

What limits tool use in nonhuman primates? Insights from tufted capuchin monkeys (*Sapajus* spp.) and chimpanzees (*Pan troglodytes*) aligning three-dimensional objects to a surface

L. T. la Cour · B. W. Stone · W. Hopkins ·
C. Menzel · Dorothy M. Fragaszy

Received: 19 November 2012 / Revised: 29 March 2013 / Accepted: 13 May 2013
© Springer-Verlag Berlin Heidelberg 2013

Abstract Perceptuomotor functions that support using hand tools can be examined in other manipulation tasks, such as alignment of objects to surfaces. We examined tufted capuchin monkeys' and chimpanzees' performance at aligning objects to surfaces while managing one or two spatial relations to do so. We presented six subjects of each species with a single stick to place into a groove, two sticks of equal length to place into two grooves, or two sticks joined as a T to place into a T-shaped groove. Tufted capuchins and chimpanzees performed equivalently on these tasks, aligning the straight stick to within 22.5° of parallel to the groove in approximately half of their attempts to place it, and taking more attempts to place the T stick than two straight sticks. The findings provide strong evidence that tufted capuchins and chimpanzees do not reliably align even one prominent axial feature of an object to a surface, and that managing two concurrent allocentric spatial relations in an alignment problem is significantly more challenging to them than managing two sequential relations. In contrast, humans from 2 years of age display very different perceptuomotor abilities in a similar task: they align sticks to a groove reliably on each attempt, and

they readily manage two allocentric spatial relations concurrently. Limitations in aligning objects and in managing two or more relations at a time significantly constrain how nonhuman primates can use hand tools.

Keywords Tool use · Spatial reasoning · *Sapajus* · *Pan troglodytes* · Alignment · Posting task

Introduction

Tool use is ubiquitous among humans and widespread in the animal kingdom (Bentley-Condit and Smith 2010; Shumaker et al. 2011). However, compared to humans, nonhuman species use tools in structurally simple ways. The basis for the human advantage over other primates in using hand tools has been deeply explored from cognitive perspectives, such as causal reasoning (e.g., Call 2010; Penn and Povinelli 2007; Sanz et al. 2012) and the complexity of coordinating actions producing force (e.g., Bril et al. 2012). Biomechanical limitations have been recognized in relation to the dexterity of action supported by various hand morphologies (e.g., Marzke 1997). We adopted a complementary approach in this work, seeking to characterize in two genera of nonhuman primates perceptuomotor abilities that are fundamental to human tool use. The perceptuomotor abilities selected for study concern manual alignment of one or more axial features of an object to features of a stationary surface. These abilities have previously been studied in humans using a “posting task” (e.g., Street et al. 2011) in which an object is fitted through a matching slot in an otherwise solid surface. Smooth performance in this task is thought to involve the dorsal visual stream, the “vision for action” system in the brain that guides manual action with objects (Jeannerod

Electronic supplementary material The online version of this article (doi:10.1007/s10071-013-0643-x) contains supplementary material, which is available to authorized users.

L. T. la Cour · B. W. Stone · D. M. Fragaszy (✉)
Department of Psychology, University of Georgia, Athens,
GA 30602, USA
e-mail: doree@uga.edu

W. Hopkins
Agnes Scott College, Emory University, Decatur, GA, USA

C. Menzel
Georgia State University, Atlanta, GA, USA

1997; Milner and Goodale 1995, 2008). Thus, performance on posting tasks is of interest to behavioral neuroscientists studying goal-directed manual actions, and clinicians working with people suffering from brain dysfunctions that affect these actions.

Performance on the posting task is also of interest to cognitive scientists because it requires management of allocentric spatial relations. An allocentric frame of reference is centered about landmarks and objects external to the body. Using a hand tool (shovel, knife, hammer, scissors, etc.) requires the management of at least one allocentric spatial relation, that is, a relationship between the tool and a surface or another object (Fragaszy and Cummins-Sebree 2005), and many common actions with tools involve more than one allocentric relationship. For example, hammering a nail into a board entails two allocentric relations: The nail must be held at the point where it should puncture the board, and the hammer must be aligned with the nail to strike it on the head. On the first strike, the nail must be held at the right angle, below the head, while the hammer strikes it—the two actions of holding and striking must overlap temporally. Nut cracking, considered the most relationally complex form of tool use by nonhuman primates routinely found in nature, involves two allocentric spatial relations (one between the nut and the anvil, and a second between the stone hammer and the nut). These relations are typically managed sequentially: the nut is placed and released on the anvil prior to striking it with the stone (Fragaszy et al. 2004; Fragaszy and Cummins-Sebree 2005). Other common forms of tool use in nonhuman primates entail controlling one allocentric relation (such as controlling the relation between a stick and a hole while probing into the hole with the stick).

Perhaps managing concurrent allocentric spatial relations constitutes a significant hindrance to nonhuman primates' use of objects as tools. In support of this proposal, a recent study by Fragaszy et al. (2011) demonstrated that both tufted capuchin monkeys (*Sapajus* spp.¹) and chimpanzees (*Pan troglodytes*) were increasingly hindered in aligning a stick to a matching groove in a solid surface as the number of features to align increased from one to two to three. However, features of the design of Fragaszy

et al.'s (2011) study limit the strength of the conclusions. Subjects received sticks of three different shapes in set order of anticipated difficulty, starting with straight sticks, followed by T-shaped sticks, followed by Tomahawk-shaped sticks. One shaft segment of all the sticks was the same length; the crosspiece in the T stick and the head segment of the Tomahawk-shaped stick were both shorter than the shaft segment. Thus, the subjects might have developed a bias to attend to the more familiar longer segment of each stick rather than the shorter and less familiar pieces of the T-shaped or Tomahawk-shaped sticks, and this may have interfered with aligning the crosspiece of the T or the head of the Tomahawk sticks to the matching groove in the surface.

