American Journal of Primatology 73:1–19 (2011)

RESEARCH ARTICLE

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

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This report addresses phylogenetic variation in a spatial skill that underlies tool use: aligning objects to a feature of a surface. Fragaszy and Cummins-Sebree's [Behavioral and Cognitive Neuroscience Reviews 4:282–306, 2005] model of relational spatial reasoning and Skill Development and Perception–Action theories guided the design of the study. We examined how capuchins and chimpanzees place stick objects of varying shapes into matching grooves on a flat surface. Although most individuals aligned the long axis of the object with the matching groove more often than expected by chance, all typically did so with poor precision. Some individuals managed to align a second feature, and only one (a capuchin monkey) achieved above-chance success at aligning three features with matching grooves. Our findings suggest that capuchins and chimpanzees do not reliably align objects along even one axis, and that neither species can reliably or easily master object placement tasks that require managing two or more spatial relations concurrently. Moreover, they did not systematically vary their behavior in a manner that would aid discovery of the affordances of the stick–surface combination beyond sliding the stick along the surface (which may have provided haptic information about the location of the groove). These limitations have profound consequences for the forms of tool use we can expect these individuals to master. Am. J. Primatol. 73:1–19, 2011. © 2011 Wiley-Liss, Inc.

Key words: allocentric; egocentric; spatial reasoning; object manipulation; alignment; tool use

INTRODUCTION

Human technical prowess relies upon moving objects with precision and efficiency. A common element of precision in moving an object is bringing it into alignment with another object or surface. Often the object to be aligned varies in more than one plane, such as a key that fits into a lock only when the long axis and the transverse elements are all aligned with the keyhole. Like other performatory skills, aligning objects has an anticipatory, intentional element. Anthropologists have long argued that the appearance of tools and tool kits in early human history reflects blossoming anticipatory skills to select appropriate objects, to transport them, modify them (e.g., manufacture tools), and use them in diverse ways [Haslam et al., 2009; Potts, 1991; Roux & Bril, 2005; Washburn, 1960].

Differences between humans and nonhuman primates in the domain of tool use may reflect the latter's more limited abilities to align objects. In general, the evidence supports this view, in that nonhuman primates spontaneously use tools in ways that involve permissive alignment and/or alignment of one dimension, such as inserting a stick into a hole [e.g., Fragaszy & Cummins-Sebree, 2005]. However, the object alignment components of tool use have received little empirical attention from psychologists studying tool use in humans or nonhuman species. Recently, Weiss et al. [2007] showed that cotton-top tamarins (*Saguinus oedipus*), a species of South American monkeys that do not spontaneously use tools, show anticipatory adjustments when reaching for an object. These monkeys adopt a less preferred grip posture when they grasp an upside down object that they must subsequently hold upright to retrieve a piece of food. The finding that nonhuman primates use anticipatory positioning of the hand to grasp objects suggests that nonhuman primates may also anticipate the positions of objects that they manipulate. With specific relevance for tool use, it will be

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Contract grant sponsors: L.S.B. Leakey Foundation; The Wenner-Gren Foundation; NIH; Contract grant numbers: HD38051; R01 HD056352; HD060563.

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Received 6 October 2010; revised 28 February 2011; revision accepted 16 April 2011

DOI 10.1002/ajp.20966

useful to know if or how nonhuman primates anticipate the position of objects that they move; that is, how they align objects to other objects. In this report, we examine how common chimpanzees (*Pan troglodytes*) and tufted capuchin monkeys (*Cebus apella*), both species that use tools spontaneously in natural and captive settings, place stick objects of varying shapes into matching grooves on an otherwise flat surface. (Note that animals identified as *C. apella* in laboratory colonies outside South America may be any combination of species—*C. apella*, *C. libidinosus*, *C. nigritus*, *C. robustus*, and *C. melanocephalus*—all previously considered as *C. apella* but recognized as separate species from 2001 [see Fragaszy et al., 2004]).

Frames of Reference and Alignment of Objects

Animals use two distinct spatial frames of reference to move themselves and objects in space: egocentric (with respect to the body) and allocentric (with respect to the external environment) [Pick & Lockman, 1981]. The egocentric frame of reference is traditionally regarded as phylogenetically and ontogenetically primary, defined by gravity, and rooted in the vestibular sense of position and movement [Berthoz, 1997/2000]. An allocentric frame of reference uses the relationship between two or more objects external to the body to define the location of things in space, as when using landmarks to locate a hidden object or to navigate in a large-scale space [Cheng et al., 2007; Potì, 2000]. When manipulating an object in relation to another object or a surface within arm's reach, the actor uses an allocentric frame of reference, and in this case the handled object moves in relation to other relevant components of the set [Lockman, 2000]. For example, putting a spoon into a bowl requires monitoring the mobile allocentric spatial relationship between the spoon and the bowl. An allocentric frame of reference permits accurate performance when the starting spatial arrangements of objects vary across occasions.

This analysis suggests why moving an object in relation to other mobile objects and in relation to substrates in a goal-directed task can be challenging. Mobile frames of reference add degrees of freedom to the system. Managing multiple degrees of freedom of movement in the body is more difficult than managing fewer degrees of freedom [Bernstein, 1967, 1996; Dounskaia, 2005]. This principle should apply in tasks requiring placing objects in relation to surfaces. Managing one relation at a time while moving an object in relation to a surface results in a reduction of the degrees of freedom to manage at a given time, although it may not be the most efficient possible strategy for solving the problem.

According to Bernstein [1967], learning a new motor skill proceeds first by reducing degrees of freedom (by ''freezing'' dimension of movement at joints), which serves to simplify the problem of motor control for the novice. This proposal continues to receive attention by movement scientists interested in skill learning [e.g., learning to play the violin; Konczak et al., 2009]. Konczak et al. [2009], as is the norm for movement scientists, focus on the degrees of freedom in the movement of the body. Less attention has been paid to the role of the degrees of freedom in moveable objects external to the body in the process of skill learning.

Theoretical Links Between Object Manipulation, Including Alignment, and Tool Use

Effectively managing mobile allocentric frames of reference is a prerequisite for tool use, in which the actor produces a specific spatial and force relation between an object and a surface or another object by moving one or more components of the set. Many manipulations of objects outside tool-using contexts (e.g., positioning an object for safe storage) also depend upon managing mobile allocentric frames of reference. Lockman [2000] suggests that humans begin to learn how to manage allocentric mobile frames of reference in the first year of life, in the course of exploratory actions, and that this process continues throughout life. In his view, effectively managing multiple, and particularly mobile, spatial frames of reference is an ontogenetic achievement that supports the gradual (continuous) emergence of tool use in humans.

Lockman [2000] developed this theory, now called Perception–Action theory, from the theory of ecological psychology developed by J.J. and E. Gibson [Gibson, 1979; Gibson & Pick, 2000]. A key tenet of Perception–Action theory is that individuals generate behavior to learn about current circumstances; they use action to generate perceptions and they use perception to guide actions. Hence, exploratory behavior is viewed as critically important for learning how to achieve a goal through action. Individuals learn about the affordances of the materials and of their actions with the materials through exploration [Gibson & Pick, 2000]. To understand how an individual learns to solve a problem, Perception–Action theory directs us to look at the structure of the problem, the particular setting of action (defining the challenge for the actor), and the ways in which an individual acts to learn about this structure in a given setting. Perception–Action theory has proven useful in understanding human infants' mastery of a variety of spatial skills, including reaching, prehension, locomotion, and acting with objects [Berger & Adolph, 2003; Bourgeois et al., 2005; McCarty et al., 2001a,b; Thelen & Smith, 1994].

Fragaszy and Cummins-Sebree [2005] extended Perception–Action theory in a comparative direction, with an eye to examining species differences in tool use. Their model incorporates some features of

Bernstein's [1967, 1996] approach to skill learning, and posits that allocentric spatial relations embodied in goal-directed object manipulation (i.e., problem-solving settings, including but not limited to tool use) can vary in several dimensions. Relevant dimensions include the number of relations, whether they must be managed concurrently or in sequence, and the nature of each spatial relation, for example, whether it must be managed over time, and if so, if it is dynamic. Fragaszy and Cummins-Sebree's [2005] model produces the predictions that increasing the number of relations to be managed concurrently increases the challenge of an object manipulation task, and that managing more than one relation at a time will present a greater challenge than managing the same number of relations sequentially. Each additional spatial relation adds at least one degree of freedom to the task.

Here, we investigate how nonhuman primates manage a spatial problem, entailing the use of mobile allocentric frames of reference to insert an object into a matching groove in a substrate. The study is designed to evaluate the hypothesis from Fragaszy and Cummins-Sebree's model of spatial reasoning that increasing the number of relations to be managed concurrently increases the challenge of a manipulation problem and two related hypotheses. The first related hypothesis, from Perception–Action theory, is that individuals generate exploratory behavior to detect spatial relations and to learn how to manage them (i.e., to detect the affordances of the problem). The second related hypothesis, from Skill Development theory [Bernstein, 1967, 1996], is that individuals act to simplify the demands for motor control when working on a difficult problem, particularly by reducing the degrees of freedom that they must manage concurrently.

