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Effective Tool Choice by Chimpanzees (Pan Troglodytes): Learning and Flexibility

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EFFECTIVE TOOL CHOICE BY CHIMPANZEES (*PAN TROGLODYTES*):
LEARNING AND FLEXIBILITY

by

LINDSAY MAHOVETZ

Under the Direction of William Donald Hopkins, PhD

ABSTRACT

Chimpanzees are proficient tool users and have been shown to use properties of weight and length to select effective tools. Researchers have, however, neglected to investigate whether chimpanzees utilize other tool properties. This study investigated whether chimpanzees use other properties to choose effective tools, how feedback influences their ability to select effective tools, and whether or not chimpanzees are flexible in effective tool selection. Sixty-one chimpanzees, ages 17-52 years, underwent four probing tasks requiring tools of differing physical properties. The results demonstrate that chimpanzees are able to utilize properties of length, surface area, and shape to select effective probing tools. Though exploration of the environment is suggested to facilitate learning and/or performance, it did not have an effect as measured through looking. Together, these results support prior research concerning effective tool selection by chimpanzees, as well as expand current knowledge and understanding of what may underlie effective tool selection.

INDEX WORDS: Tool use, Tool effectiveness, Flexibility, Learning, Optimal foraging, Cognition

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LINDSAY MAHOVETZ

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2015

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DEDICATION

I dedicate this work to my family and friends who have been there by my side through all the ups and downs. It is without them that I would not have had the courage to follow my dreams.

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LIST OF ABBREVIATIONS

AQ	Asymmetry Quotient
FO	Fronto-orbital
GM	Gray Matter
IFG	Inferior Frontal Gyrus
MRI	Magnetic Resonance Imaging
OFT	Optimal Foraging Theory
PFC	Pre-frontal Cortex
PCI	Inferior Precentral Sulcus
ROI	Region of Interest
STN	Subthalamic Nucleus
UTMDACC	University of Texas M. D. Anderson Cancer Center
YNPRC	Yerkes National Primate Research Center

1 INTRODUCTION

1.1 Tool Use

The use of tools is not only a prominent component of the everyday lives of humans, but also for many other animals including non-human primates (chimpanzees: Nishida, 1973; capuchins: Fragaszy, Izar, Visalberghi, Ottoni, & de Oliveira, 2004), otters (Hall, & Schaller, 1964), birds (crows: Hunt, 1996), and even cephalopods (Finn, Tregenza, & Norman, 2009). Previous research has shown that animals exhibit tool use both in the wild and in captivity (c.f., wild crows: Hunt, 1996; captive crows: Powell & Kelly, 1977; captive chimpanzees: Sumita, Kitahara-Frisch, & Norikoshi, 1985; wild chimpanzees: Nishida, 1973; captive capuchins: Westergaard & Fragaszy, 1987; wild capuchins: Fragaszy et al., 2004). For example, wild chimpanzees have an extensive repertoire of uses for tools including, but not limited to, probing, digging, and hunting using sticks, cracking nuts using rocks or other hammer-like objects, and sponging/wadging using leaves. Similarly, captive chimpanzees also show proficiency in many of these same activities, especially probing, nut cracking, and sponging/wadging. (*For catalogues/reviews of tool using behavior see: van Lawick-Goodall, 1968; Beck, 1980; Barber, 2003; Shumaker, Walkup, & Beck, 2011*)

The ability to use tools is an important part of survival (Wagman & Carello, 2001) as tools can be used to retrieve hidden or out of reach resources, to test the depths of bodies of water (c.f., Breuer, Ndoundou-Hockemba, & Fishlock, 2005), and to deter predators (c.f., Boinski, 1988; Fletcher & Leith, 2008). Food is essential to any living being and reaping the energetic and time benefits of food intake over expenditure can be enhanced with tools as they may reduce the costs of exploiting otherwise unattainable resources (Torrence, 1983; Foley, Lee, Widdowson, Knight, & Jonxis, 1991). In order to be adaptive, the tool must not only be

effective for the task, but the act of using tools must also be effective; otherwise, survival would be compromised as costs would outweigh benefits. From this, one can see that tool use requires a certain level of cognitive ability because this skill requires animals to be able to perceive information in the environment and act in ways that do, in fact, reduce costs and increase benefits (Foley et al., 1991).

Given the possible evolutionary advantages of tool use, there are at least two different perspectives that aid in supporting the existence of effective tool use. One perspective is ecologically based keying into the function of tool use and the other is cognitively based keying into the mechanisms underlying tool use. The ecological component utilizes the theory known as the Optimal Foraging Theory (OFT) to provide support for the existence of effective tool use based upon the energy gains facilitated by the use of tools as well as the limiting of costs. The cognitive component utilizes perception, problem solving ability, and cognitive control as support for the development of effective tool use. It must be noted that these two perspectives are not mutually exclusive; both an ecologically driven need for more effective foraging strategies and an increase in cognitive abilities in other domains may have been equally influential in the development of tool use capabilities.

1.2 Optimal Foraging Theory

Efficient exploitation of various aspects of the environment, especially of food resources, is vital to the survival of animals (Emlen, 1966). The OFT posits that the optimal diet should, or will tend to, maximize the ratio of the net gain to the net loss (e.g., Emlen, 1966; MacArthur & Pianka, 1966; Schoener, 1971; Katz, 1974; Wolf, Hainsworth, & Gill, 1975). Typically gains and losses are defined in terms of energy gained and expended, but can also include time and safety (Charnov, 1976; Pyke, Pulliam, & Charnov, 1977). Environmental selection pressures

have led to more efficient foraging behaviors, which maximized the benefits of time and energy. While maximizing energy with food intake can be achieved by consuming few highly nutritious items, or many less nutritious items, maximizing time benefits incorporates the decision to “give up” and forage elsewhere (Charnov, 1976; Pyke et al., 1977). If an individual persists to forage in an area or process foods where the gain is little or nothing at all, the individual may reach a point when it is no longer beneficial to continue. Here, the energy costs would outweigh the gains. If, however, the individual gives up and forages in a new location or finds resources more easily processed, the gains would then outweigh the costs. Thus, deciding to give up is an important component of optimal foraging and its benefits can aid in the survival of the forager.

For optimal foraging, activities should continue as long as the net “gain in time spent per unit food exceeds the loss” (p. 603; MacArthur & Pianka, 1966). Thus, in terms of natural selection, foraging with tools should be an adaptive process because it involves behaviors allowing for efficient and effective foraging, which increase the energetic gains of an individual (Winterhalder, 1981) and therefore its fitness. Indeed, tool use allows the individual to expend energy that is recompensed for by a faster and/or more bountiful reaping (Kurland & Beckerman, 1985), as well as gain access to otherwise unavailable resources. For example, Günther and Boesch (1993) state that, for a population of wild chimpanzees in Taï National Park in Cote d’Ivoire, the ratio of overall energy gains of nut cracking to overall energy expenditure is nine to one. With regard to insect fishing (i.e., ants, termites), chimpanzees forage for insects that are higher in fat content which maximize intake benefits for time spent fishing (O’Malley & Power, 2012). Even though for some chimpanzee populations insect fishing may not result in a sufficient energetic gain (O’Malley & Power, 2012), vital fats, vitamins, and minerals that are

otherwise deficient in a frugivorous diet are obtained. Accordingly, it appears that tool use is an advantageous and adaptive component of optimal foraging.

1.3 Cognition

Tool use requires certain cognitive capacities in order for animals to effectively process the information in the environment and act in ways that increases their survival. The cognitive abilities related to tool use include perception, problem solving, and cognitive control.

1.3.1 *Perception and Problem Solving*

When foraging, an animal must first recognize (i.e., perceive) there is some benefit that is hidden (i.e., nut, honey, ants). As stated by Foley and colleagues (1991):

a diet of 'embedded foods' - foods that are neither visually obvious nor available without considerable time and energy costs associated with processing...require complex cognitive skills...These are linked to perceptual abilities (the recognition that the edible component is within an inedible substrate)... (p. 64; *for more on cognition and embedded food see Gibson, 1986*)

Second, the animal must perceive, or recognize, objects possessing the physical properties allowing them to get that hidden benefit (i.e., rock for nut, stick for honey/ants). The recognition of tool properties may also be considered problem solving since the animal must determine how to get around obstacles placed in front of them. The animal must realize that in order to obtain the hidden food of nuts or out-of-reach food of honey a hammer-type tool or stick is needed to get the respective food item. It must assess how to get that hidden benefit by determining what will effectively get it that benefit and, in doing so, an animal increases its access to a variety of foods (Foley et al., 1991) and consequently survival. If the animal lacks the ability to perceive physical properties of objects and to solve the problem of getting an otherwise unattainable source of energy, its survival may be compromised.

