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Anna M. Yocom

The Ohio State University

Sarah T. Boysen

The Ohio State University

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Comprehension of functional support by enculturated chimpanzees *Pan troglodytes*

Anna M. YOCOM, Sarah T. BOYSEN*

Department of Psychology, The Ohio State University, Columbus, OH 43210, USA

Abstract Studies of causal understanding of tool relationships in captive chimpanzees have yielded disparate findings, particularly those reported by Povinelli & colleagues (2000) for tool tasks by laboratory chimpanzees. The present set of experiments tested nine enculturated chimpanzees on three versions of a support task, as described by Povinelli (2000), during which food rewards were presented in different experimental configurations. In Experiment 1, stimulus pairs included a choice between a cloth with a reward on the upper right corner or with a second reward off the cloth, adjacent to a corner, with the second pair comprised of a cloth with food on the upper right corner, and a second cloth with the reward on the substrate, partially covered. All subjects were successful with both test conditions in Experiment 1. In a second study, the experimental choices included one of two possible correct options, paired with one of three incorrect options, with the three incorrect choices all involving varying degrees of perceptual containment. All nine chimpanzees scored significantly above chance across all six conditions. In Experiment 3, four unique conditions were presented, combining one of two possible correct choices with one of two incorrect choices. Six of the subjects scored significantly above chance across the four conditions, and group performance on individual conditions was also significant. Superior performance was demonstrated by female subjects in Experiment 3, similar to sex differences in tool use previously reported for wild chimpanzees and some tool tasks in captive chimpanzees. The present results for Experiments 2 & 3 were significantly differed from those reported by Povinelli et al. (2000) for laboratory-born, peer-reared chimpanzees. One contribution towards the dramatic differences between the two study populations may be the significant rearing and housing differences of the chimpanzee groups. One explanation is that under conditions of enculturation, rich social interactions with humans and conspecifics, as well as active exploration of artifacts, materials, and other aspects of their physical environment had a significant impact on the animals' ability to recognize the support relationships among the stimulus choices. Overall, the present findings provide strong support for the hypothesis that our chimpanzee subjects based their responses on an understanding of functional support which represented one facet of their folk physics repertoire [*Current Zoology* 57 (4): 429–440, 2011].

Keywords Chimpanzees, Comparative cognition, Tool use, Causality

Tool use by wild chimpanzees is a ubiquitous feature of daily life in many chimpanzee communities across equatorial Africa, and is represented by a range of cultures within these populations that regularly use tools that can be specific to the community (Boesch and Boesch, 1990; Boesch-Achermann and Boesch, 1993; Goodall, 1986; McGrew, 1992; Sakura and Matsuzawa, 1991; Whiten et al., 1999). Since the initial discoveries by Goodall (1964), each year, particularly over the past two decades, research groups from Germany, Japan, Switzerland, the U.S., and other teams continue to report new tool types and functions by wild chimpanzees (e.g., Hernandez-Aguilar et al., 2007; Pruetz and Bertolani, 2007; Sanz and Morgan, 2009; Yamamoto et al., 2008). It is not surprising, given the extent of tool use by wild chimpanzees, that a wide array of tool-related

tasks have been explored in captive apes, as well (e.g., Bania et al., 2009; Furlong et al., 2008; Limongelli et al., 1995; Mulcahy and Call, 2006; Povinelli, 2000; Tomasello et al., 1993; Tonooka et al., 1997; Visalberghi et al., 1995; Whiten et al., 1996).

More recently, in contrast to reports of successful performance by chimpanzees on a range of tasks over the past several decades, Povinelli and his colleagues (2000) reported a series of some twenty-seven tool paradigms that resulted in poor performance by seven juvenile chimpanzees that had been laboratory-born and peer-reared as a separate social group. As a result, Povinelli (2000) reached a number of general conclusions about chimpanzees' abilities related to "folk physics". He specifically proposed that chimpanzees were apparently unable to fully grasp basic conceptual, func-

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* Corresponding author. E-mail: boysen.1@osu.edu

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tional relationships about the world around them, including concepts such as gravity, support, and connectedness, among others. In a study that contributed to this conclusion, Povinelli et al. (2000) investigated the concept of support using an approach that was similar, but not a replication, of an original task with tamarins first reported by Hauser et al. (1999). Povinelli and colleagues (2000) varied the specific design of the cloths, and used a different protocol to determine if their chimpanzees could distinguish between physical contact of the cloth and food, and perceptual containment of the food by the cloth. In the most difficult version of the task, when there was the largest amount of perceptual containment of the food surrounded by a cloth, they found their chimpanzees did not attend to the functional properties. That is, the chimpanzees pulled either cloth at random, including cloths that supported the food and those that did not. Povinelli et al. (2000) attributed their subjects' limited success to simple perceptual learning, and concluded that the chimpanzees only grasped specific perceptual rules governing the relationship between the cloth and the food. Notably, they concluded that the animals did not understand the concept of support.