Study Species

Our current understanding of each species' aptitude for using objects as tools, particularly in natural settings [reviewed in McGrew, 2004; Ottoni & Izar, 2008], and their differing dexterity at manipulating objects in the hand [Crast, 2006; Crast et al., 2009; Fragaszy, 1998], might lead us to expect that chimpanzees would have an advantage over capuchins in the alignment task. There are more reports of chimpanzees in widely distributed locations using objects as tools in various ways than there are for capuchins [e.g., compare McGrew, 2004; Ottoni & Izar, 2008]. However, note that most instances of tool use described for both species involve producing a single relation between object and surface (as in probing into an opening) or sequential management of more than one relation. Taking nut cracking as an example of the latter case, the individual places a nut on an anvil surface, then strikes the nut with a stone. This involves managing two relations in sequence [see Fragaszy & Cummins-Sebree, 2005; Visalberghi & Fragaszy, 2006, for more examples].

Moreover, a variety of findings suggest that chimpanzees, perhaps to the same extent as capuchins, are challenged by problems embodying more than one spatial relation, such as stacking blocks with an irregular surface [Hayashi & Takeshita, 2009; Stone et al., unpublished data], and that capuchins and chimpanzees approach object manipulation tasks in captivity in similar ways and with equivalent success [Anderson, 1996]. For example, individuals of both species can seriate cups in a fixed order [''nesting cups''; Johnson-Pynn et al., 1999]. They achieve equivalent mastery of this problem, creating structures with five nested cups, inserting an extra cup into the middle of the series, and using diverse strategies to combine the cups. Thus, it is unclear at present whether the species differ in anticipatory positioning of objects, in exploratory actions that provide haptic information about the spatial relation between an object and a surface, or in behavioral strategies that simplify an alignment problem by reducing degrees of freedom in some fashion. Our study addressed these issues.

Experimental Task

We presented a task requiring subjects to align a rigid object with a matching groove in a tray. We manipulated the spatial relations involved in the task by altering the shape of the objects and their matching grooves. Inserting an object with a symmetrical outer contour (for example, a circular disk or a straight stick) requires managing one relation between object and the groove; aligning a single edge serves to align the entire object. Aligning an asymmetrical object efficiently requires managing at least two spatial relations concurrently. For example, efficiently aligning a cross with one axis, set off-center into a cross-shaped groove, requires simultaneously managing the two axes of the object with respect to the groove. If the actor deals with the two axes sequentially, initially aligning the long axis of the stick with the long axis of the groove, for example, the cross piece would be at the wrong end of the long axis (i.e., the cross piece of the stick would be upside down with respect to the cross piece of the groove) half the time, on average. Each additional asymmetric feature increases the number of relations that must be managed concurrently to align the object correctly, and decreases the probability of success if the actor deals with one relation at a time.

Predictions Concerning Object Alignment

In accordance with the hypothesis that an increasing number of concurrent relations increases the challenge of a problem, we predicted that the number of asymmetrical components in the object to be inserted into a matching groove would directionally affect the number of insertion attempts per trial. Our second hypothesis is that, as the number of concurrent relations embodied in the problem increases, individuals will generate exploratory behavior to learn about the affordances of the materials and actions with the materials. This hypothesis leads to the prediction that, when encountering a new problem embodying an increased number of relations, the actor will vary its behavior; for example, it will move the object along the surface in a new way or will change the angular orientation of insertion attempts. The direction of these shifts is not predicted, only that challenging tasks will provoke exploration of the relationships among actions, object, and surface. We were particularly interested in whether subjects would increase actions moving the object on the surface in areas where the surface changes (i.e., the groove into which the object is to be inserted), as these actions could provide haptic information about the fit between tray and object. Finally, we predicted that individuals would adopt behavioral strategies that reduce the degrees of freedom of the stick's movement along the surface or otherwise increase control of the stick's motion. In our task, this could be manifest as sliding the stick across the surface or using one hand to stabilize the end of the stick at a point on the surface of the tray while the other hand grasps the shaft, as humans sometimes do when inserting a key into a lock.

METHOD

Subjects

The subjects of this study were four adult chimpanzees (*P. troglodytes*) and eight adult capuchin monkeys (*C. apella* spp). The chimpanzees, two males and two females, were 18–34 years old at the time of testing. They were housed in an indoor-outdoor facility at Georgia State University's Language Research Center, and were tested in their indoor home cage through mesh metal fencing. The capuchins, eight pair-housed males aged 13–20, were housed in a vivarium at the University of Georgia and tested in their home cages. Subjects received their usual diet and water was available ad libitum. This study complied with all local and national regulations concerning humane care and use of nonhuman animals in research, and was approved by the University of Georgia Institutional Animal Care and Use Committee. The study adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

Apparatus

The four conditions each utilized a different combination of matching stick and groove, with later conditions adding asymmetrical components to the shape of the stick and its corresponding groove in the tray (see Fig. 1 for an illustration of the tray in each condition). All conditions used the same circular base tray (46 cm diameter for chimpanzees, 15.3 cm diameter for capuchins). In Condition 0, baseline, the stick was a circular wooden rod (38 cm long and 2.5 cm diameter for chimpanzees, 11.5 cm long and 1 cm diameter for capuchins) and the groove in the tray was the entire circular base, which was just large enough to accommodate the stick at any rotational angle (the stick bisected it into two semicircles). Condition 1 used the same stick, but the tray had a single straight groove slightly larger than the stick. In Condition 2, we replaced the circular rod with a cross-shaped cuboid stick, which had to be placed into a corresponding cross-shaped groove. The long axis was again 38 cm for the chimpanzees and 11.5 cm for the capuchins; the short axis of the cross was 12.7 cm for the chimpanzees and 4.8 cm for the capuchins; and it was 2.5 cm thick for chimps and 1 cm for capuchins. In Condition 3, one half of the short bar of the cross-shape was replaced by an isosceles right triangle (hypotenuse 8.9 cm for chimpanzees, 4.7 cm for capuchins), creating a tomahawk-shaped object. The length of the long axis of the stick was roughly the length of the forearm for each species.

For testing, chimpanzee subjects were isolated in a section of the home cage (2.0 × 4.3 × 2.5 m high) and an experimenter, seated in a chair obliquely facing the cage, slid the stick and tray under the wire

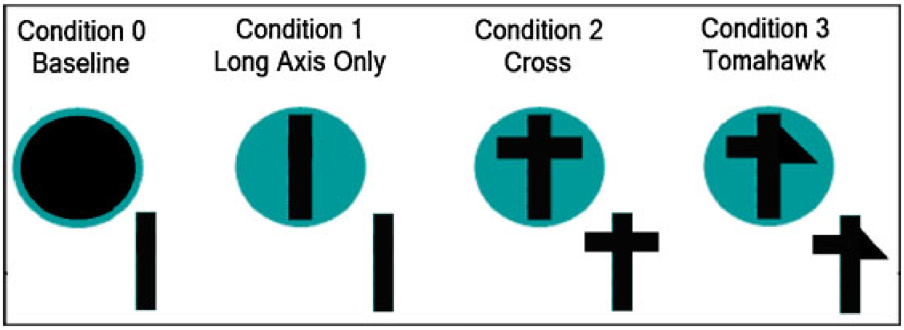


Fig. 1. The shapes of the sticks and the matching trays for each condition. Not to scale.

mesh into the cage. Trials were filmed through the wire mesh from overhead and from the side.

Capuchin subjects were sequestered in the bottom half of their home cage. A clear panel was fixed to the front of the cage. The experimental tray, attached to a flat drawer at the bottom of this panel, could slide into the cage which the subject could push back out. The experimenter handed the sticks to the monkey through the vertical cage bars and positioned the cross- and tomahawk-shaped parts vertically to fit through the bars. A tripod-mounted camera filmed straight-on through the clear panel on the transport door.

Procedure

Before baseline, we confirmed that all subjects would return the tray by sliding it out of their cage to receive a small food reward. Trials began when the stick was handed to the subjects by the experimenter, having first slid the tray in. Subjects were allowed to work with the stick until they succeeded in inserting it into the groove and sliding the tray back out, or until they stopped attending to the apparatus for longer than a minute, at which point the experimenter requested the return of the stick and the tray. Successful completion of a trial resulted in verbal praise and food reward: the chimpanzees received a 2 cm thick slice of banana or a sip of juice and the capuchins received a portion of a peanut or raisin. Intertrial interval was typically 30 sec, long enough for the subject to consume the food reward and the experimenter to prepare the next trial.

Each subject completed at least ten trials at each condition before progressing to the next, and on each subsequent testing day, subjects were presented with at least two review trials of each completed condition before beginning a new one. A testing day included a maximum of 25 trials. When presenting the tray in Conditions 1–3, the angle of the tray's groove with respect to the cage frame was roughly balanced across trials, although chimpanzees often moved the tray and subjects of both species repositioned their bodies around it throughout the trial. For Conditions 2–3, the experimenter counterbalanced the orientation of the stick when he/she handed it to the subject, with respect to the shaped or nonshaped end being closest to the subject's hand.