1.3.2 Cognitive Control

Not only must animals recognize what tools are required for a given task, they must also act appropriately by inhibiting certain responses such as choosing an ineffective tool, or impulses such as perseveration in responding when a tool is ineffective. The ability to inhibit responses, which may be ineffective or task-irrelevant, is important to effectively overcome environmental obstacles.

It is widely accepted that the prefrontal cortex (PFC) is associated with inhibitory control (Munakata, Herd, Chatham, Depue, Banich, & O'Reilly, 2011), particularly regions such as the right inferior frontal gyrus (IFG; Munakata et al., 2011; Hofmann, Schmeichel, & Baddeley, 2012). Hofmann and colleagues (2012) describe this type of inhibition as 'active' because the PFC detects goal-inconsistent responses and keeps such responses below the neural activation threshold so that these responses are never carried out. For example, Miyake, Friedman, Emerson, Witzki, and Howerter (2000) had utilized a stop-signal task to measure this. Across 48 trials, the researchers developed a prepotent response in subjects to categorize words as 'animal' or 'nonanimal'. Subjects were then told not to respond when they heard a tone. The proportion of categorization responses for trial tones was indicative of 'active' inhibition since subjects had to inhibit their prepotent categorization response. Using Go-No Go tasks, evidence suggests that one function of the right IFG is response inhibition (Munakata et al., 2011); however, other research suggests that its function involves environment monitoring of task-relevant information (Munakata et al., 2011). Additionally, the IFG projects to the subthalamic nucleus (STN), an area thought to be crucial in inhibiting motor responses until an appropriate motor plan has been determined by the motor control areas of the frontal lobe (Munakata et al., 2011).

Greater activation in the PFC and STN appear to be related to greater inhibitory control (c.f., Chikazoe, Konishi, Asari, Jimura, & Miyashita, 2007; Verbruggen & Logan, 2008). Given the relation between the PFC, specifically the right IFG, and inhibitory control, it is plausible that IFG volume may correlate with effective tool selection. If so, then animals with larger IFG volumes would be better at inhibiting responses of selecting familiar tools or other tools before properly assessing the situation (i.e., task, goal, goal-relevant solution) and make more effective tool selections than those with smaller IFG volumes who are worse at inhibiting those responses. Thus, a greater capacity for cognitive control over response inhibition may be related with IFG volume and would allow for better tool using and problem solving abilities.

1.4 Previous Research

In the act of nut cracking, choosing the best hammer is one of the most crucial factors in successfully obtaining the fruit inside. Several physical properties make one hammer more appropriate than another, such as weight, shape, size, and ease of handling (Schrauf, Call, Fuwa, & Hirata, 2012). A recent study by Schrauf and colleagues (2012) examined whether chimpanzees solely use the property of weight to select hammer tools. Weight acts as a vital factor in ascertaining the impact of a strike, thus relating to the effectiveness of a hammer for nut cracking; generally, the heavier the weight of a hammer, the fewer number of strikes would be needed to crack open a nut. The researchers hypothesized that chimpanzees would relate weight to the corresponding effectiveness of three hammer tools and choose the most effective tool. All but one subject had prior experience with nut cracking. Prior to trials one and four, each tool was given to the subject to ensure the experience of the weight differences. Throughout the study, subjects had the freedom to switch between the three hammers during each trial.

In experiment one, chimpanzees were given three cube hammers. The chimpanzees exhibited no differences in selection between the various hammer weights in their initial choice and overall. Chimpanzees also did not exhibit preferential switching from lighter to heavier or heavier to lighter. One possibility might have been that all tools were functional in that eventually, with enough strikes, the nut would be cracked. It was also suspected that handling comfort might have contributed to the lack of tool preference. A second experiment was then conducted using spheres, which are more hand-form fitting, to address the handling issue. With the spherical hammers, the chimpanzees did not exhibit preferential selection on first choices but did exhibit an overall group preference for the heaviest hammer over the lightest; minimal switching occurred and only after several strikes were made. In experiment three, the weights of the hammers were modified in order to increase the discrepancy in benefit. No selectivity emerged on first choices but the group exhibited an overall preference for the heaviest and middleweight hammers over the light. There was no significant difference between the direction of switching (i.e., lighter to heavier versus heavier to lighter), but several switches were made before using a tool, indicating perception of weight and anticipation of the outcome in relation to the selected weight. It appears that situations maximizing the benefit of particular tool by increasing the cost of switching tools (i.e., transport of the tool across a distance) may aid in making selection preferences more apparent. Based upon these results, the researchers concluded that chimpanzees select hammers based solely on weight; however, one cannot rule out shape and size, which impact handling comfort, previous experience, and the overall benefit of choosing a particular tool as factors also considered during the tool selection process. Tool benefits and switching costs of weighted tools contribute to tool selectivity, and prior experience influences how attentive an individual is to the properties and action proficiency.

Although Schrauf et al.'s study revealed that chimpanzees are capable of distinguishing differences in physical properties of tools, it only examined the property of weight. Wild chimpanzees also use probing tools to fish for insects and dip for honey; they also modify tools prior to and during probing to make them most effective. In choosing the best probing tool, several properties make the probing tool appropriate, including shape, thickness, durability and length. Since chimpanzees are capable of using the property of weight for selecting hammer tools, it is plausible that for probing tools chimpanzees would also use probing-relevant properties, such as length, to extract resources; it is not initially clear, however, whether chimpanzees will choose the most effective tool when the selection of tools includes only un-modifiable tools.

Using a probing task, Sabbatini, Truppa, Hribar, Gambetta, Call, and Visalberghi (2012) examined whether chimpanzees attend to tool features, whether visual feedback affects performance, and whether relational rules are applied when selecting tools. The researchers hypothesized that chimpanzees would learn that length was the effective property, that visual feedback would increase performance, and that relational rules were used during selection. Prior to testing, subjects underwent a familiarization phase in which they were able to experience the first set of tools to be used in the study. Phases one and two of the study included training and transfer trials in which subjects were offered three probing tools (two non-functional, one functional) in order to retrieve a reward from a tube; subjects were given only one selection opportunity per trial.

Phase one was used to determine which tool properties subjects attended to. Training included a set of trials in which the handles (irrelevant feature) of each tool never changed and only the long tool (i.e., length is relevant feature) was functional. For the transfer trials, the

handles were switched so that the functional tool was still the same length but had a different handle than in training. During training, chimpanzees did not exhibit preferences for the longest tool on trial one. During transfer, seven of the eight subjects chose the long (correct) tool above chance over the other two tools. Phase two was used to determine whether relational rules are used when selecting tools. Training included a set of trials in which the handles (irrelevant feature) of each tool changed with each trial and only the long tool (i.e., length is relevant feature) was functional. For the transfer trials, the handles of the three tools were identical, the tube was made longer, and the lengths of the tools were changed such that the tool that used to be the longest (i.e., functional) in phase one training and transfer and phase two training was now the medium length (i.e., nonfunctional) tool. Only one chimpanzee had to undergo phase two training since they had failed phase one transfer. During transfer, all subjects chose the longest (correct) tool above chance over the other two tools both on trial one and overall. Since all subjects inhibited selecting the tool that was the longest in all of phase one and in phase two training, but now was now the medium sized tool, Sabbatini and colleagues concluded that chimpanzees utilize a relational rule of relative length for selecting appropriate probing tools. In both phases, visual feedback did not influence, more specifically increase, performance accuracy. Having access to a transparent tube did not increase selection of the correct tool on trial one in either of the transfer tasks. In order to be successful, subjects had to substitute prepotent responses of selecting tools having handles previously associated with rewards with a new selection strategy of choosing the longest of the available tools.

