut with a stone, and their relation to displacement of the nut after a strike. Wild bearded capuchin monkeys (hereafter, capuchins) in Fazenda Boa Vista, Piauí, Brazil, put a whole nut in a pit on the anvil before striking the nut, and frequently reposition the nut in the same pit or move the nut to a different pit on the same anvil between strikes (Fragaszy et al. 2010a). These behaviors suggest to us that the capuchins may be evaluating the affordance of the anvil, and more specifically, the pit in the anvil in which they place the nut. Capuchins prefer some anvils to others (personal observation), which may reflect perception of differential affordances of the anvils as sites to crack nuts.

In order to detect affordances of an object, the actor must act on the object when visual perception does not provide sufficient information. Bodily action, haptic exploration, and feedback are all important in organizing actions with tools. The Perception-Action perspective that we adopt here is congruent with the increasingly prominent theory in studies of human cognition that cognition is “embodied” (e.g., Barsalou 2008; Chemero 2009) in that cognition is shaped by the body and bodily actions. We propose that the same principles apply to nonhuman species. Visalberghi et al. (2009) and Fragaszy et al. (2010b) showed that capuchins handled and tapped stones when selecting between two hammer stones of equal volume and appearance, a circumstance in which they could not judge the mass of the stones by visual cues. In the current study, we expected that capuchins would generate behaviors to detect affordances of anvils, as they do for stones when they cannot judge affordances by vision, and we expected that they would prefer the anvils which provided certain affordances.

In principle it should be easier to detect affordances when the actor acts on an object or surface directly with his or her body (Bernstein 1967; Pick and Lockman 1981) rather than indirectly, through an intermediary object. In nut-cracking, the affordances of the stone and the nut are relatively easy for capuchins to detect because they handle the stone and nut directly (e.g. tapping, pushing or lifting stone, and tapping or sniffing the nut). In contrast, the capuchins usually act on the anvils indirectly by placing the nut in various positions on the anvil and striking it with the stone. Therefore, we expect that detecting affordances of the anvil is not as clear-cut as detecting affordances of the nut and stone. Our predictions in this study were that the capuchins would be selective about pits and that they would continue exploring pits across the testing period. We also wanted to document the explorative actions the capuchins performed that could provide information about the affordances of novel pits. For example, they could feel the pits directly with fingers, move nuts in and out of pits or strike the nut in the pit with a stone.

In this study, we provided novel anvils containing ellipsoid pits of different horizontal dimensions and different depths. We reasoned that the horizontal dimensions and depth of a pit could influence two aspects of affordances in nut-cracking. One aspect is the probability that the strike will displace the nut (termed "fly-off" hereafter). For a human, striking the nut in a pit significantly reduced the rate of fly-offs compared to striking the nut on a flat surface (Fragaszy et al., 2010a). We hypothesized that the capuchins use the pits in the anvils for the same reason, because displacing the nut off the anvil costs time of retrieval and risks losing the nut or the anvil site to a competitor while the animal attempts to retrieve the nut. A very shallow or a very large pit that approximates a flat surface would increase the probability that the nut would fly off (see Figure 1 for illustration). A very small pit poses a similar risk. The second aspect is the effectiveness of the pit as a striking platform. We observed that capuchins stopped using pits when they became very deep (> 3 cm) (personal observation). We further reasoned that the capuchins avoided striking a nut where little of the nut shell is exposed above the rim of the pit, because these strikes are ineffective. Therefore, we further predicted that the capuchins would prefer the pits associated with lowest fly-off rate and/or highest effectiveness (lowest number of strikes to success) and that they would avoid using the least effective (i.e., small and/or deep) pits.

We further recognized that nut cracking occurs in a social setting and the capuchins' use of pits might be influenced by the choices of other individuals. In other settings group members have a strong effect on youngsters' choice of foraging sites. For example, young wild brown capuchins (*Cebus apella*) in Suriname were attracted to inspect and handle bamboo stalks previously opened by conspecifics (Gunst et al. 2008) even though those sites no longer contained prey. In this study, we examined how social influence plays a part in the choice of location and the enhancement of interest in a location in nut-cracking.

Methods

Site and Subjects

The study site (9°39' South, 45°25' West, altitude approximately 420 m above sea level) is located on private property (Fazenda Boa Vista) in a dry woodland plain in Piauí, Brazil (Fragaszy et al. 2004; Visalberghi et al. 2007). A group of wild bearded capuchin monkeys (*Cebus libidinosus*) routinely comes to an area where there are anvils and stones. This is the area where we carried out the field experiments. The monkeys are habituated to human observers.

Nine capuchins (six males, Chicao, Mansinho, Dengoso, Tucum, Teimoso and Jatoba; and three adult females, Chuchu, Dita and Piaçava) from a group of 15 individuals participated in this study on a voluntary basis.

Materials

We used palm nuts of one species collected from the area. The nuts the capuchins cracked in this study (*Orbignya* sp.) have an ellipsoid shape and average 4 cm in diameters and 6 cm long (Visalberghi et al. 2008). Nuts of this species were commonly cracked by the capuchins at the study site outside of the experimental period as well as during the experiment. We supplied the capuchins with a single stone (1.46 kg) that was regularly used by these monkeys at this cracking site. We only used one species of nut and one stone as efficiency of cracking is related to the weight of the stone and species and size of the nuts (Liu et al. unpublished data; Fragaszy et al. 2010b).

We manufactured three log anvils cut from fallen candeia trees (*Piptocarpha rotundifolia*, Compositae), the wood of which is moderately heavy (density 0.65 g/cm^3), hard, moderately durable, with thick rough texture and good mechanical resistance (Lorenzi 1992). The capuchins use anvils of this species of tree in other areas of our study site (Visalberghi et al. 2007). The anvils were 75 cm long and had similar cross-sections (ranges from 15 to 23 cm). We smoothed the logs by peeling them and then made pits in the center of each log with chisel, hammer and Dremel tool^{TM} (Dremel company, Wisconsin). The pits varied in horizontal dimensions and depths. To determine the various horizontal dimensions and depths of the pits used in this study, we started with the average size of the nuts (4 by 4 by 6cm). We assumed that a medium-size and medium-depth pit, corresponding to average nut size (4 cm wide, 6 cm long and 2 cm in depth) would fit the average nut snugly and thus provide the optimal horizontal dimensions for minimizing nut fly-off and maximizing effectiveness of each strike.

Design

In experiment 1, we presented pits of large, medium and small horizontal dimensions. We determined the horizontal dimensions of the pits as 1.5 times greater or smaller than the average size of the nuts. The pits measured: 9 by 6 by 2cm (Large), 6 by 4 by 2cm (Medium), and 4 by 3 by 2cm (Small, 1.5 times smaller than 4 cm is 2.7cm and we rounded to the nearest cm).

In experiment 2, we presented pits of shallow, medium and deep depths. We determined the depth as 2 times greater or smaller than the average size of the nuts. The pits measured: 6 by 4 by 1cm (Shallow), 6 by 4 by 2cm (Medium) and 6 by 4 by 4cm (Deep). The medium pits in both experiments had the same dimensions and depth. Pits of different horizontal dimensions and depths are shown in Figure 2.

We made one pit on two opposite sides of each log (6 pits total). A pit of each horizontal dimension or depth appeared on two different logs. This is illustrated in Figure 3. We did this to ensure that the capuchins' use of different pits would not be affected by unknown properties of a specific pit (e.g. minor differences in rebound properties of different logs).

Procedure

As illustrated in Figure 4, the three anvils were presented in an equilateral triangle. The logs were partially buried in the ground, so that the height above ground of the top surface was approximately 10 cm (similar to that of other log anvils the capuchins use) and the logs did not wobble when struck. Since we made two pits of each size on different logs, we rotated the logs daily to get a different combination of three pits (always 1 of each size).

At the beginning of each testing day, and periodically throughout testing, we rubbed all the pits with fresh cracked nut kernels to ensure they all had the same odor and oiliness so that these cues would not influence the monkeys' use of pits. A stone and a whole nut were presented in the center of the log triangle before each trial. A trial began when a capuchin picked up the stone and a nut and brought them to an anvil to begin cracking. A trial ended when the capuchin cracked the nut, gave up the nut or was displaced by another individual. When the trial ended, the stone was put back in the center ground of the anvil triangle and abandoned nut pieces were swept off the anvils. All trials were recorded using a Canon^{TM} GL2 miniDV camcorder.

Coding

All occurrences of four associated actions (touching pit with hand, positioning nut in pit, striking nut in pit, and switching from one pit to another) were coded for every trial. The location of these actions with the nuts was also recorded (i.e., in which pit the subject positioned the nut, in which pit the subject struck the nut and from which to which pit the subject switched). Two outcomes, fly-off (nut bounced out of the pit and off the anvil; or nut remained in place) and success (cracked or not cracked) were also recorded.

We recorded the time interval (to the nearest minute) elapsed between successive subjects using the experimental anvil site by using the minutes displayed on tape. For example if the previous subject finished cracking and left the anvils at 00:20, the next one arrived at the anvils at 00:22, the interval was recorded as 2 minutes. The time interval was recorded as zero when the next subject came to the anvil, less than 1 minute after the previous one left.

The coder re-coded 10 randomly selected trials from each experiment and the intra-coder agreement was 100% for all variables combined. Another coder who was blind to the design also coded 10 randomly selected trials from each experiment and the inter-coder agreement was 97% for all variables combined.

Analysis

We first evaluated the affordances of the pits and then analyzed the capuchins' detection of the affordances through their preferences and their strategy of detection (feel the pit, position a nut in the pit, and strike a nut in the pit with a stone), using repeated t-tests. We then looked at the patterns of switches to determine first, if they use the more energy conserving strategy (position only before switch) or the less energy conserving strategy (position and strike before switch); and second, if they switched more frequently out of ineffective pits (termed "self-correction", hereafter) than out of effective pits. For all of the above analyses, we used data from trials in which the subjects cracked a whole nut (422 trials for experiment 1 and 482 trials for experiment 2). Finally we examined if the monkeys were socially influenced in their choices of pits. For this purpose, we used the "whole nut" trials during which the subjects worked on whole nuts plus the trials during which subjects brought a piece of a nut (partial nut) from elsewhere to crack on the anvils, resulting in 446 trials in experiment 1 and 633 trials in experiment 2.

Affordances and Capuchins' Detection of Affordances

We evaluated the affordances of each pit for each individual in terms of fly-off rate and effectiveness score. Then we examined each monkey's number of first choices, number of total strikes, and number of nuts cracked when using each pit. Lastly, we evaluated how the two aspects of affordances correlated with the three behavioral variables.

Fly-off rate was defined as the total number of fly-off events in that pit divided by the total number of strikes in that pit. Effectiveness of the pit was defined as the total number of nuts cracked divided by the total number of strikes multiplied by 100. We predicted for experiment 1: Fly-off rate: medium < large < small; Effectiveness: medium > large or small; and for experiment 2: Fly-off rate: deep < medium < shallow; Effectiveness: medium or shallow > deep.