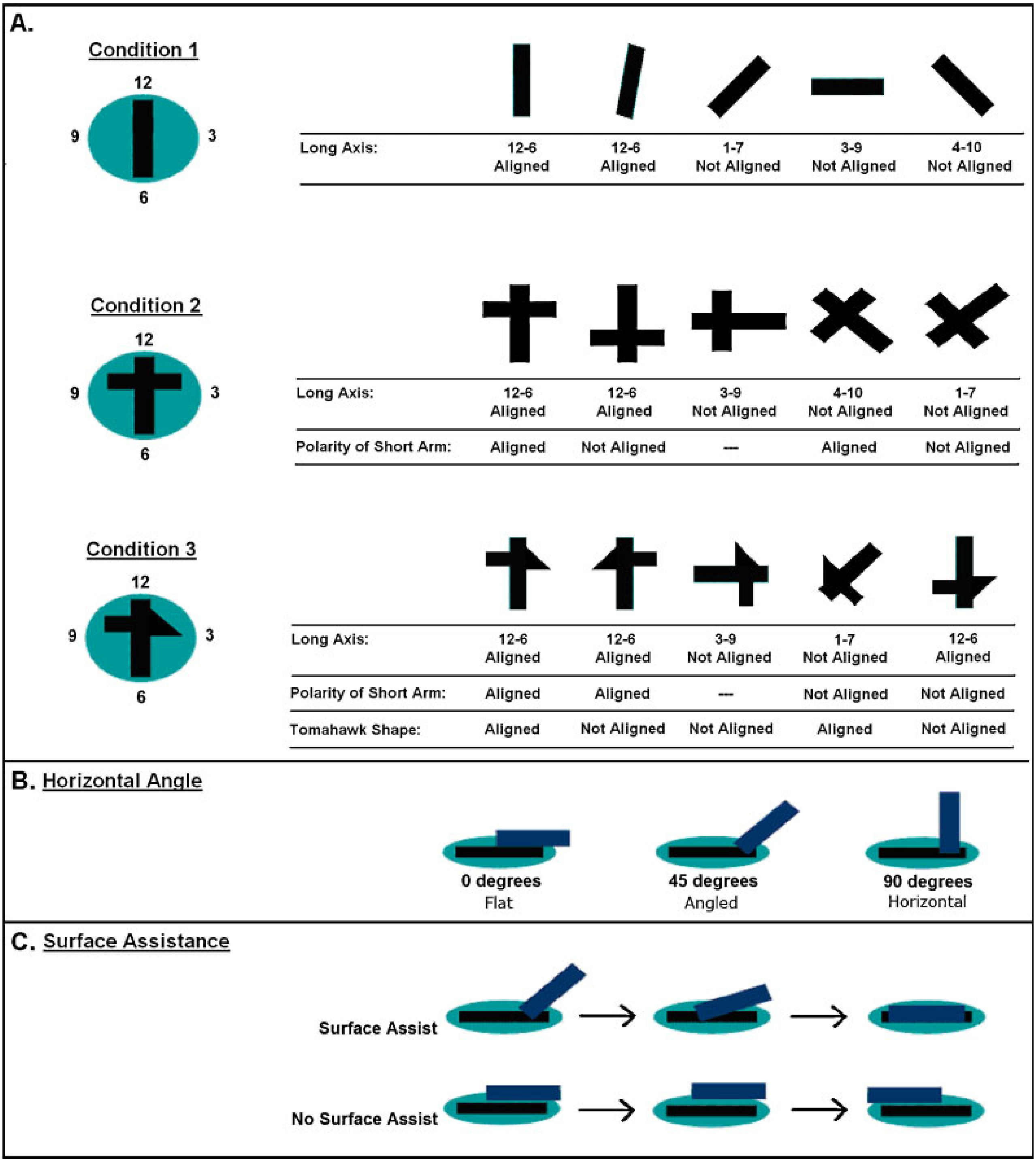
Coding

We coded behavior per trial from playback of digital video using Observer$^{\mathrm{TM}}$ 5.0 software (Noldus Information Technology, Wageningen, The Netherlands). The trial was defined as beginning the moment both the stick and tray were passed to the subject and ending when the task was solved (or rarely when the subject stopped trying and the trial was ended by the experimenter). We coded discrete attempts to place the stick during each trial. The first attempt per trial was operationally defined as beginning when the stick first contacted the tray. Subsequently, differing events delineated the beginning and ending of attempts (see below). We coded these episodes as bouts and included each bout as one attempt at placement unless another variable (e.g., angle of the stick) changed during the bout.

For each attempt, we scored the alignment of the stick with respect to the groove, the angle of contact between stick and tray, whether the subject used one or two hands, and whether the subject moved the stick across the surface of the tray. The latter three variables were used to evaluate the predictions that subjects would act in ways to reduce the degrees of freedom of the stick's movement and to explore new actions with the stick when challenged to manage more than one spatial relation at a time.

The first variable coded per attempt was the alignment of the stick with respect to the groove (see Fig. 2; Panel A). We coded alignment in three ways. First, we coded the alignment of the long axis of the stick with respect to the groove in the tray (as seen from above). We used a clock face classification rubric for this purpose (see Fig. 2). If the stick was within approximately 22.5° of the groove on either side, we considered it 12–6 alignment. If the stick was within approximately 22.5° to either side of perpendicular, we considered it 3–9 alignment. If it was between the 12–6 and 3–9 ranges, we considered it 1–7 or 4–10 alignment (each range was approximately 22.5° to either side of clock face 1.5–7.5 and 4.5–10.5). In other words, the entire clock face was broken up into four sections of equal size (each 45° wide on both sides of the axis) centered evenly around the vertical (12–6) and horizontal (3–9) axes and the two diagonals (1.5–7.5 and 4.5–10.5). This coding rubric permitted reliable judgments of alignment. In addition, for Conditions 2 and 3, we coded the alignment (''polarity'') of the cross piece of the stick with respect to the cross piece of the groove as ''aligned'' or ''not aligned,'' ignoring the 3–9 case where the cross piece is equidistant to the two ends of the groove. For Condition 3, we coded if the tomahawk shape of the stick was positioned facing in the same direction as the matching portion of the groove. If the subject contacted the tray with the stick held vertically, we counted an attempt but did not code any alignment. In several attempts, we could code one aspect of alignment but not others. For example, if the subject's arm or hand blocked sight of the cross piece of the stick but not the long axis, we were able to code alignment of the long axis but not of the cross piece or the direction of the head of the tomahawk.

The second variable coded for each attempt was a categorical judgment of the horizontal angle of the stick as it touched the tray (see Fig. 2; Panel B). If the stick was oriented within 10° of horizontal against the tray, we coded it as flat. If it was within 10° of perpendicular to the tray, we coded it as



Long Axis:	12-6 Aligned	12-6 Aligned	1-7 Not Aligned	3-9 Not Aligned	4-10 Not Aligned

Long Axis:	12-6 Aligned	12-6 Aligned	3-9 Not Aligned	4-10 Not Aligned	1-7 Not Aligned
Polarity of Short Arm:	Aligned	Not Aligned	—	Aligned	Not Aligned

Long Axis:	12-6 Aligned	12-6 Aligned	3-9 Not Aligned	1-7 Not Aligned	12-6 Aligned
Polarity of Short Arm:	Aligned	Aligned	—	Not Aligned	Not Aligned
Tomahawk Shape:	Aligned	Not Aligned	Not Aligned	Aligned	Not Aligned

Fig. 2. Illustrations of dependent variables for alignment of the long and asymmetrical portions of the stick (Panel **A**), angle of contact (Panel **B**), and surface assistance (Panel **C**, showing temporal succession of a successful attempt where the stick placement was guided by the groove). Panel A is shown in plan view, with clock face numbers used to categorize alignment of the long axis of the stick relative to the long axis of the groove (defined as 12–6). Panels B and C are shown in the side view.

vertical and the clock face alignment was ignored. If it was intermediate between these two values, in the larger range from 10–80°, we coded it as angled.

The third variable was whether the subject moved the stick along the surface so as to make contact with a non-uniform area (i.e., the groove), which in effect guided the movement of the stick (called surface assistance). Examples of surface assistance include (1) inserting one tip of the stick into the groove and then pivoting the stick around this tip; (2) inserting the tip of the stick into the groove and then sliding the tip forward while lowering the rest of the stick toward the groove (illustrated in Fig. 2; Panel C); and (3) sliding or rolling the stick flat along the tray's outer surface until it met the groove. If any of these occurred, we scored surface assistance. If, on the other hand, the subject dropped the stick onto the tray or set it down without sliding or rolling it along the surface, we did not score surface assistance. Finally, we coded whether the subject used one or two hands to place the stick.

When one of these four variables (alignment, angle, surface assistance, or use of hand(s)) changed values or if the stick was removed from the surface for more than half a second, we considered that attempt finished. A new attempt was scored if activity combining the stick and tray resumed. Thus, if the subject tapped the stick against the tray multiple times in quick succession without altering any of those variables nor removing the stick for more than half a second, the entire bout of tapping was scored as a single attempt. To take another example, if the subject began a right-handed attempt at 12–6 alignment, flat, with the shaped end of the stick over the wrong end of the tray's groove, and then spun the stick around to a 3–9 alignment, we coded two distinct attempts: (1) a right-handed, flat, 12–6 attempt, with surface assistance, and (2) a right-handed, flat, 3–9 attempt, with surface assistance. The intervening clock face positions of 1–7 or 4–10 that it passed through were ignored, unless the stick moved slowly or stopped there. When the subject switched hands or added/removed a hand, this action also ended the previous attempt and initiated a new one.