A common finding in these two studies is that the chimpanzee subjects did not exhibit an initial preference for selecting a particular tool. Since, over time, this preferential selection surfaces, it is plausible that, at some level, learning is occurring. Despite the information these

studies provide, it remains unclear which components of the experimental situation influence how chimpanzees learn about the effectiveness of tools. For example, Schrauf and colleagues (2012) allowed chimpanzees to have access to all tools during all trials, allowing them to switch between tools freely. On the other hand, Sabbatini and colleagues (2012) restricted chimpanzees to one tool choice per trial. Given these two separate testing conditions, one would suspect that rates of learning would differ since it is known that experience plays a significant role in learning about the environment and which actions are afforded. Through exploration of the environment, individuals come to determine or learn what “opportunities for action are afforded [by an object] in a given situation” (p. 191, Wagman & Carello, 2001). This discovery may lead to an increased capability in determining whether or not a given object possesses the properties relevant to a given situation (Wagman & Carello, 2001). Having a more varied experience is an elementary component in formulating flexible knowledge that allows for better and/or faster task/concept acquisition (Sabbatini et al., 2012). Based on the influence of experience in learning, it would appear that differential access to tools would affect learning, and consequently tool effectiveness. For example, those with the ability to access tools freely would learn at a faster rate than those without as a result of the increased potential for unrestricted exploration of multiple tools.

1.5 Research Questions and Hypotheses

Multiple questions remain with respect to the components of effective tool use by chimpanzees. The main question that stands is whether experience plays a role in whether chimpanzees select effective tools and in how they learn about tool effectiveness. It has been said that exploration of the environment creates opportunities for learning (Wagman & Carello, 2001) and that this experience aids in forming flexible knowledge allowing for better, faster

task/concept acquisition (Sabbatini et al., 2012). Considering that experience may play a role in effective tool selection, I hypothesized that chimpanzees would exhibit an overall selection preference for the most effective tool upon repeated exposure to the task. Additionally, this study used opaque PVC pipes (*see methods for more detailed descriptions*) so that knowledge of which tool was needed could only be achieved by looking into the pipe; without looking into the pipe, there was no way of knowing which tool was needed. Thus, I hypothesized that the percentage of trials that subjects looked into the pipe would be positively correlated with the percentage of correct choices for each task.

Also with respect to experience, I investigated whether differential access to tools influenced the rate at which chimpanzees learned about tool effectiveness. As previously stated, differential access may influence performance such that those with the ability to access tools freely would learn at a faster rate than those without, as a result of the increased potential for unrestricted exploration of multiple tools. Thus, considering that differential access to tools may influence the rate of learning about effective properties of tools, I hypothesized that chimpanzees with unrestricted access to tools (i.e., can select/explore multiple tools) would require fewer trials to choose the correct tool and have a higher percentage of correct tool choice overall than chimpanzees with restricted access (i.e., forced to select/explore one) for each task.

There is also the question of how cognitively and/or behaviorally flexible chimpanzees are in selecting effective tools when task requirements change. If chimpanzees are flexible in tool selection, then when tool requirements of a task are changed such that different physical properties are required, chimpanzees should choose the tool with the physical property matching the change. If so, then I hypothesized that chimpanzees would exhibit no differences in correct tool selection between tasks for either trial one performance and overall performance (percent of

all trials for a given task). If there were differences between each modified task and the original task, I hypothesized that the differences would be positive. Positive differences would indicate more flexibility, in which increasing positive differences would imply increasing flexibility, and negative differences would indicate less flexibility. The zero and positive instances relate to positive transfer as the general knowledge obtained in the first task would aid chimpanzee performance in the subsequent tasks. Furthermore, I hypothesized that prior performance would predict future performance such that chimpanzees with higher percentages of overall correct tool selections on the initial task would select the correct tool on more trials in the changed/modified tasks than those who had lower percentages.

Based upon previous research, the brain should also relate to tool using behavior either directly with the cognitive ability to select effective tools and/or the ability to be flexible in choices across similar but slightly different situations. Thus, I hypothesized that the volume of the IFG, specifically the right IFG in the PFC, would positively correlate with performance and flexibility. More specifically, chimpanzees with a larger right IFG would perform better and exhibit greater flexibility, on trial one and overall (percent of all trials for a given task) on each task, compared to chimpanzees with a smaller right IFG. Greater flexibility, here, reflects greater ability to inhibit selection of familiar or other tools before properly assessing the situation. However, it is also possible that the ability may depend on asymmetry between the left and right hemispheres rather than just the absolute volume of the right IFG, such that those with larger right IFG relative to the left IFG would exhibit greater flexibility.

It remains unclear which factors play into the (preferential) selection of effective tools (i.e., learning and flexibility), how the brain may be involved, and how ecology (in the form of

optimal foraging) and cognition drive effective tool use. The present study aimed to aid in our understanding of effective tool use by chimpanzees.

2 METHODS

2.1 Subjects

Subjects included of 61 captive chimpanzees (*Pan troglodytes*) from the Yerkes National Primate Research Center (YNPRC) Main Center in Atlanta, Georgia (N = 13), the YNPRC Field Station in Lawrenceville, Georgia (N = 5), and the University of Texas M.D. Anderson Cancer Center (UTMDACC) in Bastrop, Texas (N = 43). Of these subjects, 27 were male and 34 were female, and ranged in age from 17-52 years ($M = 32.88$, $SD = 10.10$). Subjects had *ad libitum* access to water and were not food deprived, as all food rewards were supplemental to their normal daily diet. Subjects were tested over the course of approximately 14 months spanning from September 4, 2013 to November 4, 2014. This study was conducted in accordance with the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates, the Committee on the Care and Use of Laboratory Animal Resources (NRC, 2011), and was approved by the local institutional animal care and use committee.

2.2 Pre-testing Habituation/Exploration

Prior to testing, subjects were exposed to all tool types to habituate them to the materials as well as to let them explore the differing physical properties. Habituation consisted of six five-minute trials in which behavioral data were recorded at one-minute intervals. The first three trials took place prior to the length task, the second two prior to the surface area task, and the sixth prior to the shape task (*see tool and task descriptions in next subsection*). Behaviors that were recorded included: exploration (e.g., sniffing, biting), manipulation (e.g., raking, probing),

and other (e.g., trading, putting down; *see Table 2.1 for detailed behavioral ethogram*). The duration of tool handling was also recorded for these trials.

Table 2.1 Habituation Ethogram

Ethogram of behavior categories, including specific behaviors and descriptions, to be recorded during habituation prior to testing

Category	Behavior	Description
Exploration	Sniffing	Individual sniffs/smells the tool using their nose
	Licking	Individual licks tool by making contact with tongue over or along the tool
	Biting	Individual bites down on the tool with teeth; includes using teeth to break tool
	Bending	Individual applies force to misshape the tool into a curved, "L", or elbow shape; breaking may occur
Manipulation	Rubbing/Raking	Individual rubs the tool against another substrate or engages in a raking motion against another substrate with the tool
	Nesting	Individual holds or uses the tool during nesting behavior
	Protoprobing	Individual attempts to insert tool into a non-probing substrate (i.e., no hole or crevice)
	Probing	Individual attempts to insert tool into a hole or crevice; excludes inserting into devices meant for probing
Other	Trade/Give Back (with exploration)	Individual attempts to give the tool back to the experimenter after prior exploration of the tool without being asked to "give" tool back
	Trade/Give Back (without exploration)	Individual attempts to give the tool back to the experimenter after no exploration of the tool without being asked to "give" tool back
	Put Down/Leave (with exploration)	Individual immediately puts down the tool after exploration of the tool; may include leaving the vicinity after putting the tool down
	Put Down/Leave (without exploration)	Individual immediately puts down the tool after no exploration of the tool; may include leaving the vicinity after putting the tool down

2.3 Experiment One: Original (Length) Probing Task

This task tested tool effectiveness based on length.

2.3.1 Materials

An approximately 25.4 cm long, 2.54 wide PVC pipe and three stick-tools were used for this experiment (Figure 2.1). Approximately one-third of the PVC pipe (toward the end furthest away from the subject) was filled with a viscous food reward (i.e., yogurt, applesauce, mustard) and secured to a metal base on the outside of the subject's cage, such that the empty part of the pipe was closest to the subject. The stick-tools for the probing task were lollipop sticks varying in length (the dimension of effectiveness being tested). The effective tool was the longest measuring 30.48 cm in length and .59 cm in diameter. This tool was considered effective as its use allowed subjects to gain maximum reward per insertion. The less effective tool was a shorter stick measuring 20.32 cm in length and .44 cm in diameter. This tool was less effective as its use only allowed minimal reward gain per insertion. The ineffective tool was a very short stick measuring 11.43 cm in length and .40 cm in diameter. This tool was ineffective because it never reached the reward on insertion.