In the current study, tufted capuchins and chimpanzees were required to align one stick or two sticks with matching groove(s) in a tray. The sticks were of equal length; only the arrangement of grooves varied. The different arrangements were presented in a balanced order, ruling out the possibility that performance could reflect differential experience with a particular shape or length. In two conditions presented in this study, two allocentric spatial relations could be dealt with sequentially, and in a third condition, subjects had to manage both allocentric relations simultaneously. Thus, the current study evaluated the relative difficulty of managing two concurrent versus two sequential allocentric spatial relations in a fitting problem. It also provided an opportunity to assess our subjects' proficiency at aligning axial features of objects to surfaces.

Working from Fragaszy and Cummins-Sebree's (2005) model of spatial reasoning, we predicted that subjects would make more attempts to place the sticks when two allocentric spatial relations had to be managed concurrently rather than sequentially. We were also interested to see whether individuals would strategically generate exploratory actions with the stick, such as moving the stick across the surface, to provide haptic information about the location and orientation of the groove, or moving the stick above the surface of the groove, evaluating alignment visually. Finally, we were interested to see whether our subjects would act to reduce the number of directions in which the stick could move with respect to the surface of the tray into which they were to place the stick. They might have done so, for example, by "pinning" one end of the stick in the groove with one hand and pivoting the stick around this point with the other hand. If they did use such actions, we predicted that they would make greater use of them as the number of spatial relations increased, and thus, the difficulty of the problem increased. We compare our findings to children's performance using a similar fitting task (Fragaszy et al. unpublished data). We conclude from these comparisons that capuchins and chimpanzees perceive the problem of aligning an object to stationary features of a surface very differently than do humans,

¹ Recent molecular analysis has revealed that capuchin monkeys, formerly identified as the single genus *Cebus*, are two genera, with the robust (tufted) forms (including *apella*, *libidinosus*, *xanthosternos*, and several other species) now recognized as the genus *Sapajus*, and the gracile forms retained as the genus *Cebus* (Lynch Alfaro et al. 2012a, b). Because colonies of tufted capuchin monkeys held in the USA are derived from animals imported from the wild prior to the elevation of subspecies of *Cebus apella* to true species, and more recently, to a species in the genus *Sapajus*, distinct from *Cebus*, monkeys in these colonies are now recognized as unknown combinations of species and hybrids of the genus *Sapajus*, rather than as *C. apella*.

and that their method of solving the problem (managing one spatial relation at a time, and relying more on haptic rather than visual information to align objects) severely limits the ways nonhuman primates can use hand tools.

Methods

Subjects

The subjects of this study included six adult capuchin monkeys (*Sapajus* spp.) and six adult chimpanzees (*P. 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 and two females (Sherman, Mercury, 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 Frigaszy 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. One or two sticks to be inserted into the groove(s) were presented, in accord with the number of grooves in the tray. 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 ($11.7 \times 1 \times 1$ cm for capuchins; $28 \times 2.6 \times 2.6$ 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 One Stick, 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 Two Sticks 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 Broken T used the same two sticks as Condition Two Sticks, but the grooves were placed perpendicular to each

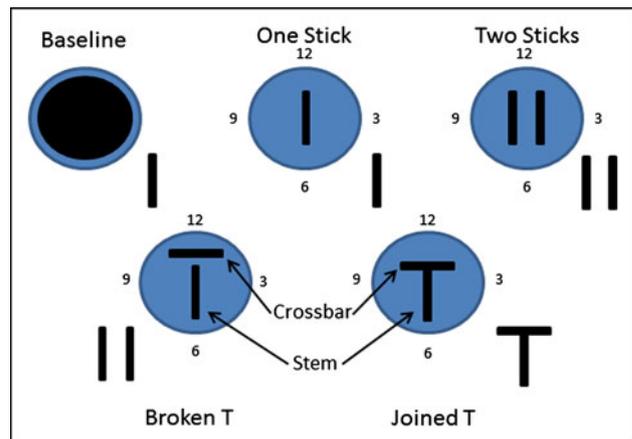


Fig. 1 The shapes of the sticks and matching trays for each condition. Not to scale

other to make a T shape with a small separation between the two grooves. Condition Joined T used a T-shaped cuboid stick. Each segment of the T-shaped stick was the same width and length as the sticks used in all previous conditions. The T-shaped groove was centered in the tray.

For testing, the capuchins were confined in the bottom half of their home cage ($90 \times 137 \times 71$ cm). 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 were confined in a section of their indoor home cage ($2.0 \times 4.3 \times 2.5$ 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 ZR 100), one tripod-mounted camera filming face-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 were confined in two outdoor sections of their home cage (each $2.3 \times 4.3 \times 2.4$ 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 did not 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 HD 40) 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 inserted it fully into the groove in the tray or until 30 s elapsed during which no interaction took place. 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. Video clips of representative trials of Condition Straight Stick and Condition Joined T (one each for a capuchin and a chimpanzee) are available in Supplementary materials (SM1 to SM4). All capuchins as well as the chimpanzees from the Language Research Center had participated in a previous study using a similar task, so that no shaping was required for those subjects to interact with the tray appropriately. The task was unfamiliar to the chimpanzees from the Yerkes National Primate Research Center and, consequently, some shaping was required. These two subjects were allowed to interact with the stick and baseline tray until they successfully placed the stick completely into the open base of the tray. Once this was achieved, as with all subsequent trials, the subjects were verbally praised and given a food reward. Testing began the day following the session in which these subjects successfully completed the baseline task 10 times. Both subjects did so the first day the tray was presented.