Next we looked at the capuchins' behaviors with each pit. We expected their pattern of behaviors would reflect the differences among pits in the fly-off rate and effectiveness measures. Because we expected small pits would have the highest fly-off rate and deep pits would have the lowest effectiveness and because they were the most visually distinctive, we predicted that the capuchins would avoid them. We predicted that the capuchins would prefer the pit with highest effectiveness and/or the lowest fly-off rate in both experiments. Their preference would be evident in the following behavioral variables: number of first choices (defined as first strikes), number of total strikes and number of nuts cracked. This prediction was evaluated by repeated-measures t-tests comparing large and medium pits in experiment 1 and shallow and medium pits in experiment 2. The low N of trials using the shallow and deep pits precluded the use of ANOVA for these analyses.

Switches and Self-correction

We assessed two behaviors through analysis of switches from one pit to another while cracking a single nut. First, we assessed if the capuchins used the more energy conserving strategy of switching (position only, then switch) more often than the less energy conserving strategy (position, strike, then switch), using a repeated measures t-test. Second, we examined if the subjects made proportionally more switches from a less effective pit (i.e. self-correction) than switches from effective pits using repeated-measures ANOVA. Data were arcsine transformed for these analyses. Effect size was calculated using Hedge's d (corrected for small sample size) for all pairwise comparisons.

Social Influence

We examined whether social influence played a part in the capuchins' choice of each pit by comparing the relative frequency with which subjects used the same pit as the preceding individual to the overall frequency with which the subjects first positioned a nut in a that pit.

Results

General results

We collected 21 to 87 trials per subject, where the number of trials corresponds to number of nuts attempted (422 trials total, including 98 trials in which nuts were not cracked). Each subject cracked an average of 36 nuts in experiment 1. In 21.3% of trials (90 trials), the subjects switched from one pit to another at least once. The subjects produced a total of 2201 strikes, with 50.3% in large pits, 46.3% in medium pits and 3.4% in small pits.

We collected 14 to 78 trials per subject (482 trials total, including 131 trials in which nuts were not cracked), with an average of 39 nuts cracked by each subject in experiment 2. The subjects switched at least once in 18.5% of these trials (89 trials). The subjects had a total of 2338 strikes, 75.4% in shallow pits, 24.1% in medium pits and 0.4% in deep pits.

We did not observe any change in frequency of switching as a function of testing days (see Table 1). Regression analyses showed that testing day did not predict the frequency of switches in experiment 1 ($B = 0.005$, $t = 0.32$, $P = 0.76$) and in experiment 2 ($B = -0.028$, $t = -2.29$, $P = 0.08$).

Across experiments, only twice did the subjects directly touch the pits by hand. In these two cases, they picked up nut pieces or dirt out of a medium pit. Smelling the pits, or smelling their hand following manual exploration were also not observed. Instead, they routinely positioned the nut in the pit and struck the nut in the pit with a stone.

Affordances and Capuchins' Detection of Affordances

<u>Experiment 1 horizontal dimension of the pit</u>

Fly-off rate did not differ significantly between large (X +SD = 0.34+0.10) and medium (X +SD = 0.30+0.09) pits, paired $t_8 = 1.69$, $P = 0.13$, however the effect size of Hedge's d is 0.40, reflecting the difference is about medium scale. Fly-off rate for the small pits (X +SD = 0.74+0.18) was not included in the test because three subjects did not strike in small pits and three subjects struck but did not crack any nuts in them. Paired t-tests revealed that the effectiveness of large pits (X +SD = 19+11) is significantly higher than the effectiveness of medium pits (X+SD = 10+4), t_8 = 3.49, P = 0.008, with an effect size of Hedge's d = 1.04. The effectiveness of small pits (X+SD = 7+9) was not included in the test due to low N (N = 3).

To summarize, there was a large difference in effectiveness between large and medium pits (large > medium) and minimal difference in fly-off rate (medium< large). Therefore, if the capuchins are sensitive to the affordances of the pits, we can predict a preference for large pits.

We analyzed capuchins' use of the pits with three variables: number of first strikes, number of total strikes and number of nuts cracked in each pit per subject. Paired t-tests comparing the number of first strikes in medium (X +SD = 19.4+14.0) and large (X +SD = 28.4+15.3) pits revealed that the capuchins preferred large pits (t $_8$ = 3.43, P = 0.009 with an effect size of Hedge's d = 0.58). The average number of first strikes in the small pits was 1.2 (SD = 1.1). Paired t-test comparing total number of strikes in medium (X +SD = 113+33) and large (X +SD = 123+65) pits revealed the capuchins struck in both pits equally often, t_8 = 0.55, P = 0.60, with an effect size of Hedge's d = 0.18, reflecting a small scale difference. The average number of total strikes in the small pits was 8.2 (SD = 11.0). Paired t-tests comparing number of nuts cracked in medium (X +SD = 12+8) and large (X +SD = 23+16) pits showed that the capuchins cracked significantly more nuts in the large pits (t_8 = 3.23, P = 0.012, with an effect size of Hedge's d = 0.83).

Table 2 shows the pits with the lowest fly-off rate and the highest effectiveness, and the pits with the highest number of first strikes, number of total strikes and number of nuts cracked for each individual. As shown, the large pits have the highest effectiveness for all individuals and are preferred by 4 individuals for all three behavioral measures, and by another 3 individuals for two out of the three measures.

Experiment 2 depth of the pit

Fly-off rate is significantly higher in shallow pits (X +SD = 0.50+0.11), compared to the medium pits (X +SD = 0.30+0.21, paired t_8 = 2.44, P = 0.04 with an effect size of Hedge's d = 1.13). Fly-off rate for the deep pits could be calculated for only one subject that struck 10 times and produced 1 fly-off in a deep pit (fly-off rate = 0.1). Paired t-tests revealed that the effectiveness of shallow pits (X +SD = 16+8) is significantly higher than the effectiveness of medium pits (X +SD = 12+7, P = 0.004, with an effect size of Hedge's d = 0.51). Effectiveness of deep pits was zero for the one subject who struck in a deep pit.

To summarize, there was a significant difference in effectiveness between shallow and medium pits (shallow > medium) and a significant difference in fly-off rate (medium< shallow). Therefore, effectiveness alone predicts preference for shallow pits and fly-off rate alone predicts preference for medium pits.

Paired t-tests comparing the number of first strikes in shallow and medium pits for each subject revealed that the capuchins preferred shallow pits (X +SD = 41+18) over medium pits (X +SD = 11+6, t_8 = 5.72, $P < 0.001$, with an effect size of Hedge's d = 2.11). Paired t-tests comparing total number of strikes in the shallow and medium pits for each subject revealed the capuchins struck more often in the shallow pits (X +SD = 196+78) than in the medium pits (X +SD = 63+43, t_8 = 4.81, P = 0.001, with an effect size of Hedge's d = 2.00). Paired t-tests comparing the number of nuts cracked in shallow (X +SD = 32+19) and medium (X +SD = 7+5) pits showed that the capuchins cracked significantly more nuts in the shallow pits ($t_8 = 4.81$, $P = 0.001$, with an effect size of Hedge's d = 1.71).

Table 2 shows the pits with the lowest fly-off rate and the highest effectiveness, and the pits with the highest number of first strikes, number of total strikes and number of nuts cracked for each individual. As shown, the shallow pits have the highest effectiveness for all individuals, and are preferred by 8 out of 9 individuals on all three behavioral measures.

Switches and Self-correction

In 52% of the trials in which the capuchins switched in experiment 1, they positioned the nut in a pit and switched to another pit ('position only' switch); in the other 48% of trials in which the capuchins made a switch, they positioned the nut in a pit and struck it with the stone before switching ('position and strike' switch). The proportion of "position only" switches (X +SD = 37%+34%) and the proportion of "position and strike" switches (X +SD = 63%+34%) did not significantly differ (paired t test on arcsine transformations: $t_8 = -0.83$, $P = 0.43$). Four of nine subjects used the more energy conserving strategy (position only) more often than the less energy conserving strategy (position and strike). In experiment 2 subjects had more 'position only' switches (X +SD = 74%+20%) than 'position and strike' switches (X+SD = 26%+20%, paired *t* test on arcsine transformations: $t_8 = 3.39$, $P = 0.009$, Hedge's d = 2.28). Seven of nine subjects used the more energy conserving strategy more often than the less energy conserving strategy.

To assess self-correction, we compared proportion of switches (out of all initial positions) out of all three pits for both experiments. Repeated-measures ANOVA on arcsine transformations showed switches out of small (X +SD = 81%+8%), medium (X +SD = 24%+8%) and large (X +SD = 12%+5%) pits were significantly different ($F_{2, 12} = 69.37$, $P < 0.001$), with an effect size of partial η^2 of 0.92. Post hoc comparisons with Bonferroni correction revealed that subjects switched out of small pits significantly more often than large pits ($P < 0.001$, Hedge's d = 9.82); switched out of small pits significantly more often than medium pits ($P = 0.001$, Hedge's d = 6.77); and switched out of medium pits more often (though NS) than large pits ($P = 0.087$, Hedge's d = 1.71).

In experiment 2, repeated-measures ANOVA on arcsine transformations revealed that switches out of deep (X +SD = 100%+0%), medium (X +SD = 25%+10%) and shallow (X +SD = 10%+4%) pits were significantly different ($F_{2, 14} = 64.77$, $P < 0.001$, with an effect size of partial η^2 of 0.90). Post hoc comparisons with Bonferroni correction showed subjects switched out of deep pits significantly more often than shallow pits ($P < 0.001$, Hedge's d = 30.23); switched out of deep pits significantly more often than medium pits ($P = 0.001$, Hedge's d = 10.08); and switched out of medium pits more often (though NS) than shallow pits ($P = 0.23$, Hedge's d = 1.87).

Social Influence

We examined if the subject's initial choice of a pit (first positioning) was socially influenced by the preceding individual. Subjects often came to an anvil right after the preceding individual, resulting in an inter-subject interval of 0 min (the median inter-subject interval = 1 min, range = 0-10 min for both experiments). In 72% of subject-pit combinations in experiment 1 and 86% in experiment 2, subjects first positioned the nut in the same pit where the preceding individual last struck at a higher frequency than their own overall frequency of first positioning in that pit. This is shown in table 3. We did not have enough cases to run Chi-square tests on each subject's use of each pit, with one exception. Piaçava had 39 trials where the preceding monkey last struck in shallow pits in experiment 2 and she followed in 32 of those trials, which is more frequent than her own overall proportion of first positioning in shallow pits (57%): $X^2 = 9.99$, $N = 39$, $P = 0.002$.

Table 4 shows the frequency with which each monkey was followed ranked by the individual's overall efficiency score in the study (efficiency = [total number of strikes / total number of nuts cracked] x 100). We did not observe less proficient individuals following more proficient individuals more often than expected.

Discussion

We adopted a Gibsonian Perception-Action perspective to examine the wild capuchin monkeys' detection of affordances of novel anvils. We predicted that the capuchins would prefer pits providing certain affordances, namely effective cracking and secure positioning for the nut. We also predicted that they would be less selective about pits than they have been shown to be with stones and nuts (Visalberghi et al. 2009; Fragaszy et al. 2010b), because it is easier to detect affordances of an object or surface directly with one's body than indirectly, as when cracking a nut through contact via intermediary object(s). We also predicted that they would prefer the most functional pits and that they would need to detect affordances of the pits through action (by positioning and striking the nuts in the pits).