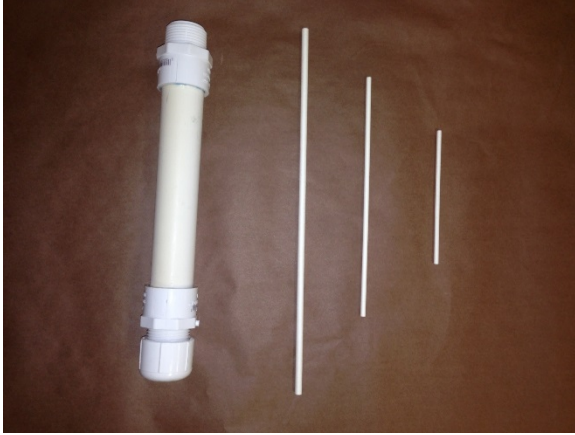


Figure 2.1 Original (length) task materials

The apparatus and tools for the original (length) task assessing the property of length.

2.3.2 Procedure

There were two conditions. Approximately half of the subjects ($N = 31$), randomly selected, were presented with restricted access. Restricted access was defined as having only one opportunity to select a tool during a trial, forcing the subject to use the first tool they selected. The remaining subjects ($N = 30$) were presented with unrestricted access. Unrestricted access was defined as having unlimited opportunities to select additional tools throughout the trial.

Subjects underwent a minimum of 20 two-minute test trials spread across separate days (minimum = 2 days, maximum = 5 days). Prior to each trial the device was filled with a viscous reward and attached to a metal base already affixed to the subject's cage, at which point the subject was able to look into the device. Next, the three tools were placed on a table with a sliding board starting from the experimenters left to the right. After placement, the sliding board was pushed toward the caging so that the subject could make a tool selection; the selection of a tool marked the beginning of each trial. For restricted access individuals, the sliding board was pulled away from the cage once a tool had been selected and the tool selected was recorded. For unrestricted access individuals, the sliding board remained in position for the duration of the

two-minute trial; during these trials the experimenter recorded the order in which the tools were selected as well as the latency from the start of the trial and whether or not the subject attempted to use the tool(s). Additionally, whether or not the subject looked into the device prior to making a selection was recorded. At the end of each trial, regardless of condition, the device was removed and the experimenter requested the tool(s) back from the subjects using the words “give” paired with the appropriate trained hand gesture. The experimenter then began the next trial by carrying out the same exact procedure as done for the first trial. Placement of the tools was randomized across trials with the restriction that each tool occurred in each location at least once and never in the same location on more than two consecutive trials. In order to move on to the modified tasks, subjects must have chosen the correct tool on 16 of 20 (80%) trials across two consecutive blocks of ten trials. For chimpanzees with unrestricted access, the correct tool must have been chosen *first* on the test trials.

2.4 Experiments Two-Four: Modified Probing Tasks

2.4.1 Procedure

Procedures for all modified probing tasks were identical to that of the original probing task with the exception that only two tools were presented during 20 test trials. Subjects were presented with the surface area probing task first, the shape task second, and the rigidity task last (*see below for detailed descriptions of each task*). To avoid carry over effects from the previous task, a tool used in more than one task was separated by a task utilizing different tools. This method reduced the probability of subjects developing a bias for choosing, or not choosing, a tool based upon its (in)effectiveness on a previous task.

2.4.2 Experiment Two: Surface Area Probing Task

This task tested tool effectiveness based on surface area.

2.4.2.1 Materials

A 25.4 cm long, 2.54 cm wide PVC pipe and two stick-tools were used in this experiment (see Figure 2.2). Approximately three-fifths of the PVC pipe (toward the end furthest away from the subject) was filled with a viscous food reward (i.e., yogurt, applesauce, mustard) and secured to a metal base on the outside of the subject's cage, such that the empty part of the pipe was closest to the subject. The stick-tools for the probing task varied in surface area (the dimension of effectiveness being tested). The effective tool was a thick wooden dowel measuring 29.85 cm in length and 1.27 cm in diameter. This tool was considered effective as its use allowed subjects to gain maximum reward per insertion by bending with the pipe. The less effective tool was a thin wooden dowel measuring 29.85 cm in length and .43 cm in diameter. This tool was less effective as its use only allowed minimal reward gain per each insertion.



Figure 2.2 Surface area task materials

The apparatus and tools for the modified task assessing the property of surface area.

2.4.3 Experiment Three: Shape Probing Task

This task tested tool effectiveness based on shape.

2.4.3.1 Materials

A 10.80 cm long, 2.54 cm wide PVC pipe and two stick-tools were used in this experiment (see Figure 2.3). Approximately three-fifths of the PVC pipe (towards the end of the pipe that was furthest away from the subject) was filled with a viscous food reward (i.e., yogurt, applesauce, mustard) and secured to a metal base on the outside of the subject's cage, such that the empty part of the pipe was closest to the subject. Within the PVC pipe was a plastic disc 3.18 cm in diameter and .64 cm in thickness with a rectangular opening measuring 1.91 cm in length and .50 cm in width. The stick-tools for the probing task varied in shape (the dimension of effectiveness being tested). The effective tool was a tongue depressor measuring 15.24 cm in length, 1.91 cm in width, and .16 cm in thickness. This tool was considered effective as its use allowed subjects to gain reward per insertion as it fit into the thin rectangular opening. The ineffective tool was a lollipop stick measuring 15.24 cm in length and .59 cm in diameter. This tool was ineffective as its use failed to penetrate the opening to gain reward per each insertion.

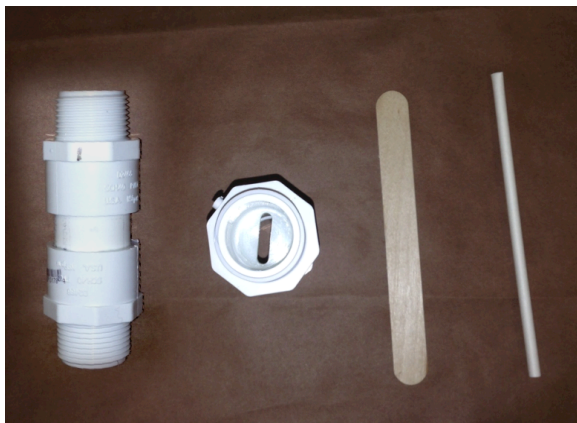


Figure 2.3 Shape task materials

The apparatus and tools for the modified task assessing the property of shape.

2.4.4 Experiment Four: Rigidity Probing Task

This task tested tool effectiveness based on rigidity.

2.4.4.1 Materials

A 25.4 cm long, 2.54 cm wide PVC pipe with two 45-degree curves and two stick-tools were used for this experiment (*see* Figure 2.4). The PVC pipe below the bend (towards the end that was furthest away from the subject) was filled with a viscous food reward (i.e., yogurt, applesauce, mustard) and secured to a metal base on the outside of the subject's cage, such that the empty part of the pipe was closest to the subject. The stick-tools for the probing task varied in rigidity (the dimension of effectiveness being tested). The effective tool was a non-rigid lollipop stick measuring 29.85 cm in length and .43 cm in diameter. This tool was considered effective as its use allowed subjects to gain reward per insertion as it bent with the pipe. The ineffective tool was a rigid wooden dowel measuring 30.48 cm in length and .48 cm in diameter. This tool was ineffective as it failed to bend with the pipe to reach the reward on insertion.

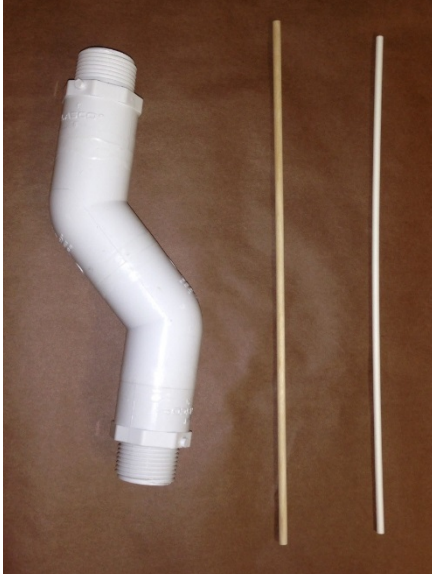


Figure 2.4 Rigidity task materials

The apparatus and tools for the modified task assessing the property of rigidity.

2.5 Brain Procedure

In vivo magnetic resonance imaging (MRI) scans were available for 52 of the 61 chimpanzees used in this study. Subject ages ranged from 17-52 years ($M = 32.04$, $SD = 10.19$), including 23 males and 29 females.