On the first testing day, the subject completed ten trials of the baseline condition before receiving the next condition. On each subsequent testing day, the subject completed three trials of baseline before receiving the next condition. The order in which each subject received the four conditions was predetermined using a Latin square. Each subject completed one trial of each condition before moving to the next condition. Two subjects each paused more than 30 s on one trial; one subject paused more than 30 s on 8 trials across all sessions. These trials were presented a second time and were completed on the second next presentation. 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 XTTM software (Noldus Information

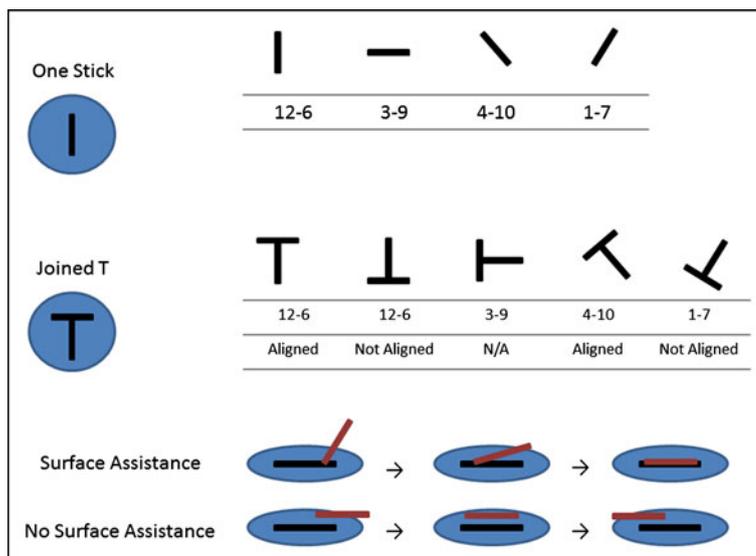
Technology). By definition, a trial began when the subject had the tray and the stick(s) in its possession and ended when it had successfully inserted the stick or sticks into the groove(s). For each trial, we coded discrete attempts in which the subject tried to place the stick in the groove. The first 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 Fig. 2) to code this variable. As seen in Fig. 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 Joined T, we coded the “polarity” of the crossbar of the T-shaped stick with respect to the crossbar of the T-shaped groove (crossbar vs. stem depicted in Fig. 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 Fig. 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.

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 were coded: one right-handed 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 was coded as two attempts (one with 12–6 alignment and one with 4–10 alignment). The clock face orientation between 12–6 and 4–10 was ignored unless the stick was paused in those orientations. The sole coder (L. la Cour) established an

Fig. 2 Illustrations of dependent variables for alignment of the stem and crossbar portions of the stick (*top* two rows), and surface assistance (temporal succession of a successful attempt where placement of the stick was guided by the groove). The *top* two rows are drawn in plan view, with clock face numbers used to categorize alignment of the stem of the stick relative to the groove in the tray (defined as 12–6). The *bottom* two rows are drawn in side view



intraobserver reliability of 92 % agreement (Cohen's $\kappa = 0.91$).

Analysis

We used the first ten trials completed by each subject to determine median values for all individuals. A Wilcoxon–Mann–Whitney test determined whether there was a significant difference between species; if not, we pooled the data from both species for all further tests. We used Wilcoxon signed ranks tests to reveal significant differences between conditions. For these tests, we used an $\alpha = 0.008$ according to the Bonferroni correction since we conducted six Wilcoxon signed ranks tests on the same data set. We performed these tests to determine whether subjects would use more attempts to align an object with two spatial relations to be dealt with sequentially rather than one spatial relation, as well as to determine whether subjects would use more attempts when dealing with two relations concurrently rather than sequentially. We also used these tests to determine whether subjects would use surface assistance more frequently in conditions requiring the management of two spatial relations rather than one spatial relation, and in conditions requiring the management of two concurrent relations rather than two sequential relations.

We used Friedman χ^2 tests within subject to evaluate bias to align the object at a 12–6 orientation, which was the correct orientation to place the stick in the groove. This was done for Conditions One Stick, Two Sticks, and Joined T. In the case of Condition Joined T, 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 area. Condition Broken T 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 the 3–9 orientation, and chance was set at 0.50. Finally, proper alignment in Condition Joined T required that the stem of the T was in a 12–6 orientation and concurrently that the crossbar of the T was aligned with the crossbar of the groove. We used χ^2 tests within subject to determine whether 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. 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.

Results

Effect of the number of sequential and concurrent relations on the number of alignment attempts

Individual subjects averaged from 1.4 (a capuchin, in Condition One Stick) to 22.8 (a chimpanzee, in Condition Joined T) attempts per trial to place the sticks into the grooves, indicating that the tasks we set for the subjects did in fact present a range of difficulties to them. Figure 3 shows the median number of attempts per condition for

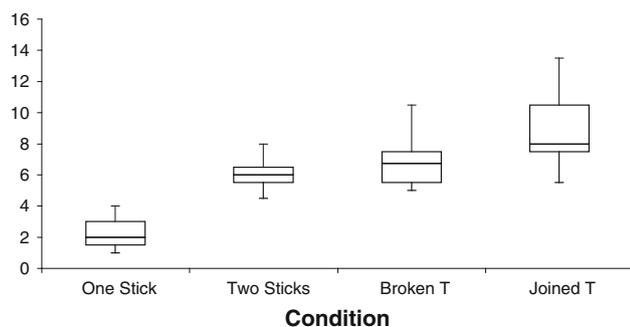


Fig. 3 Median number of attempts per condition to complete placing the stick for each species (*bars* represent IQR)