The implications of the failures reported for Povinelli's chimpanzees (2000) are problematic, relative to findings with other captive nonhuman primates (e.g., Deblauwe et al., 2006; Fragaszy et al., 2004; Sakura and Matsuzawa, 1991; Tonooka et al., 1997; Westergaard et al., 1995; Yocom and Boysen, 2010), but especially given the demonstrated prowess of wild chimpanzees in extensive and creative use of objects as tools in their environment. Why would captive chimpanzees not exhibit knowledge of physical support when such capabilities are both advantageous and necessary for their survival in the wild? For instance, to build safe nests in trees, chimpanzees would regularly need to make support judgments about which branches could hold their weight. It is possible that basic physics related to conceptual understanding of causal mechanisms about support can only emerge in developing primates within an appropriate environment. Indeed, the poor performance of Povinelli's chimpanzees (2000) on a range of tool-related tasks for which they were provided minimal or no experience with the tool or task materials prior to testing, suggests that their animals limited environmental opportunities early in development, such as exploration of novel objects, actions, and experience with manipulation of natural materials or objects, had a deleterious impact on their subsequent tool use.

The archival primate literature includes reports, some decades old that have demonstrated the negative impact of environmental and rearing conditions, especially early in development (Menzel et al., 1970; Brent et al., 1995). In addition, variations in environment and/or rearing can also account for inconsistent performances on the same tasks by different groups of chimpanzees (Bania et al., 2009; Bard and Gardner, 1996; Bering, 2004; Brent et al., 1995; Bulloch et al., 2008; Call and Tomasello, 1996; Furlong et al., 2008; Tomasello and Call, 2004; Tomasello et al., 1993). To address these issues, Call and Tomasello (1996) proposed five different early rearing categories, including: wild, captive, nursery-reared, laboratory-reared, and home-raised. They proposed that the key difference between home-raised animals and all other groups was that home-raised chimpanzees had "...daily contact with humans and their artifacts in meaningful interactions," even if they were not actually raised in a human home. Specifically, they proposed that animals in the home-raised category have undergone a process of enculturation, which includes being treated as intentional beings and engaging in triadic interactions. Such "socialization of intention" may allow enculturated apes more opportunities to learn about the world around them, in much the same way as a human child (Call and Tomasello, 1996). Others have suggested that enculturation may provide apes with a broader understanding of human behavior, which helps to redirect their attention to key features in problem-solving and other cognitive tasks (Bering, 2004; Call and Tomasello, 1996, 2004; Tomasello et al., 1993), although other contributing variables to the enculturation process may assume greater valence (Bania et al., 2009; Bulloch et al., 2008; Furlong et al., 2008). For example, Tomasello et al. (1993) found that enculturated chimpanzees performed significantly better than non-enculturated chimpanzees in an imitation task that required tool use. Remarkably, the enculturated chimpanzees performed at the equivalent level of 18- and 30-month-old children, and were able to reproduce both the means and ends of novel actions. Further tests of imitation capacities in enculturated chimpanzees have also revealed them to be quite proficient in this complex area of social cognition (Bering et al., 2000; Bjorklund et al., 2002).

If enculturation does have an effect on the cognitive capacities and behavior of chimpanzees, then a highly enculturated group of chimpanzees should perform better than Povinelli's (2000) peer-raised laboratory subjects. In particular, tool use tasks involving human arti-

facts should be easier for enculturated chimpanzees, in part, because they have had multiple opportunities to explore their enriched environment, and manipulate objects and materials around them, from a very early age.

To explore these issues further, Experiments 1–3 were conducted to examine the possible effects of enculturation on a tool task involving support. Specifically, we replicated the Support Problem (Experiments 21–24 in Povinelli, 2000) during which seven laboratory chimpanzees performed poorly, with a group of nine enculturated chimpanzees. The goals of the experiments were two-fold: 1) to determine if enculturated chimpanzees could successfully solve all variations of the Support problem over a limited amount of trials and 2) to determine if there were any specific differences in this population’s level and pattern of success versus Povinelli’s (2000) non-enculturated chimpanzees. Experiment 1 was designed to compare the two groups over the easiest of the test conditions in which there was a choice between a cloth with a reward in full contact on its surface, and the other cloth with a reward next to it, or some cases, underneath the surface (perceptual contact). All trials were conducted with no prior training with the specific task demands of the support problem, including use of the cloths.

1 Methods and Materials

1.1 Experiment 1

Subjects Subjects were nine chimpanzees *Pan troglodytes*, including three adult males (Kermit and Darrell, both 26 years old; Bobby, 19 years old), two adult females (Sarah, 47 years old; Sheba, 25 years old), two adolescents (Keeli and Ivy, both 10 years old), and two juveniles (Emma and Harper, both 6 years old) (see Table 1 for their rearing backgrounds). Since arrival at the center (ages of arrival noted in Table 1), the animals were reared in enculturated conditions, indicating that

they were engaged in a highly enriched environment, had uniquely stable relationships with one another in their social groups and with their long-term caretakers, had demands and contingencies placed on their behaviors and were encouraged to interact with their caretakers in meaningful ways.

Although the chimpanzees had participated in a wide range and number of cognitive tasks, including some involving tool use (e.g., Bania et al., 2009; Furlong et al., 2008; Limongelli et al., 1995), they had never used the materials or apparatus specifically associated with the current tasks.