2.5.1 Scanning

All chimpanzee MRI scans followed standard procedures at the YNPRC and UTMDACC. For detailed description of the procedures see Bogart, Mangin, Schapiro, Reamer, Bennett, Pierre, and Hopkins (2012).

2.5.1.1 Imaging Parameters

Of the chimpanzees scanned *in vivo*, some were scanned using a 3.0 T scanner (Siemens Trio, Siemens Medical Solutions USA, Inc., Malvern, Pennsylvania, USA) and others using a 1.5 T G.E. echo-speed Horizon LX MR scanner (GE Medical Systems, Milwaukee, WI). Please

refer to Bogart and colleagues (2012) for specific imaging parameter details of these two *in vivo* scan types.

2.5.1.2 Post-Image Processing

All chimpanzee MRI scans were skull-stripped, cropped, and reformatted at .7 cubic isotropic resolution using Analyze 8.1 software. Using the Analyze software, the raw MRI scans were aligned in the axial, coronal, and sagittal planes along the anterior commissure-posterior commissure line and virtually sliced into 1 mm sections.

2.5.1.3 Inferior Frontal Gyrus Tracing and Volume

Tracing of the region of interest (ROI), the IFG, was completed using the trace tool within Analyze 8.1 software. The brain image was first placed in the sagittal plane, where the most lateral slice with a fully visible fronto-orbital (FO) sulcus was identified. A straight line was then drawn from the most superior edge of the FO to the inferior precentral sulcus (PCI). The image was rotated into the axial plane and the slice containing the previously drawn line served as the most dorsal slice that was traced. Within the axial plane, the FO functioned as the anterior boundary and the PCI as the posterior boundary. The ROI was drawn around all matter between FO and PCI and the medial boundary was a straight line between the medial edges of the two sulci. This was repeated for all slices ventral to the first slice traced until the inferior boundary was reached. The inferior boundary was determined by the crossing of the medial boundary by the insula. In cases where PCI bifurcation arose, both anterior and posterior limbs were included only if they branched from a single, common origin; this could be confirmed in the sagittal plane. Following axial tracing, the image was returned to the sagittal plane and the first lateral slice where the insula was no longer visible was located. The ROI was extended from the bottom-left corner of this slice either along PCI if it was still apparent or

straight down if it was not. The extension continued out of the frontal cortex and back around to the bottom right corner of the original ROI. This was repeated for all slices lateral to the original extension and for both hemispheres.

Once traced, the individual gray matter (GM) areas were summed across all slices to create GM volumes for each hemisphere. Before collection of the data, reliability in the measurement of the IFG was established. To assess reliability, chimpanzee IFG were traced by two tracers and the corresponding volumes were calculated. The volumes from the two tracers were compared using an intra-class correlation coefficient, revealing that the tracers were reliable at $ICC > .90$.

3 DATA ANALYSES

For optimum clarity, data analyses will be presented in order of hypotheses and not in order of experiment.

To assess the role of experience in effective tool choice, I analyzed whether overall tool selection (number of correct trials with a correct initial tool selection divided by the total number of trials) for each task was above chance using one-sample *t*-tests. For the length task, the test value was set to .33 as there were three tools to choose from, while the modified tasks test values were set to .50 as there were only two tools to choose from. The dependent variables were the percentages of correct tool choice for each task. Additionally, for the length task, I used a one-way ANOVA to determine the differences between the selection percentages of the three tools. Even though food level remained constant across trials, food level diminished during each trial; by looking into the pipes on each trial, chimpanzees would gain the information that the pipe had been refilled. Therefore, with regard to how looking into the pipe before tool selection affected

performance, I ran a bivariate correlation for each task between percent of trials a subject looked into the pipe and the percent of trials the correct tool was chosen.

To assess, more specifically, the role of differential access to tools, I analyzed whether there were differences between unrestricted and restricted access using a Mann-Whitney U test for each task as the data violated assumptions of a repeated measures ANOVA. For this, the groups were unrestricted and restricted access, and the dependent variables were the number of trials it took to choose the correct tool and the percent of all trials the correct tool was chosen.

To assess flexibility in tool selection, I analyzed both trial one and overall performance on each task. Because trial one data are binary (1 for correct, 0 for incorrect), I used McNemar's tests to compare trial one from each task to each other. Taking into account possible colony differences, post-hoc analyses were run utilizing chi-square tests. When chi-square assumptions were violated the Fisher's Exact test was used. For overall performance, a Friedman test was used as the data violated assumptions of the repeated measures ANOVA. Post-hoc analyses on colony were run using Mann-Whitney U tests.

To investigate performance further, the difference between each modified task and the original task was calculated. Here, a large negative difference would indicate less flexibility, a large positive difference would indicate the opposite, and zero would indicate equal performance. Additionally, partial correlations were run to determine whether performance on earlier tasks correlated with performance on later tasks.

To assess the relation between brain and behavior, I analyzed whether IFG volume correlated with performance on trial one and overall for each task. For trial one data, a repeated measures ANOVA was run with hemisphere (percent left IFG and percent right IFG), correct trial one (yes or no) and sex (male or female) as between-subjects variables. For overall

performance data, percent left and right IFG data were computed into an average percent.

Asymmetry quotients (AQ) were already calculated using the formula $AQ = (R - L) / [(R + L) / 0.5]$, where R represents the volume of the right IFG and L represents the left. Here, positive values indicate a rightward asymmetry and negative values a leftward asymmetry. Correlations were run between the percent of correct tool choice and the average percent of IFG in the brain, and between the percent of correct tool choice and the AQ values. Furthermore, I investigated the possible role of the IFG in performance differences between the modified tasks and the original task by running correlational analyses using average percent IFG and AQ values.

4 RESULTS

For optimum clarity, results will be presented in order of hypotheses and not in order of experiment. All analyses use the combined data from both access groups unless stated otherwise or occur in subsection 4.2. Data from the unrestricted access group in these analyses are specifically *first* choice responses.

4.1 Experience

For the following analyses: $N = 55$, mean age 33.54 years ($SD = 10.12$), 25 male, 30 female. One-sample t -tests revealed that chimpanzees chose the correct tool significantly above chance for the length, $t(60) = 69.825, p < .001$, surface area, $t(60) = 3.054, p = .003$, and shape, $t(60) = 2.708, p = .009$, tasks, but not the rigidity task, $t(60) = -.327, p = .754$ (see Figure 4.1). A one-way ANOVA revealed that, for the length task, there was a significant difference between the percent of trials each tool length was chosen, $F(2,186) = 5690.714, p < .001$ (see Figure 4.2). Specifically, the long tool was chosen significantly more than the medium, $p < .001$, and small tools, $p < .001$, and medium tool significantly more than the small tool, $p < .001$. These results show that chimpanzees chose the most effective tool significantly above chance for three of the

four tasks. Additionally, for the length task, when chimpanzees made an incorrect tool choice, they chose the better of the wrong tools (i.e., medium length).

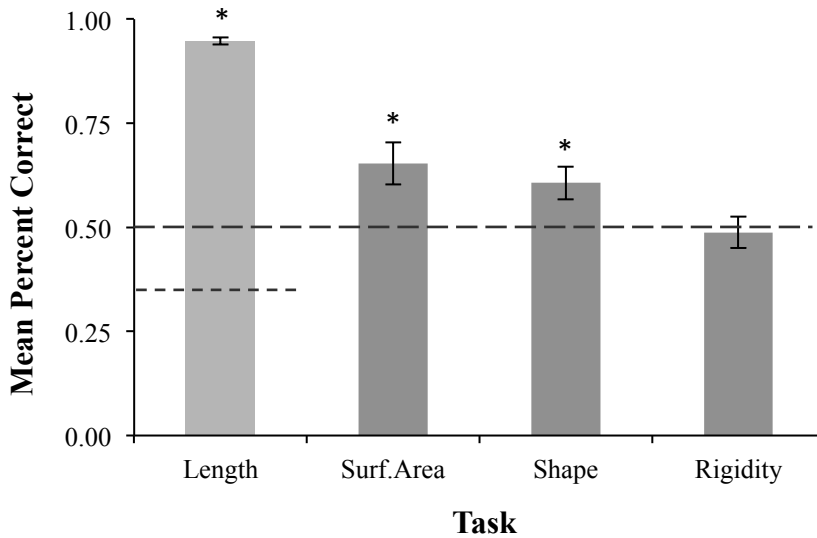


Figure 4.1 Overall performance levels on all tasks

Mean percent of correct tool choices (number of correct trials divided by all trials) as a function of task. Long dotted lines represent chance value of .50 for the surface area, shape, and rigidity tasks. Small dotted lines represent chance level of .33 for the length task. * $p < .01$.