Selectivity was confirmed by the capuchins' preference for the large and shallow pits. The findings that the capuchins preferred the two most effective pits (large and shallow, as measured by the effectiveness score) suggested they were more sensitive to the effectiveness of the pit (namely how easily they could crack a nut in the pit), than to the rate of nut fly-off, which favored the medium pit in both experiments (although not significantly so in experiment 1). In experiment 2, when the difference in fly-off rate between the shallow pit and the medium pit was larger in magnitude (as reflected by effect size) than the difference between large and medium pits in experiment 1, the capuchins still showed a stronger preference for the shallow pit.

We also confirmed that the capuchins' preference for pits was not as clear-cut as their preference for stones and nuts. The magnitude of their preference for a particular pit (50% of total strikes in the large pit in experiment 1 and 75% in the shallow pit in experiment 2) was not as large as their preference for heavier stones (94% all conditions combined, Visalberghi et al. 2009; 78% all conditions combined, in Fragaszy et al. 2010b) and nuts that were easier to crack (96% all conditions combined, in Fragaszy et al. 2010b). This is in accordance with the notion that detecting affordances embodied by the relation between surface and object(s) is more difficult than detecting affordances of a single object. The most relevant aspect of affordances of a pit, its effectiveness, is not detectable solely by visual perception. Rather, it is discovered by positioning and/ or striking a nut with a stone. This held true even in the case of the nonfunctional pits (small or deep). All subjects positioned the nut at least once in a small pit and all but one subject positioned the nut at least once in a deep pit. Three subjects struck a nut in a small pit and one subject struck a nut in a deep pit. Thus, even though the relevant dimensions of the small and deep pits may have readily been perceived by vision, subjects still occasionally used actions such as positioning and striking to detect their affordances.

The capuchins continued to explore all pits throughout the whole testing period. It is of note that they did not directly touch the pits on the anvils with their palms or fingers; instead, their actions with the pits were always indirect: they positioned nuts in the pits, and struck the nuts in the pits with a stone. During nut-cracking on a familiar anvil, before each strike, the capuchins often place the nut in a pit again and again in quick succession before releasing it and striking it with the stone. The final position of the nut is very specific with the more spherical sides of the nut against the sides of the pit (Fragaszy et al. unpublished data). The systematic final positioning of the nut suggests the capuchins attend to haptic information afforded by positioning the nut in the pit. Positioning the nut in the pit (without striking it) is a more energy conserving way to explore different pits than positioning plus striking the nut. “Position only” switches happened significantly more often than “position plus strike” switches in experiment 2 (where depth of the pits varied), but not in experiment 1 (where the horizontal dimensions varied). Perhaps depth can be detected by positioning more effectively than horizontal dimensions can be detected, or perhaps the capuchins learned to rely on positioning more over time. Our current design does not permit us to distinguish these alternative explanations.

In summary, the capuchins selected the novel pits in accord with the effectiveness of the pits for cracking nuts, where effectiveness is defined as the number of nuts cracked with 100 strikes in that pit. They detected the ‘effectiveness’ of the pits by positioning and striking nuts in them. This is similar to findings of Visalberghi et al. (2009) and Fragaszy et al. (2010b) which report that the capuchins gain information about stones through tapping and handling them. However, our findings differ from these previous studies in that the capuchins did not select the most effective pit from the first trial, as they did with nuts and stones. Nor did they consistently continue using the same pit after their first strikes, whereas the capuchins always (Visalberghi et al. 2009) or almost always (Fragaszy et al. 2010b) continued to use the same stone. In our study, they explored all the pits throughout the whole testing period, though their overall activity with pits correlated positively with the effectiveness of the different pits. Collectively, these findings support our prediction that detecting affordances of the pits in the anvils is less precise than for nuts and stones, even though the capuchins are equally experienced at cracking nuts in pits as they are at selecting nuts and stones. Thus the findings support the hypothesis that detection of affordances incorporating objects and surfaces is more difficult than detection of mass or composition of stones and resistance to cracking of the nuts, which are properties of single entities.

We also examined the role of social influence in the monkeys’ selection of pits. Capuchin groups are relatively cohesive, with members usually staying within 10 m of another group member (Fragaszy et al. 2004). In our study group, members often waited in nearby trees for their turn to crack nuts. The visibility was good, with little or no obstruction from foliage between tree limbs and the anvil. This situation could set the stage for one individual’s choice of pit to influence those that followed. Indeed, the pattern of results suggests that the capuchins were more likely to use the same pit where the preceding individual last struck, compared to their overall frequency with which they initially used the pit, even when the pit was ineffective.

Therefore, social influence could be an alternative explanation for the lower magnitude of preference for pits in this study, compared to the magnitude of preference for stones and nuts in Visalberghi et al.’s study (2009) and Fragaszy et al.’s study (2010b). However, we cannot draw the conclusion that social influence is more important for choice of pits than choice of stones, because the design of the studies about choice of stones prevented social influence on choice. We counterbalanced the positions of three anvils across testing days but the anvils had fixed positions across all trials on any given testing day. In the two studies mentioned above, the positions of stones and or nuts were randomized in every trial. Therefore, their setup prevented social influence from affecting choice of nuts and stones, whereas our setup allowed social influence to affect choice of anvil pits. Future studies should investigate to what extent social influence can change the magnitude of capuchins’ preference for heavier stones or less resistant nuts.

Social influence in foraging has been observed in many animal species, but Clayton (1978) and Rapaport (2008) reported that more studies focused on the choice of foraging item (the thing eaten) than the choice of foraging location (where the food is found or processed). Social influence in the choice of foraging location, as documented in the current study, reflects the phenomenon of “local enhancement”, in which individuals are attracted to a place associated with behavior by conspecifics in that place. Gunst et al. (2008) likewise document local enhancement in foraging activity in another species of capuchin monkey, the brown capuchin (*Cebus apella*). We consider it likely that local enhancement is a common social influence on foraging in capuchins.

Ottoni et al. (2005) noted that capuchins watched and followed the most proficient nut-crackers more often than less proficient individuals. This outcome could occur either because the capuchins recognize proficiency in others or because more proficient individuals are more likely to produce opportunities for the others to scrounge left-over pieces (Ottoni et al. 2005). However, individuals did not preferentially follow more proficient individuals in our study. Perhaps other characteristics of an individual, such as social rank and affiliation, play a larger role than proficiency in an individual's salience to others (Coussi-Korbel and Fragaszy 1995). Studies with birds (as reviewed by Tóth et al. 2009) show that observers' scrounging tactics are influenced by a variety of factors such as kinship with the provider birds, early social experience, social rank, etc. The situation is likely to be equally nuanced in capuchin monkeys, and in other animals. Thus, future studies will be necessary to unravel how social factors and foraging proficiency of all the individuals involved influence foraging behaviors in capuchins.

We now turn to the broader implications of our main finding, that capuchins are sensitive to certain properties of the pits they use in nut-cracking, preferring to crack nuts in pits where they use the fewest strikes to do so. The capuchins act to perceive the effectiveness of the pits either by positioning the nut, using the nut as an extension of their hand, or by striking the nut with the stone, thereby indirectly gaining information about the pit. In the latter situation, the stone serves as an extension of the hand, until the point of contact between nut and stone, when rebound, vibration, sound or other movement of the stone and nut inform the body. This is a naturally-occurring example in nonhuman animals illustrating that the boundary of the animal-environment system (what constitutes animal and what constitutes environment) shifts dynamically (i.e. when the nut or the stone becomes the vehicle by which affordances of the pit are perceived). By examining how actions of the animals incorporate the environment into their exploratory process, thus producing a boundary shift, we gain an ecologically relevant account of learning, perception and action.

A Perception-Action approach allows us to examine the perceptual processes that contribute to selectivity in behavior in animals, including selection of objects for a specific goal, which is certainly not limited to tool use, or to primates. For example, nest building behaviour has been widely studied in ornithology. As reviewed by Hansell (2000), birds are highly selective about nest materials and use different techniques with different materials in nest building. Early manipulative experience with materials is crucial for successful nest building in adulthood (Collias and Collias 1973), which suggests manipulative actions may play an important role in the development of selectivity. California sea otters that use stone anvils on their chest for pounding open mussels, crabs and urchins (Hall and Schaller 1964), provide another example. Hall and Schaller (1964) note that the otters use stones of particular weight for pounding, suggesting selectivity. As far as we are aware, studies on material selection in animals have primarily focused on documenting selectivity but largely ignore the exploratory behaviors that lead to selectivity. We propose that prospective studies should investigate the exploratory behaviors that support detection of affordances and lead to selectivity. Field experiments in which subjects have the full complement of experience with natural materials and activities (e.g. nest-building) would be particularly beneficial. Such studies will enrich our understanding of embodied cognition across the animal kingdom.

Acknowledgements

Thanks to R. Greenberg for help with data collection, and the Oliveira family for logistical assistance. Permission to work in Brazil was granted by IBAMA and CNPq to QL, DF and EV. Funds: IM-CleVeR (No. FP7-ICT-IP-231722) and National Geographic (CRE 8774-07).

References

Barsalou, L. 2008. Grounded cognition. *Annual Review of Psychology*, 59, 617-645.

Bernstein, N. A. 1967. The coordination and regulation of movements. Oxford, New York: Pergamon Press.

Boesch, C. & Boesch, H. 1983. Optimisation of nut-cracking with natural hammers by wild chimpanzees. *Behaviour*, 83, 265-286.

Chappell, J. & Kacelnik, A. 2002. Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). *Animal Cognition*, 5, 71-78.

Chemero, A. 2009. Radical embodied cognitive science. Cambridge, MA: The MIT Press.

Clayton, D. A. 1978. Socially facilitated behavior. *The Quarterly Review of Biology*, 53, 373-392.

Collias, E. C. & Collias, N. E. 1973. Further studies on development of nest-building behaviour in a weaverbird (*Ploceus cucullatus*). *Animal Behaviour*, 21, 371-382.

Coussi-Korbel, S. & Fragaszy, D. 1995. On the relation between social dynamics and social learning. *Animal Behaviour*, 50, 1441-1453.

Darwin, C. 1881. The formation of vegetable mould, through the action of worms with observations on their habits. London: John Murray.

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. B. & de Oliveira, M. G. 2004. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, 64, 359–366.

Fragaszy, D., Pickering, T., Liu, Q., Izar, P., Ottoni, E. B. & Visalberghi, E. 2010a. Bearded capuchin monkeys' and a human's efficiency at cracking palm nuts with stone tools: field experiments. *Animal Behaviour*, 79, 321-332.

Fragaszy, D., Greenberg, R., Visalberghi, E., Ottoni, E. B., Izar, P. & Liu, Q. 2010b. How wild bearded capuchin monkeys select stones and nuts to minimize the number of strikes per nut cracked. *Animal Behaviour,* 80, 205-214.

Gunst, N., Boinski, S. & Fragaszy, D. M. 2008. Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artefacts as an indirect social influence. *Behaviour*, 145, 195-229.