We recorded the position of the tray upon entry to the cage and also the stick's initial orientation in Conditions 1–3 (including whether the cross piece of the stick was oriented close to or far from the subject). We found no significant effect of these variables on the number of attempts per trial in either species (Wilcoxon tests, all $P > 0.05$), so we will not mention them further.

The primary coder had an intraobserver reliability of 89% agreement (Cohen's κ, $= 0.88$), based upon roughly 20% of trials rescored across 4 months. A secondary coder established interobserver reliability of 86% agreement (Cohen's $\kappa = 0.85$) based on roughly 25% of trials rescored across 4 months.

Analysis

We analyzed attempts from the first ten successful trials in each condition for each subject. We used data only from subjects that participated in Conditions 2 and 3 in inferential analyses, though some descriptive statistics on other subjects are provided in the tables. Individual subjects' participation is shown in Table I.

We analyzed the data for each species separately to test our main predictions. To test the prediction that the subjects would use more attempts to align an object with an increasing number of spatial relations to manage concurrently, we used Friedman's χ^2 for frequency count data (with three degrees of freedom), following up significant results with pair-wise Wilcoxon tests, using one-tailed $\alpha = 0.05$ for the Wilcoxon. Next, to characterize the subjects' ability to align the sticks, we used χ^2 tests within subject to evaluate bias to align the long axis of the stick to the groove (the 12–6 position) at each condition. For these analyses, chance was set at 0.25, as we scored placement using four clock face sectors (i.e., relative to the axes 12–6, 1.5–7.5, 3–9, and 4.5–10.5). We used Kruskal–Wallis tests to evaluate patterns across conditions within species in the proportions of trials, in which the long axis, the cross piece, and the tomahawk feature were correctly aligned to the groove, to evaluate the effects of increasing numbers of spatial relations on ability to achieve alignment.

TABLE I. Number of Successful Trials at Each Condition Out of Ten Attempted Trials

Species		Condition 0	Condition 1	Condition 2	Condition 3
PAN	Lana	10	10	10	10
	Mercury	10	10	8	0[a]
	Panzee	10	10	10	10
	Sherman	10	10	10	10
CEBUS	Chris	9	9	10	10
	Job	6[b]	NT	NT	NT
	Leo	6	9	7	7
	Mickey	7	5	NT	NT
	Nick	10	7	7	NT
	Solo	10	7	4	7
	Xavier	9	6	NT	NT
	Xenon	10	10	9	6

NT, not tested at that condition.

[a] Mercury stopped working on trial 1 of Condition 3 and was not tested for trials 2–10.

[b] On trial 7 of Condition 0, Job stopped working on the problem and was not tested for trials 8–10.

To evaluate the prediction that individuals would attempt to reduce the degrees of freedom in the problem, we evaluated the probability of binary variables (using surface assistance vs. no surface assistance, using two hands vs. one hand) against chance, where chance probability was defined as 0.50, using χ^2 tests for each individual, with two-tailed set at 0.05.

To evaluate the prediction that individuals encountering a new problem embodying an increased number of relations would change the angular orientation of insertion attempts, we used Wilcoxon tests within subject.

Finally, between-species comparisons for the number of attempts were made using Mann–Whitney tests, two-tailed = 0.05, to explore the possibility that the species differed in this aspect of their performance in this task.

Analyses were performed using SPSS 11.0 (SPSS Inc., Chicago). Where we conducted multiple pair-wise tests on the same data set, levels were set to 0.05 divided by the number of pair-wise tests [Bonferroni, 1936]. Effect sizes were evaluated for those tests producing statistically significant contrasts. We used odds ratios for χ^2 tests and mean difference values for Wilcoxon tests. Following Nakagawa and Cuthill [2007], we present effect sizes for pair-wise contrasts only.

RESULTS

As shown in Table I, chimpanzees attempted and completed ten trials in each condition, with the exception of Mercury, who completed eight of ten attempted trials in Condition 2 and failed to complete his one attempted trial in Condition 3. Overall, chimpanzees completed 148 trials out of 151 (98%) attempted trials. Capuchins completed between 4 and 10 of 10 attempted trials per condition, and overall completed 187 out of 237 (79%) attempted trials.

Effect of the Number of Concurrent Relations on the Number of Placement Attempts

The number of attempts with the stick per completed trial at each condition for each subject is presented in Table II. Notice that, even in baseline trials, subjects of both species on average made around 4 or 5 attempts to place the stick into the floor of the tray, with a range of 2–12 attempts on average per individual. We found a significant difference across conditions for chimpanzees (Friedman: $N = 30$, df = 3, $\chi^2 = 29.436$, $P < 0.001$). Pair-wise tests between conditions revealed a significant increase between Conditions 1 and 2 (Wilcoxon: $N = 38$, $Z = -4.336$, $P < 0.001$; mean difference = 13.8 attempts), but not between

TABLE II. Mean (Above) and Standard Deviation (Below) of the Number of Attempts Per Completed Trial at Each Condition for Each Subject

Species	Subject	Condition 0	Condition 1	Condition 2	Condition 3	All conditions
PAN	Lana	1.7	2.5	14.6	26.3	11.28
		0.95	2.51	14.28	22.74	16.49
	Mercury	12.4	10.4	37.56	–	19.52
		13.47	14.27	39.85		27.24
	Panzee	1.6	1.9	11.6	23.5	9.65
		0.97	1.29	9.2	30.58	17.84
	Sherman	1.6	2.1	8.5	16.5	7.18
		1.58	2.13	9.51	15.03	10.58
	Mean, all chimps	4.33	4.22	17.56	22.1	11.34
		8.07	7.93	23.63	23.2	18.52
CEBUS	Chris	6.33	13.33	59.1	46.4	32.42
		8.14	16.48	37.28	34.23	34.58
	Job	7.5	–	–	–	7.5
		5.09				5.09
	Leo	3.17	12.67	23.86	20.29	15.24
		0.75	13.02	16.84	23.41	16.88
	Mickey	4.23	5.2	–	–	4.67
		3.35	4.38			3.65
	Nick	2	9.14	24	–	10.5
		0.67	7.43	12.88		12.05
	Solo	2.3	4.71	29.75	34	14.75
		0.95	2.63	15.22	28.47	20.51
	Xavier	3	13.83	–	–	7.33
		2.24	8.06			7.5
	Xenon	4	5.7	27.78	26.83	14.51
		2	3.68	39.8	24.37	24.36
	Mean, all capuchins	3.9	9.38	35	33.5	16.35
		3.94	9.96	31.92	29.25	23.46

Conditions 0 and 1 (Wilcoxon: $N = 40$, $Z = -0.718$, $P = 0.473$) or Conditions 2 and 3 (Wilcoxon: $N = 30$, $Z = -0.454$, $P = 0.650$). In capuchins, we also found significant variation across conditions (Friedman: $N = 30$, df = 3, $\chi^2 = 51.152$, $P < 0.001$). Pair-wise tests revealed significant increases between Conditions 0 and 1 (Wilcoxon: $N = 42$, $Z = -3.696$, $P < 0.001$; mean difference = 5.7 attempts) and between Conditions 1 and 2 (Wilcoxon: $N = 37$, $Z = -4.604$, $P < 0.001$; mean difference = 25.8 attempts), but not between Conditions 2 and 3 (Wilcoxon: $N = 30$, $Z = -0.833$, $P = 0.405$). The species did not differ significantly in the number of attempts they made per trial in any condition (all P's = 0.09 or greater).

Effect of Concurrent Relations on Alignment of the Stick to the Groove

With respect to alignment of the long axis of the stick, as shown in Table III, three of four chimpanzees and all capuchins showed a significant bias for accurate alignment of the long axis to the groove in Conditions 1–3 (noted as 12–6 in our clock face rubric). Recall that, for these analyses, chance probability of a 12–6 alignment was defined as 0.25. Neither species showed an effect of condition on this variable (Chimpanzees: Kruskal–Wallis N1 = 4, N2 = 4, N3 = 3, $\chi^2 = 2.14$, df = 2, $P = 0.34$; Capuchins: Kruskal–Wallis N1 = 5, N2 = 5, N3 = 4, $\chi^2 = 1.02$, df = 2, $P = 0.60$). Among the

TABLE III. Number and Proportion of Attempts, Conditions 1–3, for Each Subject in Which the Long Axis of the Stick was Aligned With the Long Axis of the Groove

Species	Subject	Condition	♯ Attempts aligned/total	Proportion aligned	♯ Expected by chance	χ^2	Odds ratio
PAN	Lana	1–3	151/396	0.38	99	36.42***	1.85
		1		0.44			
		2		0.31			
		3		0.41			
	Mercury[a]	1–3	90/428	0.21	107	3.6	
		1		0.23			
		2		0.2			
		3		–			
	Panzee	1–3	178/370	0.48	93	105.37***	2.76
		1		0.33			
		2		0.43			
		3		0.52			
	Sherman	1–3	87/261	0.33	65	9.65***	1.51
		1		0.09			
		2		0.36			
		3		0.35			
	SUM	1–3	506/1,455	0.35	364		
CEBUS	Chris	1–3	381/1,033	0.37	258	119.41***	1.76
		1		0.31			
		2		0.38			
		3		0.37			
	Leo	1–3	152/399	0.38	100	11.43***	1.84
		1		0.33			
		2		0.41			
		3		0.38			
	Nick	1–3	114/226	0.5	57	78.02***	3.02
		1		0.58			
		2		0.48			
		3		–			
	Solo	1–3	157/383	0.41	96	52.22***	2.08
		1		0.58			
		2		0.44			
		3		0.37			
	Xenon	1–3	173/407	0.43	102	66.64***	2.21
		1		0.5			
		2		0.38			
		3		0.46			
	SUM	1–3	977/2,448	0.42	612		

$P < 0.001$. Each subject's overall proportion (Conditions 1–3 combined) is compared with the number expected by chance (Chance is one alignment per four attempts = 0.25) and the probability of the observed distribution, as evaluated with the χ^2 test (df = 1).

