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PAPER

Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): a Perception–action perspective

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Abstract

*How do capuchin monkeys learn to use stones to crack open nuts? Perception–action theory posits that individuals explore producing varying spatial and force relations among objects and surfaces, thereby learning about affordances of such relations and how to produce them. Such learning supports the discovery of tool use. We present longitudinal developmental data from semifree-ranging tufted capuchin monkeys (*Cebus apella*) to evaluate predictions arising from Perception–action theory linking manipulative development and the onset of tool-using. Percussive actions bringing an object into contact with a surface appeared within the first year of life. Most infants readily struck nuts and other objects against stones or other surfaces from 6 months of age, but percussive actions alone were not sufficient to produce nut-cracking sequences. Placing the nut on the anvil surface and then releasing it, so that it could be struck with a stone, was the last element necessary for nut-cracking to appear in capuchins. Young chimpanzees may face a different challenge in learning to crack nuts: they readily place objects on surfaces and release them, but rarely vigorously strike objects against surfaces or other objects. Thus the challenges facing the two species in developing the same behavior (nut-cracking using a stone hammer and an anvil) may be quite different. Capuchins must inhibit a strong bias to hold nuts so that they can release them; chimpanzees must generate a percussive action rather than a gentle placing action. Generating the right actions may be as challenging as achieving the right sequence of actions in both species. Our analysis suggests a new direction for studies of social influence on young primates learning sequences of actions involving manipulation of objects in relation to surfaces.*

Introduction

Tufted capuchin monkeys (*Cebus apella*) in semi-free conditions and in natural settings spontaneously use stones to crack nuts placed on anvil surfaces (Fragaszy, Visalberghi & Fedigan, 2004; Ottoni & Mannu, 2001; Ottoni, Resende & Izar, 2005). Young capuchins studied by Mannu (2002) were not proficient at cracking nuts before 36 months of age. To understand the ontogeny of this behavior, we analyzed the relation between spontaneous manipulation and nut-cracking in young capuchin monkeys studied longitudinally in semi-free conditions. Our analysis is framed by Perception–action theory (Lockman, 2000), according to which using an object as a tool requires producing and managing spatial relations between a held object and other object(s) or surfaces (see Fragaszy & Cummins-Sebree, 2005a, 2005b, for application of this theory to tool use in capuchin monkeys). Producing and managing spatial relations involves perceptual, attentional, and motor challenges. Learning to use an object as a tool, in this view, is accomplished through exploratory activity, which generates opportunities for learning about the affordances of actions, objects, surfaces, and spatial relations. For example, learning to use a pencil as a writing implement involves learning which end to place against the writing surface, how hard to press, and how to move the pencil with control (Lockman, 2000). Many forms of tool use also include learning a sequence of actions, and the correct order in which to produce the sequence. For example, using a spoon to bring food from bowl to mouth requires filling the bowl of the spoon, then bringing the spoon to the mouth. Initially, human infants perform both actions, but not in the correct sequence (Connolly & Dalgleish, 1989). Managing the sequence of actions in using a spoon, and monitoring that each step is accomplished effectively, requires months of practice.

In general, Perception–action theory posits that tool use is a developmentally continuous phenomenon, grounded in perceptual learning arising from action with

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objects. The theory predicts that direct actions on objects and surfaces precede actions combining an object and a surface, and that initial tool use will reflect the action routines with which the individual has acted with the relevant objects and surfaces. The actions will initially be produced with inattention to precise spatial relations, to the order of an action sequence, or to the effectiveness of a given action element. That is, both spatial and temporal aspects of the action sequence must be learned, and the actor must also learn to monitor the consequences of its actions, when actions are goal-directed. Understanding the origins of tool use, from this perspective, involves analysis of exploratory action routines with objects, coupled with an analysis of the task demands of a given tool-using context (Fragaszy & Cummins-Sebree, 2005a). Relevant dimensions of a problem include at minimum the number of spatial relations involved, whether they must be produced or maintained sequentially or concurrently, whether they require active monitoring for their maintenance (as in holding an object against a slanted surface), and whether they are managed by direct contact or through the intermediate action of an object (Fragaszy & Cummins-Sebree, 2005a). A developmental understanding of the origins of tool use further involves attention to the changing forms of action available to the individual and the changing efficiency of learning about specific task demands.

