CONCURRENT SPATIAL RELATIONS CHALLENGE CAPUCHIN MONKEYS (*SAPAJUS LIBIDINOSUS*) AND CHIMPANZEES (*PAN TROGLODYTES*) IN AN ALIGNMENT TASK AND PROVIDE IMPLICATIONS FOR TOOL USE

by

LUCY TAFT LA COUR

(Under the Direction of Dorothy Fragaszy)

ABSTRACT

Aligning an object with a surface also involves producing particular spatial relations between the object and the surface just as when using a hand tool. Gibsonian perception-action theory predicts that managing two spatial relations simultaneously in an alignment problem is more difficult than managing one relation, or managing two relations sequentially. We presented 6 captive capuchin monkeys and 6 captive chimpanzees with stick objects to insert into one groove (one relation) or two grooves (two relations). Two grooves were presented parallel to each other or as a separated T (sequential placement), or as a joined T (concurrent placement). Subjects of both species needed more attempts to insert the joined T than the parallel sticks, but not the separated T. Our findings provide strong evidence that managing two concurrent spatial relations is more challenging to non-human primates than managing two sequential relations, which restricts the problems they will solve using tools.

INDEX WORDS: tool use, perception-action theory, spatial reasoning, *Sapajus libidinosus*, *Pan troglodytes*

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DEDICATION

I would like to dedicate my thesis to my parents and my brother. Without their never-ending support and encouragement I would not have achieved all that I have.

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CHAPTER 1

INTRODUCTION

Tool use is considered an iconic aspect of human evolution and development, although the behavior is not unique to humans. Many other species, including various species of non-human primates, spontaneously use tools in their natural environment. For example, capuchin monkeys (*Sapajus libidinosus*; formerly *Cebus libidinosus*) regularly use stone hammers to crack open nuts (Fragaszy, Izar, Visalberghi, Ottoni, & Gomes de Oliveira, 2004).

An important difference between tool use in humans and tool use in non-human primates may be due to propensities of particular species to align objects to other objects or surfaces. Common forms of tool use by humans, such as hammering a nail or inserting a key into a lock, require the management of more than one allocentric spatial relation, that is, a relationship between an object and a surface or an object and another object (Fragaszy & Cummins-Sebree, 2005). The nail must be aligned with the wall while the hammer is simultaneously aligned with the nail; the key must be oriented so that the narrow end is toward the lock and the grooved side is facing upward. In contrast, non-human primates typically align only one allocentric spatial relation, and often this relation is quite permissive with respect to alignment. For instance, termite fishing in chimpanzees requires only that one end of the stick must be aligned with the termite hole (Hayashi, Mizuno, & Matsuzawa, 2005; Fragaszy & Cummins-Sebree, 2005). The most complex form of tool use by non-human primates routinely found in nature is nut cracking, which involves two spatial relations (one between the nut and the anvil, one between the stone hammer and the nut) managed sequentially (Fragaszy et al., 2004).

A recent study by Fragaszy, Stone, Scott, & Menzel (2011) demonstrated that both tufted capuchin monkeys (*Sapajus libidinosus*) and common chimpanzees (*Pan troglodytes*) are increasingly hindered in aligning an object as the number of concurrent spatial relations increases from one to two to three. The current study replicates these findings as well as delves further into the problem to determine whether increasing spatial relations also presents a problem when it is possible to manage them sequentially as opposed to concurrently.

Theoretical Links

The perception-action theory posits that individuals generate exploratory behaviors that lead to perception and perception guides subsequent actions (Lockman, 2000). These exploratory behaviors allow the individual to learn about the affordances of both the object(s) and the possible actions with those objects. According to J. J. Gibson (1979), whose theory of ecological psychology greatly influenced Lockman's theory, an affordance of an object is defined as what that object provides or offers the actor in terms of potential actions. For instance, the first time an individual picks up a hammer he/she may perceive, by wielding it, that it is light enough to swing but heavy enough on one end to provide significant force to another object. Wagman and Carello (2001) found that individuals introduced to novel "tools" could determine whether the object would afford hammering (a power task) or poking (a precision task) depending on the inertial properties and mass distribution of the object. In addition, this determination required relatively little actual experience with the object. Similarly, Hove, Riley, and Shockley (2006) found that individuals were able to decide accurately if a particular hockey stick would be best suited to exert force or be used for a precision task. Again, the decision was based upon the mass distribution, and thus the inertial properties, of the stick, which was manipulated by the researchers. In both studies, individuals were able to perceive the affordances of the objects by using dynamic touch, which involves the manipulation of an object via muscular effort (Gibson, 1966). Dynamic touch allows an individual to feel an object's inertial properties and then be able to generate the appropriate muscular effort to wield the object accordingly (Turvey, 1996).

However, an individual must learn about more than the affordances of an object to be able to use it as a tool. Another key component of tool use is the ability to manage allocentric frames of reference (Lockman, 2000; Fragaszy et al., 2011). There are two frames of reference in which individuals may work to locate and move themselves as well as objects within space. An egocentric frame of reference is centered about the body while an allocentric frame of reference is centered about landmarks and objects external to the body (Potì, 2000). The egocentric frame of reference is typically thought to develop first (Berthoz, 1997/2000). McCarty, Clifton, and Collard (2001) found that infants, ages 9 to 24 months, were more likely to plan their actions in advance when using a self-directed tool rather than an object-directed tool; they concluded that planful strategies for self-directed tools develop earlier than those for object-directed tools. When dealing with a tool and another object the individual must use an allocentric frame of reference in order to locate and align the objects appropriately with respect to each other.

When an individual uses a tool, he/she moves the tool to contact the object or surface. Thus, the allocentric frame of reference used during tool use is mobile. A mobile frame of reference adds to the degrees of freedom involved in a task by increasing the number of directions in which movement can occur. Managing more degrees of freedom is more difficult than managing fewer degrees of freedom because it means there are more movements for the individual to control (Bernstein, 1996). Additionally, tool use often requires the coordination of more than one mobile allocentric frame of reference, as when pulling in an object with a rake. During the raking action there is a mobile frame of reference between the object and the surface upon which it is moving as well as between the object and the rake pulling it. Humans begin learning to manage and coordinate such mobile allocentric frames of reference within their first year of life (Lockman, 2000). Improvements in managing allocentric frames of reference between a tool and other objects provide the basis for the continuous development of tool use seen among humans.

It could be that non-human primates are not as adept as humans at coordinating mobile allocentric frames of reference. This would partially explain why we see a repertoire of less complex tool use among non-human primates compared to humans' repertoire. Non-human primates are known to use sticks to probe or fish for insects, stab another animal, pull in or push out an object, and pry open a container. They can also use stones to dig in the dirt for insects or roots and pound nuts to crack them open (Shumaker, Walkup, & Beck, 2011). These abilities are impressive but none of the tasks involve more than two spatial relations or two concurrent relations as seen so often in human tool use, such as fitting a key in a lock or stone knapping (Bril, Roux, & Dietrick, 2005).

Fragaszy and Cummins-Sebree (2005) extended Lockman's perception-action theory in a comparative direction with the goal to examine tool use and its development across species. Their model of spatial reasoning incorporates Bernstein's (1996) idea that allocentric spatial relations can vary in a number of aspects – the number of relations involved, whether the relations can be dealt with sequentially or concurrently, and the temporality of the relations. Fragaszy and Cummins-Sebree's (2005) model predicts that the difficulty of a task increases as the number of spatial relations involved increases. Their model also predicts that a task is more difficult when the spatial relations must be dealt with concurrently rather than when the same number of relations can be managed sequentially. Fragaszy et al. (2011) provided support for the first prediction; this study aims to provide evidence for the latter prediction.

Experimental Task

Tufted capuchins and chimpanzees were presented with an object alignment task in which they had to align an object with a matching groove in a tray. Four different conditions, not including the baseline condition, required subjects to align objects in the horizontal plane with one spatial relation (one condition) or two spatial relations (three conditions) involved. The objects were single cuboid sticks or a T-shaped stick. All sticks, including both components of the T-shaped stick, were equal in length and width. Aligning a single stick in the horizontal plane presents one allocentric spatial relation because one plane must be aligned for the object to fit into the groove properly. Aligning the T-shaped stick in the horizontal plane presents two allocentric spatial relations because both the stem and the crossbar of the T must be aligned appropriately with the T shape of the groove. In two conditions presented in this study, two allocentric spatial relations could be dealt with sequentially, while one condition required subjects to manage both allocentric relations simultaneously. Subjects were allowed to manipulate the sticks in any way they wanted while trying to align them. Each time they contacted the tray with the stick was considered an attempt at alignment. We used the number of attempts per trial as our measure of the difficulty of the task.

From Fragaszy and Cummins-Sebree's (2005) model of spatial reasoning we can make several predictions. First, the number of attempts per trial will increase as the number of allocentric spatial relations involved increases from one to two. Second, the number of attempts per trial will increase when two allocentric spatial relations must be managed concurrently rather than one at a time. Finally, additional spatial relations add to the number of directions in which movement is possible. The more mobility that is possible between an object and a surface, the more movement there is that must be controlled for fine placement of the object.

From this analysis of the challenges of managing movement, we predict that non-human subjects will act to decrease the number of directions in which the stick can possibly move with respect to the groove. They might do so by moving the object across the surface of the tray and groove. Moving the stick across the surface of the tray can reduce mobility because the stick is moving in relation to a fixed surface. Subjects could also stabilize the object as they align it with the groove; for example, by "pinning" one end of the stick on the tray with one hand and pivoting the stick around this point with the other hand. In addition, we predict that they will make greater use of such actions as the number of spatial relations increases. However, moving the stick across the surface might be helpful for another reason other than reducing mobility. It can also provide haptic information about the groove, its location, and its orientation.

CHAPTER 2

METHOD

Subjects

The subjects of this study included six adult capuchin monkeys (*Sapajus libidinosus*) and six adult chimpanzees (*Pan troglodytes*). The capuchins were all male and were housed in a vivarium at the University of Georgia. They were tested in their home cages. Four of the chimpanzees, two males (Sherman and Mercury) and two females (Lana and Panzee), were housed in an indoor-outdoor facility at Georgia State University's Language Research Center. They were tested in their indoor home cage. These subjects had previously participated in Fragaszy et al.'s (2011) study. The other two chimpanzees, one male (Joseph) and one female (Christa), were housed at Emory University's Yerkes National Primate Research Center. They were tested in their outdoor home cage. These subjects had not participated in the previous study. Subjects received their typical diet, and water was available ad libitum.