each species, and Table 1 gives individual results from each condition. Wilcoxon–Mann–Whitney tests showed no significant difference in number of attempts between the two species in Conditions One Stick, Broken T, and Joined T (Wilcoxon–Mann–Whitney: $N_1 = N_2 = 6$, $df = 1$, range of $W_X = 32$ – 46 , range of P values = 0.15 – 0.35). A

significant difference between the two species was seen in Condition Two Sticks ($W_X = 23$, $P = 0.0043$). However, as this was the only significant difference seen, we pooled both species in order to analyze the effect of condition on number of attempts. Wilcoxon signed ranks tests between conditions, with corrected $\alpha = 0.008$ after the Bonferroni correction, revealed a significant increase in the number of attempts between Conditions One Stick and Two Sticks (Wilcoxon signed ranks: $N = 12$, $T^+ = 77$, $P = 0.005$), Conditions One Stick and Broken T ($T^+ = 78$, $P = 0.002$), Conditions One Stick and Joined T ($T^+ = 78$, $P = 0.002$), and Conditions Broken T and Joined T ($T^+ = 72$, $P = 0.0034$). We did not find a significant difference between Conditions Two Sticks and Broken T ($T^+ = 49.5$, $P = 0.2234$), in which the subjects placed two individual sticks, or between Conditions Two Sticks and Joined T ($N = 11$, $T^+ = 55$, $P = 0.0269$). In the case of Condition Two Sticks versus Condition Joined T, we found a $T^- = 0$ but a tie in rank produced an $N = 11$. Therefore, though the difference was in the expected direction (more attempts

Table 1 The number of attempts per completed trial of each condition for each subject (median, above, and interquartile range, below)

Species	Subject	Condition One Stick	Condition Two Stick	Condition Broken T	Condition Joined T	All conditions
<i>Sapajus</i>	Chris	2	6	6.5	12	6
		9.5	3.5	5.5	18.5	7
	Leo	2	6	7	8	6
		1.5	2.5	4.5	12.5	4
	Nick	4	6.5	5.5	7	5
		2.5	8	6.5	13	3
	Solo	1	5.5	6.5	5.5	4
		1	6.5	3.5	20.5	5
	Xavier	2	4.5	6	8	5
		8.5	5.5	3.5	19	6
	Xenon	1.5	4.5	8.5	7.5	5
		2	6	7	17	7
	Median	2	6	6	7	5
3		4	4	14	6	
<i>Pan</i>	Christa	3	6.5	11	13.5	8
		4.5	5	6	41.5	9
	Joseph	3.5	8	7.5	9	7
		8	7	4	37	5
	Lana	3	6.5	7.5	10.5	7
		2	2.5	5.5	13	5
	Mercury	2	10	7.5	8	8.43
		2	7.5	18	7.5	7
	Panzee	3	6	5	7.5	5
		0.5	2	1.5	1.5	3
	Sherman	1	6	5	7.5	5
		3.5	3.5	5.5	13.5	4
	Median	3	7	7	8	6
2		4	4	8	5	

needed for Condition Joined T than Condition Two Sticks), the reduced N produced an insignificant difference ($P = 0.027$). Eleven of twelve subjects used fewer attempts to place two sticks (in Conditions Two Sticks and Broken T) than to place one stick (in Condition Joined T).

Alignment of the stick(s) with the groove(s)

In Conditions One Stick, Two Sticks, and Joined T, only a 12–6 orientation, with respect to the clock face coding scheme, permitted alignment of the stick with the groove (and thus, placement of the stick in the groove). As shown in Table 2, most subjects aligned the sticks in a 12–6 orientation more often than expected by chance, where chance is 25 %, but the average proportion of 12–6 alignments over all conditions (0.49 for capuchins, 0.48 for chimpanzees) was far below 1.0, suggesting that this was a challenging task for the subjects. Individual proportional values for the number of attempts in which the stick was aligned correctly ranged from 0.29 to 0.80, and averaged between 0.50 and 0.65 for the Conditions One Stick and Two Sticks. In Condition Broken T, subjects had 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 Broken T. All subjects aligned the sticks with a 12–6 orientation or a 3–9 orientation more often than expected by chance (range = 0.61–0.89), with chance set at 50 %. For Condition Broken T, we checked 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). As shown in Table 4, ten subjects out of 12 aligned the stem first on at least 60 % of trials, and two of these ten did so significantly more often than aligned the crossbar first.

Condition Joined T presented different alignment requirements compared to Conditions Two Sticks and Broken T. Rather than two separate sticks to align sequentially, in 12–6 and 3–9 orientations, the T-shaped stick had to be oriented in a 12–6 alignment along the stem of the T, and concurrently, the other segment had to be aligned concurrently with the perpendicular arm of the groove (the crossbar of the T). If the crossbar was not aligned correctly, it would be upside down with respect to its groove (as shown in the second and fifth illustrations, from left to right, for Condition Joined T in Fig. 2). As shown in Table 5, 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 set at 50 %. These four individuals aligned the crossbar appropriately between 66 and 79 % of the time.

Use of actions that decrease the mobility of the stick when aligning the stick to the groove

We did not find a significant difference in the use of surface assistance (moving the stick across the surface of the tray) between the two species for any of the four conditions (Wilcoxon–Mann–Whitney: $N_1 = N_2 = 6$, $df = 1$, range of $W_X = 36$ –51.8, range of P values = 0.35–0.98). Thus, we pooled all subjects' data for analysis of surface assistance. The median number of attempts in which subjects used surface assistance declined from 93 % in Condition One Stick to 67 % in Condition Joined T (Fig. 4). Pair-wise Wilcoxon signed ranks tests between conditions, with an $\alpha = 0.008$ after the Bonferroni correction, revealed a significant decrease in the use of surface assistance between Conditions One Stick and Joined T (Wilcoxon signed ranks: $N = 12$, $T^+ = 74$, $P = 0.0017$). We did not find a significant difference between any of the other conditions. Sometimes 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 One Stick and 2 were Condition Joined T), while the chimpanzees completed 15 trials (out of 240) in a single attempt (all in Condition One Stick). In four of these cases, subjects inserted one end into the groove and rotated the stick.

