COMPOUND GRIPS: MANIPULATION AS DYNAMIC PROCESSES IN TUFTED CAPUCHIN MONKEYS (*SAPAJUS SPP* AND *SAPAJUS LIBIDINOSUS*)

by

CAROLINE ELIZABETH JONES

(Under the Direction of Dorothy M. Fragaszy)

ABSTRACT

Compound grips (the use of one hand to hold one or more objects with multiple grips) have been described in macaques, gorillas, chimpanzees, and humans, but have not been explored in any New World primate. Capuchin monkeys use both power and precision grips, and we predicted they use compound grips as well. A task to prompt compound grip was presented to captive tufted capuchin monkeys. All monkeys held 1-4 balls in one hand and dropped them individually into a tube. Wild capuchins were also filmed using compound grips naturally. Regarding the results of both samples, we conclude that capuchin monkeys hold and move multiple objects in one hand, and simple grips and independent digit movements support separate control of objects in one hand. These findings contribute to our current understanding of comparative primate dexterity, and challenge prior knowledge of the capabilities of capuchin monkeys.

INDEX WORDS: power grip, precision grip, simple grip, compound grip, manual dexterity

COMPOUND GRIPS: MANIPULATION AS DYNAMIC PROCESSES IN TUFTED CAPUCHIN MONKEYS (*SAPAJUS SPP* AND *SAPAJUS LIBIDINOSUS*)

by

CAROLINE ELIZABETH JONES

BA, Alfred University, 2012

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

MASTER OF SCIENCE

ATHENS, GEORGIA

2016

COMPOUND GRIPS: MANIPULATION AS DYNAMIC PROCESSES IN TUFTED CAPUCHIN MONKEYS (*SAPAJUS SPP* AND *SAPAJUS LIBIDINOSUS*)

by

CAROLINE ELIZABETH JONES

Major Professor:	Dorothy Fragaszy
Committee:	Laurie Reitsema
	Karl Newell
	Dean Sabatinelli

Electronic Version Approved:

Suzanne Barbour
Dean of the Graduate School
The University of Georgia
December 2016

DEDICATION

This work is dedicated to my mother, my sister, my aunt “me”, and my grandmother: the four most resilient women I know.

“*No mud, no lotus”* - Thích Nhất Hạnh

ACKNOWLEDGEMENTS

I would like to extend my sincerest and utmost gratitude to Dr. Dorothy Fragaszy for her patience, understanding, and guidance throughout the implementation of this thesis. Thank you, also, to the other members of my master’s committee. I would like to express my deepest appreciation to the Fonseca de Oliveira family, “Family M”, in Boa Vista, Brazil, for their hospitality, and field knowledge. Finally, my efforts would be futile if not for the moral support of Allison Howard, Jacqueline Newbold, Bridget Lynch, and Kate Conley.

A heartfelt thanks to:

- The University of Georgia Department of Psychology
- The UGA Research Instrument Shop
- Jungle Friends Primate Sanctuary: Kari Bagnall, Britni King
- The Etho*Cebus* Project
- Elizabetta Visalberghi
- Laurie Reitsema
- Valentina Truppa
- The University Laboratory of Archaeology: Amanda Roberts Thompson
- Luca Marino
- Kristen Wright
- Noemi Spagnoletti
- Kirsten Cook
- Kristen Morrow
- Lawrence Milburn
- Mackenzie Pryor

This research was funded by the University of Georgia Department of Psychology, the UGA LACSI Tinker Foundation Grant, and the Etho*Cebus* Project.

TABLE OF CONTENTS

Page

APPENDICES

LIST OF TABLES

Page

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Our hands are our primary instruments in every day actions. We use them to write, gesture, and perform other skilled and social activities. Non-human primates make ample use of their hands as well, but do so differently from humans. Overall, the primate hand has been studied extensively, emphasizing its importance to humans and wide variation in its use across species. The published work encompasses many aspects of hand anatomy and physiology, psychology, biomechanics, kinematics, functionality, and development. This thesis describes a technique with which capuchin monkeys grasp objects, compound grip, that has not been described before in these monkeys.

Morphology, Neuroanatomy, and Movements of the Hand

Primate hands are characterized not only by numerous shared physical features, such as five multi-jointed digits on each hand, but also by several dynamic and static capabilities, such as the ability to oppose the thumb to varying degrees. Haptic perception and dynamic touch are also thought to contribute to these capabilities (Carlson, 2013). These key shared physical features and their variation within taxa have allowed scientists to explore and compare different primates, and to speculate about their evolutionary history.

Frederic Wood Jones was one of the first to address the morphology of grips (Wood Jones, 1916). He spoke highly of Charles Darwin’s and Thomas Huxley’s work in evolution and natural selection, and applied it to the aptitude with which humans and other primates make use of their appendages. Wood Jones fashioned the phrase, “emancipation of the forelimb”, in reference to the distinct morphological and employable differences between forelimbs and hind limbs (Wood Jones, 1916; Lemelin & Schmitt, 2016). John Napier (1956, 1980) later undertook research with human hands with respect to their use in holding objects. His work on manual function has served as a general, but essential foundation for successive hand studies. Napier parsed two distinct categories of manipulation performed by humans: prehensile and non-prehensile movements. Non-prehensile movements are described as whole-hand movements, like punching or pushing. The focus of this thesis is prehensile movements, which include grips using the palm and fingers. Power and precision grips are two key prehensile grips differentiated by the size of the object being held and by the position of the object within the hand (Figure 1). Precision grips are characterized by holding an (often small) object with the distal portions of the fingers, frequently between the pads of the forefinger and the thumb. Power grips are more often used to hold larger objects, requiring the use of the palm for stability and wrapping the fingers around the object for security (Wood Jones, 1916; Napier, 1980; Aiello & Dean, 1990).

Napier (1956) also spoke to the variability within precision and power grips. These include scissor grips, which are a type of precision grip in which an object is held using the medial and lateral sides of digits two through five. A precision pinch grip uses the pads of the thumb and index finger to hold objects, as in Figure 1. Another type of precision grip comes from using flexed fingers to hold objects, as in throwing a baseball.

Power grips come in forms such as hook grips, and squeeze grips, which use the fingers and the palm (sometimes minimally) to secure an object within the hand.

In executing grips and potential dynamic movements to shift between them, all primates utilize actions of the fingers, palm, wrist, and forearm. Pronation and supination of the hand involves rotation at the wrist and elbow. The forearm, which is made up of the radius and ulna, works in tandem with the adjoining wrist to pronate and supinate the hand. In anatomical position, the entire radius is lateral to the ulna, but during a pronation of the hand, when the thumb moves medially, the distal radius rotates anteriorly and over the ulna. The radius and ulna become crossed distally, while their proximal aspects remain in anatomical position. Supination of the hand occurs when the thumb rotates laterally, back to anatomical position, thereby uncrossing the distal radius and ulna (Figure 2). The wrist contains several bones including joints to initiate movement: the wrist joint (radiocarpal) and the midcarpal joints. These allow for extension, flexion, and slight rotation of the hand. Only the wrist joint allows for ulnar or radial deviation, whereby the wrist moves the hand in the sagittal plane (Figure 3) (Napier, 1980; Aiello and Dean, 1990).

As for the fingers, digits two through five are capable of extension and flexion at the metacarpophalangeal joints, the proximal interphalangeal joints, and the distal interphalangeal joints (Figures 2, 3, and 4). The digits can also adduct and abduct as a result of the rounded shape of the metacarpophalangeal joints (Napier, 1980; Aiello and Dean, 1990) (Figure 3). Because the human thumb lacks a true middle phalanx, the only flexion and extension occurs at the metacarpophalangeal and distal interphalangeal joints.

The repertoire of grip types for humans is wide-ranging in both physical ability and preferential use especially compared to that of non-human primates. Although non-human primates use both power and precision grips, power grips are the most common type of simple grip, performed by all primates, and some non-primates, in a variety of styles. This may be due to the flexibility and ease with which power grips are performed; power grips can be performed with fewer than five digits, provide a secure grip, and require little to no fine independent digit control. In contrast, the definition of a precision grip is very narrow, and the requirements to perform such a grip are precise and well-defined (Fragaszy & Crast, 2016). One of these requirements is the presence of a saddle or carpometacarpal joint: a unique joint located between the trapezium and the first metacarpal bones (Figure 5). This joint is largely responsible for the movements required for a precision grip using the distal parts of the thumb and fingers - the ability to meet digits two through five via opposition (Napier, 1980; Aiello & Dean, 1990). Comparatively, this is where a large difference is seen in the anatomy of the hand and the gripping skills of non-human primates. Apes and all Old World monkeys have a saddle joint comparable to that of humans; New World monkeys, tarsiers, and prosimians lack a saddle joint altogether (Napier, 1961; Napier & Napier, 1967). However, studies have shown that both genera of capuchin monkeys (*Cebus* and *Sapajus*) perform a precision pinch grip using pseudo-opposition and side opposition of the thumb, counterbalancing the absence of the saddle joint (Costello & Fragaszy, 1988; Christel & Fragaszy, 2000; Spinozzi et al., 2004, 2007; Erickson, 1948; Napier, 1961) (Figure 6). This pseudo-opposition is assisted by the concavity at the posterior of the first metacarpal, and convexity of the corresponding trapezium (Aversi-Ferriera et al., 2014). The use of a precision grip by capuchin monkeys is also related to their tendency to forage extractively in the wild (Costello & Fragaszy, 1988; Parker & Gibson, 1977).

We know manipulative actions and associated independent digit movement in primates are supported anatomically and also that they are supported by neural substrates. Grasping relies on brain areas shared among humans, macaques and capuchins, including the primary motor cortex, the premotor cortex, the cerebellum, and the anterior intraparietal sulcus (AIP). Some of these areas are present in small, grasping mammals such as opossums, but the neurobiology of grasping behavior in non-primates is not well studied (Beck et al., 1996). The primary motor cortex controls movements of specific areas of the body, and neural circuits connecting it to grey matter in the spinal cord (namely, the corticospinal tract) are responsible for the overall speed of hand movement and the complex skill of moving digits independently (Carlson, 2013; Castiello, 2005). Studies have shown that the primary motor cortex and hand motoneurons in humans are connected via a monosynaptic pathway, controlling quick and independent finger movement (Kuypers, 1981; Muir & Lemon, 1983; Pehoski, 1992; Lemon, 1993). Capuchin monkeys possess direct corticospinal projections to the digits of the hand, as do Old World primates, which support independent movement of the digits. Independent movement of the digits, along with the precision grip between thumb and the other digit(s), has not been seen in other New World monkeys (Bortoff & Strick, 1993; Fragaszy, 1998). Previous neurological studies have suggested that capuchins' corticospinal tract, as well as brain areas 2 and 5 (involved in planning and execution of motor movements such as reaching, grasping, and manipulation) are proportionally as large as those of macaques, and comparable to those of other Old World primates

(Padberg et al., 2007; Heffner & Masterson, 1983). This recent association between certain areas of the cortex and digital control may not be relevant, as Iwaniuk and Wishaw (2000) report that “even species devoid of CST [corticospinal tract] are capable of performing skilled forelimb movements”. Instead, they pose an alternate pathway, the rubrospinal tract (RST), as an imperative structure for skilled forelimb movements (Iwaniuk & Wishaw, 2000). Noting capuchin monkeys’ extreme forelimb control and manual skills, Kuypers (1981) and Phillips and Porter (1977) postulate that primates rely more on the motor cortex and the corticospinal tract rather than the rubrospinal tract.

Independent digit movement, especially of the thumb and index finger, is essential for using precision grips (Lansmeer, 1993; Schieber, 1991). Like humans, Old World monkeys implement individuated movements of the digits, during movements other than opposition (Schieber, 1991). The importance of these movements to humans for handling and gripping objects was brought to light by Elliot and Connolly (1984). Capuchin monkeys have some degree of individuated finger movements, as suggested by Spinozzi and colleagues (2007). It has also been noted that capuchins’ use of a surface to support part(s) of the hand during manipulation may promote independent digit movement (Cristel & Fragaszy, 2000). In humans, sensory neurons synapse with motor neurons in the cortex. When neurons in the sensory cortex fire, they stimulate neurons in the motor cortex, allowing for better muscle firing and fine motor coordination (Carlson, 2013). This theory is buttressed with accounts of motor cortex neurons that are activated when the wrist is stabilized, rather than when it is moving (Schieber, 1990; Humphrey, 1986; Humphrey & Reed, 1983). This mechanism may also be a contributing factor to capuchins’ dexterity when manipulating objects near or on a surface.

Another feature that influences grip in primates is hand shape. New and Old World monkeys of different species move and forage in different ways, and therefore, differ morphologically. Certain morphological features of the hand, such as proportional length of the thumb relative to the other digits, vary across primate species (Napier & Napier, 1967; Fragaszy, 1998). Humans, for example, have a long thumb relative to other digits and, as mentioned previously, this assists in the many ways we grasp items (Aiello & Dean, 1990). Cristel (1993) noted short thumb length in most apes and monkeys, compared to humans. Capuchin monkeys have a hand shape similar to humans, which affects how they grasp (Napier & Napier, 1967; Fragaszy, 1998; Fragaszy & Crast, 2016) (Figures 6 and 7). Napier and Napier (1967) present average hand length measurements of most genera of living primates (Table 1), demonstrating that capuchins have proportionally much longer thumbs than squirrel monkeys (*Saimiri*), macaques (*Macaca*), and chimpanzees (*Pan*). Although a few primate species, such as spider and colobus monkeys, have only a vestigial thumb (unneeded for hanging and climbing), capuchins use their hands for many additional activities, including extractive foraging, which is aided by the use of their lengthy thumb (Fragaszy, 1998).

Quadrupedal species rely on both their hands and feet for locomotion. For this reason, the pads of their hands are slightly more pronounced and fleshy than those of humans, to cushion contact with the ground, and in some cases, the pressure of tools. The hands of quadrupedal species are not typically adapted for tool use (Napier, 1980). It was Charles Darwin who originally suggested the idea that the evolution of human hands has been influenced by the use of tools (Darwin, 1871). This is supported in both anatomical and biomedical studies, such as that by Key and Lycett (2011). Fleshy pads of the hands could serve as a preadaptation in hominins to using hand tools.