Apparatus Experimental stimuli consisted of two possible cloth and reward combinations that were presented to the chimpanzees on a raised wooden platform, with a dividing line painted down the center. Two black felt cloths (50 x 20 cm) were placed on the platform, separated by 20.3 cm between the cloth stimuli. Once baited with a food reward, a short length (3.5 cm) of each cloth was placed against the front of the test enclosure within reach of the subjects, and thus could be easily reached in order to pull the reward toward the subject. The food reward used was a half of a banana that was placed on different areas of the cloth or platform, depending on the specific experimental condition.

Procedures A notable difference from our design and that used by Povinelli and colleagues (2000) is that our subjects did not undergo an initial “orientation” phase with the test materials nor were any type of “spacer” trials presented between experimental trials. These additional procedures were not used since our animals were already familiar with a wide variety of surfaces and substrates, including human artifacts such as cloths or other pieces of material. Consequently, we deemed it unnecessary to include either orientation or “spacer” trials to sustain the animals’ motivation or provide additional training cues that such spacer trials may have provided for Povinelli’s subjects (2000).

Table 1 Subjects’ Rearing Histories

Name	Sex	Age at testing	Age at arrival OSU (years: months)	Origin & Enculturation History
Kermit	Male	26 years	3:0	Lab-born; Human-reared at OSU
Darrell	Male	26 years	3:6	Lab-born; Human reared at OSU
Bobby	Male	19 years	1:6	Zoo-born; Human-reared at OSU
Keeli	Male	10 years	1:4	Lab-born; Human-reared at OSU
Harper	Male	6 years	0:4	Lab-born; Human-reared at OSU
Sarah	Female	47 years	28:0	Wild-born; Human-reared; Language trained
Sheba	Female	25 years	2:7	Private colony; Human-reared at OSU
Ivy	Female	10 years	1:0	Lab-born; Human-reared at OSU
Emma	Female	6 years	0:1	Lab-born; Human-reared at OSU

Two unique experimental conditions were tested (Fig. 1). The first condition, “Contact/No Contact”, was a choice between a cloth with the reward on the upper right corner and a second cloth with the reward off the cloth near, but not on, the upper right corner. The second experimental condition, “Contact/Contact,” paired choices between one cloth with a reward on the upper right corner versus the second cloth that had its associated reward placed on the platform, and partially covered by the upper right corner of the cloth. These specific conditions were used because they allowed for a simple discrimination between one cloth that physically supported the reward and a second one that did not. The conditions were designed to replicate those described by Povinelli and colleagues (2000) as closely as possible. The position of the correct stimulus was counterbalanced, and each condition was presented twice per session. Order of conditions within a session was quasi-randomized, with the constraint that no more than two correct conditions were presented in a row on the same side of the platform. Four sessions were completed with four trials per session, for a total of 16 test trials per subject.

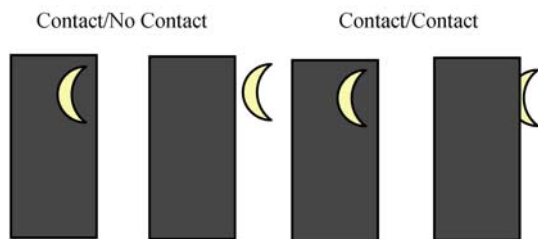


Fig. 1 Experimental conditions - Experiment 1

All subjects were tested individually. A trial began when a chimpanzee entered the test enclosure and sat in front of the platform. The experimenter next positioned both cloths on the platform, and then placed the food rewards in their respective positions (either on the cloth or platform), always from right to left. Next, the experimenter averted her head and eyes toward the floor,

at the end of the platform. At that point, the chimpanzee subject was allowed to select a cloth and pull it toward himself. A “choice” was defined as any time a subject moved one of the cloths. Any remaining reward(s) were then removed, along with the cloths. The next trial began as soon as the stimulus materials were re-arranged from the previous trial, and, if correct, the chimpanzee consumed the banana reward.

A second experimenter judged each trial as a success or failure, and recorded responses. A trial was considered a success if the subject’s first choice (i.e. the first cloth that was pulled) was the cloth that supported the reward. Similarly, a trial was considered a failure if the subject’s first choice was the cloth that did not support a reward and thus pulling the cloth did not bring the food reward within reach. All trials were also recorded with a digital color video camera. After completion of all testing, a student assistant naïve to the experimental hypotheses coded 20% of the videotaped sessions to establish inter-rater reliability. Inter-rater reliability was high, with strong agreement between the experimenter and naïve rater ($\kappa = 0.97$).

1.2 Experiment 2

Subjects Subjects were the same nine chimpanzees that participated in Experiment 1.

Apparatus The same apparatus used in Experiment 1 was used in the present study, with the exception that the cloths had different shapes for some conditions (see Fig. 2). The cloth shapes were similar to those described by Povinelli and colleagues (2000).