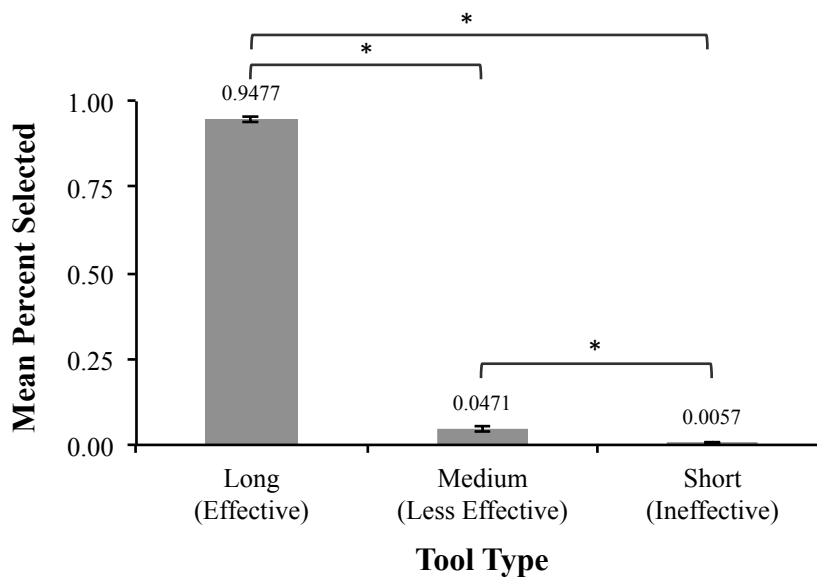


Figure 4.2 Length task tool selections

Mean percent of trials each tool was selected for the length task. * $p < .001$.

Bivariate correlation analyses revealed that the percent of trials chimpanzees looked into the pipe did not significantly correlate with performance (measured as percent of trials correct) on any task (length: $r = -.008, p = .953$; surface area: $r = -.023, p = .868$; shape: $r = .109, p = .428$; rigidity: $r = .047, p = .734$). Though looking did not predict performance, the percent of looking in the length task positively correlated with the percent of looking in the surface area, $r = .397, p = .003$, and shape tasks, $r = .281, p = .038$. Additionally, percent of looking in the shape task correlated with percent of looking on the rigidity task, $r = .414, p = .002$. These results show that whether or not chimpanzees looked into the pipe prior to tool selection did not influence performance, but that, most times, chimpanzees looked into the pipe more when they had looked in previous tasks.

4.2 Differential Access

For these analyses: $N = 61$, mean age 32.88 years ($SD = 10.10$), 27 male, 34 female. It must be remembered that the data from the unrestricted access group in these analyses are specifically *first* choice responses. Mann-Whitney U tests revealed no significant differences in the average number of trials it took to choose the correct tool in each task between the unrestricted and restricted access groups. For the percent of correct trials, there was only a significant difference between the unrestricted and restricted access groups on the rigidity task, $z = 2.176, p = .030$. Specifically, chimpanzees in the restricted access group had a higher percentage of correct choices than those in the unrestricted access group. Please see table 4.1 for full results.

Because there was a difference between the access groups on the percent of correct trials for the rigidity task, the one-sample t -test performed on chance levels for that task was reassessed. Separate one-sample t -tests were run with each access group to determine if each

group chose the correct tool above chance. The tests revealed that neither group chose the correct tool above chance (unrestricted: $t(29) = -1.880, p = 0.070$; restricted: $t(30) = 1.290, p = .207$). These and the results prior indicated that the two groups only differed on their overall performance on the rigidity task, though both groups did not perform above chance on this task.

Table 4.1 Differential access performance results

Results of Mann-Whitney U tests used to determine differences between unrestricted and restricted access groups for average number of trials chimpanzees took to choose the correct tool (trials to correct) and the percent of all trials the correct tool was chosen (percent correct)

	Unrestricted Mean Rank	Restricted Mean Rank	Mann-Whitney U	Z	p
Trials to Correct					
Length	31.62	30.40	446.50	-0.483	0.629
Surface Area	31.87	30.16	439.00	-0.467	0.641
Shape	31.10	30.90	462.00	-0.044	0.965
Rigidity	30.00	31.97	495.00	0.443	0.657
Percent Correct					
Length	30.57	31.42	478.00	0.201	0.841
Surface Area	33.83	28.26	380.00	-1.245	0.213
Shape	32.85	29.21	409.50	-0.803	0.422
Rigidity	25.98	35.85	615.50	2.176	0.030

Note. Unrestricted $N = 30$, restricted $N = 31$

4.3 Flexibility

For these analyses: $N = 61$, mean age 32.88 years ($SD = 10.10$), 27 male, 34 female, 18 YNPRC, 43 UTMDACC. For trial one performance, McNemar's tests revealed that chimpanzees selected the correct tool on trial one of the length task significantly more than the surface area, $\chi^2(1, N=61) = 4.348, p = .037$, shape, $\chi^2(1, N=61) = 32.237, p < .001$, and rigidity tasks, $\chi^2(1, N=61) = 34.225, p < .001$. Chimpanzees also selected the correct tool on trial one of the surface area task significantly more than both the shape, $\chi^2(1, N=61) = 18.581, p < .001$, and rigidity tasks, $\chi^2(1, N=61) = 18.270, p < .001$. There were no differences between the shape and rigidity tasks, $\chi^2(1, N=61) = .045, p = .831$.

Chi-square tests revealed a significant colony difference on correct trial one was present for the shape task, $\chi^2(N=61) = 4.15, p = .042$, such that chimpanzees from UTMDACC had a greater proportion of correct first trials than those from YNPRC (*see* Figure 4.3). There was no significant colony difference for the surface area task, $\chi^2(N=61) = .65, p = .420$. The values for the length and rigidity tasks failed to meet the assumptions of the chi-square test and so Fisher's Exact tests were used. The Fisher's Exact tests revealed a significant colony difference on correct trial one was present for the length task, $p = .020$, such that chimpanzees from UTMDACC had a greater proportion of correct first trials than those from YNPRC. These tests also revealed a trend toward, but no significant, colony differences for the rigidity task, $p = .055$.

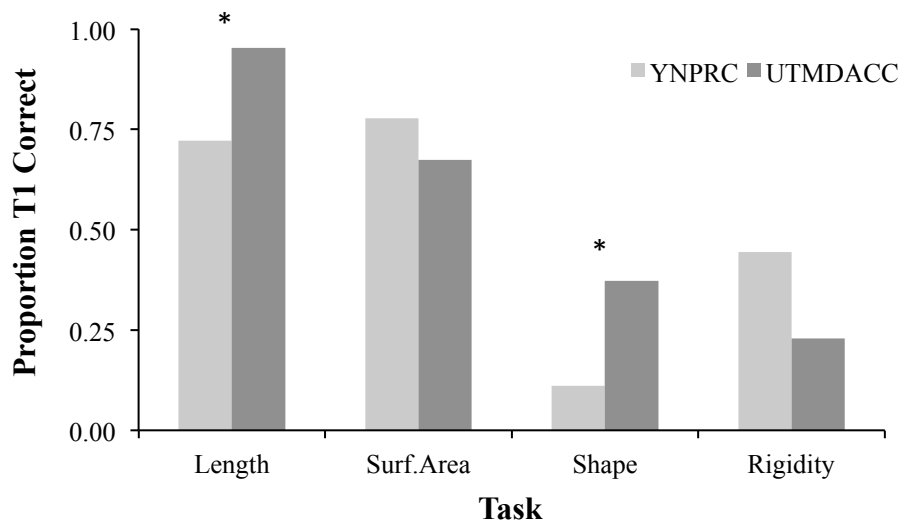


Figure 4.3 Trial one colony comparisons

Proportion of correct trial one choice as a function of task for YNPRC and UTMDACC chimpanzees. * $p < .05$.

For overall performance, the Friedman test revealed a significant effect of task, $\chi^2(3, N=61) = 75.140, p < .001$. The pairwise comparisons showed that chimpanzees had significantly higher percentages of correct tool choices for the length task than all other tasks, $p < .001$ for all, and for the surface area task than the rigidity task, $p = .010$. There were no significant

differences between the surface area and shape tasks, $p = 1.00$, or the shape and rigidity tasks, $p = .136$.