The hand has fat pads on each palmar phalanx of the digits and one on the thumb. The palm has two large fat pads on the thenar and hypothenar areas (Figure 8) (Napier & Napier, 1967; Napier, 1980). Due to these fleshy palmar pads, some primates are able to grip objects within the palm itself, without the use of the fingers (Spinozzi et al., 2004). This includes active gripping using the muscles of the palm to bring the thenar and hypothenar regions together, commonly referred to as cupping (Napier, 1980; Aiello & Dean, 1990), or as a form of power grip (Spinozzi et al., 2004). Cupping behavior has been observed in both chimpanzees and capuchin monkeys, and the position is thought to accommodate holding variable objects used as tools (Freese, 1978; Crast, 2006; Marzke, 2013; Marzke et al., 2014).

Perception-Action of Extrinsic Object Features and Function

Grasping positions and the movements connecting them are constrained by the physical properties of the object(s) being held, such as shape, size, texture, orientation, and weight (Elliot & Connolly, 1984; Pouydebat et al., 2009; Castiello, 2005). Primates assess these features using visual, tactile, and proprioceptive feedback (Fragazy et al., 2004; Fleagle, 2013). Bullock and Dollar (2011) suggested that human grips are less influenced by object shape and size than they are by goal, but other studies suggest that objects in the hand (size, shape, number, etc.) dictate hand movements and position. The way primates perceive these characteristics and the purpose/function of the object, govern how it is held (Castiello, 2005). The visual and somatosensory systems coordinate to assemble information about external stimuli. Forward facing eyes are evolutionarily key features of morphology in primates (Fleagle, 2013). Humans, chimpanzees, macaques, and capuchin monkeys process and respond to visual information at similar, rapid speeds (Proctor & Brosnan, 2013). This ability is supported by a primitive dorsal visual stream in the posterior parietal cortex of primates responsible for perception of objects' spatial location, speed, and direction. The less primitive ventral stream, which terminates in the temporal cortex, perceives visual information such as size, shape, and texture (Carlson, 2013).

Despite their good visual acuity, capuchin monkeys rely heavily on tactile information while searching for food in areas where vision is limited, such as in the cracks of cliffs and in leaf debris on the ground (Fragaszy et al., 2004). They routinely perform on par with macaques and squirrel monkeys in their abilities to find and manipulate objects by touch alone and employ a "haptic search" tactic to explore places they cannot see (Welles, 1972, 1976; Fragazy et al., 2004).

Pouydebat and colleagues (2009) determined that humans (children, n=9, and adults, n=9), chimpanzees (*Pan troglodytes*, n=14), capuchins (*Cebus apella*, n=9), orangutans (*Pongo pygmaeus*, n=7), macaques (*Macaca fuscata*, n=9), and baboons (*Papio papio*, n=9) all modulate their grasp based on object size. Capuchins use both power and precision grips to grip both large and small items, and share many similarities with humans in their methods of grasping differently sized objects. Specifically, capuchins and humans rely more on precision grips than power grips when holding one small object (Pouydebat et al., 2009; Spinozzi et al., 2004). Other studies conducted using only human adults and children found that grip is constrained contingent on the ratio of object size to hand size (Newell et al., 1989; Newell et al., 1989). Concerning weight, capuchin monkeys discriminate between objects of varying masses by lifting and lowering an object (Visalberghi and Neel, 2003), as do humans (Lederman and Klatzky, 1987, 1993; Turvey 1996; Turvey et al., 1999).

Defining Compound Grip

Since Napier's original outline of grips, researchers have shown that human hands perform many variations and extensions of power and precision grips – aptly called *simple grips*. Of particular interest to us, Napier also described *combined grips*, albeit in a vague manner. These grips are evident when a prehensile action of the human hands stops mid-movement; at this time both power and/or precision grips may be recognizable (Napier, 1956). Humans use a combined grip quite often; for example, when holding keys, a phone, and a cup of coffee in the same hand. Such complex manipulative skills likely coevolved with human cognitive capacities (Faisal et al., 2010).

MacFarlane and Graziano (2009) described the phenomenon of a combined grip, which they termed *compound grip* or *complex grip*, while investigating the grip repertoire of free-ranging rhesus macaques (*Macaca mulatta*), defining it as "holding an object with many grips simultaneously, or holding many separately controlled objects in one hand" (Figure 9). However, the literature suggests that macaques are not the only primates seen demonstrating this action, as it has been described qualitatively in other Old World monkeys such as baboons, and in apes such as gorillas and chimpanzees (Figures 10 and 11), but not specifically identified as a compound grip (Maier, 1993; Byrne & Corp, 2001; Corp & Byrne, 2002; Marzke et al., 2014). This action has not yet been explored in New World monkeys.

Capuchins, a common taxon of New World monkey, appear to be epitomical subjects for studies on compound grip use. Their hand shape and proportions are more similar to humans than those of macaques, and the length of their thumbs could support using compound grip. They possess comparable innervation from the brain to the hands and digits to Old World primates; in fact, Heffner and Masterson (1983) examined the corticospinal tract of capuchins, relative to body size, and found that it was significantly larger than that of some Old World primates, including macaques. Capuchins act dexterously, using fine movements and independent actions of the digits, and execute a modified precision grip. Capuchins also have a proportionally larger brain-to-body ratio than most primates, which indicates potential for extensive sensory integration (Fragaszy et al., 2004).

The Present Study: Hypotheses and Predictions

In this work, we aim to clarify and explore MacFarlane and Graziano's (2009) compound grip (Figure 9). We will also inquire into the capacity of capuchins to exhibit a compound grip. It is not yet documented whether capuchins have this ability, and if they do, how it is implemented. Study 1 consists of a task designed to prompt compound grip in a controlled environment. Study 2 entails video analysis of wild capuchin monkeys' activity to document occurrences of compound grip. The aim is to confirm the occurrence of compound grip in a species of New World monkey, the capuchin, and explore the variability in manipulating multiple items. We also aim to explore a practical use of compound grip in the wild. Our hypotheses and corresponding predictions are as follows:

Hypothesis 1: Species with power grip, precision grip, large and direct corticospinal tracts, independent digit movement, and analogous brain regions for complex manipulation using the hands (i.e. AIPS, premotor cortex, etc.) perform compound grips.

Prediction 1: Capuchin monkeys execute compound grips. Prior research suggests that capuchins have comparable hand morphology, neuroanatomy, and physical, dynamic hand and forearm capabilities of those primates who have displayed compound grips. I test this prediction experimentally and observationally, in captive and natural settings.

Hypothesis 2: All forms of simple grips can be used in a compound manner.

Prediction 2: Capuchins will use precision, palmar, and power grips when executing a compound grip. These simple grips have been observed in apes and New World monkeys. We will test this in experimentally, as well as in the field.

Hypothesis 3: Difficulty in maneuvering multiple objects increases with the number of objects held.

Prediction 3: Capuchins have lower success at controlling objects in one hand, as the number of objects increases.

Hypothesis 4: The number of simple grips (precision, palmar, and/or precision) used concurrently, covaries with the number of objects to be held.

Prediction 4: With each additional object held, capuchins will use more simple grips.

Hypothesis 5: The demands of managing multiple objects with one hand can be met by incorporating the use of a surface, as well as by rotating the fist/wrist/forearm.

Prediction 5: As the number of objects held increases, capuchin's use of a surface assist and rotations of the fist/wrist/forearm will increase as well. We expect that capuchins will make use of a surface as a support as an aid for object manipulation within the hand, as suggested by Costello and Fragaszy (1977).

Hypothesis 6: There is a trade-off between speed and accuracy in a task. In tasks requiring accuracy, speed will most likely reduce accuracy (Fitts, 1954; Heitz, 2014).

Prediction 6(a): Capuchin monkeys will be more accurate in a task requiring compound grip when they move more slowly.

Prediction 6(b): Alternatively, as capuchins are known to capture mobile prey with accuracy and using rapid movements, they will not conform to the speed-accuracy trade-off paradigm. Time is a strong consideration for capuchin monkeys (Proctor & Brosnan, 2013; Pouydebat et al., 2014).

We took both a hand-centric as well as an object-centric view to our problem, unlike previous literature that focuses on one or the other. Previous works in classifying, coding, and categorizing hand movements in humans and non-human primates, such as that of Bullock and Dollar (2011), have influenced the development of our coding schemes. Elliot and Connolly (1984) described intrinsic, dynamic movements of the human hand. While this schema is useful for studying the handling of objects, as opposed to gripping objects, compound grip as described by MacFarlane and Graziano (2009) was most often seen while monkeys were simultaneously storing (gripping) and manipulating (handling) objects within one hand. Most previous work that addresses primate grasping, and grasping similar to that of primates, focuses on the skillful reach-to-grasp series of movements. This study instead concentrates on the opposite problem: reach to release (Sacrey et al., 2009).

Our current study relies on a specific circumstance for defining compound grip. Our coding scheme draws upon static hand positions with respect to held objects. Elliot and Connolly (1984) were the first to recognize simultaneous and/or independent digit movement in handling and/or grasping, which is also reflected in our coding scheme.

For the purpose of this study, we defined a power grip as any grip utilizing the palm and finger(s) concurrently. We defined precision grips as any grips prehending an object with the fingers (this includes two concurrent “sub-precision grips” defined in the literature, the scissor grip and the pinch grip), without use of the palm. Palmar grips were defined as any grip using only the palm (this includes “cupping” of the hand).

CHAPTER 2

STUDY 1 METHOD

Redefining Compound Grip

Utilizing Napier's original terminology and standards for precision and power grips (namely, simple grips) (Figure 1), as well as information gathered from MacFarlane and Graziano's (2009) account of compound grip in rhesus macaques, we have fashioned a more inclusive definition and algorithmic table of grip classes and their identifying features (Table 2). This table defines compound grip as a function of the number of hands/mouth/feet used, and well as the number of objects under individual control within the hand, and the number of simple grip types (power and/or precision) used.

Subjects

Five adult male tufted capuchin monkeys (*Sapajus* spp), Xenon, Leo, Chris, Mickey, and Nick, participated in this experiment. These monkeys are housed individually in outdoor enclosures at Jungle Friends Primate Sanctuary in Gainesville, Florida, year-round. The enclosures are constructed from welded steel wire mesh, allowing monkeys to see and communicate with conspecifics. These five monkeys had previously participated in non-invasive behavioral research by the Primate Cognition and Behavior Laboratory at the University of Georgia, prior to 2014. Primary testing for this study was conducted in October of 2015.

We noted that Leo was missing the distal end of his right index finger, at approximately the distal interphalangeal joint. He was also missing the distal end of his right fifth digit, not quite as proximal as the missing part of the index finger. Leo also lacks part of the distal end of his left index finger. These deficits most likely impaired Leo's ability to grip several objects due to a lack of hand surface area for stability and volume within the hand.

Apparatus and Procedure

Using the system shown in Table 2 for identifying compound grip, an experimental ball-drop task was designed to prompt it. This task prompts the use of a compound grip, by requiring a subject to manipulate objects within the hand to deposit one ball, while storing the other ball(s).

Each monkey was given up to four conditions using wooden craft balls (1.27 cm). Subjects were required to deposit one ball, two balls, three balls, and four balls into a clear acrylic tube (12.7 cm long, 1.3 cm diam) affixed to a wooden box (16.5 cm long x 14.2 cm wide x 16.5 cm high) with an open front. The tube was positioned in the box so that the portion protruding vertically measured approximately 7.6 cm, and the portion inside the box measured approximately 5 cm. A wooden lip (16.5 cm long x 2.5 cm wide x 2.5cm high) at the front edge of the bottom of the box caught deposited items. Balls were painted with acrylic paint (red, blue, yellow, green), and coated in polyurethane (Figure 12). The apparatus was placed on a stationary surface measuring 9 cm above the ground, 18 cm long and 12.5 cm wide.

Prior to testing, positive reinforcement with food treats was used to train subjects to use one hand to deposit the items into the tube, which could be reached easily through the wire mesh. Balls were handed to the subjects by the researcher, and subjects were allowed to use either hand and position balls as they liked before depositing them. Ten trials of each condition (one ball, two balls, three balls, four balls) were recorded. Three cameras were used to record testing from different angles at 1/500 shutter speed. The left camera was a Canon HXA1S, the center camera was a Canon XF100, and the right camera was a Canon GL2. A small white board was displayed in view of all cameras before each trial with the date, subject name, condition, and trial number. This experimental set-up is displayed in Figures 13 and 14.

Behavioral variables were coded from video using Noldus Information Technology's Observer XT 10© software and Adobe Premiere Pro CC 2015 ™. Videos were coded using continuous sampling methods, frame by frame (30 frames per second). The trial started when the subject's hand crossed the plane of the mesh wire, and ended when the last object fell into the tube or out of the hand's control. Trial failures consisted of subjects missing the tube, or using two hands. When subjects "failed" to complete a condition (missed the tube) ten consecutive times or when the subject chose to stop participating, the testing session was ended.

Five successful trials per monkey, per condition were coded. The ethogram used for coding can be found in Table 3. Inter-observer reliability (80%) was calculated using 20% of the total trials coded – one from each monkey, from each completed condition.

Use of the left or right hand was coded throughout the duration of a trial. Wrist deviation/extension/flexion were not included in this coding scheme because of the difficulty in determining where a movement originated: from the wrist, the elbow, and/or the shoulder. Instead, two separate and more comprehensive variables were examined. At the beginning of each trial, a start position was marked (In Table 3, “Original Fist/Wrist/Forearm Position), using Figures 2 and 15 as guides. During pilot trials, most subjects approached the apparatus with a ventral-facing fist, which prompted the decision to designate this as “neutral”. Any subsequent rotations were coded as “fist/wrist/forearm rotation” with a corresponding direction using Figures 2 and 15. Any frames containing discernable grasping were coded for the type of simple grip used (precision, power, and/or palmar), and, when possible, the digits fabricating the grip. If more than one grip type was used in a frame, coders would indicate the presence of a compound grip in the coding scheme. Any distinct movements of independent digits from frame to frame were specified by the digit number (1-5) and the type of movement (extension, flexion, adduction, abduction) (Figures 2, 3, and 8). Contact of the object, or the hand or wrist of the monkey with the tube was coded for both frequency and duration. Finally, the number of objects remaining in the hand was indicated for each frame, to know when each object dropped.