Procedure In experiment 1, the animals could have been relying on a more finely-tuned perceptual strategy. As an example, following testing of his group of seven chimpanzees, Povinelli and colleagues (2000) proposed that their chimpanzees may simply have been following a strategy of visual contact, since their performance was poorer on the Contact/Contact trials. Consequently, they may not have had an understanding of support as the physical connection for task solution. To explore this hypothesis further, we adapted Experiment 2

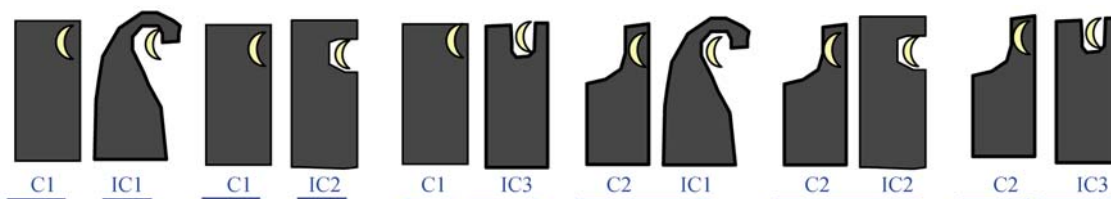


Fig. 2 Experimental conditions for Experiment 2, including two correct choices (C1 & C2) and the three incorrect choices (IC1: “Full Contact”; IC2: “Imminent Contact”; IC3: “No Contact”).

from the task originally reported by Povinelli et al. (2000), and included varying the degree of visual contact (i.e., full perceptual contact, imminent contact, or no contact) of both the correct and incorrect stimuli. If our enculturated chimpanzees were simply following a perceptual strategy in Experiment 1, we hypothesized that they would perform closer to chance as the degree of perceptual containment increased among the experimental conditions in Experiment 2.

Six unique conditions were incorporated into the experimental design for Experiment 2 (Fig. 2). Test conditions included one of two possible correct options, paired with one of three incorrect options. Correct choices were represented by a length of cloth with a food reward placed on the upper right corner of the fabric. The first correct option (C1) had the reward placed directly on the upper right corner of the cloth, while the second possible correct choice (C2) had the upper left side of the cloth removed, such that the reward appeared less perceptually contained by the cloth. The three incorrect choices all involved varying degrees of perceptual containment, as defined by Povinelli et al. (2000). An incorrect “Full Contact” option had the top portion of the cloth draped around the reward (IC1). A second incorrect option, “Imminent Contact”, had the reward resting on the platform, but inside a cut-out half circle on the upper right side of the cloth (IC2). The third incorrect choice, “No Contact”, presented the reward resting on the platform inside a cut-out half circle in the upper portion of the cloth (IC3). Specifically, for the last incorrect option (“No Contact”), the reward was inside the area of the cloth, but no portion of the cloth was above or behind it (see Fig. 2).

Subjects completed four trials per session over six sessions, for a total of 24 trials. Spatial positions of the test stimuli in each condition were counterbalanced. In addition, the order of conditions within a session was quasi-randomized such that: 1) each of the three incorrect options had to be presented once before any could be repeated; 2) no condition could be presented twice in a session; and 3) no more than two correct choices were presented in a row on the same side of the platform. The order of procedures and coding were identical to Experiment 1. Reliability ratings were again high between the judgments of the experimenter and a naïve coder ($\kappa = 0.99$).

1.3 Experiment 3

Subjects Subjects were the same nine chimpanzees that participated in the previous two experiments.

Apparatus The apparatus was the same used for

Experiments 1 and 2, with the exception that the reward consisted of a slice of banana, instead of a half banana.

Procedure It may still have been possible that the animals learned a fine perceptual discrimination between choices where the cloth and reward were touching one another, compared to stimuli in which they were not touching at all. Such a strategy could potentially have been used to respond correctly for all conditions in Experiment 2. Following similar testing, Povinelli et al. (2000) designed a final support experiment to rule out perceptual discriminations as the basis for the few successes they observed with their chimpanzee subjects. Thus, the third experiment presented here entailed presenting our animals with correct stimulus choices that had even less perceptual containment, paired with incorrect choices that depicted full perceptual containment. Among the most difficult discriminations presented in Experiment 3, the correct and incorrect choices were perceptually identical after food placement, when the animals were required to choose between them. It is likely that our chimpanzees could only be successful with the perceptually identical conditions if they had a conceptual understanding of functional support. By comparison, Povinelli’s subjects performed at chance levels on all conditions with this design (Povinelli et al., 2000). Therefore, to specifically address this issue, we replicated this experimental design with our enculturated chimpanzees in Experiment 3, in order to help clarify the extent of their knowledge of physical and functional support.

Four unique conditions were presented that combined one of two possible correct choices with one of two incorrect choices (Fig. 3). The first correct choice consisted of a cloth with a long, thin strip at the top, with the reward resting on the middle of the strip (see Fig. 3, Correct 1, “C1”). The second correct option was a cloth with a square cut from the upper portion, with the reward placed covering the uppermost middle portion of the cloth (see Fig. 3, Correct 2, “C2”). The first incorrect choice was a cloth with a square cut from the upper portion, with a small piece of the side missing, adjacent to the square (see Fig. 3, Incorrect 1, “IC1”). The reward was then placed in the center of the square. The second incorrect choice was nearly identical to the second correct option, C2, except that a small portion of the cloth above the cutout square had been removed (see Fig. 3, Incorrect 2, “IC2”). In this case, the food was placed over the missing portion of cloth such that when the rewards were in place, both C2 and IC2 looked identical. However, though perceptually similar, IC2