Young capuchins in captivity exhibit all the basic forms of manipulation seen in adults from 6 months onward, including using the thumb and index finger in a precision grip (Adams-Curtis & Fragaszy, 1994). Handling objects by turning them over or moving them from hand to hand appeared in Adams-Curtis and Fragaszy's sample by the first 8 weeks of age, and actions combining objects and surfaces became common elements in their action repertoire by 6 months of age (Adams-Curtis & Fragaszy, 1994; Fragaszy & Adams-Curtis, 1997). Juveniles between 1 and 3 years old (13 to 39 months) manipulate objects more frequently than other age groups (Byrne & Suomi, 1996; Fragaszy & Adams-Curtis, 1991). Most manipulation by juveniles in captivity is unrelated to feeding, suggesting that manipulation is intrinsically rewarding for them (Fragaszy & Adams-Curtis, 1997).

Combining an object with a surface or with another object is a minority of captive capuchins' actions at all ages (adults: 9%; juveniles: 19%; infants: 11%; Fragaszy & Adams-Curtis, 1991), but is still relatively common among juveniles (Byrne & Suomi, 1995; Fragaszy & Adams-Curtis, 1991). For example, when coded as occurring within 5 second intervals, six intervals scored per minute, actions combining an object and a substrate occurred in 64 intervals per hour per juvenile, compared to 15–17 intervals per hour per infant or per adult (Fragaszy & Adams-Curtis, 1991). Banging an object against a substrate (percussion) is a common combinatorial action performed by capuchins of all ages (Fragaszy & Adams-Curtis, 1997).

According to Perception–action theory, an individual will spontaneously percuss objects against substrates before learning to use an object to crack a nut through percussive action. Moreover, it should initially perform the elements of the action sequence in variable order before producing the correct order consistently. The acquisition of nut-cracking behavior by captive adult tufted capuchins apparently follows this pattern (Visalberghi, 1987). In Visalberghi's study, before opening a nut by striking it with a block of wood (the only suitable object available), the monkeys pounded the nut on the block and the block against the floor, among other ineffective sequences. Here, we consider whether the acquisition of nut-cracking by young monkeys in an environment with richer resources for manipulation than in Visalberghi's study follows this pattern as well.

The common chimpanzee (*Pan troglodytes*) is the only other species of nonhuman primate which spontaneously cracks nuts using stones in natural settings. Chimpanzees become proficient at this activity following years of playful activity with stones and nuts and opportunities to observe others cracking and to sample nuts cracked by others (Boesch & Boesch, 2000; Matsuzawa *et al.*, 2001). We have descriptions of the development of nut-cracking in young wild chimpanzees from two sites: Bossou, Guinea (Inoue-Nakamura & Matsuzawa, 1997) and the Taï Forest, Ivory Coast (Boesch & Boesch, 2000). These descriptions are largely convergent in timeline and pattern. Young infants first explore objects and surfaces directly, then they percuss objects against substrates and use objects to percuss other objects they have placed on a substrate. They perform all elements of the action sequence needed to crack nuts for months in a variable order and with variable objects and substrates before consistently producing the correct sequence and selecting the correct substrates and percussive tools. Once they do produce the correct sequence of actions and select appropriate objects, they still may not succeed for some time to open nuts. Similar results were reported for three captive adult chimpanzees encountering nuts and stones together for the first time (Hayashi, Mizuno & Matsuzawa, 2005). Adults generated the proper sequence with much less experience, however, than young chimpanzees (two in their first test session). One chimpanzee succeeded almost immediately. However, the third chimpanzee did not once hit the stone against the anvil or nut in the first session. This pattern of exploring objects and substrates, and later combining them, was also found by Takeshita, Fragaszy, Mizuno, Matsuzawa, Tomonga and Tanaka (2005), who studied the development of exploratory manipulation in three young captive chimpanzees. Percussion was not a prominent action at any age, although it appeared by 17 months. Instead, more common exploratory actions combining objects and substrates took the form of placing (present at 17 and 21 months), and dropping, touching and throwing (present at 21 months).