[a] Mercury and Nick completed no trials in condition 3.

TABLE IV. Number and Proportion of Attempts Per Subject With the Cross Piece of the Stick Aligned With Respect to the Cross Piece of the Groove (the Polarity of the Short Arm) Across Conditions 2 and 3, Compared With the Expected Even Distribution of such Alignments

Subject	Species	♯ Attempts aligned/total	Proportion aligned	♯ Expected by chance	χ^2 test	Odds ratio
PAN	Lana	146/304	0.48	152	0.47	
	Mercury	114/244	0.47	122	1.05	
	Panzee	135/294	0.46	147	1.96	
	Sherman	82/193	0.43	97	4.36*	0.74
	SUM	477/1,035	0.46	518		
CEBUS	Chris	275/660	0.42	330	18.33***	0.71
	Leo	129/226	0.57	113	4.53*	1.33
	Nick	66/143	0.46	72	0.85	
	Solo	125/275	0.46	138	2.27	
	Xenon	144/285	0.51	143	0.03	
	SUM	739/1,589	0.47	795		

These data exclude attempts with a 3–9 clock-face orientation.
*$P<0.05$; ***$P<0.001$.

chimpanzees, Panzee and Sherman shifted their strategy toward more 12–6 attempts in Conditions 2 and 3 compared with Condition 1, whereas Lana and Mercury failed to show that pattern. Among the capuchins, Chris and Leo made increasing proportions of alignments in 12–6 position in Conditions 2 and 3 compared with Condition 1, whereas Nick, Solo, and Xenon showed the opposite pattern.

Table IV presents data for each individual's alignment of the cross piece of the stick to the cross piece of the groove (polarity of the short arm) in Conditions 2 and 3. Note that the data in Table IV exclude attempts where the long axis of the stick was in the 3–9 position with respect to the groove; so, fewer attempts are classified in this table than in Table II for the same conditions. Aligning the cross piece of the stick presented a larger challenge for both species than aligning the long axis. As shown in Table IV, only two subjects (both capuchins) aligned the cross piece to the correct end of the long axis on more than 50% of attempts. The capuchin with the highest value (0.57) was the only subject that aligned the cross piece correctly more frequently than expected by chance. One chimpanzee and one capuchin correctly aligned the cross piece significantly less often than expected by chance. Recall that chance probability for this form of alignment was defined as 0.50.

Table V presents the data for concurrent alignment of the long axis, cross piece, and the tomahawk shape during a single attempt by subjects of each species. In Condition 2, no subject aligned the cross piece correctly on more than 54% of attempts while also aligning the long axis (chance would produce 50% alignments of the cross piece in these cases). Capuchins achieved concurrent alignment on 46% of all attempts and chimpanzees on 49%. Of the seven subjects completing Condition 3, three (one chimpanzee, two capuchins) aligned the tomahawk piece correctly on more than half of their attempts (56–76% attempts) when they also aligned the long axis and the cross piece. The deviation from chance (50%) was significant only for the capuchin that earned the score of 76% alignment. Scores for the other four individuals ranged from 15 to 46%. The two lowest scores, both for chimpanzees, were significantly lower than expected by chance.

Effect of Number of Concurrent Relations on Strategies for Holding and Moving the Stick

The proportion of attempts at a horizontal angle for each subject at each condition is presented in Figure 3. Overall, the subjects touched the stick to the tray in a horizontal (flat) position in a majority of attempts (0.7 of all attempts, chimpanzees, and 0.6, capuchins), and there was no evident shift in this bias across conditions. Panzee (chimpanzee) and Chris (capuchin) shifted to more flat (0°) attempts in Conditions 2 and 3 compared with Conditions 0 and 1 (Wilcoxon tests, Panzee: $N=20, Z=-2.78, P=0.01$; mean difference = 35%; Chris: $N=18$, $Z=-2.94$, $P=0.01$; mean difference = 17%). The other individuals did not present a trend.

Figure 4 presents the proportion of attempts across conditions on which each subject used the surface to guide the movement of the stick. Chimpanzees used the surface significantly less frequently in Conditions 0 and 1 than in Conditions 2 and 3 (Wilcoxon: $N=68$, $Z=-4.987$, $P<0.001$; mean difference = 27%). The effect derives principally from Lana and Mercury that had many more attempts than Panzee or Sherman (see Table II). Panzee and Sherman used surface assistance on a relatively high proportion of attempts throughout testing (at least 75% attempts and values cluster around 95% in Condition 3). Capuchins used the surface at a relatively high rate in Condition 0 (about 78% attempts), but all used the surface less in Condition 1 than in Condition 0 (Wilcoxon: $N=67$, $Z=-2.150$, $P=0.032$; mean difference = 4%). No

TABLE V. Distribution of Attempts Per Subject in Conditions 2 and 3 With the Long Axis Misaligned (N) or the Long Axis Aligned and the Cross Piece Aligned (YY) or Misaligned (YN), and for Condition 3, With the Long Axis Aligned, Cross Piece Aligned, and the Tomahawk Shape Aligned (YYY) or Misaligned (YYN)

Species	Individual	Condition	N	YN	YY	Sum of Y-	% of Y- that is YY	Odds ratio	Condition 3				Odds ratio
									YYN	YYY	SUM of YY-	% of YY that is YYY	
PAN	Lana	2	86	21	17	38	45						
		3	145	48	53	101	52		37	16	53	30**	0.43
	Mercury	2	259	35	31	66	47						
		3	–	–	–	–	–		–	–	–	–	
	Panzee	2	66	37	13	50	26$^{\sharp\sharp}$	0.35					
		3	114	50	72	122	59**	1.44	61	11	72	15$^{\sharp\sharp}$	0.18
	Sherman	2	53	18	12	30	40						
		3	19	27	29	56	52		11	18	29	62	
	ALL	2	464	77	73	150	49						
		3	278	125	154	279	55		109	45	154	29	
CEBUS													
	Chris	2	309	112	75	187	40$^{\sharp\sharp}$	0.67					
		3	272	80	82	162	51		46	36	82	44	
	Leo	2	89	29	34	63	54						
		3	86	20	33	53	62		8	25	33	76**	3.13
	Nick	2	85	37	40	77	52						
		3	–	–	–	–	–		–	–	–	–	
	Solo	2	66	35	16	51	31$^{\sharp\sharp}$	0.46					
		3	147	40	48	88	55		21	27	48	56	
	Xenon	2	133	38	45	83	54						
		3	77	27	39	66	59		21	18	39	46	
	ALL	2	682	251	210	461	46						
		3	582	167	202	369	55		96	106	202	52	

For this analysis, trials were discarded if any axis or alignment could not be seen on video.
$^{\sharp\sharp}P < 0.05$ below expected, χ^2 test.
$^{**}P < 0.05$ above expected, χ^2 test.

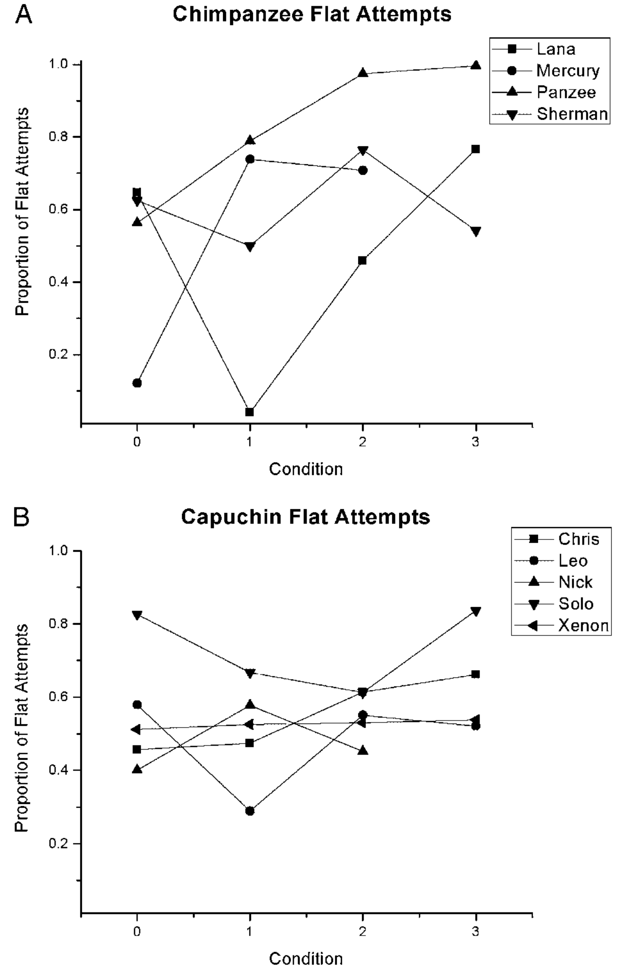


Fig. 3. Proportion of attempts at 0 degrees (flat) at each condition for each chimpanzee (Panel **A**) and each capuchin (Panel **B**).