Exploratory actions with the stick on or above the tray

All actions that could aid in aligning the stick to the groove in the tray involved the individuals bringing the stick in contact with the tray, prominently including banging the stick and sliding it across the surface. We never witnessed individuals of either species visually aligning the sticks with the groove before contact was made. We also never witnessed individuals feeling the groove with the hand directly.

Discussion

Using a hand tool involves producing one or more allocentric spatial relations between the tool and another object or surface (Fragaszy and Cummins-Sebree 2005; Cox and Smitsman 2006). Positioning an object with respect to a feature of the environment (another object or surface) requires producing allocentric spatial relations, whether or not the object is used as a tool. Thus, performance in a fitting task, like that used in the study reported here, provides insight into how an individual can use a hand tool. Overall, capuchins' and chimpanzees' performance on the fitting task presented in this study indicates that these species are severely constrained in how effectively they

Table 2 Number and proportion of attempts in Conditions One Stick, Two Sticks, and Joined T 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	Freidman χ^2	
<i>Sapajus</i>	Chris	One Stick	14/38	0.37	9.5	2.84	
		Two Sticks	39/69	0.57	17.25	44.08*	
		Joined T	57/181	0.31	45.25	4.07*	
	Leo	One Stick	14/25	0.56	6.25	12.81*	
		Two Sticks	45/62	0.73	15.5	74.86*	
		Joined T	35/99	0.35	24.75	5.66*	
	Nick	One Stick	14/42	0.33	10.5	2.13	
		Two Sticks	40/76	0.53	19	30.95*	
		Joined T	34/98	0.35	24.5	4.91*	
	Solo	One Stick	7/14	0.5	3.5	4.67*	
		Two Sticks	39/62	0.63	15.5	47.5*	
		Joined T	41/108	0.38	27	2.77	
	Xavier	One Stick	28/45	0.62	11.25	34.68*	
		Two Sticks	44/55	0.8	13.75	67.12*	
		Joined T	35/120	0.29	30	2.94	
	Xenon	One Stick	20/27	0.74	6.75	33.25*	
		Two Sticks	42/59	0.71	14.75	88.73*	
		Joined T	33/103	0.32	25.75	1.24	
	Mean	One Stick	16/32	0.5	7.96		
		Two Sticks	42/64	0.65	15.96		
		Joined T	39/118	0.33	29.54		
	<i>Pan</i>	Christa	One Stick	15/30	0.5	7.5	10*
			Two Sticks	40/64	0.63	16	48*
			Joined T	63/186	0.34	46.5	7.81*
		Joseph	One Stick	22/52	0.42	13	8.31*
			Two Sticks	34/86	0.4	21.5	9.69*
			Joined T	59/197	0.3	49.25	1.35
		Lana	One Stick	14/29	0.48	7.25	8.379*
			Two Sticks	35/64	0.55	16	30.08*
			Joined T	54/133	0.41	33.25	17.27*
Mercury		One Stick	10/21	0.48	5.25	5.73*	
		Two Sticks	53/98	0.54	24.5	44.2*	
		Joined T	32/79	0.41	19.75	10.13*	
Panzee		One Stick	21/29	0.72	7.25	34.77*	
		Two Sticks	41/67	0.61	16.75	46.81*	
		Joined T	38/70	0.54	17.5	32.02*	
Sherman		One Stick	13/19	0.68	4.75	19.11*	
		Two Sticks	32/57	0.56	14.25	29.48*	
		Joined T	47/117	0.4	29.25	14.36*	
Mean		One Stick	16/30	0.53	7.5		
		Two Sticks	39/73	0.54	18.17		
		Joined T	49/130	0.37	32.58		

* $P < 0.05$; chance set at 0.25

manage allocentric spatial relations and how well they align objects to surfaces. After specifying these constraints, we consider how tufted capuchins' and chimpanzees'

performances compare to children's performances on similar tasks, and the implications of the differences for the development of tool use in human and nonhuman primates.

Table 3 Number and proportion of attempts in Condition Broken T for each subject in which the sticks were aligned correctly (i.e., in either a 12–6 or a 3–9 orientation)

Species	Subject	# Attempts aligned/total	Proportion aligned	# Expected by chance	Freidman χ^2
<i>Sapajus</i>	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	
<i>Pan</i>	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 percent of trials in Condition Broken T in which subjects first aligned the stem of the T rather than the crossbar of the T

Species	Subject	1st Stick stem	1st Stick cross	% Stem 1st
<i>Sapajus</i>	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
<i>Pan</i>	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

Managing concurrent relations

The challenge posed by the alignment task that we presented to the chimpanzees and tufted capuchins was evident across all conditions. Individuals required on average three to four attempts to align a straight stick to a matching groove. As expected, subjects used approximately twice as many attempts to align two straight sticks (in Conditions Two Sticks and Broken T) as one straight stick (in Condition One Stick), but subjects' performance on Conditions Two Sticks and Broken T did not differ. Thus, aligning a stick was equally challenging regardless of the orientation of the groove.

However, subjects made significantly fewer attempts to place the sticks before succeeding in Condition Broken T than in Condition Joined T and eleven of twelve subjects made fewer attempts to place the sticks before succeeding in Conditions Two Sticks and Broken T than in Condition Joined T. These findings indicate that managing two concurrent spatial relationships is more difficult than managing two spatial relationships in sequence, as Fragaszy and Cummins-Sebree's (2005) model of spatial reasoning predicts, and in accord with findings by Fragaszy et al. (2011).