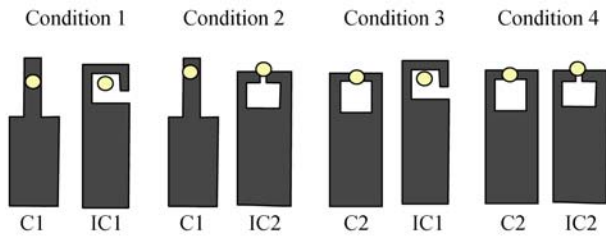


Fig. 3 Experimental conditions for Experiment 3, depicting two correct choices (C1 & C2), and two incorrect choices (IC1: “imminent contact”; IC2: “current contact”) During trials with IC2, the food reward was positioned over the small gap at the top of the cloth, and was perceptually identical to C2 when subjects chose.

was not actually supporting the reward, and therefore was not functional for obtaining the food. These choice comparisons made it critical for the subject to view placement of the rewards carefully, in order to choose correctly. In addition, it should be noted that each cloth was designed and positioned so that the rewards in each condition were the same distance from the subjects.

Four sessions were completed with each subject, and each session consisted of four trials, for a total of 16 trials per subject. Spatial positions for the comparison stimuli on all conditions were counter-balanced, and the order of the presentation of conditions within a session was quasi-randomized, with no more than two correct choices in a row presented on the same side of the platform. The order of procedures and coding was identical

to Experiment 2. When the coded responses from the experimenter and a naïve student coder were compared, inter-rater reliability was high ($\kappa = 0.98$).

2 Results

2.1 Experiment 1

As a group, the chimpanzees were successful with both test conditions in Experiment 1. It is important to note, however, that a significant difference emerged between their performances in the two conditions, such that the Contact/Contact condition was more difficult for them. This condition presented more challenging choices, because in the Contact/Contact condition, both the correct and incorrect cloths were perceptually similar; both “contained”, or surrounded, the food reward. In fact, with only a slight increase in the weight of the cloth, the incorrect choice in the Contact/Contact condition could also have been effective in obtaining the reward. However, overall, the chimpanzees performed significantly above chance in both conditions, demonstrating that they were able to distinguish between choice stimuli with mere perceptual contact, and those with full, physical, and functional support.

Table 2 presents the results for all nine chimpanzees. Binomial tests were used to compare their performance against chance, assuming a 50% probability of selecting either cloth. Each chimpanzee completed eight trials per condition, and to score significantly above chance, a subject had to choose the correct cloth on at least

Table 2 Chimpanzees’ performance for experiment 1

	Condition	Trials								Condition Total	Overall Total
		1	2	3	4	5	6	7	8		
Kermit	C/NC	+	+	–	+	+	–	+	+	6/8	12/16*
	C/C	+	–	–	+	+	+	+	+	6/8	
Darrell	C/NC	+	+	+	+	+	+	+	+	8/8*	12/16*
	C/C	+	–	+	–	+	+	–	–	4/8	
Bobby	C/NC	+	+	+	+	+	+	+	+	8/8*	12/16*
	C/C	–	+	+	–	–	+	–	+	4/8	
Keeli	C/NC	+	+	+	+	+	+	+	+	8/8*	14/16*
	C/C	+	+	–	+	+	+	–	+	6/8	
Harper	C/NC	+	+	–	+	+	+	+	+	7/8*	13/16*
	C/C	–	+	+	–	+	+	+	+	6/8	
Sarah	C/NC	–	+	–	+	+	+	+	+	6/8	13/16*
	C/C	+	+	+	+	+	–	+	+	7/8*	
Sheba	C/NC	+	+	+	+	+	+	+	+	8/8*	13/16*
	C/C	+	–	+	–	–	+	+	+	5/8	
Ivy	C/NC	+	+	+	+	+	+	+	+	8/8*	13/16*
	C/C	+	–	+	–	+	–	+	+	5/8	
Emma	C/NC	+	+	+	+	+	–	+	+	7/8*	13/16*
	C/C	–	+	+	–	+	+	+	+	6/8	
Condition Total: Contact/No Contact									66/72*	115/144*	
Condition Total: Contact/Contact									49/72*	Grand Mean	

C/NC = Contact/No Contact; C/C = Contact/Contact. *Indicates significance at the $p = 0.05$ level, one-tailed binomial test.

seven of the eight trials ($P = 0.04$, one-tailed binomial probability). With respect to individual subjects' performance, seven of the nine chimpanzees scored significantly above chance on the Contact/No Contact condition, and one animal scored significantly above chance with the Contact/Contact condition. For each condition, a total of 72 trials were completed across all subjects. As a group, the animals had to choose correctly on 44/72 trials to score significantly above chance ($p = 0.038$, one-tailed binomial probability). As a group, the chimpanzees were correct on 66/72 trials (92%) in the Contact/No Contact condition, and 49/72 trials (68%) in the Contact/Contact condition. Thus, their overall group performance was significantly above chance in both conditions ($P < 0.05$, one-tailed binomial probabilities).