Data Processing

The study design and the operational definition of a compound grip dictate that a compound grip can only be performed in this task by using two (or more) simple grips (power, precision, palmar) to grasp one or more separately controlled objects at the same time. Using two different, simultaneous grips with one hand on a spherical object is nearly impossible, hence the “one ball” condition was a starting point to allow subjects to practice the task, and provide a baseline for assessing difficulty. Trials with two or more balls were used for compound grip analysis. If monkeys can complete this task with at least two balls, we can confidently conclude that they can perform a compound grip.

Analyses

The frequency of each simple grip and each simple grip combination was collated for every condition during the experiment, and for every compound grip instance observed in the field. Using these data to address P1, P2, and P4, we determined which simple grips were used and how the frequency of compound grips changed in each condition via ANOVA, transforming the data when necessary.

In order to evaluate comparative difficulty across conditions (P3), we determined the proportion of successful trials and completed conditions. As these data were normally distributed (Shapiro Wilkes), one-way ANOVAs were used to examine the effect of condition.

To investigate the coping strategies for handling more than one object (P5), we looked at the frequency and duration of the use of a surface and well as the frequency and direction of fist/wrist/arm rotations. Frequency and duration were the units of analysis in ANOVA and condition was the independent variable.

Data concerning successful trials, as well as unsuccessful ones helped assess the application of Fitts’ Law (P6a & P6b) (Fitts, 1954; Heitz, 2014). Calculating the duration of all task attempts informed us about whether or not time is being sacrificed for accuracy, using a 2 x 4 x 5 mixed model ANOVA with repeated measures. This information was examined across conditions and subjects.

All statistical tests were performed using RStudio™ open-source software, JMP™, and/or SAS™. A 2-tailed alpha level was set at 0.05. This research complies with the International Primatological Society (IPS) Guidelines for the Use of Nonhuman Primates in Research and UGA IACUC protocol (AUP A2013 10-017-Y2-A1).

CHAPTER 3

STUDY 1 RESULTS

Hypotheses 1 and 2: Presence of Compound Grip

Successful completion of (at least) condition two (BB) by all subjects indicates that capuchin monkeys can execute a compound grip (Table 4). Capuchin monkeys use precision, palmar, and power grips when executing a compound grip. The combination of at least one power grip and one precision grip was the most frequently used compound grip that could be identified (>6% of all compound grips) (Table 5); figures 16, 17, 18, and 19 show photo examples. This unusually low percentage of even the most utilized grip may indicate the flexibility in grips that capuchins use simultaneously.

Hypothesis 3: Between Condition Difficulty

Table 6 and Figure 20 depict the percentage of successful trials per condition for each subject. The data were normally distributed (Shapiro-Wilk, p=0.2554). A one-way analysis of variance was used to determine a main effect of performance between conditions (F=9.125, dF(residuals)=12, p=0.002).

Tukey's post-hoc revealed a significant difference between condition one (B) and condition two (BB) (p=0.021) (Table 7) from a success rate of 96% to 63% (Table 6). As depicted in Figure 20, monkeys Mickey, Leo, and Chris did not complete all conditions.

Hypothesis 4: Compound Grip and Object Quantity

For each frame of each trial, for each condition, compound grips and the simple grips (palmar, precision, and power) that composed them were coded and totaled (Table 5). Simple grip combinations in the two ball (BB) condition made up 28.8% of all compound grips. Simple grip combinations in the three ball (BBB) condition made up 47.6% of all compound grips. Simple grip combinations in the four ball (BBBB) condition made up 26.4% of all compound grips. This pattern indicates that as the number of objects held increases, the percentage of compound grips out of total grips increases as well between two and three objects, and between three and four objects, but no differences in compound grip frequency between conditions were statistically significant (p=0.64, F=0.456, dF(residuals)=21).

Hypothesis 5: Hand, Wrist, and Forearm Rotation, and Support of a Surface

Table 10 displays frequency counts, percentages, and means of fist/wrist/forearm rotations, respectively. Two one-way ANOVAs were run on each rotation type (pronations and supinations), and are plotted in Figure 21 (A and B). Tukey's post-hoc tests revealed significant differences in frequency of pronations between all pairs of conditions, and differences in frequency of supinations in all pairs of conditions except between one ball and two balls (Table 11 and Figure 21) (p<.05). The use of a surface – the tube itself – to support the hand, was employed in every successful and unsuccessful trial, of every condition, by every monkey.

Hypothesis 6: Trial Duration

Three general linear models were used to examine this hypothesis. Holding condition constant, the first model yielded a main effect of duration on success, so that the longer a subject worked on a task the less successful they were (p=0.007, F=25.47, dF=4). The average successful trial took 1.62 seconds to complete, and the average unsuccessful trial took 2.43 seconds.

The main effect of condition on success was assessed in the second model and did have a significant effect (p<0.0001, F=36.05, dF=3). A third model using condition and duration as an interaction term was not significant; there was no interaction between condition and success (p=0.9394, F=0.13, dF=3). Means by success/failure are reported in Table 12 and plotted in Figure 21: A, B, C, and D.

CHAPTER 4

STUDY 1 DISCUSSION

The main hypothesis of this thesis is that species with power grip, precision grip, large and direct corticospinal tracts, independent digit movement, and analogous brain regions for complex manipulation using the hands (i.e. AIPS, premotor cortex, etc.) perform compound grips – grips that utilize more than one simple grip on one object, or one or more simple grip on several separately controlled objects simultaneously. We predicted that capuchins would use a compound grip, given a goal that required doing so. Our results show that all subjects (n=5) were able to perform a compound grip using at least two objects. Four out of five subjects (Nick, Mickey, Xenon, and Leo) were able to complete a compound grip in at least half the trials, with three objects. Two out of five subjects (Nick and Xenon) were able to perform compound grips with four objects.

The second hypothesis states that all forms of simple grips can be used in a compound manner. Identifying specific simple grips in a dynamic task, such as this one, proved to be difficult. Often, the monkey's hand obscured objects within it, prohibiting experimenters from pinpointing where the object made contact with the hand and/or digits. After identifying these simple grips to the best of the experimenter's ability, we determined that in this drop task capuchins used precision, palmar, and power grips when executing compound grips, most likely more often than our results indicate, as our coding method was quite conservative. Compound grips could only be employed (by definition), using two or more balls. Of all combinations of simple grips to create a compound grip, a combination of a precision grip (used to maneuver the focal object) and a power grip (used to store additional objects) was most common.

As predicted in hypothesis three, difficulty in maneuvering multiple objects increased in accordance with the number of objects held, but the only significant difference across conditions was between one ball and two balls. The progression of difficulty from depositing one ball 96% of the time to depositing two balls 63% of the time demonstrates the profound difference in effort between a simple grip with one object and a compound grip with two objects.

Our fourth hypothesis states that as the number of objects held in the hand increases, the number of compound grips will increase, proportionally, as well. This hypothesis was not supported, as the percentage of compound grips executed did not increase significantly with the addition of subsequent objects. Again, this may be a result of our conservative coding method, as specific simple grips within a compound grip were difficult to see.

As Costello and Fragaszy (1988) proposed, and as we predicted in hypothesis five, capuchin monkeys make use of a surface to aid object manipulation. Every monkey made contact with the tube in every trial. The same was true for the number of rotations; pronation and supination of the fist/wrist/forearm increased with each additional object held. The number of pronations and supinations increased significantly with each object added. We postulate that this is because holding numerous objects in one hand limits the amount of room in the hand, therefore decreasing the freedom to use in-hand movements. It appears that capuchins compensate for this lack of freedom with movements “outside” the hand, originating from the wrist or elbow.

Capuchin monkeys are not more accurate in a task requiring compound grip when they move more slowly, when taking condition in account; a trade-off does not exist between speed and accuracy in this task. In light of this result, several other explanations are likely. During the unsuccessful trials, nearly all subjects attempt to “fix” their mistakes (i.e. attempting to pick up dropped balls, etc.), increasing the overall duration of the trial. The trial parameters used for coding included these corrections, adding that time to the overall duration of the trial.

Nick was consistently the most skilled subject, completing ten trials of every condition, with the fewest misses overall and in each condition, with the exception of tying with Xenon in the 4-ball condition. Xenon pays close visual attention to the task, and like Nick, successfully completed ten trials of each of the four conditions. Chris was the least skilled of all the subjects. His attention was unfocused, and his movements were unpredictable and sporadic. Chris completed only the one-ball and two-ball conditions successfully, and failed the three-ball condition with ten consecutive misses. Leo’s performance during this task was average. There were several instances where he adjusted his hand position, in order to complete the same types of grips and movements seen in monkeys with average fingers, but with fewer objects. For example, due to his shortened second digit, Leo performed a precision grip using his thumb and the lateral side of his third digit (Figure 18 and Figure 19). Mickey was the only subject who voluntarily ceased participation in the task, after completing ten successful trials of both conditions one and two, and five non-consecutive successes during condition three.

Use of the left and right hand in performing this task was coded at the start of each trial, and never changed throughout. Most subjects used their right hand to complete this task; however, the sample size prevents conclusions about handedness in the population. Warren (1980) proposed that laterality in primates was task-based, and that there was no overall preference for one hand. It was later proposed that the left hand of primates was more suited for visually guided reaching, and the right for manipulation (MacNeilage et al., 1987; Forsythe & Ward, 1987). When these statements were tested with *Sapajus* (formerly *Cebus*), it was found that capuchins used more precision grips with the individually preferred hand. Overall, precision grips were more likely when reaching and precision grasping was with the right hand (Costello & Fragaszy, 1988). More recent studies have found a complete lack of hand bias in most non-human primates, with the exception of chimpanzees (Hopkins and Cantalupo, 2004; McGrewn and Marchant, 1997; Phillips and Sherwood, 2005; Hopkins, 2013). Capuchin monkeys fall into this “non-biased” category of handedness on a population level, but readily show individual biases (Fragaszy et al., 2004; McGrew and Marchant, 1997; Phillips and Sherwood, 2005; Spinozzi et al., 2004). Our results also demonstrated clear and consistent handedness in some monkeys, and less bias in others, indicative of the difficulty of the task (Table 13).

An unpublished study by Busch, Cristel, and Fragaszy found that in a reach to grasp task, capuchins use vision to obtain objects, but once acquired, directed their attention elsewhere (Fragaszy et al., 2004). This leads us to believe that to complete this task, monkeys rely more on tactile cues than visual cues, though it is suggested from the performance of Nick and Xenon that visual attention does aid in success.

CHAPTER 5

STUDY 2 METHOD

Subjects and Study Area

A group of twenty-three (n=23) wild, habituated capuchin monkeys (*Sapajus libidinosus*) (Table 14) inhabiting the EthoCebus Project field site in Boa Vista, Brazil (Piaui State) (Figure 22), were opportunistically video-recorded over a period of 2.5 months (May-July 2014). All monkeys employing compound grip were filmed with a Casio Exilim ZR-700 camera, set at 120 frames per second. A Benro A38FB Mg-Aluminum monopod was utilized frequently. Most video footage was taken in a (20 m diam) outdoor laboratory area within the monkey's natural home range. This area contains several anvils of varying sizes and materials, and was provisioned on a semi-regular basis during this study with foods typically eaten by the monkeys in this region. These foods include local kernelled corn, tucum nuts (*Astrocayum acaule* and *Astrocaryum aculaetum*), catulé nuts (*Attalea barreirensis*), piassava nuts (*Orbignya* spp), and naja nuts (*Attalea dubia*) (Figures 23, 24, and 25). For this study, tucum, piassava, and naja nuts were distributed because their size allows for multiple nuts to fit in the hand of a capuchin at one time (thus producing a compound grip).

Procedure and Analyses

More than three hundred (n=358) videos were captured during this time period. Video footage was catalogued to identify the individual monkey, the type and amount of food items utilized, grip types seen, and whether compound grips were performed while the monkey was on the ground or on an arboreal substrate. Monkeys in this habituated group are distinguishable by locals and researchers, all of whom pass identification reliability tests with 95% confidence. Due to the opportunistic nature of these observations, videos were recorded at variable angles and with variable degree of visibility – much like Macfarlane and Graziano’s (2009) experience. For this reason, no additional software was used for coding, and this more simplified method of cataloguing was implemented using Microsoft Excel while cataloguing videos.

CHAPTER 6

STUDY 2 RESULTS

Of the 358 videos collected in the field, 184 (51%) of them contained confirmed instances of compound grip. Of these compound grips, 162 (87%) of these were done with two food objects, 18 (10%) were done with three food objects, and 4 (2%) were done with more than three food objects. Individual adults Piassava, Chuchu, and Jatoba performed most of the compound grips observed (Figure 26). The youngest individual seen performing compound grips was Donzela, a six-month old juvenile.

No palmar grips were seen in any combination of compound grips in the field; however, every instance of compound grip consisted of at least one precision and one power grip. The only instances of two power grips were when a compound grip was performed with three nuts or more.

When comparing compound grips performed on the ground versus compound grips performed arboreally, we found the majority of compound grips, regardless of the number of objects held, were performed on the ground.

CHAPTER 7

STUDY 2 DISCUSSION

Compound grips were observed in a group of wild capuchin monkeys (Figures 27, 28, and 29), supporting our first hypothesis that species with power grip, precision grip, direct and large corticospinal tracts, independent digit movement, and analogous brain regions for complex manipulations using the hands perform compound grips. This opportunity presents itself when individuals have access to multiple food items (in this case, palm nuts).

We propose that the number, as well as size and other physical features of the object grasped largely influences grasping. In Figures 24 and 26 we can see that most compound grips are done with only two objects. In Figures 21, 22, and 23, the size difference in the nuts grasped is apparent. Most compound grips were performed using tucum or naja, with two tucum the most common. This may be because of their relatively small size, but may also be due to greater availability of these nuts compared to others.