Aligning an object to a groove

Subjects appropriately aligned the sticks parallel to the groove ("12–6 orientation," in our coding) in about half of their attempts to place the sticks in Conditions One Stick and Two Sticks. In Condition Joined T, subjects correctly aligned the stem of the T-shaped stick with the matching groove in 1/3 of attempts. In that condition, eight of twelve individuals (four capuchins and four chimpanzees) did not align the crossbar of the stick with the crossbar of the groove significantly more often than expected by chance. Overall, these findings indicate that the subjects brought one element into general alignment at each attempt, and they were not particularly precise about even a single element. This might be considered surprising, given the ease with which captive primates extend their hands through wire mesh or bars, and Wakita's (2008, 2012) findings that rhesus monkeys (*Macaca mulatta*) can visually discriminate a two-dimensional figure's tilt with respect to a planar axis. Thus, it is likely that the subjects in this study could visually distinguish the orientation of the stick and of the groove. However, significant differences between actions aligning the body with respect to a feature

Table 5 Number and proportion of attempts in Condition Joined T for each subject in which the crossbar of the T stick was aligned with the crossbar of the T groove

Species	Subject	# Attempts aligned/total	Proportion aligned	# Expected by chance	Freidman χ^2
<i>Sapajus</i>	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	
	<i>Pan</i>	Christa	63/131	0.48	65.5
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

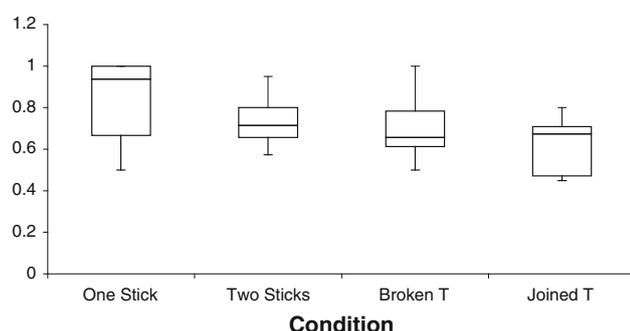


Fig. 4 Mean proportion of attempts using surface assistance across all subjects for each condition (*error bars* represent SD)

of the external environment and actions aligning an object to an external feature on the other have also been reported for young children aligning their hand or a disk to pass through a slot. Street et al. (2011) provided 18- and 24-month-old children with a flat disk to insert through a matching slot in a surface, a task quite similar to the one presented in this study to nonhuman primates. The older children could insert the disk through the slot; the younger children had difficulty with the task. However, the younger children easily inserted their hands directly into the slot, just as nonhuman primates easily pass their hands through bars or wire mesh. Street et al.'s (2011) interpretation of their findings is that orienting the disk to the slot requires integration of object properties into planned actions, a process that involves different neural substrates (the “vision for action system”; Milner and Goodale 1995, 2008; see also Gangopadhyay et al. 2010) than actions relating the body directly to objects, as when the hand is inserted into the slot. We come back to the importance of this difference between humans and nonhuman primates in the organization of visually guided action later in the discussion.

Strategies to control the stick, to explore the tray, and to align the object to the groove

The more directions of movement that must be monitored and managed, the more difficult the task (Bernstein 1967, 1996). We anticipated that tufted 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, because there would be less movement of the stick in the vertical plane when it is pressed against an unmoving surface compared to when it is moved in the air above the surface. We found that subjects of both species used surface assistance in more than half of the attempts in each condition. However, we did not find an increase in surface assistance as the tasks increased in difficulty, nor can we claim that we found a ceiling effect because all subjects of both species showed a decrease in the use of surface assistance from Condition One Stick (the easiest task) to Condition Joined T (the most complex task) while the mean number of attempts needed to achieve alignment increased fourfold (from 3.45 to 12.05) over these same conditions. Thus, we did not find evidence that our subjects used surface assistance strategically to manage the alignment problem.

Contacting the stick with the surface could instead be an exploratory procedure that generates haptic information about the tray and the groove, similar to how capuchins determine that a nut is positioned in a stable manner on the anvil before they crack the nut with a stone (Fragaszy et al. 2013). 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). Michaels et al. (2007) showed that humans preferentially use vision to assess functional attributes of tools, but when vision is limited, humans explore objects using dynamic touch in a manner that reflects their intentions to discover particular affordances for a specific purpose. 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 tufted capuchins (Fragaszy 1998), it seems plausible that chimpanzees will share EPs with tufted capuchins and humans. Therefore, we expect both species can determine an object or surface's properties through manual exploration just as humans can. Humans can also use a rigid probe held in the hand to detect object properties although they take longer to do so and are less precise in judgments about object properties when using a probe versus using the fingers directly (Lederman and Klatzky 2004). Thus, our subjects could have used the stick to locate the groove, or they could have used their hands directly. They could also have used vision in an overt way to aid alignment, by moving the sticks above the tray while checking alignment visually.

We saw no actions that qualified as overtly exploratory as those described above. 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, indicating that they were not immediately aware of the relation between the stick's movement and the location of the groove. We did not see the subjects feel the surface of the tray with their hands, nor did we see actions with the sticks above the tray that looked related to alignment. The absence of actions to align the sticks above the tray, as well as the prominence of sliding the stick back and forth across the surface of the tray, suggests that these species do not use vision or touch strategically to achieve precise alignment between two objects.

Comparison of species and subjects within species

The tufted capuchins and chimpanzees did not differ in the number of attempts they 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). Perhaps these two subjects were handicapped compared to the other subjects by their lack of practice aligning objects. The difference in the number of attempts between these two individuals and the other chimpanzees was greatest in the Joined T condition, the most challenging condition because it involved managing two concurrent spatial relations. Given that extensive practice allowed tufted capuchin monkeys to improve significantly their mastery of navigating two-dimensional mazes (Pan et al. 2011), a task requiring management of allocentric spatial relations, it is possible that practice in the fitting task presenting two concurrent relations would lead to improved performance. This is a promising topic for future research.