Mann-Whitney U tests revealed significant differences between colony for the surface area and rigidity tasks, such that chimpanzees from YNPRC had significantly higher percentages of correct tool choices than those from UTMDACC (surface area: $z = -2.006$, $p = .045$; rigidity: $z = -2.996$, $p = .003$). There were no significant colony differences for the length, $z = -.838$, $p = .402$) and shape tasks, $z = -.143$, $p = .887$) on overall performance.

Investigating performance further to determine whether chimpanzees are less flexible in changing with these tasks, the differences between each modified task and the original task were calculated (*see* Table 4.2). As indicated by the negative values, chimpanzees performed worse on the modified tasks than on the original task. Partial correlations revealed no relationship between overall performance on the first task and later tasks (length and surface area: $r = -.037$, $p = .782$; length and shape: $r = .062$, $p = .641$; length and rigidity: $r = .244$, $p = .062$).

Table 4.2 Performances differences between tasks

Mean and standard errors of the differences between each modified task and the original task

	<i>M</i>	<i>SE</i>
Surface Area - Length	-0.279	0.058
Shape - Length	-0.306	0.042
Rigidity - Length	-0.475	0.388

Combined, these results indicate that chimpanzees perform best on the length task on both trial one and overall. Chimpanzees also perform better on the surface area task than the other two modified tasks on trial one, but only better than the rigidity task overall. Additionally, there were differences between colonies such that UTMDACC chimpanzees performed better on trial one for the length and shape tasks, and YNPRC chimpanzees performed better overall on the surface area and rigidity tasks.

4.4 IFG and Performance

For these analyses: $N = 52$, mean age 32.04 years ($SD = 10.19$), 23 male, 29 female. Repeated measures ANOVAs revealed no significant effect of hemisphere (percent left IFG versus percent right IFG) on trial one performance for any tasks. There were also no significant effects of sex or any interactions between the variables. Please see table 4.3 for full results.

Table 4.3 Hemisphere and trial one performance results*Repeated measures ANOVA results assessing the effect of hemisphere on trial one performance*

	F	p
Length		
Hemisphere	0.250	0.620
Hemisphere x Sex	2.042	0.159
Hemisphere x Trial1	0.272	0.605
Hemisphere x Sex x Trial1	0.051	0.823
Sex	0.371	0.545
Trial1	0.603	0.441
Sex x Trial1	0.502	0.482
Surface Area		
Hemisphere	0.007	0.935
Hemisphere x Sex	1.879	0.177
Hemisphere x Trial1	0.026	0.873
Hemisphere x Sex x Trial1	1.258	0.268
Sex	0.036	0.851
Trial1	1.383	0.245
Sex x Trial1	0.022	0.884
Shape		
Hemisphere	0.108	0.744
Hemisphere x Sex	2.370	0.097
Hemisphere x Trial1	1.869	0.178
Hemisphere x Sex x Trial1	0.225	0.637
Sex	0.055	0.861
Trial1	2.634	0.111
Sex x Trial1	0.220	0.641
Rigidity		
Hemisphere	0.235	0.630
Hemisphere x Sex	2.191	0.145
Hemisphere x Trial1	0.562	0.457
Hemisphere x Sex x Trial1	0.238	0.628
Sex	0.162	0.689
Trial1	0.017	0.896
Sex x Trial1	1.268	0.266

Note. For F value $df = 1, 48$. Hemisphere is the factor term representing percent left IFG and percent right IFG

For overall performance on the tasks, correlation analyses revealed that the average percent IFG negatively correlates with the shape, $r = -.319, p = .021$, task and positively with the

rigidity task, $r = .300$, $p = .031$, but did not correlate with the other two tasks (Figure 4.4).

Additionally, there were no correlations between AQ values and any tasks. Correlation analyses revealed that performance differences between the shape and length task negatively correlated with average percent IFG, $r = -.337$, $p = .015$, while differences between the rigidity and length tasks positively correlated with average percent IFG, $r = .285$, $p = .041$. There were no other significant relationships. Please see Table 4.4 for full results of these analyses.

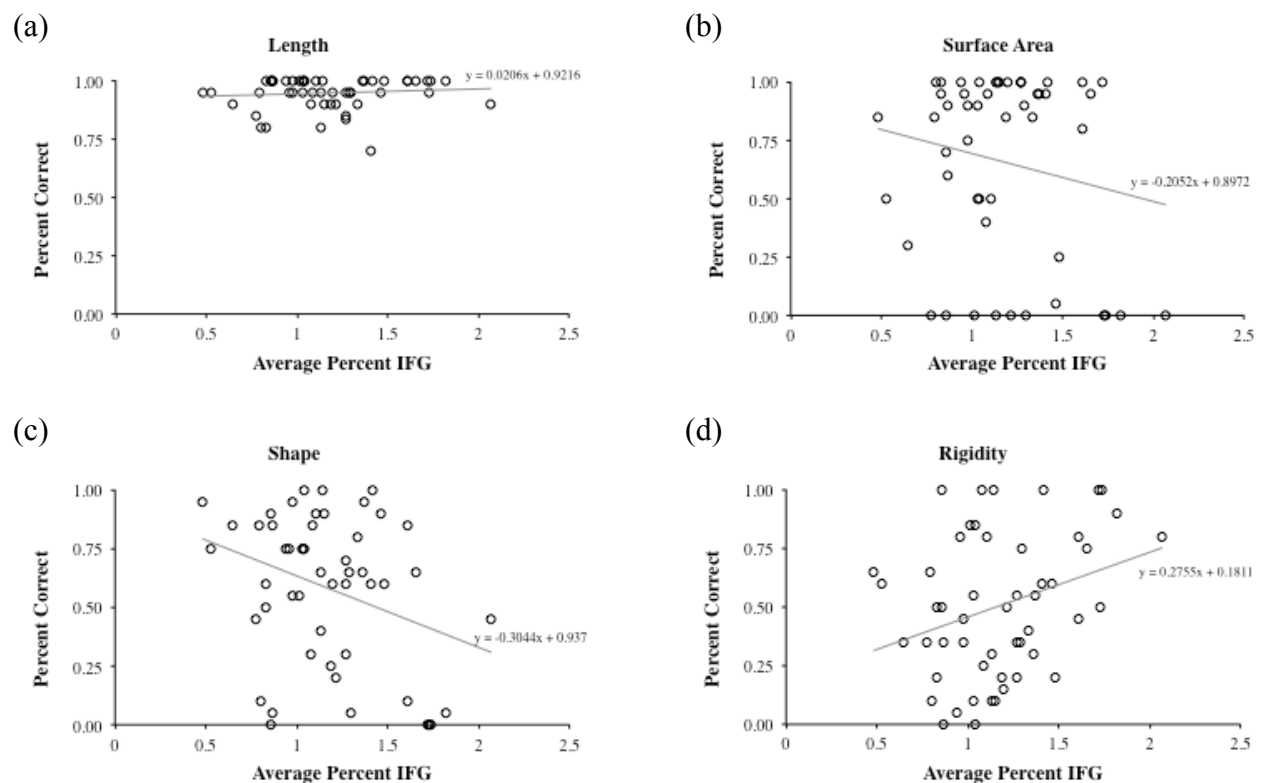


Figure 4.4 Performance and IFG correlation plots

Percent of correct tool choices as a function of average percent IFG for the (a) length, (b) surface area, (c) shape, and (d) rigidity tasks.

Table 4.4 Brain and performance correlations

Correlation results of average percent IFG and AQ values for each task and for the differences between each modified task and the original task

	<i>r</i>	<i>p</i>
Average Percent IFG		
Length	0.029	0.518
Surface Area	-0.181	0.200
Shape	-0.319	0.021
Rigidity	0.300	0.031
Surface Area – Length	0.190	0.176
Shape – Length	-0.337	0.015
Rigidity – Length	0.285	0.041
Asymmetry Quotient		
Length	0.199	0.158
Surface Area	-0.098	0.489
Shape	0.088	0.534
Rigidity	0.051	0.718
Surface Area – Length	-0.129	0.363
Shape – Length	0.045	0.753
Rigidity – Length	0.006	0.966

Together, these results suggest that, while there is no relationship between the IFG measures and performance on trial one, there is a relationship between IFG measures and overall performance. Specifically, chimpanzees with smaller average percent IFG obtained higher percentages of correct tool choices for the shape task, while those with larger average percent IFG obtained higher percentages of correct tool choices for the rigidity task. The same pattern is seen with the difference values between these two modified tasks and the length task. Finding no significant relationships with AQ values suggests that neither the left nor right IFG has greater influence on performance.