Both our second and third hypotheses were unsupported by our data collected in natural settings. No palmar grips were seen, but every instance of compound grips utilized at least one power grip and one precision grip. We expect that no palmar grips were seen due to the large size of all the nuts compared to the wooden balls presented in Study 1.

Capuchins experience within-group contest and scramble competition for food. Contest competition is highest when resources, especially those of great value, are clumped, such as in the case of our field provisioning site (Verderane et al., 2013). All capuchins take this opportunity to “hoard” resources, and compound grip helps them do so. We expect that the social setting of our field site prompts the capuchins to store as many nuts as possible, but further research about the relation between social context and the grasping of food items is needed. It was also noted that capuchins often use their wrists and arms as extensions of their hands to clutch food objects to their body, particularly during transport (Figure 25).

Throughout video coding, we came across a sample of interesting hand movements and actions, which were not quantified in our study, but merit mentioning. The monkeys used an action similar to that seen in the ancient use (now quite modernized, and popularized) of Chinese Baoding balls. A set of two balls small enough to fit in the hand, now frequently made of metal, are moved within it, allowing the two balls to switch places and still touch (or not touch, based on the user’s objective). A wild capuchin monkey at the field site used this action with two tucum nuts to adjust them within one hand – a clear demonstration of an in-hand movement described by Crast (2006).

CHAPTER 8

GENERAL DISCUSSION

Bearded capuchin monkeys use compound grips both in the wild and under experimental circumstances in captivity. In the wild, only precision and power grips were observed to constitute compound grips, although all three grips (precision, power, and palmar) were seen in the experimental study. These findings contribute to long-standing studies about the manual capabilities of capuchin monkeys – a New World monkey that has cognitive abilities comparable to those of Old World primates, but has a different morphology of the hand. We now know that despite the absence of a saddle joint, once thought to be necessary for a precision grip, capuchin monkeys can use pseudo-opposition to execute compound grips, consisting of combinations of precision and power grips. Research and developmental underpinnings have come a long way from the works of Frederick Wood Jones (1916), and John Napier (1956; 1961; 1980), although neural support for gripping movements in any primate is still lacking, and not well understood.

This thesis addresses compound grip – the ability to grasp an object with many grips simultaneously, or grasping many separately controlled objects in a hand – as it pertains to the physical, and perhaps social and practical, constraints of bearded capuchin monkeys (*Sapajus*) (MacFarlane & Graziano, 2009). In our experimental study, we concluded that capuchins make use of external space (utilizing pronations and supinations, as well as the tube for wrist/hand support), when the hand itself is constrained by “too many” objects. Capuchins also have several other methods for dealing with such a problem. It seems that despite ample evidence of tactile and haptic exploration in the capuchin literature, visually guided movements are more precise.

These findings have many implications for the way capuchins perceive their environment and cope with physical limitations. It suggests that capuchins have acute vision, as do humans and other haplorrhines, and also alludes to behavioral flexibility in capuchins. These behavioral and sensory abilities may also have coevolved with the various morphological features of capuchins' hands - fat palm pads, and proportional palm and digit lengths, as well as direct corticospinal projections (leading to high degree of dexterity).

The results of our investigation into the time-accuracy trade-off in our experimental task were puzzling, as capuchin movements of all sorts are swift and purposeful. We maintain that capuchins value time above comfort, but this may only hold true when the payoff is adequate.

In addition to the manual abilities of capuchins, our studies also indicate social correlates of manual activity. In the wild, capuchins engage in intra-group competition for food resources, and their hands aid in this phenomenon. From our field observations, it is clear that the direct competition drives their need to collect and hold as many high-demand food items (such as palm nuts) at once.

As it is clearly an effortful behavior, individuals should need a reason to use a compound grip. Collecting food seems to be the primary context in which compound grips are used by wild capuchins. We conclude that compound grip is used by capuchins when ecological and social settings allow and promote it.

Future Directions

Our video-coding methods appeared to be the most practical method considering complex kinematic assessment of non-human primate hands is difficult to execute. However, future studies may manage to use more traditional kinematic measures. As alternatives and improvements to kinematic analysis of primates' movement appear, we hope to be able to provide more detailed and precise information. In the future, we plan to use temporal and sequential methods of analysis, such as Noldus Technology's THEME™ or the sequence analysis method of Borel and colleagues (2015) that appear to be a good fit for the kind of data we collected.

Additionally, careful description of the manual behaviors of other primates is vital. Work such as that being conducted by Masi and colleagues (2015) to specify grip types in gorillas, can provide enormous insight about the variability across manual function. The derivation of evolutionary pathways of behavior is most powerful with species widely separated phylogenetically (MacLean et al., 2012).

As mentioned previously in this work, the presence of conflicting literature about the neural underpinnings of manual dexterity – especially regarding grasping – is apparent. Subsequent research should place an emphasis on the mechanisms for such skillful movements, not only in capuchins, but also in other primates. Further research should also address social influences on manual activity in the wild; capuchins are socially biased learners, and maintain close-knit and integrative group cohesion in the wild and captivity. No doubt, their activities are influences by social factors.

REFERENCES

Aiello, L., & Dean, C. (1990). *An introduction to human evolutionary anatomy*. London: Academic Press.

Aversi-Ferriera, R.A.G.M.F., Maior, R.S., Aziz, A., Ziermann, J.M., Nishijo, H., TOmaz, C., Tavares, M.C.H., & Aversi-Ferreira, T.A. (2014). Anatomical analysis of thumb opponency movement in the capuchin monkey (*Sapajus sp*). *PLoS ONE, 9*(2), 1-8.

Beck, P.D., Pospichal, M.W., & Kaas, J.H. (1996). Topography, architecture, and connections of somatosensory cortex in opossums: evidence for five somatosensory areas. Journal of Comparative Neurology, *366, 109-133*.

Borel, A., Chèze, L., & Pouydebat, E. (2015). Sequence analysis of grip and manipulation during tool using tasks: a new method to analyse hand use strategies and examine human specificities. *Journal of Archaeological Method and Theory, IN REVIEW*

Bortoff, G.A., & Strick, P.L. (1993). Corticospinal terminations in two new-world primates: further evidence that corticomotoneuronal connections provide part of the neural substrate for manual dexterity. *The Journal of Neuroscience, 13*, 5105-5118.

Bullock, I.M., & Dollar, A.M. (2011). Classifying human manipulation behavior. *IEEE International Conference on Rehabilitation Robotics*.

Byrne, R.W., & Corp, N. (2001). Manual dexterity in the gorilla: bimanual and digit roles differentiation in a natural task. *Animal Cognition*, *4*, 347-361.

Carlson, N.R. (2013). *Physiology of behavior*. Boston, MA: Pearson.

Castiello, U. (2005). The neuroscience of grasping. *Nature Reviews Neuroscience*, *6*(9), 726-736.

Corp, M., & Byrne, R.W. (2002). Leaf processing of wild chimpanzees: physically defended leaves reveal complex manual skills. *Ethology, 108,* 673-696.

Costello, M.B., & Fragaszy, D.M. (1988). Prehension in *Cebus* and *Saimiri*: I. Grip type and hand preference. *American Journal of Primatology*, *19*(1), 165-194.

Crast, J. L. (2006). A comparison of dynamic hand movements chimpanzees (*Pan troglodytes*) and capuchin monkeys (*Cebus apella*) (Master's Thesis). Retrieved from the University of Georgia Theses and Dissertations Collections Online.

Cristel, M. (1993). Grasping techniques and hand preferences in Hominoidea. In: Preuschoft, H., Chivers, D.J. (eds.), *Hands of primates* (pp. 91-108). New York: Springer-Verlag.

Cristel, C.I., and Fragaszy D. (2000). Manual function in *Cebus apella*. Digital mobility, preshaping, and endurance in repetitive grasping. *International Journal of Primatology*, *21*(4), 697-719.

Elliot, J.M., & Connolly, K.J. (1984). A classification of manipulative hand movements. *Developmental Medicine and Child Neurology, 26*, 283-296.

Erickson, O.E. (1948). The morphology of the forelimb of the capuchin monkey, *Cebus capuchinus*. Dissertation, Department of Biology. Harvard University.

Faisal, A., Stout, D., Apel, J., & Bradley, B. (2010). The Manipulative Complexity of Lower Paleolithic Stone Toolmaking. *PLoS ONE, 5*(11), 1-11.

Fitts, P. (1954). The Information Capacity of the Human Motor System in Controlling the Amplitude of Movement. *Journal of Experimental Psychology, 47*, 381- 391.

Fleagle, J.G. (2013). *Primate adaptation and evolution, 3rd ed*. San Diego, CA: Academic Press.

Forsythe, C., & Ward, J. (1987). The lateralized behavior of the ruffed lemur (*Varecia variegata*). *American Journal of Primatology*, *12*(3), 342-342.

Fragaszy, D.M. (1998). How non-human primates use their hands. In K.J. Connolly (ed.), *Psychobiology of the Hand* (pp. 77-96). London: Mac Keith Press.

Fragaszy, D.M., & Crast, J. (2016). Functions of the hands in primates. In: T.L. Kivell, P. Lemelin, B.G. Richmond, & D. Schmitt (eds.), The Evolution of the Primate Hand: Anatomical, Developmental, Functional, and Paleontological Evidence (pp. 5-13). New York: Springer.

.

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

Freese, C.H. (1978). The behavior of white-faced capuchins (Cebus capucinus) at a dry-season waterhole. *Primates*, *19*(20), 275-286.

Heffner, R.S., & Masterson, R.B. (1983). The role of the corticospinal tract in the evolution of human digital dexterity. *Brain, Behavior, and Evolution, 23*, 165-183.

Heitz, R.P. (2014). The speed-accuracy tradeoff: history, physiology, methodology, and behavior. *Frontiers in Neuroscience, 8*, 1-19.

Hopkins, W.D. (2013). Comparing human and nonhuman primate handedness: challenges and modest proposal for consensus. *Developmental Psychobiology, 55*(6), 621-636.

Hopkins, W.D., & Cantalupo, C. (2004). Handedness in chimpanzees (*Pan troglodytes*) is associated with asymmetries of the primary motor cortex: a review and hypothesis. *Journal of Comparative Psychology, 109*, 291-297.

Howard, A.M., Nibbelink, N., Bernardes, S., Fragaszy, D., & Madden, M. (2015). Remote sensing and habitat mapping for bearded capuchin monkeys (*Sapajus libidinosus*): landscapes for the use of stone tools. *Journal of Applied Remote Sensing, 9*(1), 096020.

Humphrey, D.R. (1986). Representation of movements and muscles within the primate precentral motor cortex: historical and current perspectives. *Federation Proceedings, 45*(12), 2687-2699.

Humphrey, D.R., & Reed, D.J. (1983). Separate cortical systems for control of joint movement and joint stiffness: reciprocal activation and coactivation of antagonist muscles. In J.E. Desmedt (ed.), *Motor Control Mechanisms in Health and Disease* (pp.347-372). New York: Raven Press.

Iwaniuk, A.N., & Wishaw, I.Q. (2000). On the origin of skilled forelimb movements. *Trends in Neuroscience, 23*(8), 372-376.

Johnson-Pynn, J., Fragaszy, D.M., Hirsh, E.M., Brakke, K.E., & Greenfield, P.M. (1999). Strategies used to combine seriated cups by chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscu*s), and capuchins (*Cebus apella*). *Journal of Comparative Psychology, 113*(2), 137-148.

Kaas, J.H., Jain, N., & Hui-Xin, Q. (2001). The Organization of the somatosensory system in primates. In: R.J. Nelson (ed.), The Somatosensory System: Deciphering the Brain’s Own Body Image (pp. 1-25). Boca Raton: CRC Press.

Lemelin, P., & Schmitt, D. (2016). On primitiveness, prehensility, and opposability of the primate hand: The contributions of Frederic Wood Jones and John Russell Napier. In: T.L. Kivell, P. Lemelin, B.G. Richmond, & D. Schmitt (eds.), The Evolution of the Primate Hand: Anatomical, Developmental, Functional, and Paleontological Evidence (pp. 5-13). New York: Springer.

Kuypers, H.G.J.M. (1981). Anatomy of the Descending Pathways. *Comprehensive Physiology, 597–666*.

Lansmeer, J.M.F. (1993). Evolution and the hand. Adaptations in the hands of cercopithecoids and callitrichids. In: H. Preuschoft & D.J. Chivers (eds.), Hands of Primates (pp. 191-198). New York: Springer-Verlag.

Lederman, S.J., & Klatzky, R.L. (1987). Hand movements: a window into haptic object recognition. *Cognitive Psychology, 19*, 342-368.

Lederman, S.J., & Klatzky, R.L. (1993). Extracting object properties through haptic exploration. *Acta Psychologica, 84*, 29-40.

Lemon, R.N. (1993). Cortical control of the hand. *Experimental Physiology, 78*, 263-301.

McGrew, W.C., & Marchant, L.F. (1997). On the other hand: current issues in and meta-analysis of the behavioral laterality of hand function in non-human primates. *Yearbook of Physical Anthropology, 40*, 201-232.

Masi, S., Meulman, E.J.M., San-Galli, A., Aubaile, F., Krief, S., Todd, A., Breuer, T., & Pouydebat, E. (2015, August). Food manipulation and hand preference in wild western gorillas. In D. Fragaszy and V. Truppa (Chairs), *Contemporary studies of manual function: methodological and taxonomical diversity*. Symposium conducted at the meeting of the European Federation of Primatology, Rome, Italy.

MacFarlane, N.B.W., & Graziano, M.S.A.. (2009). Diversity of grip in *Macaca mulatta*. *Experimental Brain Research, 197*, 255-268.

MacLean, E.L., Matthews, L.J., Hare, B.A., Nunn, C.L., Anderson, R.C., Aureli, F., Brannon, E.M., Call, J., Drea, C.M., Emery, N.J., Haun, D.B.M., Herrmann, E., Jacobs, L.F., Platt, M.L., Rosati, A.G., Sandel, A.A., Schroepfer, K.K., Seed, A.M., Tan, J., van Schaik, C.P., & Wobber, V. (2012). How does cognition evolve? Phylogenetic comparative psychology. *Animal Cognition, 15*, 223-238.