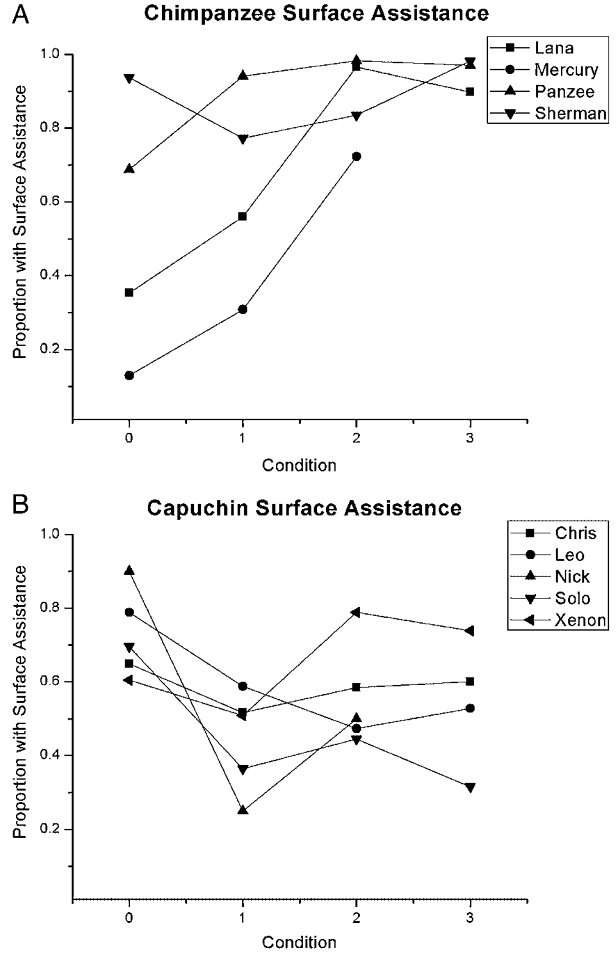


Fig. 4. Proportion of attempts involving surface assistance (SA) at each condition for each chimpanzee (Panel **A**) and each capuchin (Panel **B**).

trends are apparent in the capuchins' use of surface assistance beyond the drop between Conditions 0 and 1. Apparently, variation in the number of concurrent relations to manage across Conditions 1–3 had little effect on either species' use of the surface.

Individuals of both species routinely used a transverse hook power grip [Marzke & Wullstein, 1996] to grasp the stick, with the long axis of the stick oblique to the wrist and digits 2–5 flexed around the stick and the thumb adducted or opposing the other digits This is a normal manual posture for both species when holding a long object [Marzke & Wullstein, 1996] and it is also a common grip in young children in similar circumstances (manipulating a long narrow stick) [Manoel & Connolly, 1998]. Manoel and Connolly refer to this as a kind of "rigid grip," because it does not allow movement of the digits.

Over all conditions, individuals of each species used two hands in just over a quarter of their attempts. The proportion of bimanual attempts for each individual at each condition is presented in Table VI. Panzee, Sherman, and Lana used two hands more often in Conditions 2 and 3 (asymmetrical) vs. Conditions 0 and 1 (symmetrical) (Wilcoxon, $N=20$, $Z=-2.54$ to -3.725, $P\leq 0.01$ all cases; mean difference = 33% Panzee, 19% Sherman, and 29%, Lana). Mercury showed no consistent shift. Shifts among capuchins were both more varied in direction and of smaller amplitude. Solo shifted to an increasingly bimanual strategy in Conditions 2 and 3 vs. Conditions 0 and 1 ($N=11$, $Z=-1.89$, $P=0.06$; mean difference = 30%), as did Nick in Condition 2 vs. Conditions 0 and 1 ($N=7$, $Z=-1.83$, $P=0.07$; mean difference = 3%) (recall that Nick did not complete Condition 3). Leo and Chris showed no trend and Xenon shifted to a less bimanual strategy ($N=15$, $Z=-1.85$, $P=0.06$; mean difference = 9%). In all these cases, we used the proportion of bimanual attempts per trial as the data for the Wilcoxon tests.

Evaluation of Individual Strategies

Examining each individual's scores for the several dependent variables measured in this study, we can see in Table VII that no particular pattern of behaviors is associated with the proportion of attempts in which the individual aligned the long axis, the cross piece, or the tomahawk feature of the stick. Individuals that aligned the long axis rather well were not more likely to align the cross piece. Only one individual (capuchin Leo) scored well on aligning both the cross piece and the direction of the tomahawk (he ranked first in both variables). Across all subjects, use of two hands, surface assistance, or placing the stick flat against the tray varied independently of each other and of the probability of aligning any part of the stick to the groove.

DISCUSSION

From the perspectives of motor skill development and Perception–Action theories [Fragaszy & Cummins-Sebree, 2005; Latash et al., 1996; Lockman, 2000], how individuals move objects in relation to surfaces provides insight into how they use objects as tools. This view is premised on an understanding of tool use as a subset of goal-directed activity combining objects and surfaces (combinatorial activity). Tool use is differentiated from other subsets of goal-directed combinatorial activity by details of the spatiotemporal structure of the problem. We sought to evaluate key predictions from these theoretical perspectives relating manipulative behavior to the spatiotemporal structure of a problem, and for this purpose, we deliberately adopted a problem that

TABLE VI. Proportion of Attempts Made With Two Hands by Each Subject Per Condition

Species	Subject	Condition 0	Condition 1	Condition 2	Condition 3	All conditions
PANZEE	Lana**	0.00	0.00	0.23	0.26	0.23
	Mercury	0.01	0.14	0.17	–	0.13
	Panzee**	0.19	0.74	0.54	0.86	0.73
	Sherman**	0.00	0.00	0.25	0.22	0.20
	All chimpanzees	0.05	0.22	0.30	0.37	0.30
CEBUS	Chris	0.18	0.19	0.21	0.21	0.20
	Jobe	0.27	–	–	–	0.27
	Leo	0.42	0.40	0.34	0.16	0.30
	Mickey	0.40	0.00	–	–	0.21
	Nick**	0.00	0.05	0.05	–	0.05
	Solo**	0.44	0.52	0.77	0.76	0.72
	Xavier	0.19	0.07	–	–	0.10
	Xenon##	0.42	0.20	0.23	0.31	0.26
	All capuchins	0.28	0.20	0.23	0.31	0.26

**Significantly increased proportion of attempts that were bimanual in asymmetrical conditions (2/3) compared with symmetrical conditions (0/1), $P < 0.05$.
##Significantly decreased proportion of attempts that were bimanual in asymmetrical conditions (2/3) compared with symmetrical conditions (0/1), $P < 0.05$.

TABLE VII. Individual Performance

Species	Subject	# Attempts/ trial condition 1	# Attempts/ trial condition 3	Proportion aligned long axis conditions 1–3	Proportion aligned long axis and cross piece conditions 2–3	Proportion aligned long axis, cross piece, and tomahawk condition 3	% SA[a]	% Flat[b]	% 2H[c]
PAN									
	Lana	2.5	26.3	0.38	0.48	0.30	88	62	23
	Mercury	10.4	–	0.21	–	–	52	59	13
	Panzee	1.9	23.5	0.48	0.47	0.15	96	96	73
	Sherman	2.1	16.5	0.33	0.43	0.62	92	61	20
CEBUS									
	Chris	13.3	46.4	0.37	0.42	0.44	59	61	20
	Leo	12.7	20.3	0.38	0.57	0.76	53	48	30
	Nick	9.1	–	0.50	0.46	–	47	48	5
	Solo	4.7	34.0	0.41	0.46	0.56	38	76	72
	Xenon	5.7	26.8	0.43	0.51	0.46	73	53	10

[a] Surface assistance.
[b] Horizontal angle = 0–10°.
[c] Two hands.

could not be described as involving using a "tool." We presented capuchins and chimpanzees with a placement problem, fitting a stick into a matching groove. By altering the shape of the stick (from straight stick to asymmetric cross to tomahawk shape), we varied the number of spatial relationships between stick and groove from one to three. Aligning a straight stick requires matching the long axis of the stick to the groove; aligning the tomahawk, in contrast, requires matching the long axis, the head of the tomahawk to one end of the long axis, and the left–right direction of the head of the tomahawk.