Apparatus

All five conditions involved the use of a circular tray (15.3 cm in diameter for the capuchins, 46 cm in diameter for the chimpanzees). The tray was flat for the baseline condition and had one or two grooves for the experimental conditions as well as one or two sticks to be inserted into the groove(s). The capuchins' sticks and trays were made of PVC covered in non-toxic paint, while the chimpanzees' sticks and trays were made of wood covered in non-toxic paint and non-toxic sealant.

Figure 1 shows all five conditions, including tray and stick(s) used. In the baseline condition, the stick was cuboid (11.7 x 1 x 1 cm for capuchins; 28 x 2.6 x 2.6 cm for chimpanzees) and the groove encompassed the entire base of the tray (i.e., the surface of the tray was flat and large enough to accommodate the stick at any rotational angle). In Condition A, the same stick could be inserted into a single groove in the middle of the tray. The groove was slightly wider and longer than the stick. Condition B used two cuboid sticks of the same size, and the sticks could be inserted into two matching grooves placed parallel to each other in the tray. Condition C used the same two sticks as Condition B, but the grooves were placed perpendicular to each other to make a T shape with a small separation between the two grooves. In Condition D, a T-shaped cuboid stick replaced the sticks. Each segment of the T-shaped stick was the same width and length of the sticks used in all previous conditions. The groove was T-shaped and placed in the center of the tray.

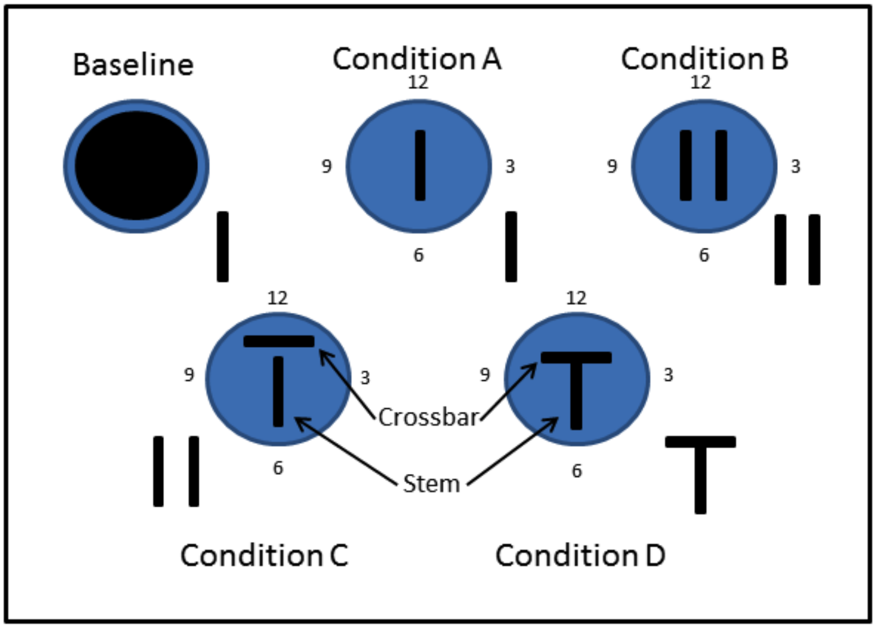

Figure 1. Diagrams for All Conditions (Sticks and Trays)

For testing, the capuchins were confined in the bottom half of their home cage. A clear panel was attached to the front of the cage, and the experimenter slid in the trays using a drawer at the bottom of the panel. The experimenter handed the stick(s) to the monkey through the vertical cage bars to the left of the panel. Once the subject was finished with the trial he could push the drawer back out of the cage. Trials were videotaped using a video camera (Canon NTSC Elura 100) mounted on a tripod. The camera was positioned to film the tray through the clear panel.

The chimpanzees at the Language Research Center (Sherman, Mercury, Lana, and Panzee) were confined in a section of their indoor home cage (2.0 x 4.3 x 2.5 m). The experimenter was seated in a chair facing parallel to the home cage and slid the trays and sticks under the wire mesh of the cage to the subject. When the subject finished a trial, it could slide the tray back under the mesh to the experimenter. Trials were filmed using two video cameras (Canon NTSC Elura 100 and Canon NTSC 2R 100), one tripod-mounted camera filming straight-on and one camera held by an experimenter filming from an oblique angle above the subject.

The chimpanzees at the Yerkes National Primate Research Center (Joseph and Christa) were confined in two outdoor sections of their home cage (each 2.3 x 4.3 x 2.4 m). The experimenter placed the tray in one section of the cage (Section A) while the subject was confined in the other section (Section B). Then the experimenter admitted the subject into Section A. The straight sticks were handed to the subject through the wire mesh of the cage; the T-shaped stick was placed beside the tray because it didn’t fit through the mesh. When the trial was completed the experimenter called the subject back to Section B then removed the tray from

Section A. Trials were filmed by a video camera (Canon Vixia HD40) mounted on a tripod positioned directly in front of Section A.

Procedure

Trials began once the tray and stick(s) were presented to the subject. Subjects were allowed to work with the stick until they successfully inserted it into the groove in the tray. Completion of a trial was followed by verbal praise and a food reward: the capuchins received a piece of a cashew; the chimpanzees at the LRC received a slice of a banana, a sip of juice, or a grape; the chimpanzees at Yerkes received a piece of green pepper, sweet potato, onion, banana, or a grape.

On the first testing day, the subject completed ten trials of the baseline condition before moving on to the next condition. On each subsequent testing day the subject completed three trials of baseline before moving on. The order in which each subject received Conditions A through D was predetermined using a Latin Square. Each subject completed one trial of each condition before moving to the next condition. The order of conditions was repeated until the subject had completed ten trials of each condition. Subjects completed a maximum of 25 trials in a testing day.

Coding

Each trial was coded from the digitized videos using Observer 10 XT^{TM} software (Noldus Information Technology). By definition, a trial began when the subject had the tray and the stick(s) in its possession and ended when it had successfully inserted the stick or sticks into the groove(s). For each trial we coded discrete attempts in which the subject tried to place the stick in the groove. The first attempt was defined as the first instance in which the stick touched the tray. For each attempt we coded the alignment of the stick with respect to the groove, whether the stick slid across the tray surface or groove, and which hand the subject used to hold the stick.

The alignment of the stick with respect to the groove was the first variable coded for each attempt in a trial. We used a clock face classification rubric (depicted in Figure 1) to code this variable. As seen in Figure 2, if the stick was placed parallel to the groove, or within approximately 22.5° of parallel, we coded a 12-6 alignment. If the stick was placed perpendicular to the groove, or within 22.5° of perpendicular, it was considered a 3-9 alignment. If the stick was placed somewhere between the ranges of 12-6 and 3-9 alignment, this was considered either 1-7 alignment or 4-10 alignment. In addition, for Condition D, we coded the "polarity" of the crossbar of the T-shaped stick with respect to the crossbar of the T-shaped groove (crossbar versus stem depicted in Figure 1). If the stick was placed so that its crossbar was located in the same hemisphere (across 3-9) as the groove's crossbar, then the stick was considered "aligned." If this was not the case, the stick was considered "not aligned." This can be seen in Figure 2.

The second variable coded for each attempt was surface assistance. Surface assistance involved moving the stick along the surface of the tray so as to make contact with the groove. For example, a subject could place the stick on the tray and slide it across the tray until it hit the groove. A subject could also place the tip of the stick into the groove and then slide it in order to lower the rest of the stick into the groove. Figure 2 depicts examples of surface assistance and no surface assistance. Lastly, the third variable coded was which hand subjects used for each attempt (right, left, or both).

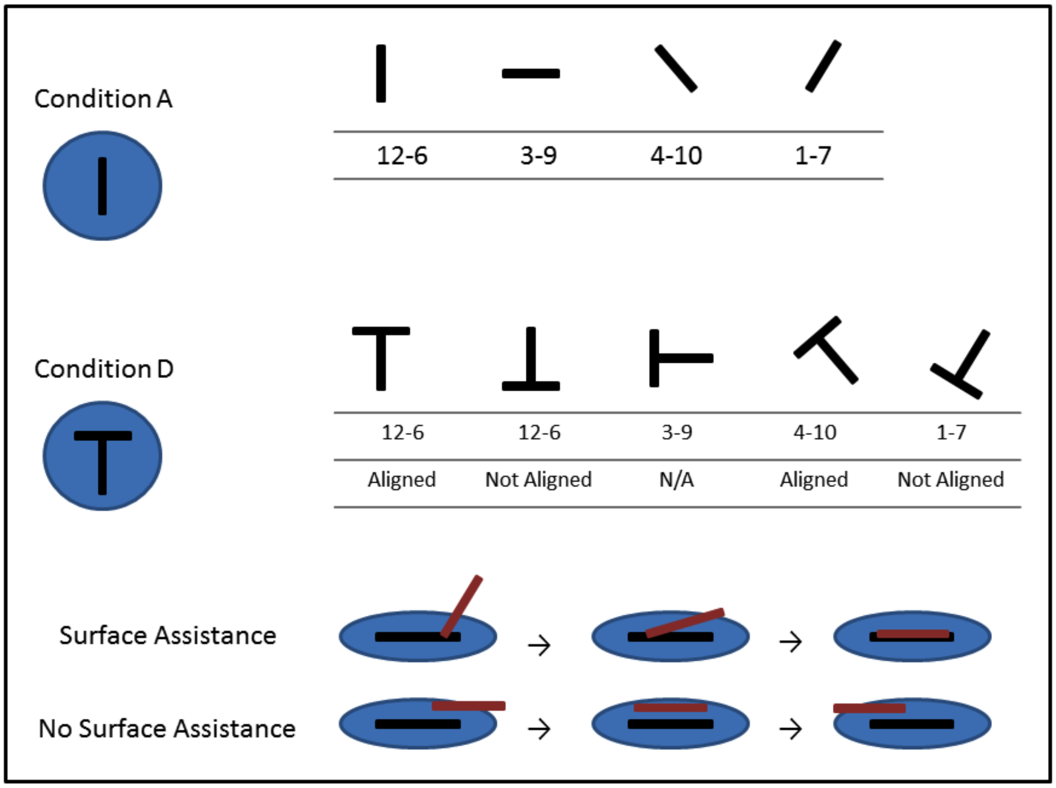

Figure 2. Stick Alignment Possibilities and Examples of Surface Assistance

An attempt ended and a new one began when the stick was removed from the tray and then brought back in contact or if any one of the above variables changed: clock face alignment (and polarity where applicable), surface assistance, or hand used. For example, if the subject placed the stick in a 12-6 orientation with its right hand, then removed the stick before placing it in a 1-7 orientation with its right hand, two attempts would be coded: one right-hand attempt in 12-6 alignment and one right-handed attempt in 1-7 alignment. In another example, if the subject placed the stick in a 12-6 alignment and then spun it until it landed in a 4-10 alignment, this would be coded as two attempts (one with 12-6 alignment and one with 4-10 alignment). The clock face orientations between 12-6 and 4-10 would be ignored unless the stick was paused in those orientations. The sole coder (L. la Cour) established an intraobserver reliability of 92% agreement (Cohen's κ = 0.91).