Hall, K. R. L. & Schaller, G. B. 1964. Tool-using behavior of the California sea otter. *Journal of Mammalogy*, 45, 287-298.

Lorenzi, H. 1992. *Arvores Brasileiras. Manual de identificacao e cultivo de plantas nativas do Brasil.* Nova Odessa, SP: Editora Plantarum, Brasil.

Ottoni, E. B., Resende, B. D. & Izar, P. 2005. Watching the best nut-crackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. *Animal Cognition*, 24, 215-219.

Pick, H. L.& Lockman, J.J. 1981. From frames of reference to spatial representations. In: *Spatial representation and behavior across the lifespan*, (Ed. by L.S. Liben, A.H. Patterson & N. Newcombe). New York: Academic Press.

Rapaport, L. G. & Brown, G. R. 2008. Social influences on foraging behavior in young nonhuman primates: learning what, where, and how to eat. *Evolutionary Anthropology*, 17, 189-201.

Semaw, S., Rogers, M. J., Quade, J., Renne, P. R., Butler, R. F., Dominguez-Rodrigo, M., Stout, D., Hart, W. S., Pickering T. & Simpson, S. W. 2003. 2.6-Million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *Journal of Human Evolution*, 45, 169-177.

Tóth, Z., Bókony, V., Lendvai, A. Z., Szabó, K., Pénzes, Z., Liker, A. 2009. Effects of relatedness on social-foraging tactic use in house sparrows. *Animal Behaviour*, 77, 337-342.

Visalberghi, E., Fragaszy, D., Ottoni, E., Izar, P., de Oliveira, M. G. & Andrade, F. R. D. 2007. Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys

(*Cebus libidinosus*) to crack open palm nuts. *American Journal of Physical Anthropology*, 132, 426-444.

Visalberghi, E., Sabbatini, G., Spagnoletti, N., Andrade, F.R.D., Ottoni, E., Izar, P. & Fragaszy, D. (2008). Physical properties of palm fruits processed with tools by wild bearded capuchins (*Cebus libidinosus*). *American Journal of Primatology*, 70, 884-891.

Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P. & Fragaszy, D. 2009. Selection of effective stone tools by wild bearded capuchin monkeys. *Current Biology*, 19, 213-217.

Table 2.1. Number of trials and switches per testing day

Testing Days	*Total number of trials*	*Total number of switches*
Exp. 1 Day 1	40	12
Exp. 1 Day 2	5	0
Exp. 1 Day 3	56	6
Exp. 1 Day 4	8	2
Exp. 1 Day 5	96	24
Exp. 1 Day 6	10	5
Exp. 1 Day 7	51	16
Exp. 1 Day 8	45	9
Exp. 1 Day 9	69	7
Exp. 1 Day 10	42	9
Exp. 1 Total	422	90
Exp. 2 Day 1	92	20
Exp. 2 Day 2	64	15
Exp. 2 Day 3	79	17
Exp. 2 Day 4	88	14
Exp. 2 Day 5	96	20
Exp. 2 Day 6	63	3
Exp. 2 Total	482	89

Table 2.2. Pits with the lowest fly-off rate, the highest effectiveness, the highest number of first strikes number of total strikes and highest number of nuts cracked for each individual

Experiment 1	Affordances of the pit		Three behavioral measures for monkey's preference		
Dimension (L = large, M = medium)	Pit with the lowest fly-off rate	Pit with the highest effectiveness	Pit with the highest number of first strikes	Pit with the highest number of total strikes	Pit with the highest number of nuts cracked
Chicao	M	L	L	M	L
Chuchu	M	L	L	M	M
Dengoso	M	L	L	L	L
Dita	M=L	L	M	M	M
Jatoba	L	L	L	M	L
Mansinho	L	L	L=M	M	L
Piaçava	L	L	L	L	L
Teimoso	M	L	L	L	L
Tucum	M	L	L	L	L

Experiment 2	Affordances of the pit		Three behavioral measures for monkey's preference		
Depth (S = shallow, M = medium)	Pit with the lowest fly-off rate	Pit with the highest effectiveness	Pit with the highest number of first strikes	Pit with the highest number of total strikes	Pit with the highest number of nuts cracked
Chicao	M	S	S	S	S
Chuchu	M	S	S	S	S
Dengoso	M	S	S	S	S
Dita	M	S	S	M	M=S
Jatoba	S	S	S	S	S
Mansinho	M	S	S	S	S
Piaçava	M	S	S	S	S
Teimoso	M	S	S	S	S
Tucum	M	S	S	S	S

Table 2.3. Number of subjects whose proportion of following the preceding monkey in using a given pit was higher than its own overall proportional use of that particular pit

	Small	Medium	Large
Experiment 1	5 out of 7*	6 out of 9	7 out of 9
	Deep	**Medium**	**Shallow**
Experiment 2	2 out of 4*	9 out of 9	8 out of 9

* Note: the Ns in these cells are smaller than 9 because some monkeys never followed another monkey when it had last struck in the small or deep pit.

Table 2.4. Frequency of one monkey using the same pit as last used by another monkey. (*Note: “number of trials followed” means number of trials in which an individual was followed by the next subject in using the same pit)

Experiment 1 Dimension	Efficiency Rank	Number of trials ending in large	*Number of trials followed in large	Number of trials ending in medium	Number of trials followed in medium	Number of trials ending in small	Number of trials followed in small	Sum of trials	Sum of trials followed	Overall % followed
Mansinho	1	20	16	16	13	1	1	37	30	81
Dengoso	2	17	12	13	9	3	1	33	22	67
Chicao	3	6	3	9	6	1	0	16	9	56
Teimoso	4	17	8	12	8	4	2	33	18	55
Jatoba	5	9	5	3	1	0	0	12	6	50
Piassava	6	19	15	12	10	1	1	32	26	81
Dita	7	7	3	20	14	1	0	28	17	61
Chuchu	8	15	11	12	10	0	0	27	21	78
Tucum	9	22	15	14	11	6	1	42	27	64
Experiment 2 Depth	Efficiency Rank	Number of trials ending in shallow	Number of trials followed in shallow	Number of trials ending in medium	Number of trials followed in medium	Number of trials ending in deep	Number of trials followed in deep	Sum of trials	Sum of trials followed	Overall % followed
Mansinho	1	36	29	12	7	0	0	48	36	75
Dengoso	2	37	31	9	3	1	0	47	34	72
Chicao	3	30	21	7	1	0	0	37	22	59
Teimoso	4	29	24	9	5	0	0	38	29	76
Jatoba	5	15	12	3	0	0	0	18	12	67
Piassava	6	32	25	12	5	1	0	45	30	67
Dita	7	16	14	9	5	0	0	25	19	76
Chuchu	8	41	30	7	2	0	0	48	32	67
Tucum	9	43	36	13	8	2	1	58	45	78

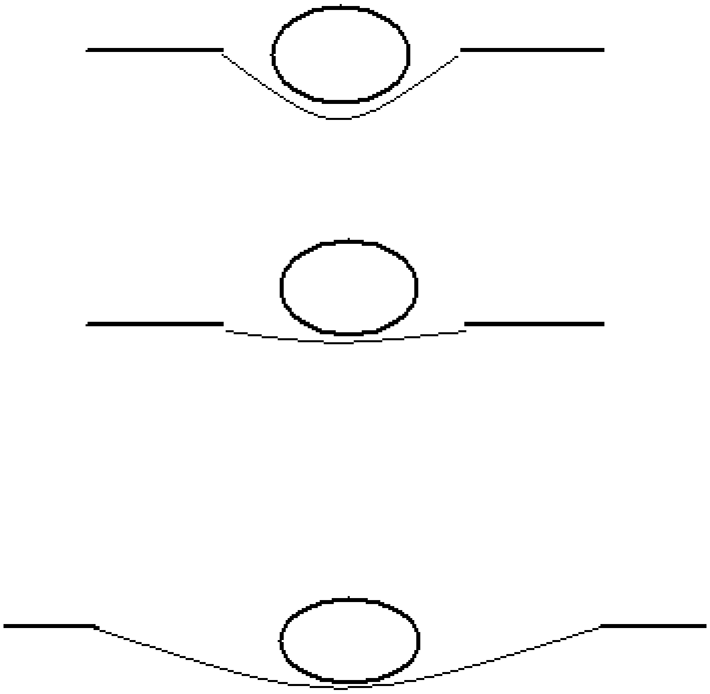

Figure 2.1. Illustration of the sagittal view of a medium pit (top, 6 cm wide and 2 cm deep), a shallow pit (middle, 6 cm wide and 1 cm deep) and a large pit (bottom, 9 cm wide and 2 cm deep).

Figure 2.2. Photos of pits (left side from top to bottom: small, medium and large pit; right side from top to bottom: shallow, medium and deep pit)

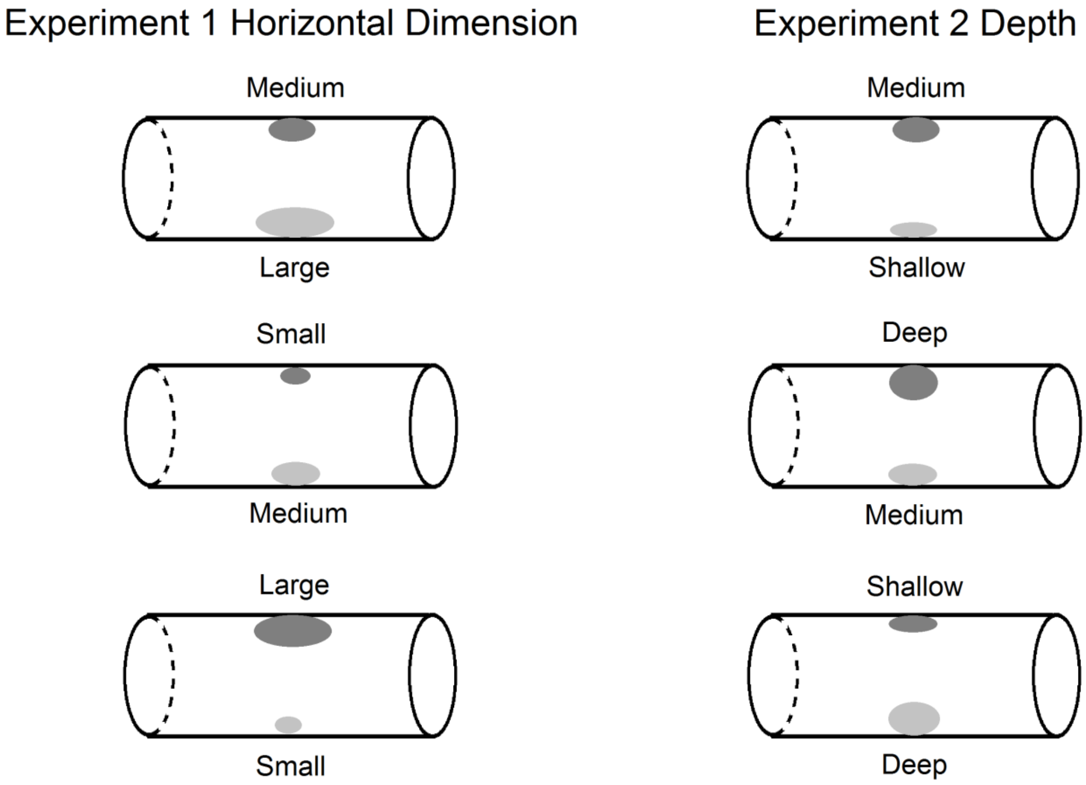

Figure 2.3. Illustration of two pits made in each anvil

Figure 2.4. Experimental layout (3 logs were arranged in an approximate perfect triangle with a 1.46 kg stone and a nut in the center)