MacNeilage, P.F., Studdert-Kennedy, M.G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioral and Brain Sciences, 10*, 247-263.

Maier, W. 1993. Adaptations in the hands of cercopithecoids and callitrichids. In: Preuschoft, H., Chivers, D.J. (eds.), Hands of primates. Springer-Verlag, New York, pp. 191-198.

Marzke, M.W. (2013). Tool making, hand morphology and fossil hominins. *Philosphical Transactions of the Royal Society B, 368*(1630).

Marzke, M.W., Marchant, L.F., McGrew, W.C., & Reece, S.P. (2014). Grips and hand movements of chimpanzees during Feeding in Mahale Mountains National Park, Tanzania. *American Journal of Physical Anthropology, 156*(3), 317-326.

Muir, R.B., & Lemon, R.N. (1983). Corticospinal neurons with a special role in precision grip. *Brain Research, 261*(2), 312-316.

Napier, J.R. (1956). The prehensile movements of the human hand. *The Journal of Joint and Bone Surgery, 38B*(4), 902-913.

Napier, J. R. (1961). Prehensility and opposability in the hands of primates. *Symposia of the Zoological Society of London, 5*, 115-132.

Napier, J.R. (1980). *Hands.* Princeton: Princeton University Press.

Napier, J.R., & Napier, P.H. (1967). *A handbook of living primates*. London: Academic Press.

Newell, K. M., Scully, D. M., McDonald, P. V., & Baillargeon, R. (1989). Task constraints and infant grip configurations. *Developmental Psychobiology, 22,* 817-832.

Newell, K.M., Scully, D.M., Tenenbaum, F., & Hardiman, S. (1989). Body scale and the development of prehension. *Developmental Psychobiology, 22,* 1-14.

Padberg, J., Franca, J.G., Cooke, D.F., Soares, J.G., Rosa, M.G., Fiorani, M., Gattass, R., & Krubitzer, L. (2007). Parallel evolution of cortical areas involved in skilled hand use. *Journal of Neuroscience*, *27*(38), 10106-10115.

Parker, S.T., and Gibson, K.R. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *Journal of Human Evolution, 6,* 623-241.

Pehoski, C. (1992). Central nervous system control of precision movements of the hand. In J. Case-Smith and C. Pehoski (eds.), *Development of Hand Skills in the Child* (pp. 1-11). Bethesda: American Occupational Therapy Association, Inc.

Phillips, C.G., & Porter, R. (1977). Corticospinal neurons: their role in movement. *Monographs of the Physiological Society*, (34), 5-12.

Phillips, K.A., & Sherwood, C.C. (2005). Primary motor cortex asymmetry is correlated with handed in capuchin monkeys (*Cebus apella*). *Behavioral Neuroscience, 119*(6), 1701-1704.

Pouydebat, E., Gorce, P., Coppens, Y., & Bels, V. (2009). Biomechanical study of grasping according to the volume of the objects: human versus non-human primates. *Journal of Biomechanics*, *42*, 266-272.

Pouydebat, E., Borel, A., Chotard, H, & Fragaszy, D. (2014). Hand preference in fast-moving versus slow-moving actions in capuchin, *Sapajus spp.*, and squirrel monkeys, *Saimiri sciureus, Animal Behaviour*, *97*, 113-123.

Proctor, D. & Brosnan, S.F. (2013). Visual processing speed in capuchin monkeys (*Cebus apella*) and rhesus macaques (*Macaca mulatta*). *International Journal of Comparative Psychology, 26*, 166-175.

Sacrey, L.R., Alaverdashvili, M., & Wishaw, I.Q. (2009). Similar hand shaping in reaching-for-food (skilled reaching) in rats and humans provides evidence of homology in release, collection, and manipulation movements. *Behavioural Brain Research, 204*, 153–161.

Schieber, M.H. (1990). How might the motor cortex individuate movements? *Trends in Neuroscience, 13*(11), 440-445.

Schieber, M. (1991). Individuated finger movements of rhesus monkeys: a means of quantifying the independence of the digits. *Journal of Neurophysiology, 65*, 1381-1391.

Spinozzi G., Truppa, V., and Lagana, T. (2004). Grasping behavior in tufted capuchin monkeys (*Cebus apella*): grip types and manual laterality for picking up a small food item. *American Journal of Physical Anthropology*, *125*, 30-41.

Spinozzi, G., Lagana, T., & Truppa, V. (2007). Hand use by tufted capuchins (*Cebus apella*) to extract a small food item from a tube: digit movements, hand preference, and performance. *American Journal of Primatology, 69*, 336-352.

Turvery, M.T. (1996). Active touch. *American Psychologist, 51*, 1134-1152.

Turvey, M.T., Shockley, K., and Carello, C. (1999). Affordance, proper function, and the physical basis of perceived heaviness. *Cognition, 73*, B17-B26.

Verderane, M.P., Izar, P., Visalberghi, E., & Fragaszy, D.M. (2013). Socioecology of wild bearded capuchin Monkeys (Sapajus libidinosus): an analysis of social relationships among female primates that use tools in feeding. *Behaviour, 150*, 659-689.

Visalberghi, E., & Neel, C. (2003). Tufted capuchins (*Cebus apella*) use of weight and sound to choose between full and empty nuts. *Ecological Psychology, 15*, 215-228.

Warren, J.M. (1980). Handedness and laterality in humans and other animals. *Physiological Psychology, 8*(3), 351-359.

Welles, J.F. (1972). The anthropoid hand: A comparative study of prehension. Doctoral Dissertation, Tulane University.

Welles, J.F. (1976). A comparative study of manual prehension in anthropoids. *Säugetierlaundliche Mitteilungen, 24*, 26–38.

Wood Jones, F. (1916). *Arboreal Man*. New York: Longmans, Green and Company.

TABLES

Table 1. *Hand Indices by Napier and Napier (1976)*

GENUS:	*Saimiri*	*Cebus*	*Macaca*	*Pan*	*Homo*
Hand Length Index	28	27	27	30	(highly variable)
(Total length of hand x 100)					
(humerus + radius + hand length)					
Phalangeal Index	54	52	49	50	49
(Phalangeal Length x 100)					
Hand Length					
Thumb Length Index	46	50	39	33	(highly variable)
(Thumb length x 100)					
Total Hand Length					
Hand to Thumb Ratio	0.61	0.54	0.69	0.91	(highly variable)
Hand Length Index					
Thumb Length Index					

Table 2. *Requisites for Classifying Simple and Compound Grips*

No. of Hands/Feet/Mouth/Tail	No. of Object(s)	No. of Simple Grip Types	Simple or Compound
1	Any	1	simple (unimanual)
2	Any	1	simple (bimanual)
1	>1	≥1	Compound
1	1	>1	Compound
2	1	>1	compound (bimanual) – aspect of control and hand position

Table 3. *Compound Grip Experimental Ethogram*

Action Group	**Action Group Type**	**Action**	**Action Type**	**Description**
Hand Use	mutually exclusive, exhaustive	Right Hand	Initial State Event	Hand use was determined at the beginning of each trial. Either a left or right hand could be used, no modifiers.
		Left Hand	State Event	
Original Fist/ Wrist/ Forearm Position	start-stop	Pronated	Point Event	Original Fist/Wrist/Forearm Position was coded using Figure 14 at the start of each trial (frame 1). No modifiers.
		Neutral	Point Event	
		Supinated	Point Event	
		Position Unknown	Point Event	
Fist/ Wrist/ Forearm Rotation	mutually exclusive, exhaustive	No Rotation	Initial State Event	Fist/Wrist/Forearm Rotation was coded using Figure 14 for every frame, relative to the previous frame. No modifiers.
		Pronating	State Event	
		Supinating	State Event	
		Rotation Unknown	State Event	
Simple Grips	start-stop	Precision Grip	Point Event	Every simple grip performed in each frame was coded: precision, power, palmar, or unknown. If more than one simple grip occurred, a mandatory modifier was coded to indicate the presence of a compound grip. Additionally, any digits that could be seen forming these grips were coded.
		Power Grip	Point Event	
		Palmar Grip	Point Event	
		Simple Grip Unknown	Point Event	
Object Drop	start-stop	Object 1 Drops	Point Event	When an object was seen in the tube, not in control of the hand, it was coded.
		Object 2 Drops	Point Event	
		Object 3 Drops	Point Event	
		Object 4 Drops	Point Event	
Tube Use	mutually exclusive, exhaustive	Tube Contact	State Event	Any contact (or lackthereof) of the hand or object with the tube was coded.
		No tube contact	Initial State Event	
		Tube Use Unknown	State Event	
Independent Digit Movement	start-stop	D1	Point Event	Any digits that were seen moving independently, or even in tandem with another finger, as well as their positions (adducted, abducted, extended, flexed) were coded.
		D2	Point Event	
		D3	Point Event	
		D4	Point Event	
		D5	Point Event	

Table 4. *Trials Completed Per Condition*

	One Ball (B)	Two Balls (BB)	Three Balls (BBB)	Four Balls (BBBB)
Nick	10	10	10	10
Mickey	10	10	5	0
Xenon	10	10	10	10
Chris	10	10	0	0
Leo	10	10	8	0

Table 5. *Simple grip combinations that constitute compound grips for the two, three, and four ball conditions. The order of simple grips in each combination is arbitrary.*

	Compound Grip Combination	**Compound Grip Frequency**	**% all Compound Grips**	**% all Compound Grips in Condition**
BB	precision/power	50	3.35%	11.7%
	precision/unknown	125	8.39%	29.1%
	palmar/unknown	13	0.87%	3.0%
	unknown/unknown	232	15.57%	54.1%
	palmar/precision	6	0.40%	1.4%
	power/unknown	3	0.20%	0.7%
Total		**429**	**28.78%**	**100.0%**
BBB	power/precision/palmar	5	0.34%	0.7%
	power/precision/unknown	167	11.21%	23.5%
	unknown/unknown/precision	173	11.61%	24.4%
	unknown/unknown/unknown	262	17.58%	36.9%
	power/unknown/unknown	80	5.37%	11.3%
	palmar/unknown/precision	10	0.67%	1.4%
	palmar/unknown/unknown	11	0.74%	1.5%
	power/power/precision	1	0.07%	0.1%
	power/palmar/unknown	1	0.07%	0.1%
Total		**710**	**47.64%**	**100.0%**
BBBB	precision/unknown/unknown/unknown	67	4.50%	17.0%
	palmar/unknown/unknown/unknown	10	0.67%	2.5%
	power/unknown/unknown/unknown	5	0.34%	1.3%
	unknown/unknown/unknown/unknown	150	10.06%	38.1%
	palmar/precision/unknown/unknown	9	0.60%	2.3%
	palmar/precision/power/unknown	89	5.97%	22.6%
	power/power/precision/palmar	15	1.01%	3.8%
	power/precision/unknown/unknown	43	2.89%	10.9%
	power/power/unknown/unknown	6	0.40%	1.5%
Total		**394**	**26.44%**	**100.0%**
Total		**1490.4**		

Table 6. *All attempts, successful and unsuccessful, by each subject, across condition.*

SUBJECT	CONDITION	No. Trials Completed	Total Attempts	Successes	Failures	Success Ratio (%)
Chris	B	10	10	10	0	100
	BB	10	13	10	3	77
	BBB	0	10	0	10	0
	BBBB	0	0	–	–	–
Leo	B	10	11	10	1	91
	BB	10	21	10	11	48
	BBB	8	23	8	15	35
	BBBB	0	0	–	–	–
Mickey	B	10	11	10	1	91
	BB	10	24	10	14	42
	BBB	5	17	5	12	29
	BBBB	0	0	–	–	–
Nick	B	10	10	10	0	100
	BB	10	12	10	2	83
	BBB	10	16	10	6	63
	BBBB	10	20	10	10	50
Xenon	B	10	10	10	0	100
	BB	10	14	10	4	71
	BBB	10	20	10	10	50
	BBBB	10	18	10	8	56
AVERAGE	B	10	10	10	0	96
	BB	10	17	10	7	64
	BBB	7	17	7	11	35
	BBBB	4	8	10	9	53

Table 7. *Tukey's Post-Hoc Test of Between Condition Difficulty, All Attempts* (α=.05)

	Diff.	Lower	Upper	P Value
BB-B	-0.331	-0.614	-0.049	0.021*
BBB-B	-0.494	-0.793	-0.194	0.002*
BBBB-B	-0.408	-0.782	-0.034	0.031*
BBB-BB	-0.162	-0.462	0.137	0.410
BBBB-BB	-0.077	-0.451	0.297	0.927
BBBB-BBB	0.086	-0.301	0.473	0.911

Table 8. *Welch 2-Sample T-Test* ($\alpha = 0.05/3 = 0.1667$)

	t	dF	95% confidence interval		mean of X	mean of Y	P Value
B-BB	3.944	4.601	0.110	0.553	0.964	0.632	0.013*
BB-BBB	1.229	6.052	-0.160	0.485	0.632	0.485	0.265
BBB-BBBB	-0.820	3.000	-0.418	0.247	0.470	0.556	0.472

Table 9. *Frequency of fist/wrist/forearm rotations, across all subjects, per condition.*

Condition	Sample Size	Pronations	Supinations	No Rotations	Unknown Rotations	Total
B	5	278	140	406	4	828
BB	5	622	396	656	34	1708
BBB	4	890	708	798	30	2426
BBBB	2	750	656	720	16	2142

Condition	Sample Size	% Pronations	% Supinations	% No Rotations
B	5	34	17	49
BB	5	36	23	38
BBB	4	37	29	33
BBBB	2	35	31	34

Condition	Average Pronations	Average Supinations	Average No Rotations	Average Rotations Unknown
B	11.08	5.6	16.24	0.16
BB	24.88	15.84	26.24	1.36
BBB	43.9	36	40	1.5
BBBB	75	65.6	72	1.6