We found that individuals of each species were challenged by the problems in the expected directions, producing greater numbers of attempts to make each placement when the number of spatial alignments to be managed increased (from one to two for chimpanzees, from zero to one and from one to two for capuchins). The chimpanzees moved the stick along the surface of the tray more in the two conditions with two or more spatial relations, compared with the two conditions with no or one spatial relation to achieve between the stick and a groove. Surface assistance could be interpreted as generating perceptual information and/or simplifying the demands for movement control. However, the range of behavioral adjustments to relational structure in the problems varied across individuals, species, and conditions in a complex way. We first discuss the theoretical implications of our findings for understanding manipulative problem solving in nonhuman animals, and then address the nature, extent, and implications of the small differences in performance between chimpanzees and capuchins on the placement tasks.

Aligning One Axis

Despite each species' considerable digital dexterity and eye–hand coordination [Fragaszy, 1998], both species displayed inefficient alignment of the long axis of the stick with the long axis of the groove—the first step in our placement problem. We did not anticipate that they would have as much difficulty with this problem as they did, but their travails were revealing. All our subjects required multiple attempts to align the long axis of the stick to the groove, whether the stick was simply straight (in Condition 1) or had additional features (in Conditions 2 and 3). Humans, in contrast, typically hold the stick above the groove, align it visually, and then lower it directly into to the groove, and they do this from the first attempt [Fragaszy, unpublished data]. Although occasionally a subject slid the stick into the groove from one end (an efficient solution from the point of view of economy of movement and one revealing effective perception of the stick–slot contact), none of our subjects ever precisely laid the stick directly into the long groove in a horizontal orientation as humans do from 4 years of age [Fragaszy et al., unpublished data]. No monkey or ape ever did this, suggesting a fundamental difference in how we perceive the relation between objects and surfaces compared with how they perceive this relation. We automatically match the line of a stick to a line on a surface; our nonhuman primate subjects, apparently, did not.

This brings us to consider how acting with precision relative to a point is different from acting with precision relative to a line. A point is a simpler geometric entity than a line. The monkeys and apes can readily and precisely bring a finger to a point on a surface, as they do when picking up an object. They can also precisely bring an object to a point on a surface, as when inserting a stick or piece of grass into a small opening [a common form of tool use; e.g., McGrew, 2004; Visalberghi & Fragaszy, 2006]. They must take two points into account to do this: the point on the surface and the terminal end of the finger or the object that will contact the surface. In contrast, a line connects two points, and thus is a relational geometric entity. The placement task required is that the subjects bring one line (stick) precisely parallel (and overlapping) to a second line (groove in the tray). There are at least four points to take into account to do this, two on the surface (defining the axis of the groove) and two on the stick (defining the axis of the stick). In this sense, aligning a stick to a groove is a more complicated relational problem than bringing a finger or a held object to a point. It would be interesting to explore whether aligning a shorter stick to a shorter groove would affect the subjects' accuracy at alignment. If the above reasoning is correct, shortening the stick and the groove would not make the problem easier for them. A line is still a relational entity, and it should remain difficult for them to make one line parallel to another. On the other hand, if managing fine movements of the stick contributed to the difficulty of the problem, a shorter stick could lead to a greater accuracy in alignment.

A telling example from a different scale of action with a stick comes from Menzel's [1972] report of how several young chimpanzees housed in a large fenced enclosure developed the technique of bracing a fallen tree branch (a very long stick) against a tree trunk at a point above wiring around the trunk meant to deter the chimpanzees from climbing the tree (and stripping its bark). Several individuals worked out an effective method of placing one end of the stick on an elevated wooden plank runway about 3 m above the ground and the other end against the trunk while standing on the runway, subsequently climbing the stick to the tree trunk and beyond. One individual, however, persisted in placing the top of the stick against the tree trunk while holding the bottom of the stick with his foot, against the side of the runway, rather than bracing it on top of the runway. He managed to position the top ‘‘point’’ almost immediately, but required several days of practice to master both ends of the ‘‘line.’’

Effects of Multiple Spatial Relations on Performance

The primary prediction derived from Fragaszy and Cummins-Sebree’s [2005] extension of Perception–Action theory that managing additional relations increases the challenge of the placement task was clearly supported by our results. Individuals of both species made approximately four times as many attempts per trial to achieve placement in Condition 2 (with a cross-shaped stick) than in Condition 1 (with a straight stick), and this shift was statistically significant for both species. All three chimpanzees that participated in Condition 3 (with a tomahawk-shaped stick) made more attempts (although not significantly so) in this condition than in Condition 2. The four capuchins that participated in Condition 3 made equivalent number of attempts as in Condition 2, suggesting that they encountered a ceiling for increasing difficulty when the second relation entered the problem in Condition 2.

Accuracy of alignment on each attempt also indicates that the number of spatial relations defined the challenge of the problem for our subjects. Three of four chimpanzees and all five capuchins aligned the long axis of the stick to the long axis of the groove more often than expected by chance across Conditions 1–3. However, the picture is quite different for alignment of the cross piece of the stick in Conditions 2 and 3. Considering concurrent alignments, in Condition 2, one chimpanzee and two capuchins aligned the long axis but in the same attempt, misaligned the cross piece of the stick more often than expected by chance, and no subject jointly aligned the cross piece and long axis of the stick significantly more often than expected by chance. In Condition 3, one capuchin monkey concurrently aligned the long axis, cross piece, and tomahawk shape more often than expected by chance. No other individual aligned the three components more often than expected by chance and two (two chimpanzees) did so less often than expected by chance. Altogether, these findings support the hypothesis of the spatial–relational model that the number of concurrent spatial relations defines the challenge of a manipulation task. When the task embodied two or more relations, the subjects worked systematically only with the most familiar one (which may also have been the most obvious one), the long axis of the stick.

Potì et al. [2009] studied how adult chimpanzees modeled constructions with three blocks demonstrated to them by a human. The constructions involved positioning blocks into a line, cross stack, or arch. The latter two constructions involve two dimensions, the line, just one. The authors comment that the chimpanzees occasionally produced the cross stack, but suggest that ‘‘constructing in two dimensions constitutes a cognitive challenge for chimpanzees and probably taps the upper boundary of their construction skills.’’ We agree that two dimensions is likely their upper boundary for positioning objects in these types of constructive and placement tasks. Hayashi and Takeshita [2009] presented the same subjects with cubic blocks with two irregular sides to stack into four-block towers. Like Potì et al. [2009], Hayashi and Takeshita [2009] found that juvenile chimpanzees did not readily anticipate the placement of the irregular side of the cube when positioning it in relation to another block or the floor. Positioning a block with some irregular sides is, like positioning a cross-shaped stick or making a cross stack construction, a problem embodying at least two spatial relations. Thus, it seems that managing two spatial dimensions concurrently challenges chimpanzees (and, we predict, capuchins) across tasks.

In our task, capuchins and chimpanzees tended to align the long segment of the stick with the long segment of the groove, but did not show this tendency for the other segments of the stick. One explanation for this pattern is the challenge for both species of reasoning about more than one spatial relation at a time, in accord with Fragaszy and Cummins-Sebree’s [2005] model of spatial reasoning. But, other explanations may also be advanced for this general finding. Perhaps the long axis was the most perceptually obvious plane of the stick and/or the groove because of its absolute length. Alternatively, it may have been the segment which the subjects had the most practice aligning. To determine the influence of physical prominence and familiarity, one could give subjects a short stick to place first and a longer T-shaped stick second, or a second stick of equal dimensions (X rather than T shaped).

Behavioral Adjustments to Challenging Problems

Motor skill theory and Perception–Action theory lead to predictions about behavior in a challenging placement task, such as we used in this study. Motor skill theory predicts that individuals will act in ways that simplify the demands of the problem for motor control. Perception–Action theory predicts that behaviors that provide information about the affordances of the problem should be more common when the task is more difficult. We anticipated that using the surface to guide the movement of the stick might serve both to simplify movement control and that the same behavior might be used in an exploratory manner in more difficult conditions. Using the surface to guide the movement of the stick reduces the degrees of freedom to control the stick, because the actor can press the stick against the substrate using constant pressure rather than raising and lowering the stick.

Maintaining contact between stick and surface may also support other kinds of movements. Christel and Fragaszy [2000] report that capuchin monkeys moved single digits independently when retrieving small pieces of food from a groove when the fingers were resting on the surface of the board, but not when they grasped the food from the top of a column where the hands were unsupported by a substrate. The passive support at the substrate evidently enabled coordination of single digits for diverse grips requiring greater control than the whole hand grips that capuchins use unless the situation demands more. Christel and Fragaszy [2000] suggest that tactile stimuli during prehension may have enhanced perception of limb movements—kinesthesia—thereby enhancing the control of single fingers. A similar process might occur when the hand holds a stick in contact with a substrate.

In sum, moving the stick across the surface of the tray in the course of attempting to place it into a groove may have multiple consequences: it may reduce the degrees of freedom the actor must control to move the stick smoothly, and it concomitantly may provide kinesthetic and haptic information about the surface and the relation between the stick and the surface (i.e., when the stick crosses a boundary into the groove). Thus, for several reasons, sliding the stick across the surface could aid placement. Capuchins use a set of actions with the hands identified in humans as ‘‘exploratory procedures’’ [Klatzky & Lederman, 1987] in a haptic search task [Lacreuse & Fragaszy, 1997], suggesting that under some circumstances they seek haptic information to organize movement. We presume that chimpanzees do the same, although to our knowledge no data bear on this issue directly.