CHAPTER 3

WILD BEARDED CAPUCHIN MONKEYS (CEBUS LIBIDINOSUS) ADAPT ACTIONS IN RESPONSE TO VARIED HAMMER STONES AND NUTS IN NUT-CRACKING[1]

---

[1] Liu, Q., Fragaszy, D. & Visalberghi, E. 2011. To be submitted to *Animal Behaviour*

Abstract

Do wild capuchin monkeys modulate their tool use actions in response to tools of various weights? In the present study, I examined if and how monkeys adapted their striking actions to task constraints (weight of the hammer stone and weight of the nut). Eight wild capuchin monkeys (body mass: 2.0-4.3 kg) cracked nuts (14-64 g) with five different hammer stones (0.57-3.47 kg). Using standard 2-D kinematics procedures and digitizing in Peak Motus©, I calculated, per nut- cracking episode per monkey, the maximum velocity of the stone during the downward striking phase and the maximum height to which the stone was lifted in the highest strike. Results showed the monkeys lifted lighter stones higher and added more kinetic energy to the stone in the downward striking phase than when they lifted heavier stones, thus achieving the appropriate kinetic energy with hammer stones of different weights. They also lifted stones higher when they cracked heavier nuts. These findings showed wild capuchin monkeys spontaneously adjusted their actions in response to task constraints, as do humans and chimpanzees. Thus this study shows that adaptation of behavior with a tool to accommodate task constraints is evident beyond the hominid lineage.

Keywords: motor control, action adaptation, motor skill, capuchin, Cebus libidinosus, embodied cognition, nut cracking, perception-action, tool use

Introduction

Skills in tool use can be reflected in two ways: choosing the most effective tool for a given task and accommodating actions with a variety of tools for a given task. Humans have been demonstrated to show both selectivity and accommodation for a given task. As early as 2.6 million years ago, our ancestors were already selective about materials when processing animal carcasses (Semaw et al. 2003). Skilled tool users can also adapt their actions with varied tools. For example, Bril et al. (2010) showed that human stone knapping experts were able to finely adjust the velocity of the hammer to maintain the appropriate amount of kinetic energy when detaching stone flakes from a flint core using hammer stones of different weights.

The Perception-Action perspective on tool use posits that skilled tool users can detect affordances of different tools and different task demands and regulate their actions according to the environmental changes (Bril et al. 2009; Smitsman 1997; Wagman and Carello 2003). In some sense, the ability to fine-tune one’s actions in response to environmental changes is an important part of skill that supports flexible and complex tool use behavior.

In nonhuman animals, complex percussive tool use involving objects and surfaces in the form of spontaneous nut-cracking has been observed and studied in wild chimpanzees (*Pan troglodytes*) and capuchin monkeys (*Cebus libidinosus*) (e.g. Fragaszy et al. 2004; Matsuzawa 2001). In nut-cracking, both species place a nut on an anvil surface and use a hammer (stone or log) to crack open the nut using percussive actions.

Wild capuchin monkeys routinely use heavy hammer stones to crack open hard palm nuts in Fazenda Boa Vista, Piau į Brazil (Fragaszy et al. 2004). Recent studies showed that these monkeys were selective about the weight of the hammer stones, preferring the heavier stone even when the ratio of the two stones was as close as 1.3:1 (Fragaszy et al. 2010a; Visalberghi et al. 2009). We also know the capuchins routinely crack different species of palm nuts and other encased foods which vary greatly in resistance to cracking (Visalberghi et al. 2008). When given a choice, the monkeys preferred to crack nuts that were easier to crack (Fragaszy et al. 2010a). This demonstrates skill is reflected via selectivity with tools and materials to be exploited in nut-cracking by capuchins.

However we do not know if capuchins show the other aspect of skill (accommodating to different tools). Recently, captive chimpanzees were shown to be able to adjust active and passive striking force to successfully crack open macadamia nuts (by reaching the threshold of necessary kinetic energy required for cracking) and also not to smash the kernels (i.e. kinetic energy is maintained just beyond the threshold) (Bril et al. 2009). We know that the capuchins routinely use a wide range of hammer stones. Spagnoletti et al.(2011) reported the capuchins living in Boa Vista use hammer stones ranging from 100 to 3000 grams, which is 2-158% of their body weight (weights obtained from Fragaszy et al. 2010b, smallest adult female = 1900g, largest adult male = 4400g). Therefore, they must be able to accommodate their actions with such a varied range of stones.

To the extent to which individuals can accommodate to different tools partly depends on individual’s action capabilities since nut-cracking is a strenuous activity for capuchins (Liu et al. 2009). Fragaszy et al. (2010b) studied the relationship between nut weights, individual body weight, maximum height of lifting and efficiency of nut cracking (defined as the number of nuts opened per 100 strikes). The monkeys in the study used one hammer stone of 1.465 kg. They reported a significant positive correlation (r = +0.75, N = 9) between individual's body weight and efficiency of cracking whole nuts. They found the maximum absolute height to which the capuchin lifted the stone was also significantly positively correlated with efficiency (r = +0.83, N = 8) and that more efficient capuchins raised the stone proportionally higher. They also found that the diameter of the nut (which highly correlates with the weight of the nut, r = +0.87, N = 89) also predicted whether a capuchin would crack a nut on a given strike. Therefore body weight, lifting height of the stone, and size of the nut all correlated with efficiency of nut cracking when the monkeys used the one stone in the study. The role of individual body weight was also mentioned in Liu et al's (2009) study on kinematics and energetics of nut-cracking in the same population of capuchins. They found that the two male adult monkeys added force in the downward phase during striking, thus creating more kinetic energy to be transferred to the nut (and thus they cracked nuts in fewer strikes) than the two female monkeys in the study. Since capuchins are highly sexually dimorphic (males are usually 1.5-2 times heavier than females, Fragaszy et al. 2004b), it is reasonable to say that the described gender difference may be partly due to difference in body weight.

Therefore, this study aimed to systematically examine the relationship among the weight of stone, the weight of nut, individual's own body weight and individual's nut-cracking actions. With stones of different weight, the monkeys could possibly monitor the force they put on the stone to achieve the same amount of kinetic energy, as the human experts did in stone knapping. Or, they could simply lift the stone higher since lifting height is positively correlated with efficiency (Fragaszy et al, 2010b) and let gravity do its job of increasing kinetic energy at the point of contact with the nut. When cracking nuts of varied weights, the monkeys could adjust the velocity of the stone or the height of the stone (lower either or both for smaller nuts). In summary, there are several degrees of freedom in the system and we do not know if or how the monkeys manage them, or if monkeys maintain a stable efficiency when exploiting various materials in nut-cracking.

Based on previous studies and the prediction posited by the Perception-Action perspective, I specifically predicted wild capuchin monkeys would adapt their actions while using stones of different weights to crack nuts of different weights and that their own individual body weight would also play a role in how they lift and strike hammer stones.

Methods

Site and Subjects

The study site (9 °south, 45 °west, altitude approximately 420 m above sea level) was located on private property (Fazenda Boa Vista) in a dry woodland plain in Piauí, Brazil (Visalberghi et al., 2007). A group of wild capuchin monkeys routinely came to an area where there were anvils and stones. This was the area where I carried out the field experiment.

Eight wild capuchin monkeys (5 males and 3 females) participated. I obtained their body weight by provisioning water near a digital scale on a tree (see Fragaszy et al. 2010b). The individual information is shown in Table 1.

Design

This study utilized a within-subject repeated measures design. A trial was defined as a nut-cracking episode (one nut). In each trial, the subject was provided with one (out of the five) stone and a nut (previously weighed and marked). All subjects had a number of episodes with each stone, and cracked nuts of different weights (for a summary see Table 2). The independent variables were stone weight (5 levels) and nut weight (continuous scale). The dependent variable was the number of strikes, vertical height of the stone and the maximum downward velocity of the stone during the highest strike per trial.

Materials

I used an existing log anvil (1 m long, 12 cm high and 12 cm wide) in the study area. This anvil was frequently used by the monkeys and it allowed good visibility for filming.

I supplied natural stones that the monkeys routinely use as hammer stones for the study. The existing hammer stones were quartzites/ siltstones. Although they differed a little in size and smoothness, they were all roughly ellipsoid shaped (see Figure 1). The five stones weighed 0.57 kg, 0.93 kg, 1.42 kg, 1.92 kg and 3.47 kg. Visalberghi et al. (2007) reported a range of 0.25-2.53 (kg) for stones found on 42 anvils surveyed in the study area. Spagnoletti et al. (2011) reported a range of 0.1-3 (kg) for stones used by two habituated wild groups observed for a one-year period in the same area. In addition, half a kg is the lower limit of weight of hammer stones that the monkeys routinely use in the nut-cracking area (personal observation). The three stones in the middle are all within the range of the stones the monkey usually use and are approximately 500 grams apart. The heaviest 3.47 kg stone is outside the upper limit and was chosen to reveal how monkeys would use extremely heavy stones as hammers, if they would use it at all.

I supplied the most resistant species of nuts that monkeys routinely crack, which was the piaçava nuts (*Orbignya sp*.). They had an oval shape and on average are 4 cm by 6 cm in size (Fragaszy et al. 2004a). Only mature nuts with the mesocarp removed were supplied and the nuts were weighed before the experiment using an electronic scale (Polder™) and marked using markers. The nuts ranged from 14 to 60 grams in weight.

A GL2 Canon DV camcorder and a sturdy tripod were used to video-record the study. A 2D calibration square was used as in the standard 2D kinematics recording procedure.

Procedure

A stone and a nut were presented on the log anvil when a monkey approached the anvil and seemed interested in cracking nuts (i.e. looking for stones/nuts). The nut was pre-marked with its weight to ensure identification. The monkey's actions were recorded on the camcorder with the stone weight and the nut weight recorded by the experimenter on tape. I tried to collect at least 10 trials per monkey per stone (see Table 2), whenever possible. I also tried giving each monkey nuts that varied in weights when they used each of the five stones. Specifically, I tried to give each monkey with each stone, three small nuts, four medium nuts and three large nuts. Nuts smaller than 25 grams were considered small, 26-40 grams were considered medium and nuts above 40 grams were considered large. This helped to ensure that all the subjects used all five stones to crack a variety of nuts.

Data Capture Setup

Standard two-dimensional motion measurement methodology was used during video-recoding (Robertson et al. 2004). Sixty Hz sampling rate and minimum exposure time of 1/2000s were used. The camera was placed approximately 6 meters away from the anvil to capture sagittal plane views (field of view was approximately 1.5 m) of the monkeys during nut-cracking. Before and after the experiments each day, I videotaped a 1m by 1m calibration square with reflective markers as calibration video.