Analysis

The first ten completed trials were analyzed for all individuals. Data from each species were analyzed separately where pairwise comparisons indicated that the species differed. We used a Freidman's χ^2 to test the prediction that more attempts would be necessary to align an object with two spatial relations to be dealt with sequentially, rather than one. We used the same test to evaluate the prediction that more attempts would be necessary when two relations had to be dealt with concurrently rather than sequentially. For both predictions we followed up significant results with pair-wise Wilcoxon tests, using one-tailed α=0.05. This allowed us to see the overall trend in the number of attempts among conditions for both species. We then used a Friedman's χ^2 within subjects, followed by pair-wise Wilcoxon tests for significant results, to test these two predictions for individual subjects.

We used χ^2 tests within subject to evaluate bias to align the object at a 12-6 orientation, which was typically the goal orientation of the task. This was done for Conditions A, B, and D. In the case of Condition D, we evaluated whether the stem of the T was aligned in a 12-6 orientation. Chance was set at 0.25 since there were four possible clock face orientations (12-6, 1-7, 3-9, and 4-10), each covering one fourth of the tray's circle. Condition C involved two goal orientations: 12-6 for the stem of the separated T and 3-9 for the crossbar of the separated T. Thus, for this condition we evaluated the bias to align the sticks in either the 12-6 or 3-9 orientation and chance was set at 0.50. Finally, proper alignment in Condition D required not only that the stem of the T was in a 12-6 orientation but also that the crossbar of the T was aligned with the crossbar of the groove. We used χ^2 tests within subject to determine if the T was aligned more often than expected by chance, which was set at 0.50 according to the two alignment options for the crossbar (aligned or not aligned).

To evaluate the prediction that subjects would increasingly use surface assistance as the conditions moved from one to two spatial relations and from sequential to concurrent, we used pair-wise Wilcoxon tests within subject. We also used pair-wise Wilcoxon tests within subject to determine if individuals expressed a hand bias.

Analyses were conducted using SPSS 17.0 (SPSS Inc., Chicago, IL). Where multiple pair-wise tests were conducted on the same data set, α levels were set at 0.05 divided by the number of tests (Bonferroni, 1936).

CHAPTER 3

RESULTS

Effect of the Number of Sequential and Concurrent Relations on the Number of Alignment Attempts per Trial

Pair-wise comparisons showed no significant difference in number of attempts between the two species for any of the four conditions (Friedman: $N = 60$, df = 1, range of $\chi^2 = 0.001$-1.723, range of P values = 0.189-1.000). Thus, we pooled both species in order to analyze the effect of condition on number of attempts. We found a significant difference in the number of attempts per trial across conditions (Friedman: $N = 120$, df = 3, $\chi^2 = 142.922$; $P < 0.001$). Pair-wise Wilcoxon tests between conditions, with an $\alpha=0.008$ after the Bonferroni correction, revealed a significant increase in the number of attempts between Conditions A and B (Wilcoxon: $N = 120$, $Z = -7.566$, $P < 0.001$), Conditions A and C ($Z = -7.91$, $P < 0.001$), Conditions A and D ($Z = -8.104$, $P < 0.001$), Conditions B and D ($Z = -4.385$, $P < 0.001$), and Conditions C and D ($Z = -3.223$, $P = 0.001$). Figure 1 shows the average number of attempts per condition for each species. Refer to Table 1 for individual results from each condition.

Effect of the Goal Orientation on Alignment of the Stick(s) with the Groove(s)

In Conditions A, B, and D, only a 12-6 orientation, with respect to the clock face coding scheme, could lead to successful alignment of the stick with the groove. As shown in Table 2, most subjects aligned the sticks in a 12-6 orientation more often than expected by chance. Since the 12-6 orientation was one of four possible orientations that we coded, chance was set at 25%.

In Condition C, there were two goal orientations. Subjects needed to place one stick in a 3-9 orientation and one stick in a 12-6 orientation. Table 3 shows the number and proportion of attempts made by each subject in a 12-6 or a 3-9 orientation in Condition C. All subjects aligned the sticks with a 12-6 orientation or a 3-9 orientation more often than expected by chance. Chance was set at 50%.

Condition D presented still one more alignment requirement. Not only did the T-shaped stick need to be oriented in a 12-6 alignment, but the crossbar of the T needed to be aligned with the crossbar of the groove. If not aligned correctly, the T stick would be upside down with respect to one groove. As shown in Table 4 only four subjects (two capuchins and two chimpanzees) aligned the crossbar of the T stick with the groove significantly more often than expected by chance, which was defined at 50%. These four individuals aligned the crossbar appropriately between 66% and 79% of the time.

For Condition C we also checked to see whether subjects chose to align the first stick with the stem of the separated T (a 12-6 orientation) or the crossbar (a 3-9 orientation). Because the other conditions included mostly grooves of a 12-6 orientation, subjects became more familiar with this alignment and this could cause them to prefer aligning the stem of the T first rather than the less familiar crossbar. As shown in Table 5, only two subjects (two chimpanzees) chose to align the crossbar first more often than the stem of the separated T. All other subjects aligned the stem first on at least 60% of trials.

Use of Actions That Decrease the Mobility of the Stick when Aligning the Stick to the Groove

Among both capuchins and chimpanzees, the average proportion of the use of surface assistance decreased as the conditions increased in difficulty (see Figure 4). However, as in the analysis of the number of attempts, we did not find a significant difference in the use of surface assistance between the two species for any of the four conditions (Friedman: $N = 120$, df = 1, range of $\chi^2 = 0.083$-0.421, range of P values = 0.516-0.773). Thus, we pooled all subjects' data for our analysis of surface assistance. The mean number of attempts in which surface assistance was used declined from 80% in Condition A to 60% in Condition D. We found a significant difference in the use of surface assistance per trial across conditions (Friedman: $N = 120$, df = 3, $\chi^2 = 21.837$; $p < 0.001$). Pair-wise Wilcoxon tests between conditions, with an $\alpha = 0.008$ after the Bonferroni correction, revealed a significant decrease in the use of surface assistance between Conditions A and D (Wilcoxon: $N = 120$, $Z = -4.799$, $P < 0.001$) and Conditions B and D ($Z = -3.316$, $P = 0.001$).

Some individuals expressed a significant bias for one hand but no directional bias for the group was found. Three of 12 individuals chose to use two hands more often than one hand. Five individuals used their left hand significantly more often than the right hand while three individuals used their right hand significantly more often than the left hand. One individual chose to use his left and right hands at an approximately equal rate; he used his right hand in 45% of attempts and his left hand in 46% of attempts. Table 6 shows the percent use of right, left, and both hands for each subject across all conditions. It also shows the handedness index (HI), which portrays the subject's hand bias on a continuum from a strong left-hand preference (-1.0) to a strong right-hand bias (1.0) (Hopkins, 1995). Positive values correspond to a right-hand bias while negative values correspond to a left-hand bias.

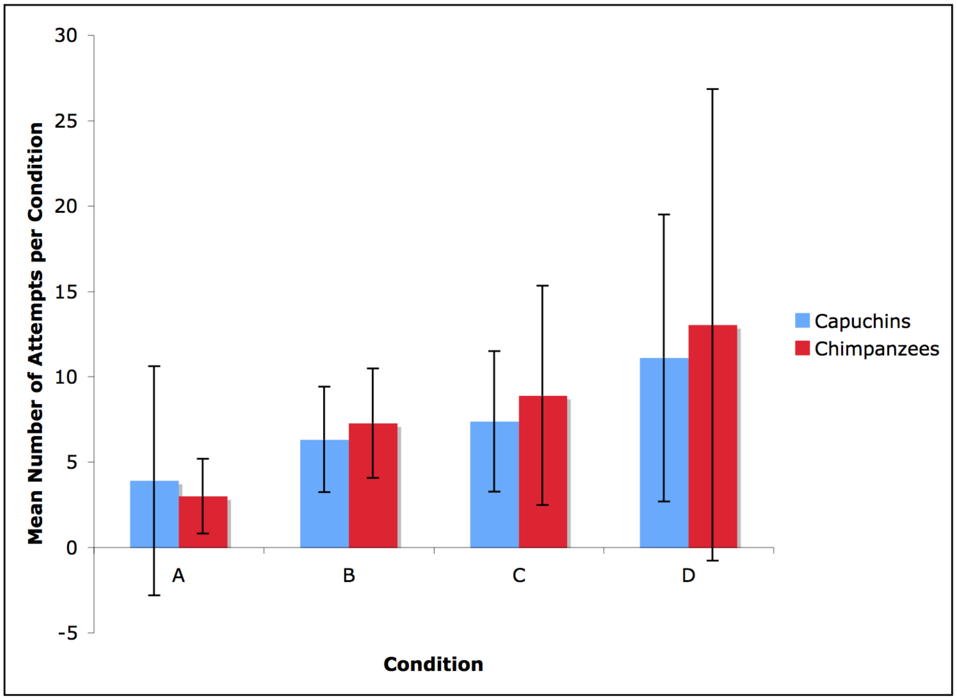

Figure 3. Mean Number of Attempts per Condition for Each Species

Table 1. The Number of Attempts per Completed Trial of Each Condition for Each Subject (Mean, Above, and Standard Deviation)