Additional analyses were conducted to examine possible differences between the group's performances for the two experimental conditions. A Mann-Whitney U test revealed a significant difference between conditions ($P = 0.002$) (Siegel and Castellan, 1988), indicating that the animals performed significantly better with the Contact/No Contact condition. Similarly, we tested for possible sex differences using the same statistical approach (Mann-Whitney U). No differences were found between males and females in the Contact/No Contact condition ($P = 0.786$), the Contact/Contact condition ($P = 0.519$), or across all trials ($P = 0.273$).

2.2 Experiment 2

Findings from Experiment 2 revealed successful performance by the animals across all conditions. Our chimpanzees showed no difficulty with any experimental conditions. For choices between two cloths with similar levels of perceptual containment or those in which the incorrect cloth actually depicted greater perceptual containment of the reward than the correct cloth (e.g., C2/IC1), our subjects performed significantly above chance. Furthermore, their performance on these conditions did not differ from results with any of other conditions. On trials during which they were presented with two novel choices (e.g., C2/IC1, C2/IC2, C2/IC3), their performance was no different than those trials whose choices could have been recalled from Experiment 1 (e.g., C1/IC1, C1/IC2, and C1/IC3).

Binomial tests were completed to compare the chimpanzees' performance with chance (50% probability of selecting either cloth). To score significantly above chance, a subject had to choose the correct cloth at least 17 times ($P = 0.033$, one-tailed binomial probability). All nine chimpanzees scored significantly above chance

across the six conditions. Binomial tests were also performed to look at group performance for each experimental condition. To score significantly above chance, the group had to choose correctly on 24/36 trials ($P = 0.034$, one-tailed binomial probability), which they accomplished for each test condition. A Chi square test was used to determine if there were any significant differences in group performance among the six conditions, but no significant differences were found ($P = 0.586$). In addition, a Mann-Whitney U was conducted to examine for possible sex differences, however, no differences were found between males' or females' performances over the six conditions ($P = 0.310$).

2.3 Experiment 3

Binomial tests were conducted to compare the animals' performance with chance, assuming a 50% probability of selecting either cloth. Among the nine chimpanzees, six (including Bobby, Harper, Sarah, Sheba, Ivy, and Emma) scored significantly above chance across the combined four conditions, which required at least 12/16, or 75% correct responses each ($P = 0.04$, one-tailed binomial). Additional binomial tests also examined group performance. Over all conditions, the subjects needed to choose correctly at least 83/144, or 58%, of the total possible trials to reach statistical significance ($P = 0.04$, one-tailed binomial). The chimpanzees were correct on 108/144 (75%) of the trials, and therefore were not responding by chance ($P < 0.05$, one-tailed binomial probabilities). Group performance for each of the individual conditions was also significantly above chance ($P < 0.05$, one-tailed binomial probabilities). A Chi square test conducted to look for differences among the four conditions revealed none ($P = 0.56$). Further, a Mann-Whitney U was conducted to examine possible sex differences, collapsed across the four conditions. This analysis revealed a significant difference between male and female performance, with females (87.5% correct) outperforming males (65% correct; $P = 0.024$).

2.4 Comparing the OSU and POV chimpanzees

Both groups of chimpanzees were successful with both conditions of the first support problem (Experiment 1). A Mann-Whitney U was conducted to examine possible differences between the performances of the OSU and POV groups in Experiment 1. No significant differences were found for either the Contact/No Contact ($P = 0.198$) or the Contact/Contact ($P = 0.869$) conditions.

The results of Experiment 2 (Table 3) revealed that Povinelli et al.'s (2000) chimpanzees performed at lev-

els significantly below chance on three of the six test conditions: C2/IC1, C2/IC2, and C2/IC3, whereas our subjects were significantly above chance on all six conditions. A Mann-Whitney U was conducted to determine if there were significant differences between the performances of the two groups. The results showed that the OSU animals performed significantly better than Povinelli's et al.'s (2000) subjects during four conditions: C1/IC1 ($P = 0.037$), C2/IC1 ($p = 0.004$), C2/IC2 ($p = 0.001$), and C2/IC3 ($p = 0.003$). For two test conditions (C1/IC2 and C1/IC3), there were no significant differences between the two populations. The conditions during which the New Iberia chimpanzees performed the best (C1/IC1, C1/IC2, and C1/IC3) and were most similar to our group (C1/IC2 and C1/IC3) all involved choices in which the correct answer was the full cloth, a condition that had been exposed to the New Iberia subjects previously during Experiment 1 (Povinelli et al., 2000).

In Experiment 3, group performance revealed that our chimpanzees performed significantly above chance during all conditions, whereas Povinelli's animals performed below chance throughout the experiment (see Table 4). Moreover, as a group, the chimpanzees were successful with all test conditions presented in Experiment 3. A Mann-Whitney U was used to determine if there were statistical differences between the two groups. Several significant differences emerged, including Condition 1 (C1/IC1) ($P = 0.027$), Condition 2 (C1/IC2) ($p = 0.023$), and Condition 4 (C2/IC2) ($P = 0.022$). For each condition, the chimpanzees in the present study

performed significantly better than the seven juvenile animals reported by Povinelli et al. (2000). For Condition 3 (C2/IC1), however, there were no significant differences between the two groups ($P = 0.087$).