Coding

I collected a total of 463 nut-cracking episodes (30-95 per monkey). For each stone condition per monkey, if they had more than 10 successful episodes, I randomly selected 10 for coding. If they did not have 10 episodes, I coded all episodes. Table 2 showed the number of coded trials per stone per subject.

For the behavioral coding, number of strikes was recorded. For the biomechanics coding, I first identified the highest strike from each episode and coded the highest strike per episode. For each highest strike, the metacarpophalangeal joint (MCP point) on the monkey's body and the nut were manually digitized (Peak Motus™ by Vicon, version 9.0) in each field of video (60 fields per second). The MCP point of the third finger was used as a proxy as the center of the hammer stone.

For each strike, three critical events were marked: "start of lifting", "MCP joint of third digit zenith" and "stone-nut contact". Start of lifting was defined as the instant when the stone begins to move upward. The MCP zenith point was the very instant when the MCP joint reaches the highest vertical height. Because the MCP joint was used as a proxy for the stone's center of mass, this instant was referred to as stone zenith point. The stone-nut contact occurred in the subsequent downward phase, at the instant when the stone contacted the nut.

After manually digitizing the points, raw coordinates of the points were filtered using a fourth-order Butterworth filter with cut-off frequency of 10Hz (Jackson, 1979). Filtered coordinates were then scaled to actual measurement units using calibration video. From these datasets, I obtained maximum vertical height of the stone and the mechanical energetics (the maximum gravitational potential energy and the maximum kinetic energy) for each trial.

Analysis

A stepwise multiple regression analysis in SPSS was conducted to test if the weight of the nut, the weight of the stone and the weight of the subjects predicted the number of strikes necessary to crack the nut. Each nut-cracking episode was used as the unit of analysis for this regression analysis.

A separate stepwise multiple regression analysis was conducted to examine if the same three variables predicted the maximum vertical height to which the stone was lifted. The highest strike per nut was used as the unit of analysis.

From the mechanical energetics (the maximum gravitational potential energy and the maximum kinetic energy) for each trial, a k/p ratio (maximum kinetic energy divided by the maximum gravitational potential energy) was calculated to evaluate if the monkey added additional work (meaning instead of letting the stone free fall, the monkey added force downward to the stone) onto the stone in the downward striking phase. Because in a free fall, the maximum gravitational potential energy should all be turned into the maximum kinetic energy just prior to contact point, the k/p ratio would be equal to one. A k/p ratio bigger than 1 indicated the monkey put additional work (added downward force onto the stone) in that trial. Therefore, a separate stepwise multiple regression analysis was conducted to examine if the same three variables predicted k/p ratio. The highest strike per nut was used as the unit of analysis.

Similar stepwise multiple regression analysis was also performed within each individual to examine difference in individual patterns.

Results

General Results

On average, the monkeys struck 4.6 (SD=4.9) times to crack open a nut. Linear multiple regressions were run to analyze how body weight, stone weight and nut weight predicted number of strikes to crack the nut, height to which the stone was lifted and how much additional force the monkeys added onto the stone during striking (as reflected by k/p ratio).

Regression showed the three variables significantly predicted the number of strikes to crack open the nut ($R=0.48$, $p< 0.0001$): monkey's body weight ($\beta= -0.17$, $p = 0.001$), stone weight ($\beta= - 0.31$, $p <0.0001$), nut weight ($\beta= 0.35$, $p< 0.0001$). Regression also showed the three variables significantly predicted the height to which the stone was lifted ($R=0.65$, $p< 0.0001$): monkey's body weight ($\beta= 0.59$, $p<0.0001$), stone weight ($\beta= -0.20$, $p <0.0001$), nut weight (beta= 0.11, p= 0.02). A third regression analysis showed monkey body weight (beta= 0.19, p<0.0001) and stone weight (beta= -0.45, p<0.0001) significantly predicted the k/p ratio (R=0.49, p<0.0001). Nut weight was not a significant predictor in this analysis.

Individual Patterns

For Mansinho, stone weight (beta=-.315, p=0.006) and nut weight (beta=0.580, p<0.001) both significantly predicted the number of strikes (R=0.657, p<0.001). Stone weight (beta=-.631, p<0.001) and nut weight (beta=0.323, p=0.03) both significantly predicted the height lifted (R=0.705, p<0.001). Stone weight (beta=-.768, p<0.001) significantly predicted the k/p ratio and nut weight was not significant predictor.

For Dengoso, stone weight (beta=-.356, p=0.01) and nut weight (beta=0.377, p=0.006) both significantly predicted the number of strikes (R=0.495, p=0.002). Stone weight and nut weight both were not significant predictors for the height lifted. Stone weight (beta=-.757, p<0.001) significantly predicted the k/p ratio and nut weight was not significant predictor.

For Teimoso, stone weight (beta=-.529, p<0.001) and nut weight (beta=0.264, p=0.03) both significantly predicted the number of strikes (R=0.589, p<0.001). Stone weight (beta=-.625, p<0.001) significantly predicted the height lifted and nut weight was not a significant predictor. Stone weight (beta=-.367, p=0.009) significantly predicted the k/p ratio and nut weight was not significant predictor.

For Jatoba, stone weight (beta=-.322, p=0.049) significantly predicted the number of strikes (nut, NS). Stone weight (beta=.400, p=0.013) significantly predicted the height lifted (nut, NS). Stone weight (beta=-.545, p<0.001) significantly predicted the k/p ratio (nut, NS).

For Tucum, stone weight (beta=-.338, p=0.026) and nut weight (beta=0.324, p=0.033) significantly predicted the number of strikes (R=0.499, p=0.006). Stone weight (beta=.433, p=0.004) and nut weight (beta=0.301, p=0.038) significantly predicted the height lifted. Stone weight (beta=-.545, p<0.001) significantly predicted the k/p ratio (nut, NS).

For Piacava, only nut weight (beta=0.584, p=0.001) significantly predicted the number of strikes (stone, NS). Stone weight (beta=-.559, p=0.002) significantly predicted the height lifted (nut, NS). Stone weight (beta=-.562, p=0.002) significantly predicted the k/p ratio (nut, NS).

For Dita, only nut weight (beta=0.565, p=0.003) significantly predicted the number of strikes (stone, NS). Stone weight (beta=-.485, p=0.012) significantly predicted the height lifted (nut, NS). Stone weight (beta=-.784, p<0.001) significantly predicted the k/p ratio (nut, NS).

For Chuchu, stone weight and nut weight both were not significant predictors for the number of strikes and the height lifted. Stone weight (beta=-.692, p=0.002) significantly predicted the k/p ratio (nut, NS).

In summary, individual patterns varied greatly as described above. In terms of number of strikes, Mansinho, Dengoso, Teimoso and Tucum had fewer strikes when using heavier stones and when cracking lighter nuts. Jatoba had fewer strikes when using heavier stones. Both

Piacava and Dita had more strikes with heavier nuts. Number of strikes did not change with different stones. For Chuchu, stone and nut weight did not predict number of strikes.

In terms of lifting height in response to stones and nuts, Mansinho lifted lighter stones higher and lifted higher when cracking heavier nuts. Dengoso did not adjust lifting height in response to stone weight and nut weight. Teimoso lifted lighter stones higher but did not lift differently in response to nut weight. Both Jatoba and Tucum lifted heavier stones higher and lighter stones lower (inverse response compared to Mansinho and Teimoso). Tucum also lifted higher when cracking heavier nuts. Both Piacava and Dita lifted lighter stones higher but did not do so when cracking heavier nuts. Chuchu did not change lifting height in response to stones or nuts. In terms of additional force, all the monkeys put more additional force on lighter stones but did not change force in response to nuts.

Figure 2 showed the maximum kinetic energy (vs. hypothetical kinetic energy in a free fall, which is equal to the maximum potential energy from the same lifting height) across trials (lighter stones to heavier stones in ascending order) in a male and a female subject. This showed the monkeys added extra force (thus adding kinetic energy) during the downward striking phase with all stones.

Discussion

The overall regression analysis results strongly supported the prediction derived from the Perception-Action perspective that the monkeys would modify their actions in response to the weight of the hammer stone and the weight of the nut. Their own body weight was also a significantly predictor. More specifically, the first regression analysis on number of strikes showed that bigger monkeys had fewer strikes, fewer strikes were necessary to crack a nut with a heavier stone and that more strikes were necessary to crack bigger nuts. The second regression analysis on lifting height showed that bigger monkeys lifted the hammer stone to a higher distance than did smaller monkeys, that they lifted lighter stones to a higher distance than heavier stones, and that they lifted hammer stones higher when they were cracking bigger nuts than when they were cracking smaller nuts. The third regression analysis on k/p ratio showed that bigger monkeys added more work onto the stone and they added more work onto the lighter stones during the downward striking phase.

The individual regression analyses showed that the extent to which one individual can accommodate and adapt to stones of different weights to crack different nuts greatly depends on the individual's action capability. It is clear that the three big males (Mansinho, Dengoso and Teimoso) showed more adjustment and regulation in their movements, as compared to the two sub-adult males (Jatoba and Tucum) and the three females (Dita, Piacava and Chuchu). Within the three big males, Mansinho showed more adjustment and regulation (effectively adjusting both lifting height and additional force) than Dengoso and Teimoso. This is in agreement with the fact that Mansinho had the biggest body weight and was also the most efficient individual as showed in another study conducted two years earlier (Fragaszy et al. 2010b). Mansinho was also described as the most skilled individual in the group by all researchers during the year the study was conducted (personal communication and observation). He was always observed to have the greatest amount of control with stones in nut-cracking (personal communication and observation). The two young males Jatoba and Tucum had a somewhat confusing strategy of adjustment (lifting heavier stones higher), which could be a statistical artifact due to their low number of trials with the 0.57 stone (1 trial for Jatoba and 0 for Tucum) as the increased lifting height was the most pronounced with this stone in the three big males. However, these two young males were able to use the 3.47 stone just fine, therefore somehow showing a positive beta value. In contrary, the three females who also had few trials with the 0.57 stone, had great difficulty lifting the heaviest 3.47 stone, therefore they showed the expected negative beta value. Jatoba, even though much heavier in body weight than Tucum, ranked lower in efficiency than Tucum (Tucum 5th out of 11 and Jatoba 9th) two years ago and was still less efficient than Tucum during the time of the current study (Fragaszy et al. 2010b; personal observation). He was also very peripheral in terms of social ranking, which might also have influenced his nut-cracking behavior because he had to constantly look out for other individuals and was always in a hurry (personal observation).

Within the three females, Dita and Piacava showed more adjustment and regulation than Chuchu. This is also congruent with reported efficiency rankings (Dita 4th out of 11, Piacava 6th and Chuchu 8th) for these three individuals in Fragaszy et al.' study (2010b). Even though Chuchu weighed a little more than the other two females, she was visibly pregnant at the time of this study (personal observation), so the extra body weight was not associated with higher efficiency or better control of the stones as with other individuals.