Table 10. *ANOVAs and Tukey's Post-Hoc Tests of Fist/Wrist/Forearm Rotations* (α=.05)

ANOVA (Pronations as a function of Condition)

	dF	Sum of Squares	Mean Squares	F Value	p	
Condition	3.000	33517.000	11172.000	55.000	0.000	*significant
Residuals	76.000	15438.000	203.000			

Tukey's Post-Hoc (Pronations as a function of Condition)

	diff	Lower	upper	p	
BB-B	13.800	3.211	24.389	0.005	*significant
BBB-B	32.820	21.588	44.052	0.000	*significant
BBBB-B	63.920	49.912	77.928	0.000	*significant
BBB-BB	19.020	7.788	30.252	0.000	*significant
BBBB-BB	50.120	36.112	64.128	0.000	*significant
BBBB-BBB	31.100	16.600	45.600	0.000	*significant

ANOVA (Supinations as a function of Condition)

	dF	Sum of Squares	Mean Squares	F Value	p	
Condition	3.000	30313.000	10104.000	35.810	0.007	*significant
Residuals	76.000	21446.000	282.000			

Tukey's Post-Hoc (Pronations as a function of Condition)

	diff	Lower	upper	p	
BB-B	10.240	-2.241	22.721	0.145	
BBB-B	30.400	17.162	43.638	0.000	*significant
BBBB-B	60.000	43.490	76.510	0.000	*significant
BBB-BB	20.160	6.922	33.398	0.001	*significant
BBBB-BB	49.760	33.250	66.270	0.000	*significant
BBBB-BBB	29.600	12.510	46.690	0.000	*significant

Table 11. *Successful and unsuccessful trial duration means, measured in seconds.*

		Chris	**Leo**	**Nick**	**Mickey**	**Xenon**	**Total Avg**
B	Successful Trials	0.84	0.47	0.67	0.49	0.51	**0.60**
	Unsuccessful Trials	None	0.20	None	0.30	None	**0.25**
BB	Successful Trials	1.96	0.88	1.81	0.89	1.58	**1.42**
	Unsuccessful Trials	3.53	1.45	3.24	0.79	0.91	**1.98**
BBB	Successful Trials	None	2.21	2.86	1.47	1.95	**2.12**
	Unsuccessful Trials	None	1.98	4.42	1.74	3.14	**2.82**
BBBB	Successful Trials	None	None	4.86	None	3.14	**4.00**
	Unsuccessful Trials	None	None	4.27	None	4.23	**4.25**

Table 12. *Percentage of right hand use.*

Nick	**B**	**BB**	**BBB**	**BBBB**	**%**	**% Overall**
1	R	R	R	R	100	100% Use of Right Hand
2	R	R	R	R	100	
3	R	R	R	R	100	
4	R	R	R	R	100	
5	R	R	R	R	100	
%	100	100	100	100		
Chris	**B**	**BB**	**BBB**	**BBBB**	**%**	
1	L	R			50	60% Use of Right Hand
2	L	R			50	
3	R	R			100	
4	L	L			0	
5	R	R			100	
%	40	80				
Leo	**B**	**BB**	**BBB**	**BBBB**	**%**	
1	R	R	L		67	53% Use of Right Hand
2	R	R	R		100	
3	L	R	L		33	
4	R	L	L		33	
5	L	L	R		33	
%	60	60	40			
Mickey	**B**	**BB**	**BBB**	**BBBB**	**%**	
1	L	L	R		33	67% Use of Right Hand
2	L	R	R		67	
3	R	R	R		100	
4	L	R	R		67	
5	R	R	L		67	
%	40	20	80			
Xenon	**B**	**BB**	**BBB**	**BBBB**	**%**	
1	L	R	L	L	25	25% Use of Right Hand
2	L	L	R	L	25	
3	L	L	R	L	25	
4	L	L	L	L	0	
5	L	L	R	R	50	
%	0	20	60	20		

Table 13. *Sapajus libidinosus group members in Fazenda Boa Vista, May-July 2014.*

Individual Name	**Sex**	**Age at Beginning of Data Collection**
Amarelinha	f	UA
Cachaca	m	2 years, 2 months
Catu	m	7 years, 3 months
Cenoura	u	5 months
Chani	f	3 years, 7 months
Chuchu	f	UA
Coco	m	4 years, 10 months
Dita	f	UA
Divina	f	1 year, 6 months
Donzela	f	1 year, 4 months
Doree	f	6 years, 6 months
Jatoba	m	UA
Mansinho	m	UA
Pacoca	f	5 years, 4 months
Pamonha	f	5 years, 4 months
Patricia	f	1 year, 4 months
Piacava	f	UA
Presente	m	3 years, 3 months
Thais	f	3 years, 3 months
Teimoso	m	UA
Teninha	f	UA
Titia	f	1 year, 4 months
Tomate	m	7 years, 5 months

Table 14. *Frequency of compound grips per food item.*

Food Item Combination	Compound Grip Frequency
Tucum + Tucum	117
Naja + Naja	21
Naja + Naja + Naja	12
Piassava + Piassava	8
Unknown	7
Naja + Piassava	4
Piassava + Tucum	4
Tecum + Tucum + Tucum	3
Naja + Naja + Piassava	2
Piassava + Piassava + Piassava	2
Naja + Corn	1
Naja + Piassava + Tucum	1
Naja + Tucum	1
Tucum + Tucum + Naja	1
Naja + Naja + Tucum	0
Total	184

FIGURES

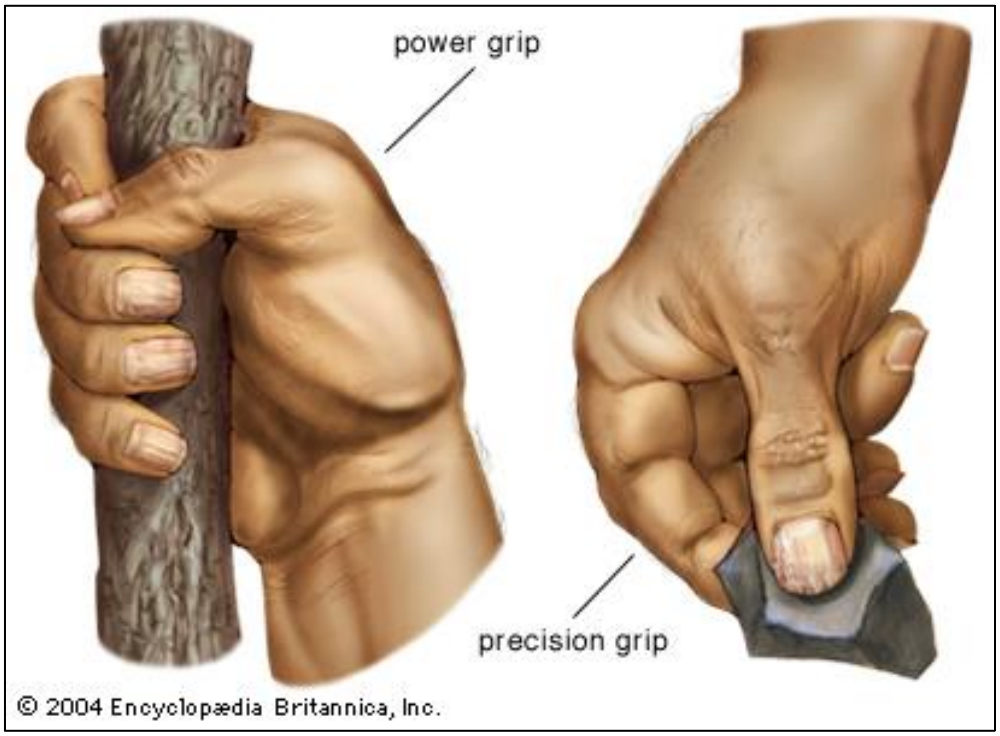


Figure 1. Human power and precision grips. By courtesy of Encyclopedia Britannica, Inc., copyright 2004; used with permission.

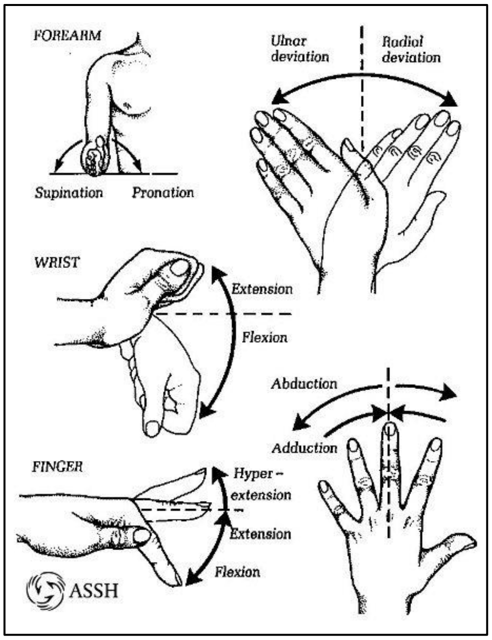


Figure 2. Dynamic movements of the forearm, wrist, and digits. Published with permission from the American Society for Surgery of the Hand.

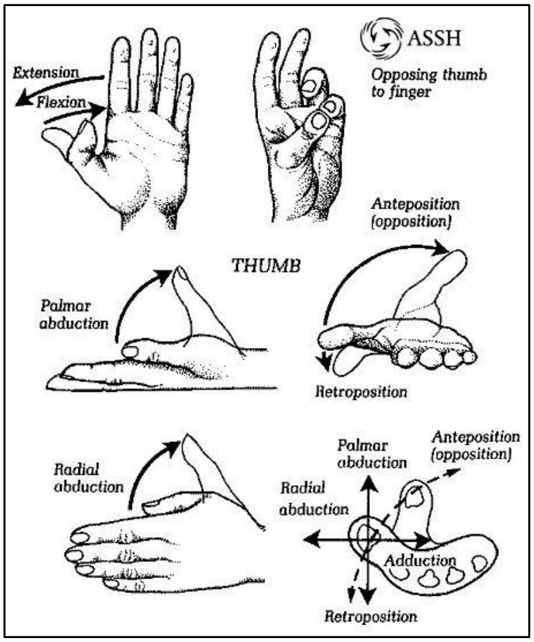


Figure 3. Dynamic movements of the digits and opposition of the thumb. Published with permission from the American Society for Surgery of the Hand.

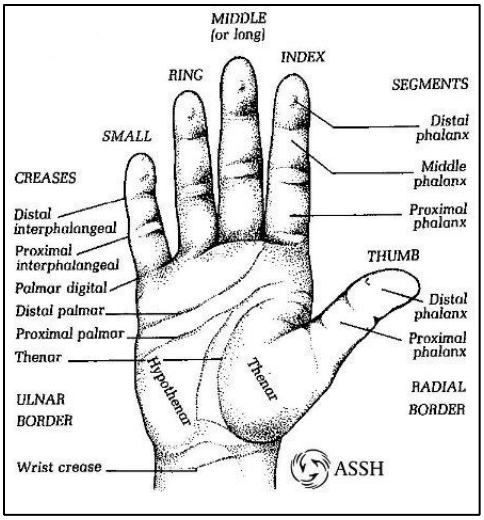


Figure 4. Human hand area and digit segments. Published with permission from the American Society for Surgery of the Hand.

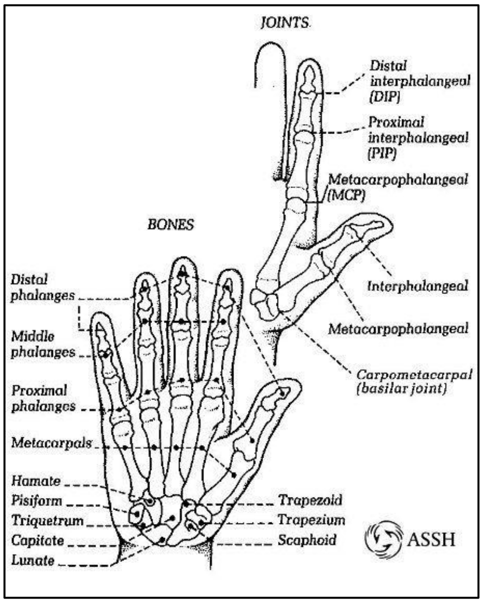


Figure 5. Bones and joints of the human hand, fingers, and wrist. Published with permission from the American Society for Surgery of the Hand.