Did our subjects move the stick across the surface of the tray in ways that could aid alignment? Generally, yes. Most individuals of both species did move the stick across the surface of the tray on most attempts, although there were large individual differences in the use of this strategy. Two chimpanzees did so on most of their trials in all conditions; two others, that required more attempts at every condition than the first two individuals, did so more often as the number of relations to manage increased. The three chimpanzees that completed Condition 3 used the surface on more than 80% of their attempts. The capuchins used this strategy as often as the chimpanzees overall, but did not consistently adjust the frequency of using the surface across conditions; in Conditions 2 and 3, the individual range was 32–79%. These findings do not strongly support the prediction that subjects would increasingly adopt behaviors that reduce degrees of freedom in moving the stick in more challenging conditions.

Using two hands might increase the ease of manipulation or the stability of contact with the stick. However, our subjects did not consistently use two hands to solve this problem, nor did their use of two hands differ consistently across conditions. Subjects differed widely in how often they used two hands (range from 0.02 to 0.73 for all attempts) and no consistent trend across conditions was evident in how often subjects used two hands.

Adopting a particular angle of contact between stick and tray might aid placement, either by increasing the haptic information generated by motions of the stick across the surface or by making it easier to move the stick in a controlled manner. As shown in Table VII, all except two individuals placed the stick flat against the tray on half or more of all attempts across all conditions (recall that ‘‘flat’’ covered only 10° out of a possible 90°). Variation in this variable across conditions was large across and within subjects, with no apparent directional trend. Thus, placing the stick flat against the surface seemed to be a standard approach to the placement problem, rather than a strategy to cope with increasing demands for managing concurrent spatial relations.

Overall, it seems that use of the surface was a common strategy in both species, and there is a slight suggestion that chimpanzees use the surface more often as the task becomes more difficult. The other two behaviors, which we predicted might vary in accordance with task difficulty, did not vary in the expected manner. Still, among chimpanzees, the two subjects that made the fewest attempts per trial to place the stick (an index of efficiency) used two hands, moved the stick on the surface, and moved it flat against the surface more often than the other two chimpanzees. The chimpanzee with the least success at this task used all these behaviors the least often. The capuchins did not present as clear a picture linking any particular behavior with efficiency at placement. Thus, we have weak support for our predictions that specific behaviors would be associated with efforts to place the stick into the groove.

Comparison of the Species in This Task

Capuchins did not vary from chimpanzees in number of attempts used to place the stick, efficiency at aligning the long axis of the stick (virtually all the subjects did this at above-chance levels), or efficiency of concurrently aligning more than one element of the stick (most individuals of both species did not do this well consistently). One capuchin but no chimpanzee achieved good success at aligning both the cross piece and the tomahawk shape. There is no evidence from this study that either species had an advantage relative to the other in recognizing or producing the correct alignment of a stick to place it into a matching groove. There was some evidence that two chimpanzees and one capuchin modified their actions across conditions in response to the challenge of the task (i.e., they increased the use of two hands or the use of surface assistance). Individual variation was prominent in our study; differences between species were not evident.

According to Fragaszy and Cummins-Sebree's [2005] model of spatial reasoning, an individual's behavior in placement tasks should predict that individual's aptitude for mastering relations present in tool tasks containing the same relational structures. Our findings in this study suggest that capuchins and chimpanzees will master tool tasks of equivalent structure, but that there will be wide differences across individuals in aptitude for these tasks. One source of individual differences might be early rearing conditions. Menzel et al. [1970] reported that apes reared for the first year or two in natural environments were better able to solve manipulation problems (tool-using tasks) than those reared entirely in captive settings. All the subjects in our study were laboratory born and raised, although their rearing histories varied with respect to how intensively they interacted with humans and with how many conspecific companions they lived.

Wider Theoretical Implications

Weiss et al. [2007] show that cotton-top tamarins move their hands into an awkward position, with the thumb facing downward, to grasp the stem of an upside down glass that they then turn upright and retrieve a piece of food adhering to the inside of the glass. They do not grasp the glass with the normal grip, thumb facing up, and then turn it over after prehending it. Their behavior in this circumstance illustrates in a nonhuman species the phenomenon known as the ''End-state comfort effect,'' documented widely in humans, where actors adopt initially awkward postures to meet later task demands [Rosenbaum et al., 2006]. These findings, with a species that does not routinely use tools in nature or captivity, are at first glance surprising in relation to the relatively ineffective planning shown by chimpanzees and capuchins in this study that even in the straight stick condition were not very accurate at initial placements. Why might grasping an upside down glass elicit more effective planning than the placement task we presented in this study?

We suggest that one difference between planning where to place the hand and planning where to place an object held in the hand is owing to the privileged perception and control of the body. Although a wide body of evidence indicates that peripersonal space representation is malleable and can be affected by experience moving held objects [e.g., Làdavas & Serino, 2008], a held object remains distinct from the body with respect to ''ownership.'' ''Ownership'' is indicated by responding to touches to the object as touches to the body, and humans also report that they sense that the body is located where the object is [Makin et al., 2008]. Tools do not acquire this status [De Preester & Tsakiris, 2009] and we should not expect that other objects would acquire ownership status either.

A second possible reason that positioning the hand to grasp the stem of a glass is easier than positioning a stick into a groove is that the stem of the glass is a single plane, equivalent in our task to the long axis of the stick. Our subjects did manage to align the single long axis of the stick to the groove at above-chance levels, albeit with less precision than the tamarins achieved at placing their hands along the shaft of the glass. However, the tamarins had direct haptic information about contact with the glass, whereas in our task the monkeys and apes were feeling the surface of the tray indirectly through the stick. Less direct perception should generate a wider margin of error in positioning, especially when the actor does not systematically seek information through action [as humans often do when faced with an unfamiliar object or surface; Klatzky & Lederman, 1987]. Thus tamarins, despite having a less flexible prehensile repertoire than chimpanzees or capuchins, were able to place their hands in good alignment with the long stem of the glass.

A third possible reason that the tamarins managed to position their hands to grasp the glass efficiently for retrieving the food, and that the chimpanzees and capuchins in this study did not manage to position a stick into a groove efficiently, is that the tamarins' actions with the glass (and its content, food) were self-directed, whereas the chimpanzees and capuchins' actions in this study were object directed. As McCarty et al. [Claxton et al., 2009; McCarty et al., 2001a,b] show, young children (between 9 months and 2 years old) are better able to plan the correct grip for a tool that is directed toward themselves rather than directed to another (for example, using a spoon to feed themselves vs. using a spoon to feed another). In our study, the subjects' actions were directed at an object rather than themselves and there was no food retrieval (a self-directed action) involved in the task.

In any case, a major difficulty faced by our subjects concerned the additional planes present in the cross-shaped stick and the tomahawk, which presented two or three axes to position rather than the single long stick. The difficulty of positioning objects, in the terms of Fragaszy and Cummins-Sebree's [2005] model of spatial reasoning, increases in concert with the number of concurrent relations to be managed, and this may apply to the body as well. This view leads to the prediction that if given a task requiring concurrently preshaping of the hand in a certain way and rotation of the forearm to a particular angle, for example, the anticipatory alignment of the body would be compromised compared with the situation presented to tamarins by Weiss et al. [2007].

The single most important conclusion we draw from our work is that nonhuman species, just as humans, have embodied minds, but their minds are constrained differently than ours when it comes to perceiving and acting with objects in space. Humans from 3 to 4 years of age have greater aptitude to manage more than one dimension concurrently when positioning objects [Fragaszy et al., unpublished data] in circumstances that challenge chimpanzees and capuchins [this study; Hayashi & Takeshita, 2009; Potì et al., 2009]. Surely these differences impact each species' aptitude to act with objects in a flexible goal-directed manner, as in tool use. Our findings help us understand why wild populations of chimpanzees and capuchins exhibit only relatively simple (in relational terms) forms of tool use involving moving an object toward a point rather than aligning an object to a plane and sequential rather than concurrent relations. For example, chimpanzees and capuchins exhibit several variations of probing skills, inserting a stick into a small opening, and they crack nuts by placing the nut on an anvil and then striking the nut with a hammer stone [e.g., Boesch & Boesch-Achermann, 2000; Mannu & Ottoni, 2009; Sanz & Morgan, 2007]. Managing more than one allocentric relation of objects and surfaces concurrently, and managing alignment of a line rather than a point, lies at the upper boundary of their manipulative spatial skills. Further attention to the physical and experiential circumstances which govern spatial reasoning and spatial planning in diverse species will help us understand the genesis of flexible tool use.

ACKNOWLEDGMENTS

We thank John Kelley for assisting with the chimpanzee experiments, and Jen Benoit and Philip Webber for assistance with coding. Research was supported by the L.S.B. Leakey Foundation, the Wenner-Gren Foundation, and HD38051, R01 HD056352, and HD060563 from NIH. The content is the responsibility of the authors and does not necessarily represent the official views of NIH. All research complied with applicable local and national animal care regulations.

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