Therefore, the extent to which individuals can accommodate action to different tools also depends on the individual's action capabilities. It is clearly shown in Table 2 that smaller females had fewer trials with the heavier stones. With heavy stones, larger individuals might have more room and options to adjust their actions than smaller individuals since the latter are challenged to lift the heavy stones at all, as shown above. Therefore, skill in this case is a follow-on to size. However, in our sample, size was not the only predictor of skill level, as shown with Jatoba and Chuchu. Therefore, individual’s social rank, reproductive status and long-term nut-cracking pattern should be taken into consideration. Individual differences in skill and action capabilities were also noted in nut-cracking by captive chimpanzees (Bril et al. 2009). In their study, one female had significantly larger amplitude of movement so that she consistently lifted the hammer stone to a higher distance and achieved higher potential energy with all three different stones. Future studies could examine how skilled individuals adjust and control their actions differently from non-skilled individuals in nut-cracking in finer aspects (e.g. coordination, precision of movement etc.)

Accommodation of action in skilled tool use is usually studied in relation to task constraints in the motor control literature (Bril et al. 2010; Newell 1986). In the situation of tool use, constraints within a given tool use task can include changes of the relevant objects and surfaces. Therefore, in nut-cracking, task constraints can be an unusually heavy or light stone or an unusually tough nut or an unusually slippery anvil surface. Investigating how skilled individuals use tools in such situations by examining their actions will inform us about both bodily skills and cognitive abilities in tool use. Unfortunately this area of research in tool use is rather lacking, as pointed out by Bril et al. (2010). Bril et al. (2010) studied how human stone knapping experts finely adjusted the velocity of the hammer to maintain the appropriate amount of kinetic energy when detaching stone flakes from flint core using hammer stones of different weights. In the same study, they also showed that human tool users also adapted their actions accordingly when they were asked to produce flakes of different sizes (a different task constraint) and that they were able to accommodate concurrent changes in the task (tool weight and flake size to produce). Captive chimpanzees can also accommodate hammer stones of different weights to some extent: three out of five subjects did so with two out of three experimental stones (Bril et al. 2009). The current study provided comparable data from wild capuchin monkeys. The wild capuchins were able to adapt their actions in response to task constraints such as weight of the tool and the weight of the nut to be cracked by adjusting the lifting height and the force put on the stone. However, we did not find that the capuchins maintained the same amount of kinetic energy with different tools as in human stone knapping experts. It is highly possible that the reason lies in the difference between the tasks and the tool weight/ body weight ratio. The stone knapping task calls for relatively fine movement of one’s hand and fingers while nut-cracking in capuchins calls for a whole body movement which is a relatively gross movement. The hammer stones were 13% to 171% in proportion of the monkeys’ body weight in the current study. In Bril et al.’s study (2010) the average body weight of the human participants was 75.7 kg and all the hammer stones weighed around1 kg or less, which was 1% of their body weight. Moreover, the large changes in the weight of the hammer stones made it impossible for the monkeys to maintain the kinetic energy by altering lifting height or force put on the stone, because the monkeys were limited in how high they can lift or how much force they can put on the stone. Nonetheless, the results still demonstrated that in such a strenuous tool use activity with such heavy tools, the capuchins were able to accommodate their whole body movement in response to changes in tools and nuts to crack.

Another interesting point worth mentioning is the difference between nut weight as a predictor and stone weight as a predictor. Nut weight only predicted lifting height in Mansinho and Tucum out of eight subjects with low beta values (0.323 and 0.301, respectively) while stone weight did predict expectedly for four individuals (2 had inverse correlation and 2 others no correlation) with relatively high beta values (-0.485 to -0.631). Nut weight did not predict k/p ratio in all eight subjects while stone weight significantly predicted k/p ratio in all subjects with relatively high beta values (-0.367 to -0.784). If the monkeys were adjusting their actions in response to relevant materials (stones and nuts), why did they only adjust in response to stone weight but not at all or only a little bit in response to nut weight? This may seem puzzling but one possible explanation is that monkeys directly manipulated stones in their hands, but they did not directly manipulate nuts when they lifted the stone and struck the nut. The nut was in indirect contact with the body and therefore might not influence the action regulation as much as the stones. In fact, the object to be struck or hit as a task constraint should be examined carefully and differently than the handheld tool as a task constraint. Most relevant studies only examined the handheld tool/object (e.g. hammer stone in nut-cracking by chimpanzees, Bril et al. 2009; dart in target throwing by humans, Campos et al. 2011) or examined another task relevant object other than the tool but this object was still in direct contact with the body (e.g. flake to be produced from the handheld stone core, Bril et al. 2010). It would be interesting to examine if humans adjust their actions in response to the task relevant object that is comparable to the nut in the case of nut-cracking. For capuchins (and also chimpanzees), future studies should include more species of nuts that vary more widely in resistance. For example, if a capuchin has to crack a relatively soft nut using a heavy stone, the pattern of accommodation should be even more pronounced. Maybe a significantly softer or harder nut would facilitate more adjustment and regulation of actions even though the nut is still not in direct contact with the body as the stone is.

To examine further how capuchins can adapt and regulate their actions in response to different task relevant materials, future studies can examine accommodation to changes in anvil surface. For example, when forced to use a soft surface, will the monkey increase the kinetic energy? When forced to use a slippery surface, will the monkey change the striking angle? Further analysis on consecutive strikes within each nut-cracking episode is also necessary to examine if and how individuals regulate their actions in response to real-time feedback. Such studies will provide valuable information about skill in nut-cracking and the extent to which capuchins can accommodate within their action capabilities.

Acknowledgements

Thanks to the Oliveira family for logistical assistance. Permission to work in Brazil was granted by IBAMA and CNPq to QL, DF and EV. Funds: The University of Georgia LACSI Tinker Graduate Research Award awarded to QL.

References

Bril, B., Dietrich, G., Foucart, J., Fuwa, K., & Hirata, S. (2009). Tool use as a way to assess cognition: how do captive chimpanzees handle the weight of the hammer when cracking a nut? *Animal Cognition, 12*, 217-235.

Bril, B., Rein, R., Nonaka, T., Wenban-Smith, F., & Dietrich, G. (2010). The role of expertise in tool use: skill differences in functional action adaptation to task constraints. *Journal of Experimental Psychology: Human Perception and Performance, 36*, 825-839.

Campos, C. E., Benda, R. N., Couto, C. R., Profeta, V. L. S., Andrade, A. G. P., & Ugrinowitsch, H. (2011). Effect of the dart weight and target distance on the kinematic variables of the movement control of the underarm throw task. *Progress in Motor Control VIII*, Cincinnati, OH.

Fragaszy, D. M., Izar, P., Visalberghi, E., Ottoni, E. B., & de Oliveria, M. G. (2004a). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology, 64*, 359–366.

Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004b). *The complete capuchin: The biology of genus cebus*. Cambridge, UK: Cambridge University Press.

Fragaszy, D., Greenberg, R., Visalberghi, E., Ottoni, E. B., Izar, P. & Liu, Q. (2010a). How wild bearded capuchin monkeys select stones and nuts to minimize the number of strikes per nut cracked. *Animal Behaviour, 80,* 205-214.

Fragaszy, D., Pickering, T., Liu, Q., Izar, P., Ottoni, E. B. & Visalberghi, E. (2010b). Bearded capuchin monkeys' and a human's efficiency at cracking palm nuts with stone tools: field experiments. *Animal Behaviour*, *79*, 321-332.

Jackson, K. (1979). Fitting mathematical function to binmechanical data. *IEEE Trunsuctions of Biomedical Engineering*, *26*, 172-124.

Liu, Q., Fragaszy, D., Wright, B., Wright, K., Izar, P., & Visalberghi, E. (2011). Wild bearded capuchin monkeys (*Cebus libidinosus*) place nuts in anvils selectively. *Animal Behaviour, 81*, 297-305.

Matsuzawa, T. (2001). Primate foundations of human intelligence: a view of tool use in nonhuman primates and fossil hominids. In T. Matsuzawa (Ed.), *Primate Origins of Human Cognition and Behavior* (p 3-25). Tokyo: Springer-Verlag.

Newell, K.M. (1986). Constraints on the development of coordination. In M.G. Wade & H.T.A. Whiting (Eds.), *Motor development in children: Aspects of coordination and control* (pp. 341–361). Amsterdam: Nijhoff.

Robertson, G. E., Caldwell, G., Hamill, J., Kamen, G. & Whittlesey, S. (2004). *Research methods in biomechanics*. Champaign, IL: Human Kinetics.

Semaw, S., Rogers, M. J., Quade, J., Renne, P. R., Butler, R. F., Dominguez-Rodrigo, M., Stout, D., Hart, W. S., Pickering T. & Simpson, S. W. (2003). 2.6-Million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *Journal of Human Evolution, 45*, 169-177.

Smitsman, A. W. (1997). The development of tool use: Changing boundaries between organism and environment. In C. Dent-Read and P. Zukow-Goldring (Eds.), *Evolving explanations of development: Ecological approaches to organism–environment systems,* 301-329. Washington, DC: American Psychological Association.

Spagnoletti, N., Visalberghi, E., Ottoni, E., Izar, P. & Fragaszy, D. (2011). Stone tool use by adult wild bearded capuchin monkeys (*Cebus libidinosus*). Frequency, efficiency and tool selectivity. *Journal of Human Evolution, 61*, 97-107.

Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P. & Fragaszy, D. (2009). Selection of effective stone tools by wild bearded capuchin monkeys. *Current Biology, 19*, 213-217.

Visalberghi, E., Fragaszy, D., Ottoni, E., Izar, P., de Oliveira, M. G. & Andrade, F. R. D. (2007). Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. *American Journal of Physical Anthropology, 132*, 426-444.

Visalberghi, E., Sabbatini, G., Spagnoletti, N., Andrade, F.R.D., Ottoni, E., Izar, P., Fragaszy, D., 2008. Physical properties of palm fruits processed with tools by wild bearded capuchins (*Cebus libidinosus*). *American Journal of Primatology,70*, 884-891.

Wagman, J. B., & Carello, C. (2003). Haptically creating affordances: The user-tool interface. *Journal of Experimental Psychology: Applied, 9*, 175-186.

Table 3.1. Individual information

Individuals	Mansinho	Dengoso	Teimoso	Jatoba	Tucum	Piassava	Dita	Chuchu
Sex	M	M	M	M	M	F	F	F
Body Weight (kg)	4.28	3.63	3.59	3.44	2.45	2.03	2.23	2.32

Table 3.2. Number of coded trials per stone per individual

	Stones (weight in grams)					Total
	3470	1960	1420	930	570	N = 295
Mansinho	10	10	10	10	10	50
Dengoso	10	9	10	9	9	47
Teimoso	10	10	10	10	10	50
Jatoba	10	9	9	9	1	38
Tucum	9	10	10	10	0	39
Piassava	1	10	8	9	0	28
Dita	1	9	8	8	0	26
Chuchu	1	6	6	4	0	17

Figure 3.1. Photos of five hammer stones used in the study (photo by E. Visalberghi).