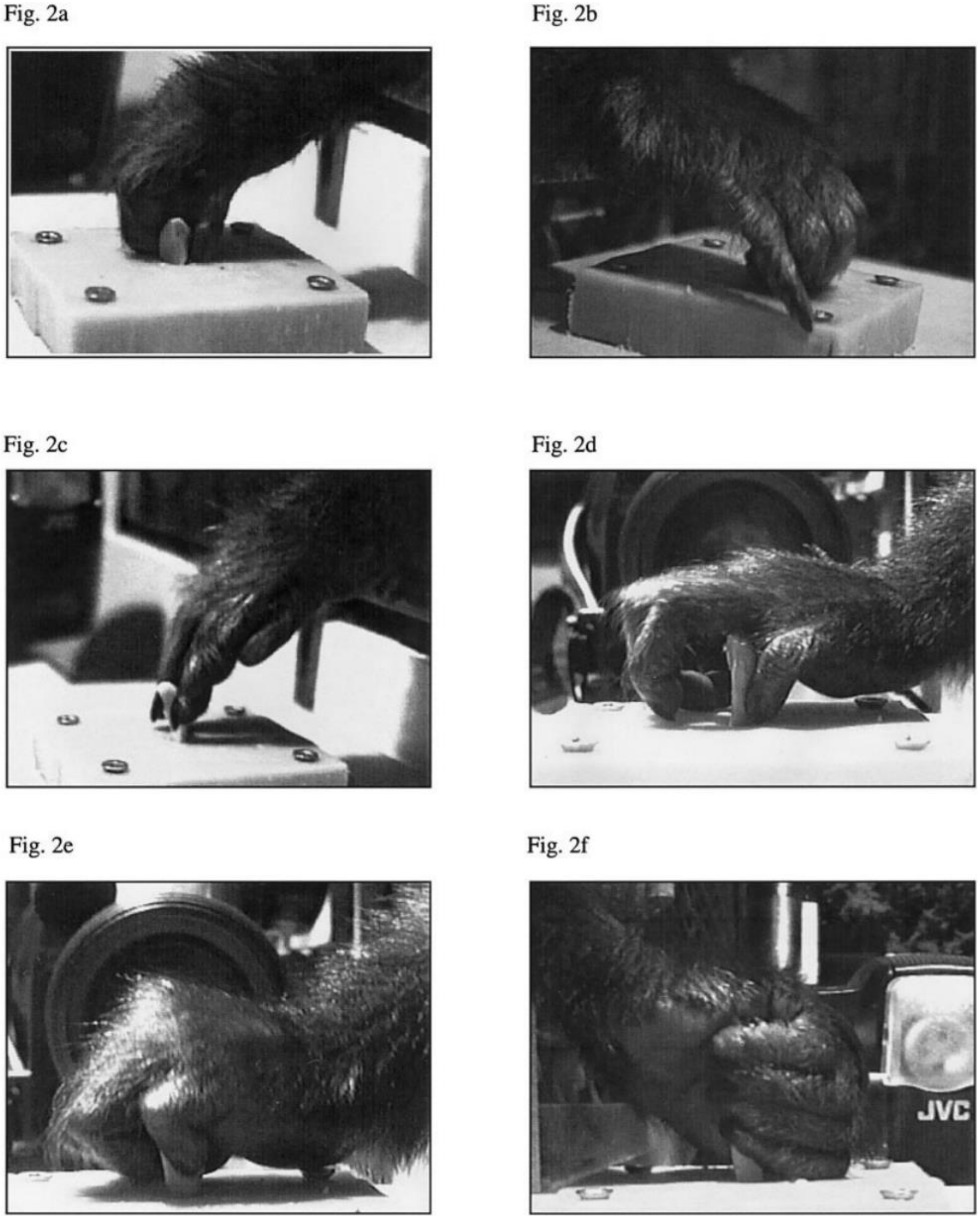


Fig. 2a

Fig. 2b

Fig. 2c

Fig. 2d

Fig. 2e

Fig. 2f

Figure 6. Capuchin monkey grips (Spinozzi et al., 2004). Used with permission.

Figure 7. Comparison of primate hands, including relative size and thumb position. Image used with permission from Cambridge University Press, originally printed in Schultz, 1956.

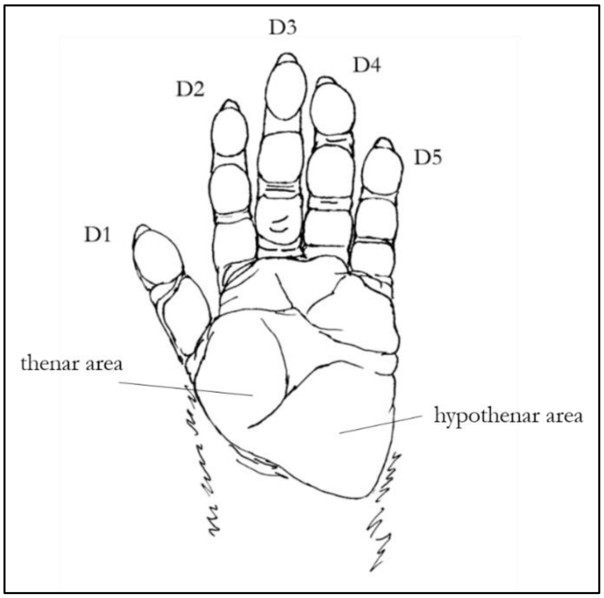
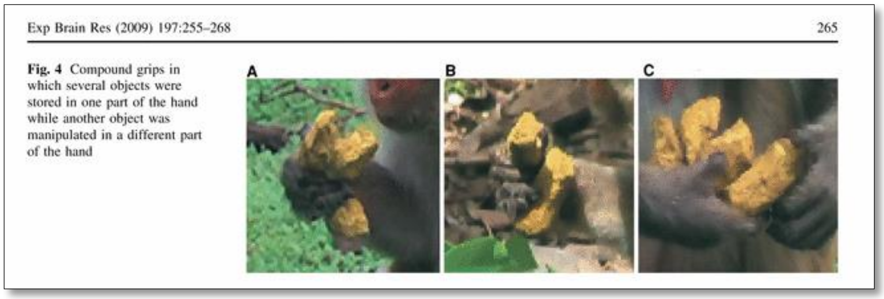


Figure 8. Tufted capuchin (*Sapajus spp*) hand diagram. Sketch by Kirsten Cook.



Exp Brain Res (2009) 197:255–268 265

Fig. 4 Compound grips in which several objects were stored in one part of the hand while another object was manipulated in a different part of the hand

Figure 9. Original documentation of compound grip in Cayo Santiago rhesus macaques by MacFarlane and Graziano, 2009. Image used with permission of Springer.

Figure 10. Chimpanzee holding fruits with compound grips in each hand, and simple bimanual grips in each foot. Photo obtained via open source social media, courtesy of GRASP-UNEP.

Figure 11. Western lowland gorilla using compound grips to hold multiple tokens. Photos used with permission from Lincoln Park Zoo, Chicago, IL, USA.

Figure 12. Testing apparatus and balls to be deposited.

Figure 13. Testing set-up at Jungle Friends Primate Sanctuary in Gainesville, Florida

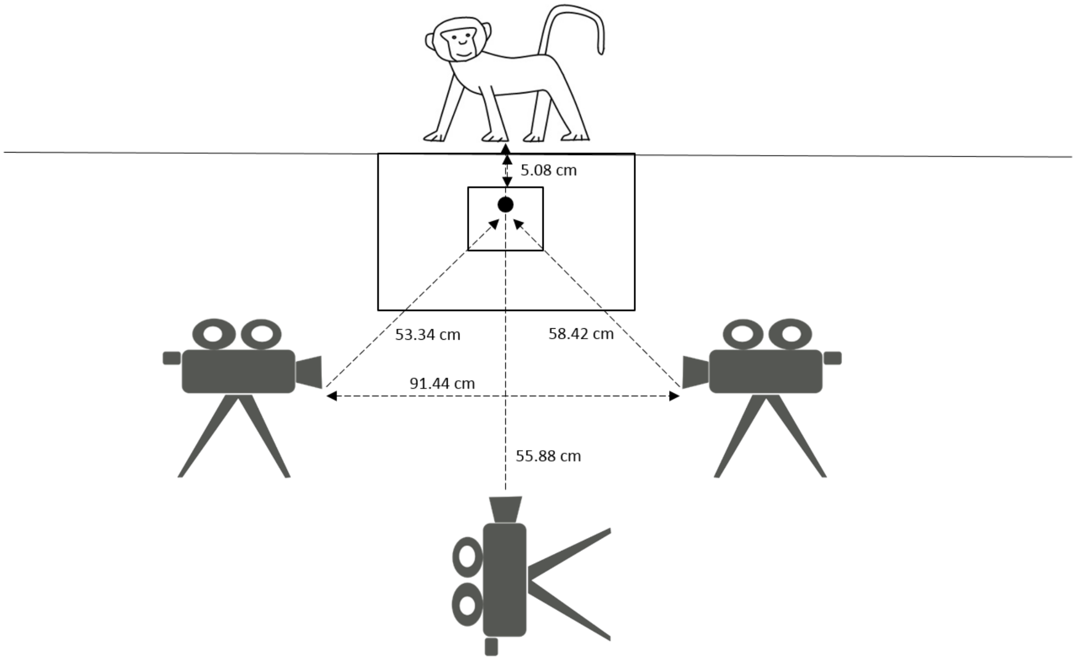


Figure 14. A diagram of the experimental set-up.

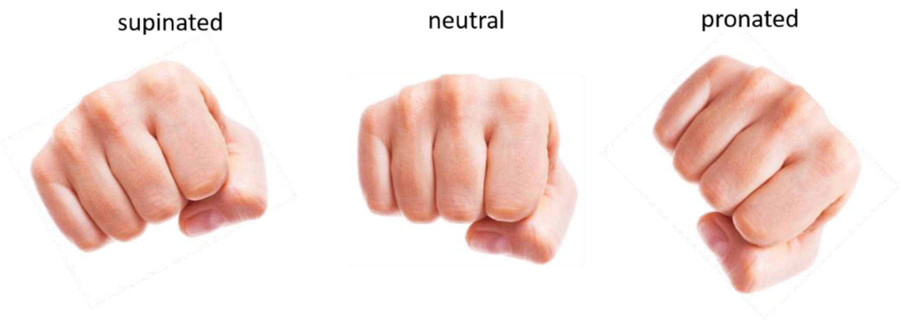


Figure 15. Ethogram reference for coding fist/wrist/forearm position and rotation.

Figure 16. Chris deposits one ball, while storing another, assisted by finger and object contact with the tube.

Figure 17. Nick holds four balls in one hand. Depositing them one at a time, while storing the other three, constitutes a compound grip.

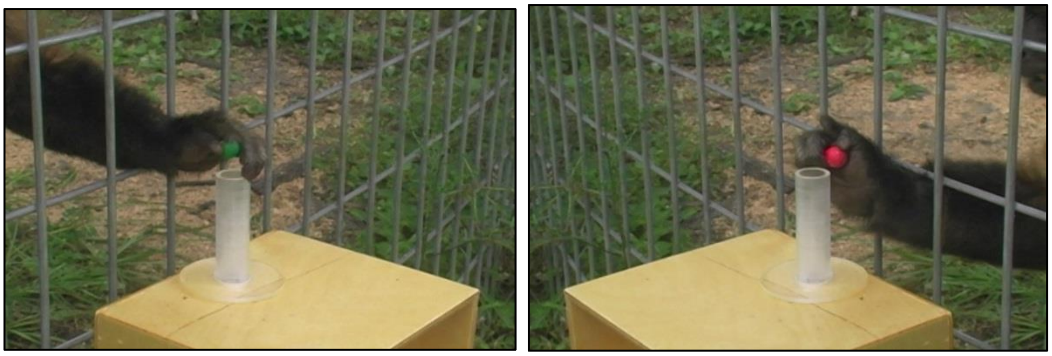


Figure 18 and Figure 19. Leo lacks the medial and distal end of his second digits, but is still able to perform both power and precision grips with the use of this thumb, palm, and the lateral part of his third digit.

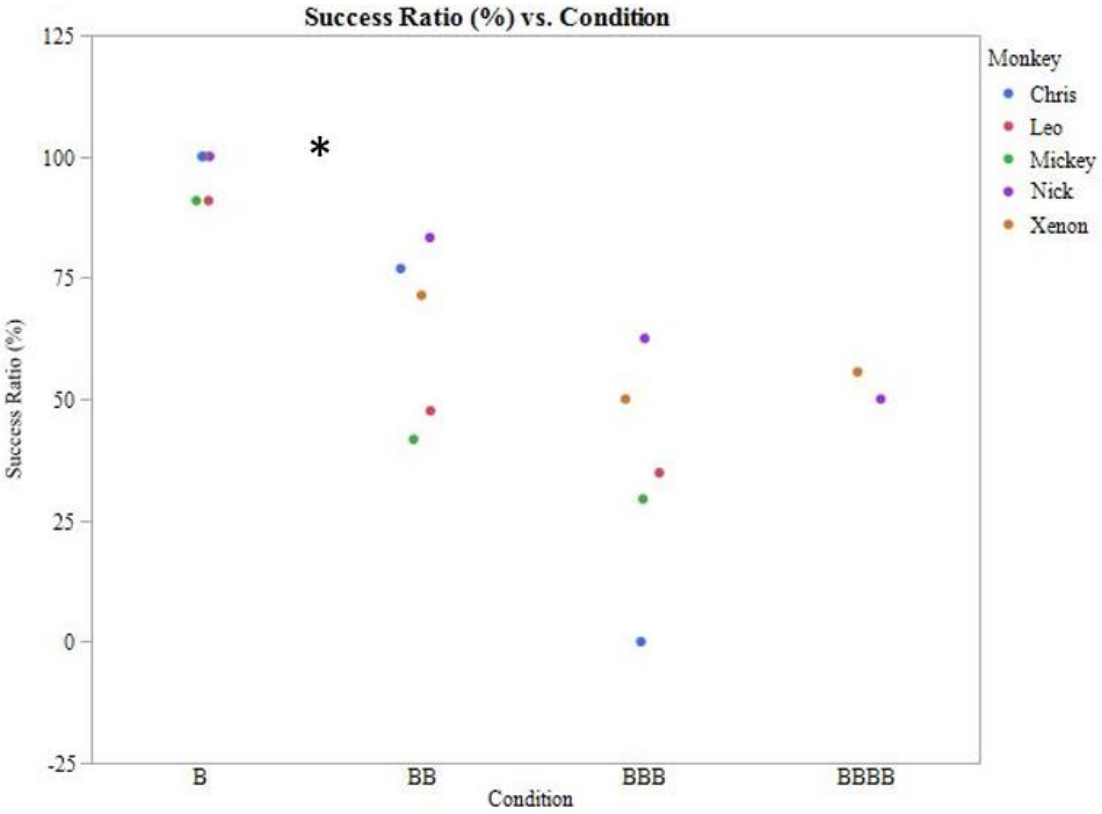
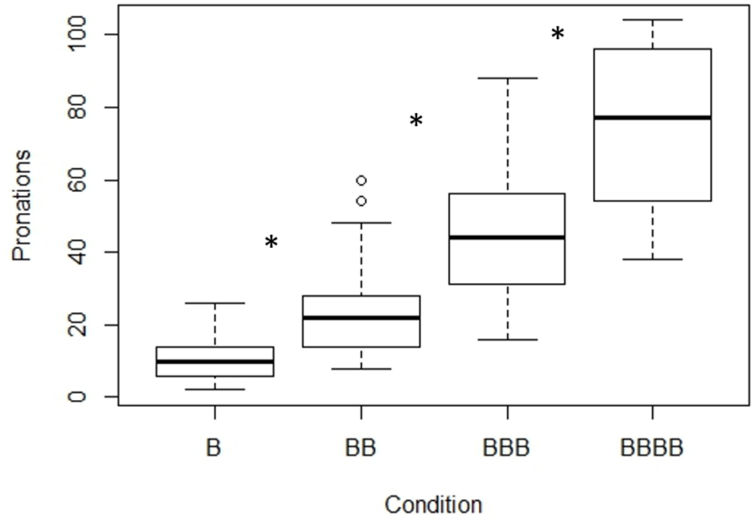
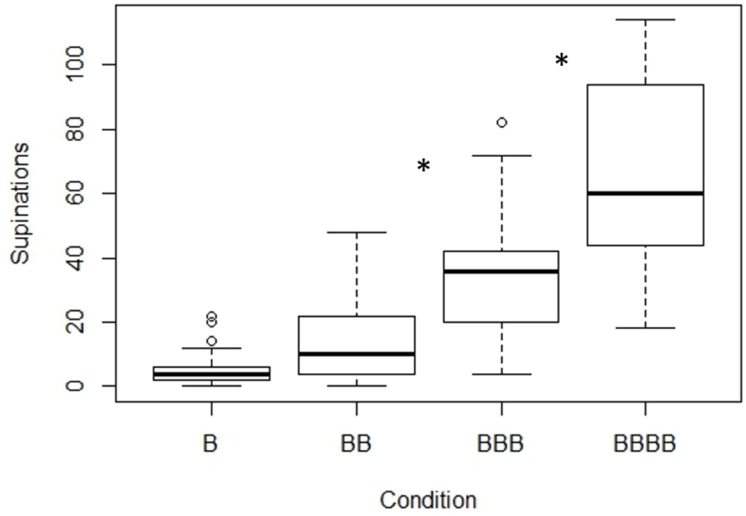


Figure 20. A scatter-plot which demonstrates the successful completion of each condition by each subject. Monkeys Mickey, Leo, and Chris did not complete all conditions.