5 DISCUSSION

Chimpanzees have been documented as proficient tool users and studies have investigated whether chimpanzees use properties like weight and length to select the most effective tool for their given tool-using problem. However, researchers have neglected to investigate whether chimpanzees utilize other tool properties, such as surface area, shape, or rigidity. Thus, this study investigates whether chimpanzees do use other properties to choose effective tools, how experience influences their ability to select effective tools, and whether or not chimpanzees are flexible in effective tool selection.

This study revealed that chimpanzees do use properties other than weight and length to select effective tools. Although performance was best for the length task, chimpanzees were able to successfully utilize properties of both surface area and shape to determine which tools were effective for the task, indicated by their above chance performance. While chimpanzees did choose the effective tool for the rigidity task on some trials, they did so less than chance, contrary to my original hypothesis. A possible explanation for the poor performance on the rigidity task could be attributed to similarities between the tools. While the tools differed on the dimension of rigidity, material, and color, they looked quite similar to each other given their equal shape and length. This similarity in shape and length may have proved difficult to overcome leading to incorrect tool choices.

The results from the length task are in agreement with prior research detailing the ability of chimpanzees to choose effective tools based on length (Sabbatini et al., 2012). Chimpanzees, in this study, selected the most effective tool (long) for the task more than the other two tools. However, when incorrect choices were made, chimpanzees chose the medium tool (less effective compared to long) over the small tool (ineffective). This suggests that, although they did not

choose the most effective tool, chimpanzees still chose a tool that was not completely ineffective. These data support the notion that chimpanzees forage optimally as selecting the long tool gains them a larger and/or faster harvest. What is also interesting with regard to tool selection is that during the surface area task chimpanzees chose the most effective tool significantly more than chance, and thus more than the less effective tool. This is interesting because both tools allowed chimpanzees to gain reward, the only difference being the amount of reward. Additionally, the small tool looked similar to the most effective tool from the length task which was the first task chimpanzees experienced. Therefore, the results from the surface area task also support the notion that chimpanzees optimally forage.

It is known that exploring the environment facilitates, or at least creates opportunities for, learning (Wagman & Carello, 2001). It is said that having a varied experience is fundamental to forming flexible knowledge allowing for better, faster task/concept acquisition (Sabbatini et al., 2012). Taking the influence of environmental exploration into account, this study investigated whether or not looking into the pipe prior to tool selection affected performance. By looking into the pipe prior to tool selection, chimpanzees potentially were able to gain information regarding food level and the type of tool needed. In contrast to my hypothesis, these data showed no significant relationship between looking and performance. This relationship absence, however, is in agreement with Sabbatini et al.'s (2012) finding that visual feedback did not increase performance. Though this study used opaque pipes, access to a transparent tube did not increase selection of the correct tool on trial one in the study by Sabbatini and colleagues. Overall, these data do not provide support for the perception aspect of problem solving as chimpanzees failed to gain the perceptual information from the pipe for the tool needed for the task. While the food level and pipe type remained constant across trials, food levels diminished

within trials. Because food levels diminished within trials, it would appear beneficial to look into the pipe to make sure that levels were replenished. It is also plausible that chimpanzees need not look into the pipe after a number of trials in a single task if an expectation of replenishment and/or pipe type develops. It should be noted that the total number of trials completed in succession on a single day varied between chimpanzees, which would likely affect the development of such expectations. This is a limitation of this study and is something to investigate in future work.

Based on the influence of experience, it seemed likely that differential access to tools would affect learning about tool effectiveness. This study utilized two groups of chimpanzees, one with unrestricted access to tools during each trial and one with restricted access. Mostly, these data were in disagreement with my initial hypothesis that differential access to tools would influence performance. However, differential access did influence overall performance on the rigidity task such that those with restricted access were more successful. An explanation for this finding is that choosing the wrong tool was more costly to chimpanzees with restricted access than to those with unrestricted access. This is plausible since the unrestricted individuals could choose the effective tool after initially selecting the ineffective tool, thus incurring a lesser cost than restricted individuals.

Though no study has specifically assessed flexibility in tool use, Sabbatini demonstrated that chimpanzees can be flexible in their tool selection on the dimension of length. They found that when tool length options changed for a task presented previously, chimpanzees chose tools using a rule of relative length, rather than absolute length. More specifically, when the longest tool in the first task became the medium tool in the subsequent task, chimpanzees chose the 'new' longest tool. For this study, if chimpanzees exhibited flexibility in tool use, then they

should have performed equally as well, or better, on trial one and overall for each task.

However, these data show that chimpanzees were not flexible as they performed better on the length task than any of the other tasks. The poorer performance on the modified tasks indicates that chimpanzees in this study may be less flexible in tool selection when tool properties deviate from length.

Since the subject pool of this study included chimpanzees from two different colonies, I investigated potential differences in performance between the colonies. There were indeed differences between the two colonies in the number of correct trial one choices for two of the tasks. Chimpanzees from UTMDACC had a higher proportion of correct trial one choices for the length and shape tasks than chimpanzees from YNPRC. It is plausible that these differences are an effect of experience, specifically that of enrichment and testing experience involving tools for probing. A possible explanation for these differences is that the YNPRC chimpanzees are heavily experienced with utilizing lollipop sticks of various sizes as probing tools, as compared to UTMDACC chimpanzees. The UTMDACC chimpanzees also have experience utilizing lollipop sticks as probing tools, but perhaps less extensively since a wider range of enrichment and experimental devices requiring different, non-lollipop stick tools have been used. This explanation can also extend to the difference found with overall performance on the rigidity task where YNPRC chimpanzees performed better than the UTMDACC chimpanzees. These results suggest that, while extensive experience with one or few tool-types can aid performance, it also has the potential to hinder performance.

In order to select appropriate tools, animals must be able to inhibit certain responses or perseverate when tools are ineffective. The PFC is now known to be associated with inhibitory control (Munakata et al., 2011). Specifically, goal-irrelevant responses are detected by the PFC

and are kept below the neural activation threshold such that they are never carried out (Hofmann et al., 2012). There is also evidence suggesting that IFG activation plays an important role in inhibitory control (c.f., Chikazoe et al., 2007; Verbruggen & Logan, 2008). Given the relationship between the IFG activation and inhibitory control, this study investigated whether IFG volume also plays a role response inhibition. No relationships between performance and AQ values were found, suggesting that neither the left nor right IFG has greater influence on performance. Relationships were only found with the average percent IFG values for two tasks. Specifically, chimpanzees with smaller average percent IFG obtained higher percentages of correct tool choices for the shape task, whereas those with larger average percent IFG obtained higher percentages of correct tool choices for the rigidity task. The result for the shape task was surprising given the lollipop stick presented was similar to those presented in the length task and was of similar shape, but not length, to the thin dowel in the surface area task. Because of these similarities the tool may have been more familiar as a probing tool than the tongue depressor; thus, it seems plausible that chimpanzees would need to inhibit the response of choosing the more familiar tool. If this was the case, given the literature mentioned above, one would suspect there to be a positive correlation with IFG volume, which is opposite our finding. Taken as a whole, these data do not provide evidence supporting an important role of IFG volume (neither average percent of whole brain nor difference between left and right) in response inhibition ability when making effective tool selections. The case here may be that IFG activation does not directly translate to IFG volume; thus future work should look both at behavior patterns and brain activation during the moments prior to tool selection, if possible.

In summary, the results of this study demonstrate that chimpanzees are able to utilize properties of length, surface area, and shape to select effective tools supporting the notion that

chimpanzees select tools based upon effective properties. Although chimpanzees performed best on the length task, they also excelled at the surface area and shape tasks by performing significantly above chance. The surface area results provide marked evidence supporting the notion that animals optimally forage. It must be acknowledged that individual differences occur within each task. What is efficient for one individual may not necessarily be for another individual, and these may have influenced results. Future work should look more deeply into individual differences with regard to effective tool use. Though exploration of the environment is suggested to facilitate learning and/or performance, it did not appear to have an effect in this study as measured through looking. Together, these results support prior research concerning effective tool selection by chimpanzees, as well as expand current knowledge and understanding of what ecological and cognitive factors may be at play.

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