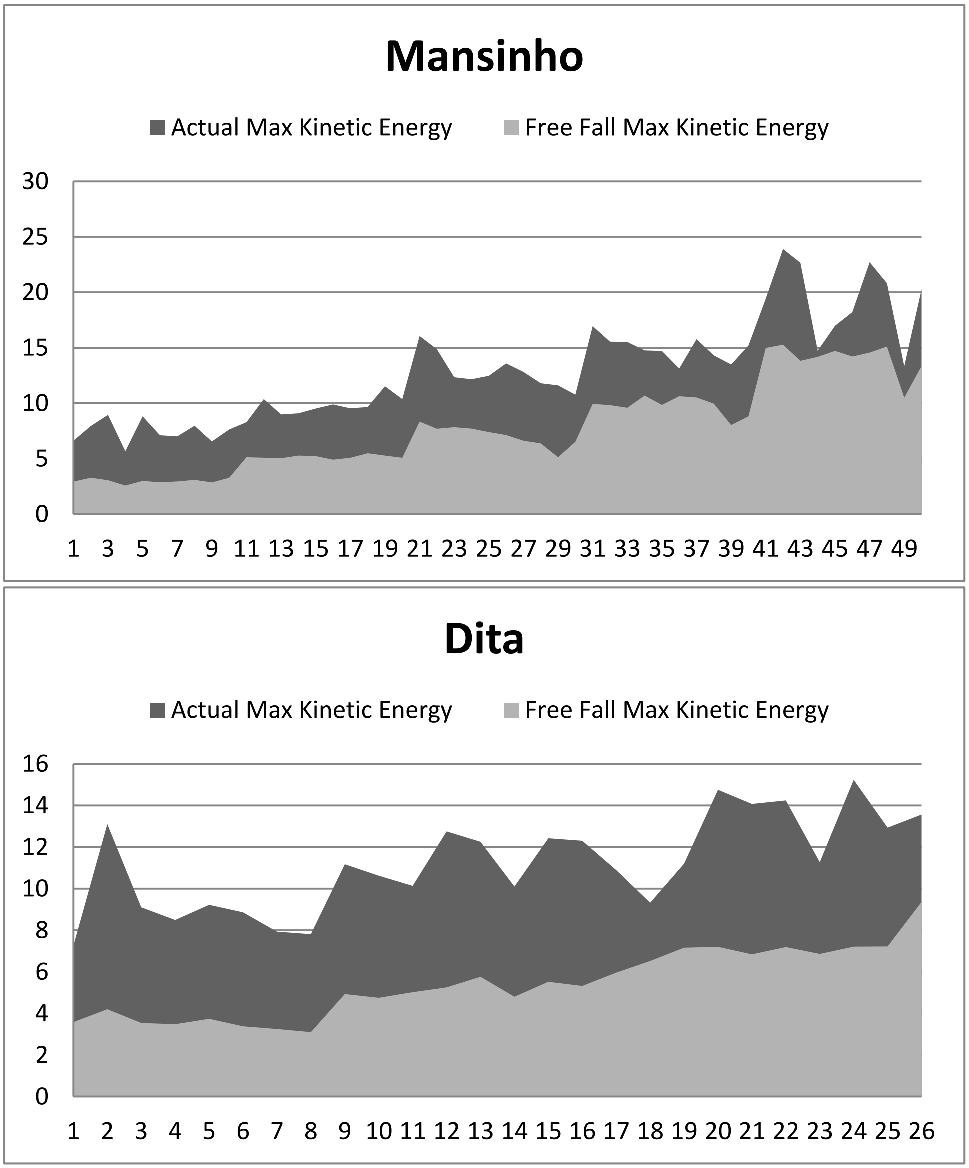

Figure 3.2. The maximum kinetic energy (vs. hypothetical kinetic energy in a free fall, which is equal to the maximum potential energy from the same lifting height) across trials (lighter stones to heavier stones in ascending order on X axis) in a male and a female subject. X axis is trial numbers and Y axis is kinetic energy in Joules.

CHAPTER 4

GENERAL CONCLUSIONS

This research aimed to apply a Perception-Action perspective to animal tool use and to test hypotheses derived from this theoretical framework. The Perception-Action perspective emphasizes the coupling of perception and action and it views tool use as a process during which the actor detects affordances of objects and surfaces in relation to his or her own action capabilities, executes action on the environment and gains new perceptual information from the action, leading to better detection of affordances and effective goal directed action (Lockman, 2000). Therefore, perception and action are linked. The Perception-Action perspective does not treat cognitive abilities involved in tool use as something that only happens in the mind but posits that cognition and action cannot be separated. In the case of animal tool use, we can study skill and cognition from studying the act of tool use.

From the Perception-Action perspective, we can study how individuals of any species or age detect affordances of objects or surfaces using species-typical exploratory routines and how they accommodate their actions in response to changing affordances. Applying the

Perception-Action framework to tool use in nonhuman animals leads to the following hypotheses:

1) Animals detect affordances of objects and of object/ surface/ action combinations using species-typical exploratory actions.

2) Detecting affordances by direct contact with the body (that is, via one relation) should be easier than by indirect contact, because indirect contact adds at least one additional degree of freedom to the system. Evaluating or managing additional degrees of freedom increases the challenge of an activity.

3) Animals will modify their actions in response to varying affordances when they use tools.

The results of the first study (Liu et al. 2011) showed that the wild capuchin monkeys successfully detected affordances (effectiveness and fly-off rate) of novel anvil pits and did so via species-typical exploratory actions (positioning and striking, not direct touching), and that detecting affordances by indirect contact (the anvils) was more difficult than by direct contact with the body (when compared to detecting affordances of nuts and stones directly). Therefore the first two hypotheses were supported. The results of the second study showed that the wild capuchin monkeys modified their percussive actions in response to varying affordances of hammer stones and nuts in nut-cracking, namely they lifted lighter hammer stones higher and put more force onto lighter hammer stones compared to heavier stones and that they lifted stones higher with more force when they were cracking heavier bigger nuts. Individual differences also clearly demonstrated that the extent to which an individual can adapt and regulate their actions in response to environmental affordance changes (stone and nut weight) clearly depends on individual's action capabilities and skill level. Therefore the third hypothesis was also supported.

This work also demonstrates the Perception-Action perspective affords systematic study of complex tool use behavior in a nonhuman primate species, especially behaviors reflecting selectivity and adaptive actions to accommodate new challenges. In fact, more recent studies are adopting it as the theoretical framework; for example, two recent studies examined how wild bearded capuchin monkeys detected affordances of nuts and stones using routine exploratory actions and selected more effective hammer stones for nut-cracking (Fragaszy et al. 2010; Visalberghi et al. 2009). Another study used this perspective to examine the development of nut cracking in capuchins (Resende et al. 2008). The Perception-Action perspective posits that young animals explore their environment and learn about different spatial and force relations and interrelations among different objects and surfaces. In this process, young animals act directly on objects and surfaces before they combine them and that early tool use acts will reflect their routine actions with which animals had used to explore the relevant objects and surfaces. Resende et al. (2008) reported that the development of spontaneous tool use in semi-free ranging tufted capuchins strongly supported the predictions posited above. They found that young monkeys showed percussive actions very early and readily struck nuts and other objects against a surface in their first half year of life. The monkeys explored single object/surface (nut/stone/anvil surface) long before they showed the correct sequence of actions supporting tool use: placing a nut on a surface and then releasing it before striking it with a stone.

The Perception-Action perspective has also been adopted to study nut-cracking in captive chimpanzees. Bril and colleagues reported captive chimpanzees adapted to hammer stones of various weights during nut-cracking by adjusting passive and active forces (Bril et al. 2009). The work with chimpanzees and capuchins illustrates how skill in tool use is reflected in animals' adaptive and flexible tool-using actions. Therefore, researchers should not only focus on the Piagetian tradition of testing in tool use but should also pay attention to the animals' tool using actions.

The Perception-Action perspective can also be adopted to study selectivity, affordance detection and skilled action in other kinds of object manipulation, tool use and problem-solving in animals. Prospective studies should investigate the exploratory behaviors that support detection of affordances and lead to selectivity. Studying everyday exploration in animals in different situations can be very informative. Starting from natural observation of individuals in their natural environment enables researchers to document detailed descriptions of individuals' exploratory routines.

How skill and embodied cognition is manifested in actions is a line of research that is of significant promise in research on human and animal tool use. When individuals encounter new environmental challenges (such as new surfaces, or new objects, or even new "forms" of body: e.g. teenager's growth spurt, pregnancy induced bodily change in humans), researchers can examine the behavioral changes on an individual basis. How individuals learn about affordances and fine-tune their detection of different affordances also depends on the individuals' body and action capabilities. Therefore the Perception-Action perspective on tool use affords a case-by-case naturalistic examination of the “functional and cognitive hallmarks of tool use” (Adolph and Lockman 2002, symposium, as cited in Berger and Adolph 2003). Such a framework encourages researchers to consider individual differences (side bias, prior experience, age, and predisposition etc.) in development of tool use and problem-solving. This approach provides a theoretical framework within which different species are granted full consideration of their different species typical action routines and different developmental trajectories.

In conclusion, this dissertation research has shown that the Perception-Action perspective is a promising alternative theoretical framework for studying tool use and object manipulation in animals, compared to the traditional representational approach. Adopting the Perception-Action approach enables researchers to ask new questions from new angles, and leads to productive scientific studies as shown above. From a comparative psychology point of view, this approach provides explanations about taxonomic differences in problem-solving and tool use that the traditional account of “cognitive differences” has failed to provide. From a developmental psychology point of view, the perception-action perspective also provides a rich theoretical framework that supports the study of perceptual learning, motor and skill development and how perception-action routines support development of manual skills and tool use. In tool use and problem-solving in which actions are involved, the Perception-Action perspective is a promising theoretical framework, as shown in this work.

References

Berger, S. E., & Adolph, K. E. (2003). Infants use handrails as tools in a locomotor task. *Developmental Psychology, 39,* 594-605.

Bril, B., Dietrich, G., Foucart, J., Fuwa, K., & Hirata, S. (2009). Tool use as a way to assess cognition: how do captive chimpanzees handle the weight of the hammer when cracking a nut? *Animal Cognition, 12*, 217-235.

Fragaszy, D., Greenberg, R., Visalberghi, E., Ottoni, E. B., Izar, P. & Liu, Q. (2010). How wild bearded capuchin monkeys select stones and nuts to minimize the number of strikes per nut cracked. *Animal Behaviour, 80,* 205-214.

Liu, Q., Fragaszy, D., Wright, B., Wright, K., Izar, P., & Visalberghi, E. (2011). Wild bearded capuchin monkeys (*Cebus libidinosus*) place nuts in anvils selectively. *Animal Behaviour*, *81,* 297-305.

Lockman, J. (2000). A perception–action perspective on tool use development. *Child Development, 71*, 137-144.

Resende, B. D., Ottoni, E. B., & Fragaszy, D. M. (2008).Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): a Perception–action perspective. *Developmental Science, 11*, 828–840.

Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P. & Fragaszy, D. (2009). Selection of effective stone tools by wild bearded capuchin monkeys. *Current Biology, 19*, 213-217.