Tool use in natural settings in nonhuman primates

The most important conclusion we draw from our findings is that nonhuman primates will be more likely to use hand tools to produce a single spatial relation or two sequential relations rather than two or more concurrent relations. A second important conclusion is that nonhuman primates will be unlikely to use tools in any format that requires precise axial alignment of objects with other objects or surfaces. Extant field data provide support for both of these ideas. Most reports of tool use among wild nonhuman primates involve producing a single relation between an object and a point, such as using a probe or striking something (Shumaker et al. 2011). For example, using a probe to retrieve termites from their nest requires that the individual align one end of the probe to touch the hole in the termite nest. Once this is accomplished, haptic information arising from the pressure where the probe has been inserted against the wall of the nest can aid in orienting the probe for insertion. Thus, this is a relatively permissive alignment problem requiring management of one allocentric relation (between stick and hole). 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 tufted capuchins; Souto et al. 2011). Note that the skill achieved in these instances, and others described for animals in natural environments, rely primarily upon the use of active touch (Turvey 1996; Jones and Lederman 2006) of objects in contact with a surface, not precise alignment of an object with another object, nor use of vision to move an object in relation to a surface.

Comparison with humans

To our knowledge, there have been no published reports of wild nonhuman primates spontaneously using tools in a way that incorporates actively managing two concurrent relations, although chimpanzees and tufted capuchins have each occasionally been seen to use two or more single relation tools in succession (Biro et al. 2006; Falotico 2011; Sanz and Morgan 2009). Humans, on the other hand, master a variety of tasks involving two concurrent allocentric relations with fine control of the angle and production of force. Stone knapping, a skill that goes beyond the mere production of stone flakes and is thought to be critical to early humans, involves two concurrent relations (Roux and Bril 2005). Many other examples could be provided; skilled use of hand tools involving management of two or more mobile, allocentric spatial relations is prevalent across cultures.

The other feature of our experimental task that challenged our subjects was aligning axes of a stick held in the hand with a fixed feature of a surface (a groove, in this study). Wakita (2008) provides data on rhesus macaques (*M. mulatta*) learning to judge whether a given line matched a line shown in the immediately previous displays. The lines fell in one of the two cardinal orientations (horizontal or vertical) or one of four oblique orientations, in gradations of 3° angular departure in each direction. The monkeys learned to discriminate the oblique lines from cardinal orientations and to discriminate oblique orientations by degree, direction, or both. Using a psychophysical approach, Vásques et al. (2000) directly compared discrimination of line orientation in humans and rhesus monkeys presented with a reference line, followed 1 s later by a test line, which varied from 1° to 5° angular departure from the reference line. Participants indicated the direction of tilt of the test line with respect to the reference line viewed immediately previously. Humans and monkeys performed equivalently in these tasks. Together, these findings show that rhesus monkeys can visually detect departures from collinearity far smaller than used in our clock face coding scheme (in which we judged the stick as aligned, that is, collinear, if it was within 22.5° angular departure in either direction, of the long axis of the groove). We think it is probable that our subjects could visually perceive the angle of the stick and the angle of the groove with respect to each other, but that they had difficulty managing that allocentric spatial relation through manual action. That is, the production of alignment was the challenge, rather than perception of alignment. Studies with nonhuman primates on judgment of alignment are needed to confirm this proposal.

The human advantage compared to nonhuman primates at aligning object features and managing concurrent

relations appears early in life, in accord with children's growing mastery of a variety of hand tools in early childhood (McCarty et al. 2001). Already at 2 years of age, children inserted a straight (Bar) stick into a matching groove in 2.5 attempts, on average, and a T-shaped stick in five attempts. At 3 and 4 years of age, they inserted a T-shaped stick in two attempts, on average, and in one attempt for a Bar stick (Fragaszy et al. unpublished data). Chimpanzees and tufted capuchins in Fragaszy et al.'s (2011) study and in the present study made nearly four times as many attempts to insert the Joined T stick into the tray compared to the Bar stick. In precision of alignment, the comparison is equally stark. Three- and four-year-old children aligned the long axis of the Bar or T sticks with the groove in nearly all attempts (Fragaszy et al. unpublished data). Even 2-year-old children were proficient at aligning the long axis of the stick to the groove, doing so on 80 % of attempts with Bar stick. The nonhuman primates in the current study aligned the long axis of the Bar stick with the groove on 52 % of attempts. Finally, children use vision strategically to aid them in placing the stick. Beginning at about 3 years of age, children start to hold the stick above the groove, align it visually, and then place it directly into the groove (Fragaszy et al. unpublished data). Our nonhuman subjects never did this. Thus, the human advantage over other primates in perceptuomotor skills fundamental to using hand tools is already evident at 2 years of age and amplifies quickly as children become more strategic at using their perceptual resources to align objects and better able to manage concurrent mobile spatial relations (Lockman 2000; Örnkloo and von Hofsten 2007).

Acknowledgments Supported by NIH Grants HD060563 and HD056352 to Georgia State University. The contents of this article do not necessarily represent the official views of NIH. We thank John Kelly, Jennifer Schaeffer and Jamie Russell for assistance with testing.