Species	Subject	Condition A	Condition B	Condition C	Condition D	All Conditions
CEBUS	Chris	8.1	6.5	8.8	13.8	9.3
		14.73	2.55	6.78	8.88	9.38
	Leo	2.5	6.2	6.5	9.9	6.28
		1.78	1.75	2.32	6.12	4.28
	Nick	4.2	7.6	6.9	9.8	7.13
		3.29	3.83	5.22	6.96	5.24
	Solo	1.4	6.2	6.4	10.8	6.2
		0.7	3.29	2.12	10.36	6.31
	Xavier	4.5	5.5	6.8	12	7.2
		4.58	2.84	2.82	9.57	6.19
	Xenon	2.7	5.9	8.9	10.3	6.95
		3.37	4.01	3.6	9.26	6.16
	Mean	**3.9**	**6.32**	**7.38**	**11.1**	**7.18**
		6.7	3.08	4.12	8.4	6.47
PAN	Christa	3	6.4	10.8	18.6	9.7
		1.76	3.03	3.65	18.85	11.08
	Joseph	5.2	8.6	8.9	19.7	10.6
		3.82	4.09	4.89	22.82	12.78
	Lana	2.9	6.4	8.4	13.3	7.75
		1.73	2.41	3.34	8.79	6.08
	Mercury	2.1	9.8	13.9	7.9	8.43
		0.99	3.79	12.59	3.96	7.89
	Panzee	2.9	6.7	5.9	7	5.63
		0.57	1.77	1.6	2.4	2.32
	Sherman	1.9	5.7	5.5	11.7	6.2
		1.45	2.11	2.42	11.06	6.61
	Mean	**3**	**7.27**	**8.9**	**13.03**	**5.68**
		2.2	3.21	6.42	13.82	8.61

Table 2. Number and Proportion of Attempts (Conditions A, B, and D) for Each Subject in which the Stick Was Aligned in a 12-6 Orientation

Species	Subject	Condition	# Attempts Aligned/Total	Proportion Aligned	# Expected by chance	Chi Square
CEBUS	Chris	A	14/38	0.37	9.5	2.84
		B	39/69	0.57	17.25	44.08*
		D	57/181	0.31	45.25	4.07*
	Leo	A	14/25	0.56	6.25	12.81*
		B	45/62	0.73	15.5	74.86*
		D	35/99	0.35	24.75	5.66*
	Nick	A	14/42	0.33	10.5	2.13
		B	40/76	0.53	19	30.95*
		D	34/98	0.35	24.5	4.91*
	Solo	A	7/14	0.5	3.5	4.67*
		B	39/62	0.63	15.5	47.5*
		D	41/108	0.38	27	2.77
	Xavier	A	28/45	0.62	11.25	34.68*
		B	44/55	0.8	13.75	67.12*
		D	35/120	0.29	30	2.94
	Xenon	A	20/27	0.74	6.75	33.25*
		B	42/59	0.71	14.75	88.73*
		D	33/103	0.32	25.75	1.24
	Mean	**A**	**16/32**	**0.5**	**7.96**	
		B	**42/64**	**0.65**	**15.96**	
		D	**39/118**	**0.33**	**29.54**	
PAN	Christa	A	15/30	0.5	7.5	10*
		B	40/64	0.63	16	48*
		D	63/186	0.34	46.5	7.81*
	Joseph	A	22/52	0.42	13	8.31*
		B	34/86	0.4	21.5	9.69*
		D	59/197	0.3	49.25	1.35
	Lana	A	14/29	0.48	7.25	8.379*
		B	35/64	0.55	16	30.08*
		D	54/133	0.41	33.25	17.27*
	Mercury	A	10/21	0.48	5.25	5.73*
		B	53/98	0.54	24.5	44.2*
		D	32/79	0.41	19.75	10.13*
	Panzee	A	21/29	0.72	7.25	34.77*
		B	41/67	0.61	16.75	46.81*
		D	38/70	0.54	17.5	32.02*
	Sherman	A	13/19	0.68	4.75	19.11*
		B	32/57	0.56	14.25	29.48*
		D	47/117	0.4	29.25	14.36*
	Mean	**A**	**16/30**	**0.53**	**7.5**	
		B	**39/73**	**0.54**	**18.17**	
		D	**49/130**	**0.37**	**32.58**	

*P<0.05; chance set at 0.25.

Table 3. Number and Proportion of Attempts (Only Condition C) for Each Subject in which the Sticks Were Aligned in either a 12-6 or a 3-9 Orientation

Species	Subject	# Attempts Aligned/Total	Proportion Aligned	# Expected by chance	Chi Square
CEBUS	Chris	72/88	0.89	44	35.64*
	Leo	44/65	0.68	32.5	8.14*
	Nick	49/69	0.71	34.5	12.19*
	Solo	39/64	0.61	32	3.06
	Xavier	58/68	0.85	34	33.88*
	Xenon	73/89	0.82	44.5	36.51*
	Mean	**56/74**	**0.76**	**36.92**	
PAN	Christa	83/108	0.77	54	31.15*
	Joseph	55/89	0.62	44.5	4.96*
	Lana	54/84	0.64	42	6.86*
	Mercury	91/139	0.65	69.5	13.3*
	Panzee	47/59	0.8	29.5	20.76*
	Sherman	46/55	0.84	27.5	24.89*
	Mean	**63/89**	**0.7**	**44.5**	

*$P<0.05$; chance set at 0.5.

Table 4. Number and Proportion of Attempts for Each Subject in which the Crossbar of the T Stick Was Aligned with the Crossbar of the T Groove (Only Condition D)

Species	Subject	# Attempts Aligned/Total	Proportion Aligned	# Expected by chance	Chi Square
CEBUS	Chris	32/57	0.56	28.5	0.86
	Leo	16/35	0.46	17.5	0.257
	Nick	16/34	0.47	17	0.12
	Solo	31/47	0.66	23.5	4.89*
	Xavier	28/41	0.68	20.5	5.49*
	Xenon	16/33	0.48	16.5	0.03
	Mean	**23/41**	**0.56**	**20.58**	
PAN	Christa	63/131	0.48	65.5	0.19
	Joseph	68/145	0.47	72.5	0.56
	Lana	41/52	0.79	26	17.31*
	Mercury	25/32	0.78	16	10.13*
	Panzee	24/38	0.63	19	2.63
	Sherman	25/42	0.6	21	1.52
	Mean	**41/73**	**0.56**	**36.67**	

*P<0.05; chance set at 0.5.

Table 5. Number and Percent of Trials in which Subjects First Aligned the Stem of the T versus the Crossbar of the T (Condition C Only)

Species	Subject	1st stick stem	1st stick cross	% stem 1st
CEBUS	Chris	7	3	70
	Leo	7	3	70
	Nick	8	2	80
	Solo	7	3	70
	Xavier	8	2	80
	Xenon	9	1	90*
	Mean	**7.67**	**2.33**	**77**
PAN	Christa	3	7	30
	Joseph	8	2	80
	Lana	6	4	60
	Mercury	8	2	80
	Panzee	9	1	90*
	Sherman	3	7	30
	Mean	**6.17**	**3.83**	**62**

*$P<0.05$; chance set at 0.5.

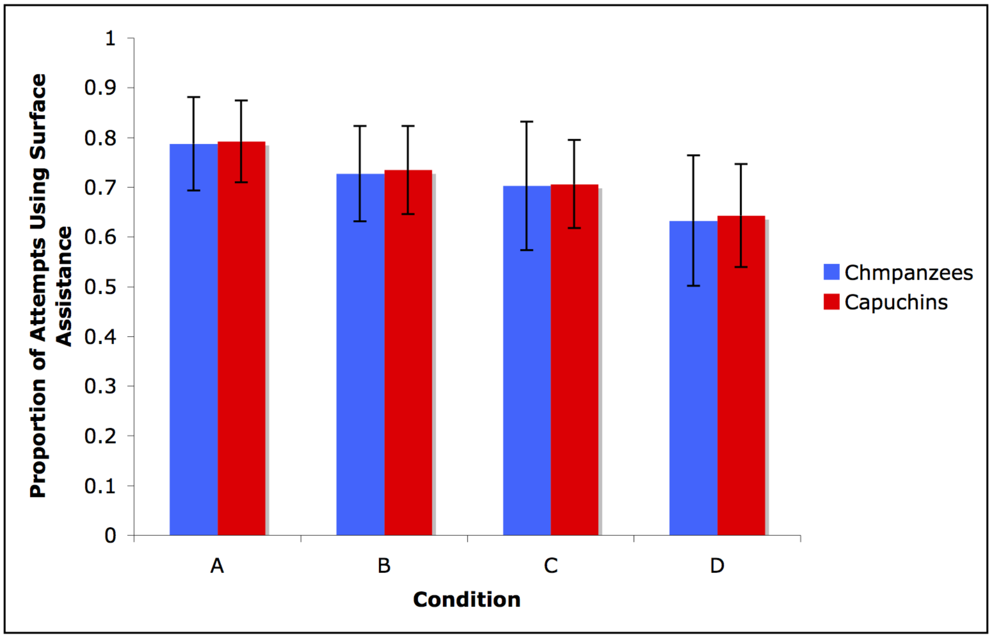

Figure 4. Mean Proportion of Attempts Using Surface Assistance Across All Subjects for Each Condition

Table 6. Percent Use of Each Hand and the Handedness Index (HI) for Each Subject Across Trials

Species	Subject	% Right	% Left	% Both	HI
CEBUS	Chris	45	46	9	-0.01
	Leo	37	16	47	0.38
	Nick	94	4	2	0.92
	Solo	13	14	73	-0.04
	Xavier	42	50	8	-0.08
	Xenon	29	65	6	-0.38
	Mean	**43.33**	**32.5**	**24.17**	**0.13**
PAN	Christa	19	40	41	-0.35
	Joseph	100	0	0	1
	Lana	29	39	31	-0.15
	Mercury	8	54	38	-0.75
	Panzee	10	15	75	-0.21
	Sherman	67	13	20	0.68
	Mean	**38.83**	**26.83**	**34.17**	**0.21**

CHAPTER 4

DISCUSSION

By definition, tool use involves producing one or more allocentric spatial relations between the tool and another object or surface (Fragaszy et al., 2011). In order to understand how an individual might go about learning to use a tool, the ecological perspective (Gibson, 1979; Smitsman, 1997) and Lockman's perception-action theory (2000) direct us to look at the affordances of the objects and relations involved, how to produce the needed allocentric relations, and how to manage them. Beginning at age three or four, humans are able to manage more than one spatial relation concurrently when positioning objects into a groove or onto an image (Fragaszy, Kuroshima, & Stone, manuscript in preparation), but data from Fragaszy et al. (2011) have shown that adult capuchins and chimpanzees are challenged by such a task. In the current study, individuals were required to align one stick or two sticks with the matching groove(s) in a tray. As with using a hand tool, the task required the individual to manage one or two allocentric spatial relations between hand-held objects and a fixed surface and, in the case of two relations, to manage them either sequentially or concurrently.