3 Discussion

As a group, the OSU chimpanzees were able to solve all the variations of the Support problem that were presented to them within a relatively small number of trials per condition. Given the small number of trials used, it is unlikely that extensive learning occurred within each condition or experiment. For example, while there was slight variation in the success rate across the three experiments for the OSU chimpanzees, the group did not perform successively better with each experiment (see Fig. 4), which would be expected if they had learned important test features from earlier trials. More importantly, their overall performance remained much more consistent than the performance of the New Iberia chimpanzees (Povinelli et al., 2000), who were tested with the same conditions and the same order of experiments. Povinelli and colleagues (2000) concluded that their chimpanzees had based their responses on the perceptual features of the problem, and not on an understanding of functional support. They further proposed that their chimpanzees either attended to whether the cloth and reward *appeared* to be touching or if contact between the cloth and the reward was imminent. In contrast, our chimpanzees were attentive at a more conceptual level beyond simple perceptual features, since they were able to make the correct selection even when the

Table 3 Comparison of performance between OSU & POV chimpanzees for experiment 2

	Experimental Condition					
	C1/IC1**	C1/IC2	C1/IC3	C2/IC1**	C2/IC2**	C2/IC3**
OSU	94.4%*	88.9%*	83.3%*	91.7%*	94.4%*	97.2%*
POV	67.9%*	67.9%*	67.9%*	46.4%	50.0%	64.3%

* Indicates significant from chance, $p = 0.05$, one-tailed binomial. ** Indicates significant difference between OSU & POV groups by condition, $P < 0.05$, Mann-Whitney U.

Table 4 Comparison of performance between OSU & POV groups for experiment 3

	Experimental Conditions			
	C1/IC1**	C1/IC2**	C2/IC1**	C2/IC2**
OSU	75.00%*	80.56%*	66.67%*	77.78%*
POV	39.29%	53.57%	50.00%	50.00%

* Indicates statistically different from chance. ** Indicates significant difference between OSU & POV groups by condition, $P < 0.05$, Mann-Whitney U.

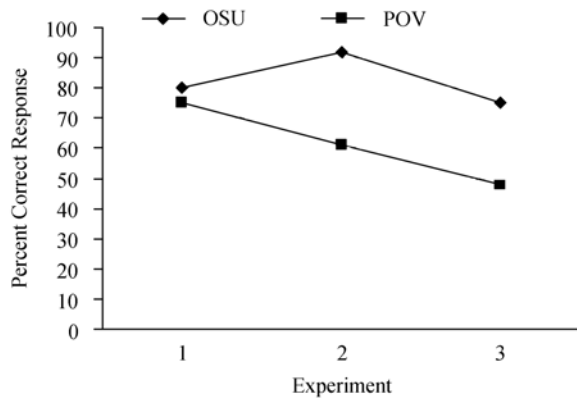


Fig. 4 Performance by OSU & POV Subjects across Experiments 1–3

two choices were perceptually identical. An important question is why our subjects were able to perform significantly better than the New Iberia group.

The results of the present set of experiments offer a number of indications that the constellation of experiences, including the acquisition of a range of concepts related to how the world works (i.e., folk physics), falling under the general term “enculturation”, has a positive effect on the expression of chimpanzee cognitive capacities (Bania et al., 2009; Bulloch et al., 2009; Furlong et al., 2008), including problem solving that requires tool use. Contributions from these processes may explain, in part, why laboratory-born, peer-reared juvenile chimpanzees had very limited success with the support problem (Povinelli et al., 2000). The overall performances reported here for our chimpanzees on the support problem demonstrated that enculturated subjects performed significantly better than results from peer-reared laboratory chimpanzees reported by Povinelli et al. (2000). These differences were especially apparent under the more difficult test conditions in Experiments 2 and 3.

One possible contribution towards the observed differences between the two chimpanzee populations may be the impact of enculturation on the animals’ ability to recognize the functional support relationships inherent in the task. Indeed, there is precedent for better performance on several tasks with captive apes during which enculturated animals tested performed better than other groups (e.g., Bania et al., 2009; Bulloch et al., 2008; Call and Tomasello, 1996; Furlong et al., 2008). Since Povinelli’s subjects were raised under laboratory conditions as an isolated peer group, the type and extent of human contact they received may have been more limited. While they may have had constrained interactions with caregivers and some research assistants, and

received food and other care from staff members, published reports have suggested that they may not have been encouraged to explore, interact, and understand their environment, and had limited, if any, access to human artifacts or natural materials (Povinelli, 2000). In contrast, the chimpanzees tested in the current set of experiments were raised in a highly stimulating environment from an early age, in most cases (2–3 years old), and two subjects arrived as very young infants (ages 4 months and 5 weeks). They were specifically encouraged to interact with objects and materials in their environment, with most having quasi-free range within the facilities until adolescence, and were permitted to investigate and discover how things worked throughout the human culture in which they were immersed. While it is possible that one of the single variables that differed between Povinelli’s (2000) chimpanzees and the OSU chimpanzees, such as enrichment, training, or housing, may have been most influential in the performance differences observed, it was not possible to systemically test these variables with the captive populations in the present study. Recent studies, however, indicate that varying levels of several of the enculturation variables mentioned, as well as variations in the age when these differences were encountered, are correlated with varying levels of success in a tool use task among chimpanzee groups (Furlong, et al., 2008).