References

- Bentley-Condit VK, Smith EO (2010) Animal tool use: current definitions and an updated comprehensive catalog. *Behaviour* 147(2):185–221, A1–A32
- Bernstein N (1967) *The coordination and regulation of movement*. Pergamon Press, New York
- Bernstein N (1996) On dexterity and its development. In: Latash M, Turvey M, Bernstein N (eds) *Dexterity and its development*. Lawrence Erlbaum, Mahway, pp 3–237
- Biro D, Sousa C, Matsuzawa T (2006) Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: case studies in nut-cracking and leaf-folding. In: Matsuzawa T, Tomonaga M, Tanaka M (eds) *Cognitive development in chimpanzees*. Springer, New York, pp 476–508
- Bril B, Smaers J, Steele J, Rein R, Nonaka T, Dietrich G, Biryukova E, Hirata S, Roux V (2012) Functional mastery of percussive

- technology in nut-cracking and stone-flaking actions: experimental comparison and implications for the evolution of the human brain. *Phil Trans R Soc B* 367(1585):59–74
- Call J (2010) Trapping the minds of apes: causal knowledge and inferential reasoning about object–object interactions. In: Lonsdorf E, Ross S, Matsuzawa T (eds) *The mind of the chimpanzee*. Chicago University Press, Chicago, pp 75–84
- Cox RFA, Smitsman AW (2006) The planning of tool-to-object relations in young children. *Dev Psychobiol* 48:178–186
- Falótico T (2011) *Uso de ferramentas por macacos-prego (Sapajus libidinosus) do parque nacional Serra da capivara - PI* [Doctoral Thesis]. Universidade de São Paulo, São Paulo, Brazil
- Fragaszy DM (1998) How non-human primates use their hands. In: Connolly K (ed) *The psychobiology of the hand*. Cambridge University Press, Cambridge, pp 77–96
- Fragaszy D, Cummins-Sebree S (2005) Relational spatial reasoning by a nonhuman: the example of capuchin monkeys. *Behav Cogn Neurosci Rev* 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. *Am J Primatol* 64:359–366
- 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. *Am J Primatol* 73:1012–1030
- Fragaszy DM, Liu Q, Wright BW, Allen A, Brown C, Visalberghi E (2013) Bearded capuchin monkeys (*Sapajus libidinosus*) strategically place nuts in a stable position during nut-cracking. *PLoS One* 8(2):e56182. doi:10.1371/journal.pone.0056182
- Gangopadhyay N, Madary M, Spicer F (eds) (2010) *Perception, action and consciousness*. Oxford University Press, Oxford
- Jeannerod M (1997) *The cognitive neuroscience of action*. Blackwell, Cambridge
- Jones LA, Lederman SJ (2006) *Human hand function*. Oxford University Press, New York
- 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. *Cogn Psychol* 19:342–368
- Lederman SJ, Klatzky RL (2004) Haptic identification of common objects: effects of constraining the manual exploration process. *Percept Psychophys* 66:618–628
- Lockman JJ (2000) A perception-action perspective on tool use development. *Child Dev* 71:137–144
- Lynch Alfaro JW, Boubli JP, Olson LE, Di Fiore A, Wilson B, Gutiérrez-Espeleta GA, Chiou KL, Schulte M, Neitzel S, Ross V, Schwochow D, Nguyen MTT, Farias I, Janson CH, Alfaro ME (2012a) Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. *J Biogeogr* 39:272–288
- Lynch Alfaro JW, de Sousa e Silva J Jr, Rylands AB (2012b) How different are robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. *Am J Primatol* 74:273–286
- Marzke M (1997) Precision grips, hand morphology, and tools. *Am J Phys Anthro* 102:91–110
- McCarty ME, Clifton RK, Collard RR (2001) The beginnings of tool use by infants and toddlers. *Infancy* 2:233–256
- Michaels CF, Weier S, Harrison SJ (2007) Using vision and dynamic touch to perceive the affordances of tools. *Perception* 36:750–772
- Milner AD, Goodale MA (1995) *The visual brain in action*. Oxford University Press, Oxford
- Milner AD, Goodale MA (2008) Two visual systems re-viewed. *Neuropsychologia* 46:774–785
- Örnkloo H, von Hofsten C (2007) Fitting objects into holes: on the development of spatial cognition skills. *Dev Psychol* 43:404–416
- Pan J, Kennedy EH, Pickering T, Menzel CR, Stone BW, Fragaszy DM (2011) Development of maze navigation by tufted capuchins (*Cebus apella*). *Behav Process* 86:206–215
- Penn D, Povinelli D (2007) Causal cognition in human and nonhuman animals: a comparative, critical review. *Annu Rev Psychol* 58:97–118
- Roux V, Bril B (2005) Stone knapping: the necessary conditions for a uniquely hominin behaviour. *McDonald Institute Monographs*, Cambridge
- Sanz CM, Morgan DB (2009) Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. *Int J Primatol* 30:411–427
- Sanz C, Boesch C, Call J (eds) (2012) *Tool-use: cognitive requirements and ecological determinants*. Cambridge University Press, Cambridge
- Shumaker RW, Walkup KR, Beck BB (2011) *Animal tool behavior: the use and manufacture of tools by animals*. Johns Hopkins University Press, Baltimore
- 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. *Biol Lett*. doi:10.1098/rsbl.2011.0034
- Street SY, James KH, Jones SS, Smith LB (2011) Vision for action in toddlers: the posting task. *Child Dev* 82:2083–2094
- Teleki G (1974) Chimpanzee subsistence technology: materials and skills. *J Hum Evol* 3:575–584
- Turvey MT (1996) Dynamic touch. *Am Psychol* 51:1134–1152
- Vásques P, Cano M, Acuña C (2000) Discrimination of line orientation in humans and monkeys. *J Neurophysiol* 83:2639–2648
- Wakita M (2008) Orientation perception in rhesus monkeys (*Macaca mulatta*). *Anim Cogn* 11:535–545
- Wakita M (2012) Monkeys perceive the orientation of objects relative to the vertical axis. *Anim Cogn* 15:1205–1209