All attempts to align objects seen in this study consisted of the individuals bringing the stick in contact with the tray, including banging the stick, dragging it across the surface, or inserting one end into the groove and rotating the stick to align it. We never witnessed individuals of either species visually aligning the sticks with the groove before contact was made. In contrast, beginning at the age of about four, children are able to hold the stick above the groove, align it visually, and then place it directly into the groove on the very first attempt

(Fragaszy, Kuroshima, & Stone, manuscript in preparation). We did see a few instances in which subjects slid the stick into the groove on the first attempt; the capuchins completed 23 trials (out of a total of 240 trials) in a single attempt (21 trials were Condition A and 2 were Condition D) while the chimpanzees completed 15 trials (out of 240) in a single attempt (all in Condition A). However, these single-attempt trials were accomplished using surface assistance rather then visual alignment alone, as humans do from a young age. This suggests that non-human primates rely less on vision to achieve alignment than do humans. If not by vision, how do non-human primates align axes of objects? We shall argue below that they do so primarily haptically, but first we shall examine the effects of the number of spatial relations on performance in the task.

Form and Number of Attempts to Align Sticks to Groove

The challenge posed by this alignment task was evident across all conditions. We found that, as seen in Fragaszy et al. (2011), subjects did find two spatial relations more difficult to manage than a single relation, as reflected by the significantly greater number of attempts per trial needed to align the object in Conditions B, C, and D than in Condition A. We also found that subjects were more challenged by the management of two concurrent relations than by management of two sequential relations, as evidenced by the significant increase in number of attempts from Condition B to Condition D. Even when the task involved the alignment of just one spatial relation individuals required multiple attempts each trial to accomplish their goal (on average, three to four attempts). We predicted these findings based on Fragaszy and Cummins-Sebree's (2005) model of spatial reasoning, a comparative expansion of Lockman's (2000) perception-action theory.

More specifically with regard to alignment, we found that subjects appropriately aligned the sticks in the 12-6 orientation significantly more often than expected by chance (25%) in Conditions A, B, and D. However, although above chance, the subjects were still rather inexact in their alignment. In each of these conditions, the 12-6 orientation was the only orientation in which the stick was properly aligned with the groove. Subjects managed to align the stick roughly to the 12-6 orientation on 49% of attempts across all trials in Conditions A, B, and D. For Condition C, with two sticks separately forming a T when both are placed in the tray, chance was defined as 50% to reflect the two goal orientations – 12-6 for the stem of the T and 3-9 for the crossbar (as seen in Figure 1). In this case, the subjects aligned each stick in either a 12-6 or a 3-9 orientation in 70-76% of attempts, which is significantly different from chance. Thus, all individuals except one capuchin aligned the sticks in either a 12-6 or a 3-9 orientation, as opposed to a 1-7 or a 4-10 orientation, significantly more often than expected by chance, but far from universally. The lowest score for alignment in Condition C was earned by one capuchin that aligned the sticks correctly on 61% of attempts (not significantly different from chance).

In Condition D the task presented a concurrent second spatial relation, which involved the alignment of the crossbar of the T stick with the crossbar of the groove. We analyzed how many attempts individuals made in the 12-6 orientation that also involved the appropriate alignment of the crossbar. Again, chance was set at 50% to reflect the two possibilities that the T was upside down (the crossbar was not aligned) or right side up (the crossbar was aligned). Four individuals (two capuchins and two chimpanzees) appropriately aligned the crossbar of the stick with the crossbar of the groove significantly more often than expected by chance (66% to 78% of attempts) and at about the same rate as they aligned the parts of the T in Condition C (as described above).

In this study we intentionally made each stick and portion of the T the same width and length so that no aspect of the objects would become more perceptually obvious than another. However, by virtue of the conditions subjects might have become more familiar with placement in the 12-6 orientation since only Condition C involved an instance in which alignment required the 3-9 orientation. Thus, we analyzed each trial of Condition C for each subject to determine how often individuals placed the first stick in the stem of the separated T groove rather than the crossbar groove (seen in Figure 1). We found that ten of twelve subjects (which is significantly more than expected by chance; p=0.019) did in fact place the first stick in the stem groove at least 60% of the time, although only two of these subjects did so significantly more than expected by chance (at least 90% of the time). These findings were consistent for the ten subjects regardless of the orientation of the grooves in relation to the subject when the tray was given to the subject. One interpretation of this finding is that these ten subjects perceived one portion of the T (as seen in Figure 1) as the stem and worked to align the object first with that portion. Thus, when the subjects were required to manage two spatial relations they dealt first with the most familiar part of the task. The fact that the 3-9 orientation was only required for alignment in one condition, and thus less familiar to the subjects, could be the reason why we did not find a significant difference in the number of attempts made between Conditions C and D (both of which produce a T shape). Dealing with this unfamiliar alignment required more attempts and, thus, increased the number of total attempts in Condition C compared to Condition B.

Our current findings along with those of Fragaszy et al. (2011) provide strong support for the central predictions of Fragaszy and Cummins-Sebree's (2005) model of spatial reasoning, that increasing the number of spatial relations involved makes placement more difficult and managing concurrent relations is more difficult than managing the same number of sequential relations. The subjects required a 1.5-2 fold increase in the number of attempts to align an object embodying two relations rather than one, which is a significant increase. In addition, when the second spatial relation was concurrent with the first, subjects needed significantly more attempts than when the two relations could be managed sequentially; the number of attempts doubled from Condition B to Condition D. When the stick was T-shaped, the subjects aligned the stem of the T consistently more often than expected by chance (aligned in 33% of all attempts in Condition D). Chance in this case was defined as 25% considering there were four orientations in which the T could be placed (12-6, 1-7, 3-9, and 4-10). However, when they aligned the stem, they were unable to align the crossbar of the T concurrently more often than expected by chance (aligned in 56% attempts in Condition D), where chance was defined as 50% since the T could be placed right side up (crossbar aligned) or upside down (crossbar not aligned).

These findings help us to interpret the instances of spontaneous tool use seen among chimpanzees and capuchins in their natural habitats. Most instances of tool use seen among non-human primates involve a single point relation (object to a point), such as when probing or termite fishing (Hayashi et al., 2005; Fragaszy et al., 2011). Termite fishing requires that the individual align one end of the stick to touch the hole in the termite nest. Once this is accomplished the stick can be rotated to achieve the correct orientation for insertion, with haptic information arising from the pressure where it has been inserted against the wall of the nest. Thus, this is a relatively permissive alignment problem. Once inserted, a variety of finely tuned, haptically-guided maneuvers with the probe object may be used, from delicately moving the probe to follow irregular tunnels (seen in chimpanzees; Teleki, 1974) to twisting the probe, which appears to reduce the probability of breaking the probe (seen in capuchins; Souto, Bione, Bastos, Bezerra, Fragaszy, & Schiel, 2011). Note that the sophistication of skill achieved in these instances, and others described by field workers, rely primarily upon the use of active touch (Turvey, 1996; Jones & Lederman, 2006) of objects already in contact with a surface. Non-human primates share with humans a wide array of skills mediated by active touch (Fragaszy & Crast, in review).

The most structurally complex form of tool use seen among non-human primates is nut cracking using a hammer (Fragaszy et al., 2004; Inoue-Nakamura & Matsuzawa, 1997). Nut cracking requires producing two sequential allocentric spatial relations – placing the nut upon the anvil and striking the nut with the hammer. There have been no instances, to our knowledge, reported of non-human primates spontaneously using tools in a way that incorporates producing two concurrent relations or more than two spatial relations in sequence in their natural habitats. Wild chimpanzees and capuchins have each occasionally been seen to use two or more single-relation tools in succession (Sanz & Morgan, 2009; Falotico, 2010). Humans, on the other hand, perform such tasks on a daily basis; every day many of us lock and unlock our front door, which requires the concurrent management of two spatial relations (the narrow end of the key and the grooved side of the key in relation to the lock). With practice, we master a variety of tasks involving two concurrent allocentric relations with fine control of the angle and production of force. An example of this is seen among expert glass bead knappers in India (Bril et al., 2005). These expert knappers produce beads by holding a glass block against an iron bar (used as an anvil) with one hand and removing flakes from the glass block by hitting it with a buffalo horn hammer on the end of a flexible wooden stick, held in the other hand. The knappers adjust the angle of the glass against the iron bar and the amount of force with which the hammer hits the glass in order to remove the appropriately sized flake. The result is a beautiful ellipsoid bead.

Strategies to Manage Multiple Spatial Relations

An increase in the number of spatial relations involved in a task increases the number of directions in which movement is possible, and the more directions of movement that must be monitored and managed, the more difficult the task becomes. We predicted that the capuchins and chimpanzees would act in some way that would reduce some of the mobility involved in the alignment task. Using the fixed platform of the tray to guide the stick, which we called "surface assistance," might serve this purpose. If the individual used the tray to guide the stick there would be less movement of the stick in the vertical plane because it is pressed against an unmoving surface. We also predicted that such actions would increase in frequency as the number of spatial relations inherent in the task increased.

We found that subjects of both species used surface assistance in more than half of the trials in each condition**.** Across all subjects and all trials in that condition, surface assistance was used in 281 attempts of 412 total attempts in Condition A, 566 of 815 attempts in Condition B, 648 of 976 attempts in Condition C, and 867 of 1437 attempts in Condition D. This is strong evidence for the hypothesis that these species solve an alignment problem differently than do adult humans, who align objects primarily visually (Fragaszy, personal experience). However, we did not see the predicted increase in surface assistance as the tasks increased in difficulty, nor can we claim that we found a ceiling affect because surface assistance decreased from Condition A (used in 79% of attempts) to Condition B (used in 73% of attempts) for 5 chimpanzees and 4 capuchins. Four subjects of each species showed a decrease in surface assistance from Condition B to Condition C (70%), while four subjects of each species also showed a decrease from Condition C to Condition D (64%). All subjects of both species showed a decrease in the use of surface assistance from Condition A (the easiest task) to Condition D (the most complex task) while the mean number of attempts needed to achieve alignment increased four fold from 3.45 to 12.05 over these same conditions. This decrease suggests that individuals explore new actions when they fail to achieve their goal.

The use of two hands might be another way that subjects could stabilize the stick during alignment. However, subjects seemed to make the choice to use their right hand, left hand, or both hands at the beginning of testing and this preference stayed relatively consistent across trials. Only two subjects (one capuchin and one chimpanzee) used a bimanual strategy the majority of the time. All other subjects showed a unimanual bias except one capuchin that used his right and left hands at an equal rate. Thus, it seems that though the task results in a hand preference on an individual basis, it does not produce a population-level hand bias, and most subjects did not adopt a bimanual pattern.