The potential effects of enculturation have far-reaching consequences in the domains of behavior and cognition. When enculturated chimpanzees are compared to less enculturated groups, they appear to excel at engaging with objects, mirror recognition, gestural communication, and joint attention (Call and Tomasello, 1996). These are all critical social-cognitive abilities, and may result from a combination of personality and behavioral differences that have already emerged in enculturated chimpanzees from a young age (Bard and Gardner, 1996). Compared to nursery or laboratory-reared chimpanzees, enculturated chimpanzees have also been described as more alert and cooperative, and perhaps most importantly, have shown the longest attention span compared to less enculturated animals (Bard and Gardner, 1996). Attracting the attention of a chimpanzee (or a young child) is often paramount for success with many cognitive experiments. The attentional component seems to be a critical link that enculturated chimpanzees use to their advantage in many social and learning contexts, including tool use. Most notably, our chimpanzees were more successful than Povinelli’s subjects in Experiment 3, when atten-

tion would have been paramount to their success for discriminating between functional and non-functional stimulus choices that were perceptually identical. Specifically in Conditions 2 and 4, the animals had to watch closely where the food was placed on the cloth since once the reward was in position, both cloths looked as if they could be correct. Under these challenging conditions, the chimpanzees we tested excelled compared to the New Iberia group tested previously on the same task (Povinelli et al., 2000).

Another intriguing finding from Experiment 3 was the fact that female chimpanzees performed significantly better than the males tested. These findings demonstrated that the animals were making choices based on their understanding of support as form of physical connection. Interestingly, under these conditions, female chimpanzees significantly outperformed the males, suggesting that they may have had a better understanding of the physical support concept, at some level. Such differences have been reported among captive and wild chimpanzees engaged in tool use (Boesch-Achermann and Boesch, 1993; Furlong et al., 2008; Lonsdorf, 2005). Specifically, Lonsdorf (2005) found that wild chimpanzee females began termite fishing at an earlier age and initially spent more time engaged in such tool use than young males. Even after both sexes had acquired tool using skills, females remained the more proficient tool users. Lonsdorf (2005) attributed these differences to the fact that females used a technique similar to their mothers, while males did not. These results suggest that early in development, male chimpanzees may not be as interested in tool use, and thus it may be more difficult for them to focus attention on observing and learning the most efficient technique. Such sex differences may also reflect, in part, the differing social constraints placed on males and females. While males need to build social relationships early and can join in cooperative hunts as a source of supplemental protein, tool use would be an ideal way for females to garner a protein source, while remaining safer and closer to the center of the community's territory. Consequently, it may be that sex differences in learning and attention observed for male chimpanzees in the wild are reflected in similar attenuated attentional capacities in captive males, perhaps reflecting a more hard-wired sex difference that is attenuated through rearing, resulting in the capacity of enculturated females to outperform, especially when attention to task details is key. Therefore, when a conceptual understanding of support was crucial, as in Experiment 3, where even a strict perceptual rule

would have been fruitless, enhanced attentional resources may have allowed for better performance by female chimpanzees.

Similarly, our enculturated group likely had an advantage over the laboratory, peer-reared New Iberia animals in a number of domains. Critically, we hypothesize that the process of socializing attention with our chimpanzees as they developed allowed them to focus their attention on the most important features of a problem. In turn, they were able to recognize the most important aspect of the task - physical support - and not some other irrelevant variable, including perceptual or imminent contact. It is likely that prior experiences and the processes that subservise enculturation also help to explain other positive results on tasks for which they have outperformed the Povinelli (2000) group (e.g., Bania et al., 2009; Bulloch et al., 2009; Furlong et al., 2008). Indeed, many of the tool use tasks reported were relatively straightforward (Povinelli, 2000). Consequently, if an animal had the capacity to recognize what part of a tool problem required attention, through some combination of experience, training, or more global contributions from enculturation, they would likely have a distinct advantage over subjects without a similar background of object manipulation and exploration of natural materials, among others.

The present findings mesh well with reported results from infant studies using similar tasks to address the concept of functional support (e.g., Schlesinger and Langer, 1999; Sommerville and Woodward, 2005). For example, Schlesinger and Langer (1999) found that infants were able to pull the correct cloth in order to bring a toy within reach (causal action) by the age of 8 months, although they could not identify an impossible event within the same type of task using a preferential looking approach until they were 12 months of age (causal perception). These results suggest that, at least for the concept of support, human infants first learn to solve the problem through their own actions, and then are able to identify a solution perceptually. These conclusions also support with the relationship between experience and enculturation for chimpanzees. Through enculturation, our apes were encouraged to learn about the world through exploration, using their own actions, along with the active guidance of adults. It follows naturally that, after causal experience, perceptual discriminations would follow, prior to responding. Subsequently, based upon the experiences inherent during the process of enculturation, our chimpanzees were able to apply their knowledge of the world and the resultant

folk physics, and, in the case of the support problems, select the cloths that supported the reward. That is, their rich and varied environmental and social experiences contributed to improved performance on a tool use task that required the conceptual understanding of support. Future investigations, including additional studies of tool use in other nonhuman primate species, may help to clarify the range and extent to which the experiences derived from enculturation impact on the expression of cognitive capacities in apes.

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