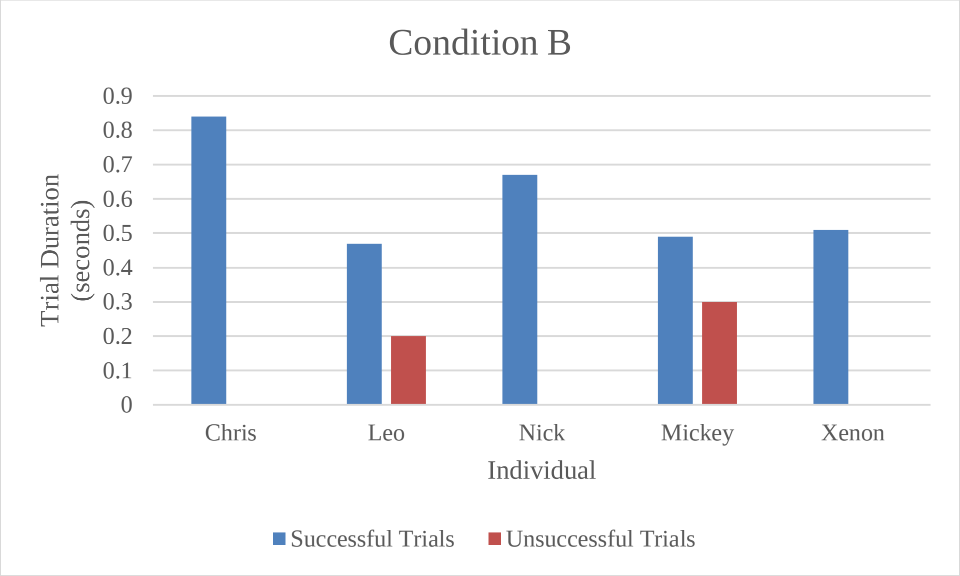


(A)

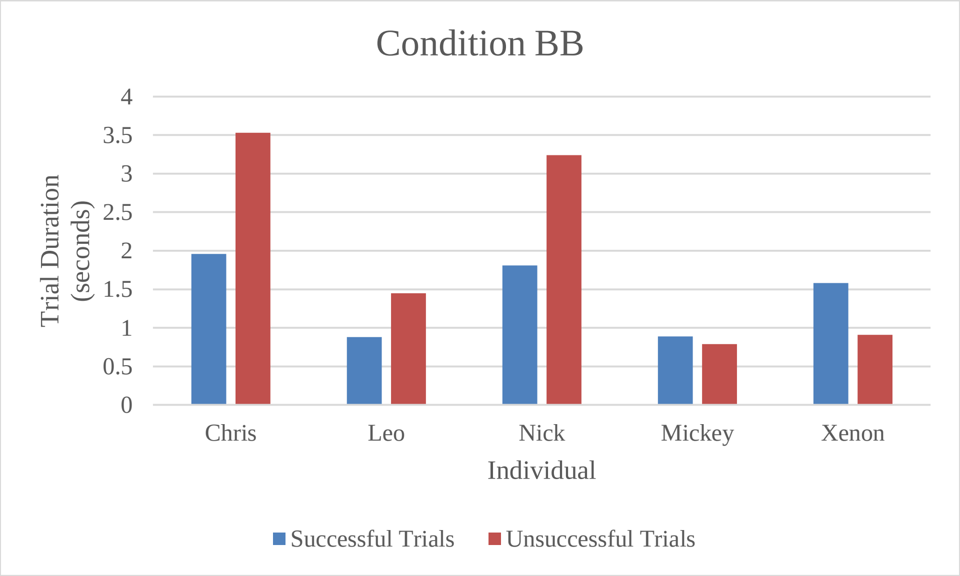


(B)

Figure 21. (A) Box plot depicting the frequency of pronations per condition. All differences are significant. (B) Box plot depicting the frequency of supinations per condition. All differences are significant, except between B and BB.


Condition B
Trial Duration (seconds)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Chris
Leo
Nick
Mickey
Xenon
Individual
Successful Trials
Unsuccessful Trials

(A)


Condition BB
Trial Duration (seconds)
4
3.5
3
2.5
2
1.5
1
0.5
0
Chris
Leo
Nick
Mickey
Xenon
Individual
Successful Trials
Unsuccessful Trials

(B)

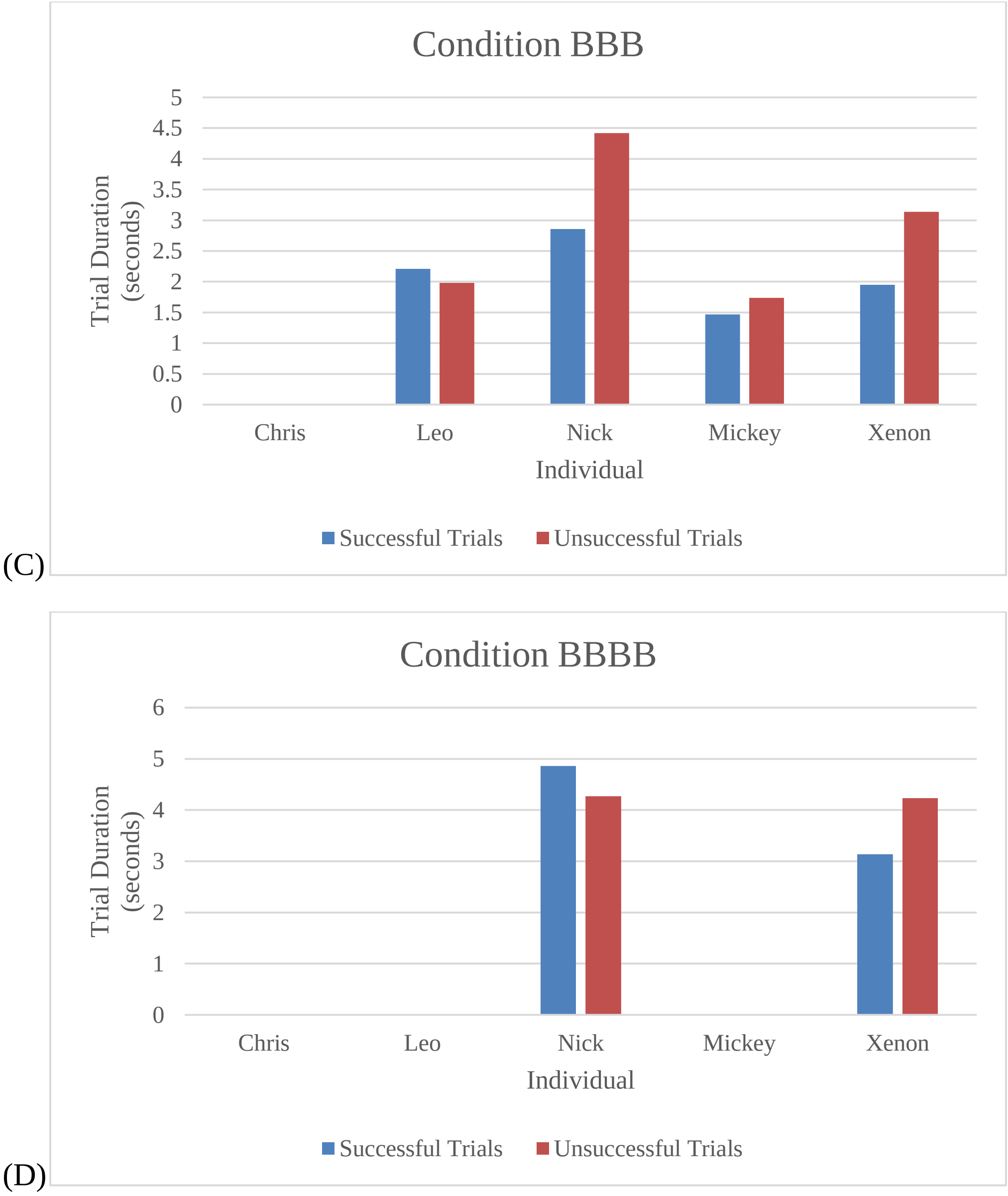


Figure 22. Successful versus unsuccessful trial durations. A time of “0” indicates that the individual monkey did not attempt and/or complete the condition.

Figure 23. The field site in Fazenda Boa Vista lies in the southeast of the state of Piaui, in northeastern Brazil. Image used with permission from Howard and colleagues (2015).

Figure 24, 25, and 26. Comparison of Piassava (large nut), tucum (medium-sized nut), and naja (small nut).

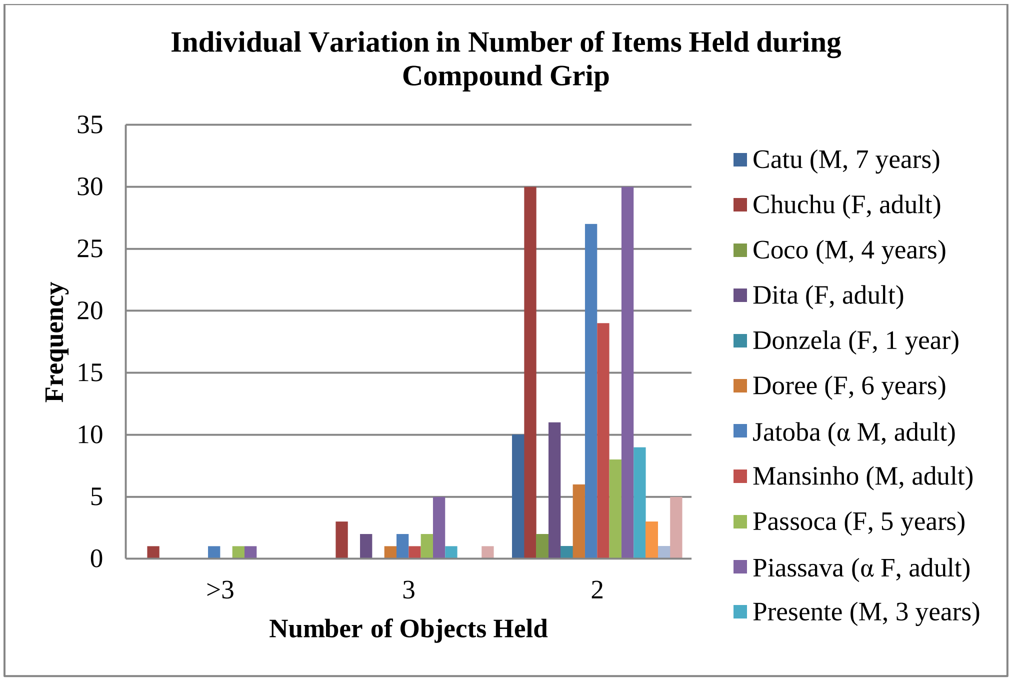


Figure 27. Frequency of number of food items gripped, per individual.

Figure 28. Catu performs a compound grip, but also uses his arm to clutch addition nuts to his body.

Figures 29 and 30. Wild capuchin monkeys at Fazenda Boa Vista, perform compound grips.

APPENDIX I

LITERATURE REVIEW

Comparative understanding of primate somatosensory and motor systems is an area of ongoing research which is hindered by the lack of clarity due to species variability (Kaas et al., 2001). To the author's knowledge, little research has been done on how other more specific features of objects are gleaned and internalized in the non-human primate brain.

Tactile stimuli are perceived via kinesthetic feedback from the somatosensory system. Primates have exceedingly haptically-sensitive hands due to epidermal ridges, Miessner's corpuscles, and overlapping areas of sensitivity on the skin of the hands (Fragaszy et al., 2004). Studies with rhesus macaques show that once again, the anterior intraparietal sulcus is influenced by the shape of the object held, but after contact is made with said object, firing of neurons in the somatosensory cortex increases rapidly until the object is secured in the hand (Castiello, 2005).

Complex manipulative skills are thought to correlate with "higher cognitive function" across primates (Parker & Gibson, 1977). For example, chimpanzees and capuchin monkeys are two genera that forage extractively – no doubt an application of complex manipulation. Parker and Gibson (1977) hypothesize that this is because they are intelligent enough to apply problem-solving tactics. This argument proves to be quite circular, as extractive foraging requires problem solving skills, and problem solving is evidence of “intelligence”. Complex manipulation is synonymous with problem-solving and extractive foraging.