In conclusion, we did not identify a strategy to reduce the mobility in this task across subjects that was responsive to increasing demands for management of allocentric relations. All subjects used surface assistance on over 50% of attempts but the number of attempts using surface assistance decreased as the mobility inherent in the task increased. In terms of hand preference, only two individuals used both hands more often than one hand. To further explore the possible use of strategies we examined the three subjects that required the most attempts across conditions to complete the task and thus had the most difficulty with the task. We thought we might see a particular strategy emerge from the increased number of attempts that would reflect how the subject was dealing with the difficulty. However, these subjects, one capuchin and two chimpanzees, did not show a specific pattern of actions that differed from other individuals' patterns. They did not use surface assistance less than other subjects, nor did they show a distinctive pattern of hand bias (one used both hands most often, one used its right and left hands equally often, and one its right hand for all trials). These findings do not support our prediction that subjects will adopt a manual strategy to reduce mobility as the number of directions of movement involved in the task increases.

Contacting the stick with the surface, as in surface assistance, could instead be an exploratory procedure that generates haptic information about the tray and location of the groove in addition to or rather than as a way to reduce the degrees of freedom involved in the task. Lederman and Klatzky (1987) described exploratory procedures (EPs), which are highly stereotyped movements of the hand that humans use to explore an object or surface. EPs identified by Lederman and Klatzky (1987) include lateral motion, pressure, static contact, unsupported holding, enclosure, and contour following, and humans use them to explore objects and surfaces for different properties (such as weight, volume, texture, etc). Lacreuse and Fragaszy (1997) compared EPs in humans and capuchins and found that capuchins perform the same EPs as seen among humans when manually exploring an object. Comparable data are not yet available for chimpanzees. However, because this species displays similar manual function during the manipulation of objects as well as relatively similar hand anatomy, it seems plausible that they too will share EPs with capuchins and humans. We expect both species can determine an object or surface's properties through manual exploration just as a human can.

Lederman and Klatzky (1987) defined EPs as actions in which the hand explores the object. For instance, according to Lederman and Klatzky (1987), contour following occurs when the hand remains in contact with the contour of the object. It is used to determine the shape and/or volume of the object. In this study, we saw the subjects make some alignment attempts in which the stick followed the surface of the tray even as it dipped down into the groove. This form of active contact with the tray and groove can provide subjects with information concerning location of the groove and its width or length, and thus, its shape. Applying torque or force to an object produces the “pressure” EP (Lederman & Klatzky, 1987). In this study, we extend the concept of EPs to include the stick’s exploration of the tray. Lederman and Klatzky (1987) did not address such indirect exploration but it may be just as useful as manual exploration in some instances, as in the pressure EP. By applying force to the tray via the stick the subject can learn about the hardness of the tray’s material just as it would if it used its hand to do so. Using the stick to explore an object may not produce as many EPs as manual exploration; for instance, it will not allow an individual to determine the temperature of the tray as would static contact between the object and hand. However, exploration of the tray via the stick may be the reason that our subjects commonly used surface assistance in this study.

Comparison of Species in the Task

In general, the capuchins and chimpanzees did not differ in the number of attempts made across conditions, the efficiency at which they aligned the sticks, or the rate at which they used surface assistance. The two subjects that made the most attempts across conditions were both chimpanzees. Neither of these subjects had participated in the previous object alignment study done by Fragaszy et al. (2011); this study was their first encounter with an experimental object alignment paradigm, whereas all the other subjects had participated in the study by Fragaszy et al. (2011). This could be the reason that these two subjects required more attempts across conditions to align the objects.

Although this study did not involve tool use, the subjects’ ability to manage relations in this task should be reflected in their ability to manage similar relations in tasks that do involve tool use (Fragaszy & Cummins-Sebree, 2005). Thus, we should see that capuchins and chimpanzees are similar in their abilities to use tools in nature (restricting tool use to the management of one relation at a time), and they appear to be. Both capuchins and chimpanzees crack nuts using stone hammers as well as use sticks to probe for insects, including fishing for termites (Shumaker et al., 2011; Souto et al., 2011). Chimpanzees dip for ants and use different tools sequentially to extract honey from bee hives and termite mounds, both in trees and underground (Boesch, in press; Sanz & Morgan, 2009). Capuchins excavate tubers with stones and flush vertebrate prey with sticks (Falotico, 2010). These forms of tool use involve managing one spatial relation at a time rather than concurrently.

In this study, we also found evidence of species-typical approaches to alignment problems central to tool use. Capuchins banged the sticks against the surface of the tray more often than did the chimpanzees. The chimpanzees produced more rolling and sliding rather than percussive movements. Banging and pounding objects appears in a capuchin's manipulation repertoire within the first year of life (Fragaszy & Adams-Curtis, 1991; Byrne & Suomi, 1996). Dogo de Resende, Ottoni, and Fragaszy (2008) conducted a longitudinal study focusing on the development of tool use, particularly nut cracking. They found that percussive actions between objects and surfaces appear very early in young capuchins' development and, in accord with this action bias, capuchins readily strike nuts against stones at a very early age. However, release of the nut on the stone so that it can be struck with another object (the stone hammer) appears much later. Young chimpanzees, on the other hand, readily place and release objects but do not produce percussive actions very often (Takeshita, 2001). Thus, although individuals of both species become excellent nut crackers, the two species go about learning the skill in ways that build upon actions most common in their repertoire – percussion in capuchins and placement in chimpanzees.

Regardless of the differences in how chimpanzees and capuchins acquire their tool use, the types of tool use seen within these two species are similar concerning the number and temporality of spatial relations. The findings from Fragaszy et al. (2011) as well as this study provide us with an explanation for this similarity. Subjects participating in Fragaszy et al.'s (2011) study seemed to reach a ceiling in ability to manage relations when the number went beyond 2 concurrent spatial relations. In this study we found that 2 concurrent relations is more difficult to manage than 2 sequential relations. The most important conclusion we can draw from our findings is that non-human primates will be more likely to use tools to produce a single spatial relation or two sequential relations rather than two or more concurrent relations. This limitation constrains the types of problems they solve using tools in comparison to humans. In the future, we plan to study chimpanzees' and capuchins' abilities to manage spatial relations when using a tool, together with the exploratory procedures they use to discover the properties of the tool and the spatial relations involved in the task.

REFERENCES

Bernstein N. 1996. On dexterity and its development. In: Latash M, Turvey M, Bernstein N, editors. Dexterity and Its Development. Mahway, New Jersey: Lawrence Erlbaum. p 3-237.

Berthoz A. 1997/2000. Le sens du mouvement. Paris: Editions Odile Jacob. Translated and published as The brain's sense of movement. Cambridge, MA: Harvard University Press.

Boesch C. In press. Ecology and cognition of tool use in chimpanzees. In: Sanz C, Boesch C, Call J, editors. Tool Use in Animals: Cognition and Ecology. Cambridge University Press.

Bril B, Roux V, Dietrick G. 2005. Stone knapping: Khambhat (India), a unique opportunity? In: Roux V, Bril B, editors. Stone Knapping: The Necessary Conditions for a Uniquely Hominin Behaviour. McDonald Institute Monographs.

Byrne G, Suomi SJ. 1996. Individual differences in object manipulation in a colony of tufted capuchins. Journal of Human Evolution 31:259-267.

Dogo de Resende B, Ottoni EB, Fragaszy DM. 2008. Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): a perception-action perspective. Developmental Science 11:828-840.

Falotico T. 2011. Uso de ferramentas por macacos-prego (*Sapajus libidinosus*) do parque nacional Serra da capivara - PI [Master's Thesis]. Universidade de São Paulo, São Paulo, Brazil.

Fragaszy DM, Adamas-Curtis LE. 1991. Generative aspects of manipulation in tufted capuchin monkeys (*Cebus apella*). Journal of Comparative Psychology 105:387-397.

Fragaszy D, Crast J. In preparation. Functions of the hand in primates. In: Lemelin P, Richmond B, Schmitt D, Kivell T. The Evolution of the Primate Hand: Perspectives from Anatomical, Developmental, Functional, and Paleontological Evidence. Springer Publishing.

Fragaszy D, Cummins-Sebree S. 2005. Relational spatial reasoning by a nonhuman: the example of capuchin monkeys. Behavioral and Cognitive Neuroscience Reviews 4:282-306.

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

Fragaszy D, Kuroshima H, Stone B. 2011. How young children align objects with surfaces: effects of dimensionality and spatial structure. Manuscript in preparation.

Fragaszy DM, Stone BW, Scott NM, Menzel C. 2011. How tufted capuchin monkeys (*Cebus apella* spp) and common chimpanzees (*Pan troglodytes*) align objects to surfaces: insights into spatial reasoning and implications for tool use. American Journal of Primatology 73:1012-1030.

Gibson JJ. 1966. The senses considered as perceptual systems. Boston: Houghton Mifflin.

Gibson JJ. 1979. The ecological approach to visual perception. Boston: Houghton Mifflin.

Hayashi M, Mizuno Y, Matsuzawa T. 2005. How does stone-tool use emerge? Introduction of stones and nuts to naïve chimpanzees in captivity. Primate 46:91-102.

Hopkins WD. 1995. Hand preferences for a coordinated bimanual task in 110 chimpanzees (*Pan troglodytes*): cross-sectional analysis. Journal of Comparative Psychology 109:291-297.

Hove P, Riley MA, Shockley K. 2006. Perceiving affordances of hockey sticks by dynamic touch. Ecological Psychology 18:163-189.

Inoue-Nakamura N, Matsuzawa T. 1997. Development of stone tool use by wild chimpanzees (*Pan troglodytes*). Journal of Comparative Psychology 111:159-173.

Jones LA, Lederman SJ. 2006. Human Hand Function. New York: Oxford University Press.

Lacreuse A, Fragaszy DM. 1997. Manual exploratory procedures and asymmetries for a haptic search task: a comparison between capuchins (*Cebus apella*) and humans. Laterality 2:247-266.

Lederman SJ, Klatzky RL. 1987. Hand movements: a window into haptic object recognition. Cognitive Psychology 19:342-368.

Lockman JJ. 2000. A perception-action perspective on tool use development. Child Development 71:137-144.

McCarty ME, Clifton RK, Collard RR. 2001. The beginnings of tool use by infants and toddlers. Infancy 2:233-256.

Potì P. 2000. Aspects of spatial cognition in capuchins (*Cebus apella*): frames of reference and scale of space. Animal Cognition 3:69-77.

Sanz CM, Morgan DB. 2009. Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. International Journal of Primatology 30:411-427.

Schick KD, Toth K, Garufi G. 1999. Continuing investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). Journal of Archaeological Science 26:821-832.

Shumaker RW, Walkup KR, Beck BB. 2011. Animal tool behavior: the use and manufacture of tools by animals. Baltimore, Maryland: Johns Hopkins University Press.

Smitsman AW. 1997. The development of tool use: changing boundaries between organism and environment. In: Dent-Reed C, Zukow-Goldring P, editors. Evolving Explanations of Development. Washington, DC: American Psychological Association. p 301-329.

Souto A, Bione CBC, Bastos M, Bezerra BM, Fragaszy D, Schiel N. 2011. Critically endangered blonde capuchins fish for termites and use new techniques to accomplish the task. Biology Letters DOI:10.1098/rsbl.2011.0034.

Takeshita H. 2001. Development of combinatory manipulation in chimpanzee infants (*Pan troglodytes*). Animal Cognition 4:335-345.

Teleki G. 1974. Chimpanzee subsistence technology: materials and skills. Journal of Human Evolution 3:575-584.

Toth N, Schick K. 2009. The Oldowan: the tool making of early hominins and chimpanzees compared. Annual Review of Anthropology 38:289-305.

Turvey MT. 1996. Dynamic touch. American Psychologist 51:1134-1152.

Wagman JB, Carello C. 2001. Affordances and inertial constraints on tool use. Ecological Psychology 13:173-195.

APPENDIX

Tool use is considered an iconic aspect of human evolution and development, although the behavior is not unique to humans. Many other species, including various species of non-human primates, spontaneously use tools in their natural environment. For example, capuchin monkeys (*Cebus apella*) regularly use stone hammers to crack open nuts (Fragaszy, Izar, Visalberghi, Ottoni, & Gomes de Oliveira, 2004).

An important difference between tool use in humans and tool use in non-human primates may be due to propensities of particular species to align objects to other objects or surfaces. Common forms of tool use by humans, such as hammering a nail or inserting a key into a lock, require the management of more than one allocentric spatial relation, that is, a relationship between an object and a surface or an object and another object (Fragaszy & Cummins-Sebree, 2005). The nail must be aligned with the wall while the hammer is simultaneously aligned with the nail; the key must be oriented so that not only is the narrow end toward the lock but the grooved side is facing upward. In contrast, non-human primates typically align only one allocentric spatial relation, and often this relation is quite permissive with respect to alignment. For instance, termite fishing in chimpanzees requires only that the stick must be aligned with the termite hole (Hayashi, Mizuno, & Matsuzawa, 2005; Fragaszy & Cummins-Sebree, 2005). The most complex form of tool use by non-human primates routinely found in nature is nut cracking, which involves two spatial relations (one between the nut and the anvil, one between the stone hammer and the nut) managed sequentially (Fragaszy et al., 2004).

A recent study by Fragaszy, Stone, Scott, & Menzel (2011) demonstrated that both tufted capuchin monkeys (*Cebus apella* spp.) and common chimpanzees (*Pan troglodytes*) are increasingly hindered by an object alignment task as the number of concurrent spatial relations increases. The current study replicates these findings and delves further into the problem to determine whether increasing spatial relations also presents a problem when it is possible to manage them sequentially as opposed to concurrently.

Theoretical Links

The perception-action theory posits that individuals generate exploratory behaviors that lead to perception and this perception then guides subsequent actions (Lockman, 2000). These exploratory behaviors allow the individual to learn about the affordances of both the object(s) and the possible actions with those objects. According to J. J. Gibson (1979), whose theory of ecological psychology greatly influenced Lockman's theory, an affordance of an object is defined as what that object provides or offers the actor in terms of potential actions. For instance, the first time an individual picks up a hammer he/she may perceive, by wielding it, that it is light enough to swing but heavy enough on one end to provide significant force to another object. Wagman and Carello (2001) found that individuals introduced to novel "tools" could determine whether the object would afford hammering (a power task) or poking (a precision task) depending on the inertial properties and mass distribution of the object. In addition, this determination required relatively little actual experience with the object. Similarly, Hove, Riley, and Shockley (2006) found that individuals were able to accurately decide if a particular hockey stick would be best suited to exert force or be used for a precision task. Again, the decision was based upon the mass distribution, and thus the inertial properties, of the stick, which was manipulated by the researchers. In both studies, individuals were able to perceive the affordances of the objects by using dynamic touch, which involves the manipulation of an object via muscular effort (Gibson, 1966). Dynamic touch allows an individual to feel an object's inertial properties and then be able to generate the appropriate muscular effort to wield the object accordingly.

Such accurate perception of the affordances of a tool is impressive because tools inherently change the boundaries between the actor and the environment (Smitsman, 1997). The tool extends the actor's capabilities not only to act upon his/her environment but to perceive it as well. It becomes temporarily embodied by the actor (Iriki, Tanaka, & Iwamura, 1996; Berti & Frassinetti, 2000; Hirose, 2002), such that the tool and the actor are now a single system with new action possibilities. This system is dynamic in that the inertial properties of the actor, more specifically the limb handling the tool, are influenced and changed by the inertial properties of the tool and vice versa (Smitsman, 1997; Thelen & Smith, 1994). For example, Bril, Dietrich, Foucart, Fuwa, & Hirata (2009) found that chimpanzees are able to perceive differences in weight of stone hammers when attempting to crack open nuts. Accordingly, they adjust the amplitude of their striking movement as well as the velocity to ensure they can crack the nut. When the hammer was heavier (1000 grams) the chimpanzees seemed to rely almost completely upon the potential energy produced by the weight of the stone to crack the nut. However, when the hammer was lighter (300 or 600 grams) the individuals used active muscular force to produce kinetic energy in addition to the stone's potential energy. Thus, the chimpanzees perceived the affordances of the tool at hand and then modified their actions in accordance.

The ecological perspective (Gibson, 1979; Smitsman, 1997) and perception-action theory (Lockman, 2000) have been used to explain how children develop spatial skills and cognition. Berger and Adolph (2003) found that toddlers who were faced with a narrow bridge could use a handrail to help them. They perceived this handrail as a possible solution and used it to help them balance on the bridge. Infants given blocks that are partially spongy and partially wooden are able to correctly orient the hard side so that they may bang the blocks on a table to make noise (Lockman, 2000). This occurs by the age of about 6 months, though it takes slightly longer for the infants to learn to orient the hard sides of two blocks to bang them against each other in order to make noise (two spatial relations to manage). This represents the development of infants' perceptions regarding spatial relations between objects and surfaces. Cox and Smitsman (2006) found that though 3-year-olds establish a clear preference in hand choice during a retrieval task using a stick, they will switch hands depending on the location to which they need to bring the object. If the object must be brought to their right they typically use their left hand and vice versa. The goal location changes the children's perceptions of the task and allows them to act upon the stick and object more efficiently. Bourgeois, Khawar, Neal, and Lockman (2005) allowed infants to explore multiple objects and types of surfaces in order to see if they tailor their manual exploration depending on the properties of these objects and surfaces. Even at the age of 6 months, infants do manipulate objects in differentiated manners (e.g., squeezing soft objects, scratching hard objects) as well as surfaces. Eight to 10-month-old infants also began exploring the relations between the objects and surfaces – banging hard objects against rigid surfaces more often than liquid surfaces, pressing objects against a flexible surface more often than against a rigid surface. Thus, the infants are taking into account the properties of both the objects and the surfaces and using them to create relations between the object and surface. All of these studies indicate a steady increase in infants' development of spatial cognition as they age, which provides the basis for the gradual and continuous development of tool use in children (Lockman, 2000).

Lederman and Klatzky (1987) described what they called exploratory procedures (EPs), which are highly stereotyped movement patterns that humans use to haptically explore an object or surface. These EPs include lateral motion, pressure, static contact, unsupported holding, enclosure, and contour following, and humans use them to explore objects and surfaces for different properties (such as weight, volume, texture, etc). These EPs help to inform an individual's haptic perception of an object or surface. Lacreuse and Fragaszy (1997) compared EPs in humans and capuchins and found that capuchins perform all of the same EPs as seen among humans. Thus capuchins are capable of determining an object or surface's affordances through manual exploration just as a human can.

However, an individual must not simply learn about the affordances of an object to be able to use it as a tool. Another key component of tool use is the ability to manage allocentric frames of reference (Fragaszy et al., 2011). There are two frames of reference in which individuals may work to locate and move themselves as well as objects within space. An egocentric frame of reference is centered about the body while an allocentric frame of reference is centered about landmarks and objects external to the body (Potì, 2000). The egocentric frame of reference is typically thought to develop first (Fragaszy et al., 2011). McCarty, Clifton, and Collard (2001) found that infants, ages 9 to 24 months, were more likely to plan their actions in advance when using a self-directed tool rather than an object-directed tool; they concluded that planful strategies for self-directed tools develop earlier than those for object-directed tools. In an object-location task, Potì (2000) found that capuchins have a much stronger egocentric frame of reference than allocentric frame, and they use this egocentric frame more often. When dealing with a tool and another object the individual must use an allocentric frame of reference in order to locate and align the objects appropriately.

Tools are not stationary objects; thus, an allocentric frame of reference used during tool use is a mobile frame of reference as opposed to fixed. A mobile frame of reference adds to the degrees of freedom involved in a task by increasing the number of directions in which mobility can occur. Managing more degrees of freedom within the body is more difficult than managing fewer degrees of freedom because it means there are more movements for the individual to control (Bernstein, 1996). Additionally, tool use often requires the coordination of more than one mobile allocentric frame of reference, as seen when pulling in an object with a rake. During the raking action there is a mobile frame of reference between the object and the surface upon which it's moving as well as between the object and the rake pulling it. Humans begin learning to manage and coordinate such mobile allocentric frames of reference within their first year of life (Lockman, 2000).

It could be that non-human primates are not as adept in their coordination of mobile allocentric frames of reference. This would at least partially explain why we see a repertoire of less complex tool use among non-human primates in relation to humans' repertoire. Non-human primates are known to be able to use sticks to probe or fish for insects, stab another animal, pull in or push out an object, and pry open a container. They can also use stones to dig in the dirt for insects or roots and pound nuts to crack them open (Fragaszy & Cummins-Sebree, 2005; Shumaker, Walkup, & Beck, 2011). These abilities are impressive but none of the tasks involve more than two spatial relations or two concurrent relations as seen so often in human tool use.

Fragaszy and Cummins-Sebree (2005) extended Lockman's perception-action theory in a comparative direction with the goal to examine tool use and its development across species. Their model of spatial reasoning incorporates Bernstein's (1996) idea that allocentric spatial relations can vary in a number of aspects – the number of relations involved, whether the relations can be dealt with sequentially or concurrently, and the temporality of the relations. Fragaszy and Cummins-Sebree's (2005) model predicts that the difficulty of a task increases as the number of spatial relations involved increases as well as when the spatial relations must be dealt with concurrently rather than when the same number of relations can be managed sequentially. Each additional allocentric spatial relation adds at least one degree of freedom to the task (Fragaszy et al., 2011) because each new relation presents its own directions of mobility. Thus, as the number of spatial relations increases, the amount of mobility to be controlled between the object and the surface increases. Such mobility must be controlled in order to produce the precise actions needed in a placement task.

Most of the literature to date has dealt with degrees of freedom found within the body. Each of the body's limbs has multiple degrees of freedom resulting from the possible movements of the joints. These degrees of motion must be managed in some way both while the individual is learning the skill and once the skill has been mastered. According to Bernstein (1967) the acquisition of a motor skill relies upon an individual's ability to coordinate and manage multiple degrees of freedom involved in the skill. Bernstein (1967) proposed that individuals freeze some of these degrees of freedom, by restricting movement of joints, while they are learning a new skill. As they master it, the individual releases degrees of freedom, affording modulations of activity in the face of changing circumstances. Current literature, however, paints a more complex picture.

Hong and Newell studied individuals learning to use a ski-simulator apparatus. They found that the freezing and freeing of degrees of freedom depended on both the limb in question and the direction of movement. For example, they found an increase followed by a decrease in movement of the head and torso on the superoinferior axis, but the same body part showed little difference across trials on the anteroposterior axis. The authors conclude that degrees of freedom within the body were both recruited and suppressed during this task. Konzcak et al. found similar results when studying shoulder movement in beginning violin players. Shoulder movement was not frozen and then released as Bernstein (1967) proposed. Instead, only the degree of freedom allowing shoulder flexion and extension was restricted while the other two degrees remained the same with practice. Thus, whether an individual freezes or frees the degrees of freedom involved in a task, and in what order this occurs, seems to depend greatly on the task at hand and involves a long learning process.

In the current study we are focused on the degrees of freedom that occur outside instead of within the body. We present subjects with objects that must be aligned and placed within a matching groove in the surface of a tray. As we increase the number of spatial relations involved in the task from one to two, we simultaneously increase the degrees of freedom involved. Taking Bernstein's (1967) perspective, we predict that individuals will use a strategy that allows them to freeze some of these degrees of freedom, especially as the number of relations increases. Such a strategy might include using the fixed surface of the tray to guide the stick during alignment. This strategy could provide the subject with haptic information about the location of the groove as well as reducing the mobility of the stick. If the stick is pressed against the fixed surface of the tray, the number of directions in which it might move is limited. This could ease the burden of aligning the object by decreasing the degrees of freedom that must be controlled by the subject. Fragaszy et al. (2011) did find that most subjects of both species did use such a strategy on most of their attempts to align the object with the groove. However, strong evidence for an increase in this strategy as the number of relations between the object and surface increased was not found. Therefore, Bernstein's (1967) proposed pattern of managing degrees of freedom may not be the most efficient way to approach the object alignment task presented by Fragaszy et al. (2011).

Another interesting finding from Fragaszy et al. (2011) as compared to Fragaszy, Kuroshima, and Stone (manuscript in preparation) is the complete lack of the use of visual alignment among capuchins and chimpanzees. Humans, even from the very first attempt, use vision to align an object with a groove and then place the object into the groove appropriately. This use of visual alignment was not seen in the capuchins' and chimpanzees' attempts to align objects with matching grooves in Fragaszy et al. (2011). All attempts to align the stick by non-human primates were made by banging the stick, dragging it across the surface, or inserting one end of it and rotating to align it. These results, however, should not be surprising based up on the literature concerning visual attention during tasks in non-human primates.

During reaching and grasping tasks, capuchins typically look at the object until they have it in a secure grasp but no longer than that (Fragaszy, Visalberghi, & Fedigan, 2004). After securely grasping the object, capuchins will return to monitoring their surroundings. The longer it takes to reach and grasp an object, the longer the capuchins will monitor their surroundings afterward. In nature, this monitoring would allow the individuals to be vigilant of possible predators in the area and, thus, visual monitoring seems to be a priority of capuchins. Nevertheless, this pattern of visual attention is seen even when the capuchins are in a laboratory setting when predators are not a concern. Simons and Holtkotter (1986) found that capuchins preferentially choose to open a latch on a closed door by sliding the latch's handle with one hand until it rests in the appropriates spot by the other hand, again monitoring the task manually. However, when the subjects were prevented from using two hands to accomplish the task, they did rely upon vision to guide their hand's movement on the latch. Thus, capuchins will visually monitor a task if need be, but they prefer to monitor manually in order to free the visual system to be vigilant of their surroundings.

Not only do chimpanzees and capuchins use tools spontaneously in nature, but they are also capable of moving their fingers independently of one another as well as using a precision grip in tasks (Christel & Fragaszy, 2000; Fragaszy et al., 2004; Crast, Fragaszy, Hayashi, & Matsuzawa, 2008). A precision grip typically involves grasping an object between the pad of the thumb and the pad of the index finger to allow fine control of the object, as opposed to a power grip use, which uses the whole hand to control larger objects (Napier, 1956). Both humans and chimpanzees have a saddle joint between their thumb and index finger that allows the use of a precision grip, although this grip is somewhat limited in chimpanzees due to the short length of the thumb (Crast et al., 2008). Capuchins do not have this saddle joint but are still able to form a functional precision grip even if it is not the same pad-to-pad opposition as seen in the human precision grip (Fragaszy et al., 2004). The precision grip allows capuchins and chimpanzees to grasp small objects and pieces of food as well as perform finer movements, such as in a placement task.

REFERENCES

Berger SE, Adolph KE. 2003. Infants use handrails as tools in a locomotor task. Developmental Psychology 39:594-605.

Bernstein N. 1996. On dexterity and its development. In: Latash M, Turvey M, Bernstein N, editors. Dexterity and Its Development. Mahway, New Jersey: Lawrence Erlbaum. p 3-237.

Berti A, Frassinetti F. 2000. When far becomes near: Remapping of space by tool use. Journal of Cognitive Neuroscience 12:415-420.

Bourgeois KS, Khawar AW, Neal SA, Lockman JJ. 2005. Infant manual exploration of objects, surfaces, and their interrelations. Journal of Infancy 8:233-252.

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

Christel M, Fragaszy D. 2000. Manual function in *Cebus apella*: digital mobility, preshaping, and endurance in repetitive grasping. International Journal of Primatology 21:697-719.

Cox RFA, Smitsman AW. 2006. Action planning in young children’s tool use. Developmental Science 9:628-641.

Crast J, Fragaszy D, Hayashi M, Matsuzawa T. 2008. Dynamic in-hand movements in adult and young juvenile chimpanzees (*Pan troglodytes*). American Journal of Physical Anthropology 138:274-285.

Fragaszy D, Cummins-Sebree S. 2005. Relational spatial reasoning by a nonhuman: the example of capuchins monkeys. Behavioral and Cognitive Neuroscience Reviews 4:282-306.

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

Fragaszy D, Kuroshima H, Stone B. 2011. How young children align objects with surfaces: effects of dimensionality and spatial structure. Manuscript in preparation.

Fragaszy DM, Stone BW, Scott NM, Menzel C. 2011. How tufted capuchin monkeys (*Cebus apella* spp) and common chimpanzees (*Pan troglodytes*) align objects to surfaces:

insights into spatial reasoning and implications for tool use. American Journal of Primatology 73:1012-1030.

Fragaszy D, Visalberghi E, Fedigan L. 2004. The complete capuchin. New York: Cambridge University Press.

Gibson JJ. 1966. The senses considered as perceptual systems. Boston: Houghton Mifflin.

Gibson JJ. 1979. The ecological approach to visual perception. Boston: Houghton Mifflin.

Hayashi M, Mizuno Y, Matsuzawa T. 2005. How does stone-tool use emerge? Introduction of stones and nuts to naïve chimpanzees in captivity. Primate 46:91-102.

Hirose N. 2002. An ecological approach to embodiment and cognition. Cognitive Systems Research 3:289-299.

Hong SL, Newell KM. 2006. Change in the organization of degrees of freedom with learning. Journal of Motor Behavior 38:88-100.

Hove P, Riley MA, Shockley K. 2006. Perceiving affordances of hockey sticks by dynamic touch. Ecological Psychology 18:163-189.

Iriki A, Tanaka M, Iwamura Y. 1996. Coding of modified body schema during tool use by macaque postcentral neurons. Neuroreport 7:2325-2330.

Ko YG, Challis JH, Newell KM. 2003. Learning to coordinate redundant degrees of freedom in a dynamic balance task. Human Movement Science 22:47-66.

Konczak J, Van der Velden H, Jaeger L. 2009. Learning to play the violin: motor control by freezing not freeing degrees of freedom. Journal of Motor Behavior 41:243-252.

Lacreuse A, Fragaszy DM. 1997. Manual exploratory procedures and asymmetries for a haptic search task: a comparison between capuchins (*Cebus apella*) and humans. Laterality 2:247-266.

Lederman SJ, Klatzky RL. 1987. Hand movements: a window into haptic object recognition. Cognitive Psychology 19:342-368.

Lockman JJ. 2000. A perception-action perspective on tool use development. Child Development 71:137-144.

McCarty ME, Clifton RK, Collard RR. 2001. The beginnings of tool use by infants and toddlers. Infancy 2:233-256.

Napier JR. 1956. The prehensile movements of the human hand. Journal of Bone and Joint Surgery 38: 902-913.

Potì P. 2000. Aspects of spatial cognition in capuchins (*Cebus apella*): frames of reference and scale of space. Animal Cognition 3:69-77.

Shumaker RW, Walkup KR, Beck BB. 2011. Animal tool behavior: the use and manufacture of tools by animals. Baltimore, Maryland: Johns Hopkins University Press.

Simons D, Holtkotter M. 1986. Cognitive process in cebus monkeys when solving problem-box tasks. Folia Primatologica 46:149-163.

Smitsman AW. 1997. The development of tool use: changing boundaries between organism and environment. In: Dent-Reed C, Zukow-Goldring P, editors. Evolving Explanations of Development. Washington, DC: American Psychological Association. p 301-329.

Thelen E, Smith LB. 2004. A dynamic systems approach to the development of cognition and action. Cambridge, MA: The MIT Press.

Wagman JB, Carello C. 2001. Affordances and inertial constraints on tool use. Ecological Psychology 13:173-195.