Thus, for chimpanzees, the combined data on the development of exploratory manipulation outside of tool use, and goal-directed action using an object as a tool, fit easily into the Perception–action framework, as predicted by Takeshita *et al.* (2005). For chimpanzees, it appears that percussion is the latest-appearing action element in nut-cracking, and that the sequence of placement followed by percussion, jointly with correct selection of substrate, objects to place, and objects to percuss, take months to refine.

We report here a joint analysis of the development of manipulation and of tool use (cracking nuts using stones) in young capuchin monkeys. Our purposes were to test predictions drawn from Perception–action theory linking development of manipulation and the onset of tool use, and to generate findings for comparison with those from chimpanzees, as reviewed above. Given the differences between capuchins and chimpanzees in the typical exploratory action routines of young individuals (placing and gentle actions by chimpanzees; percussion by capuchins), we anticipated that the course of learning to use a stone to crack a nut would follow different developmental trajectories in capuchins than in chimpanzees. From Perception–action theory, we predicted that capuchins would spontaneously bang diverse objects against diverse substrates in playful contexts before using an object to crack a nut: Young capuchin monkeys, like young chimpanzees, would perform the action elements involved in cracking nuts in variable order for some period before consistently producing the correct order, and before consistently selecting appropriate anvil substrates and percussors. Finally, in line with the hypothesis drawn from Perception–action theory that species-typical forms of exploratory action support the ontogeny of species-typical forms of goal-directed action (Lockman, 2000), we predicted that capuchins would have difficulties in producing the correct sequence of actions in nut-cracking at a different point in the sequence than chimpanzees. This prediction arises from our knowledge that capuchins routinely percuss an object against another object or against a substrate (the last step in the sequence of nut-cracking) from an early age, whereas young chimpanzees do not routinely perform this action (Takeshita *et al.*, 2005), and that striking the nut with the stone is the last action in the cracking sequence to appear in chimpanzees (Inoue-Nakamura & Matsuzawa, 1997). We also considered the order in which various action elements involved in nut-cracking appeared in the behavioral repertoire outside of nut-cracking, to understand the appearance of nut-cracking in relation to spontaneous activity, and for comparisons with chimpanzees.

Method

Subjects and study area

Tufted capuchin monkeys living in one group in Tietê Ecological Park (hereafter, PET), encompassing an area of 200,000 m^2, in São Paulo, Brazil, were observed for this study. The monkeys have been considered *Cebus apella*. Recent taxonomic revisions (reviewed in Fragaszy *et al.*, 2004) have raised the previous subspecies of *C. apella* (*C. a. apella*, *C. a. nigritus*, and *C. a. libidinosus*) to species level, but given that the population in PET is constituted by hybrids descended from released animals, we will, in this paper, use *Cebus apella* in the old sense (*Cebus spp* would include the non-tufted species of capuchins). During data collection, group size varied from 23 to 16 individuals. This group is provisioned with food daily but also forages on naturally available foods (fruits, leaves, small birds and mammals) (Ferreira, Resende, Mannu, Ottoni & Izar, 2002; Resende, Greco, Ottoni & Izar, 2003). The natural environment provides abundant vegetation and other natural objects (e.g. stones) for monkeys to manipulate, in addition to food. Many specimens of the palm *Syagrus romanzoffiana* grow in the park and produce nuts, which the monkeys crack with the aid of stones to eat the kernel (Ottoni & Mannu, 2001). Capuchins collect palm nuts from the ground, place them on abundant 'anvil' surfaces of stone or concrete permanently available in the park, and strike them with stones ('hammers') to crack them open. We knew from previous work that monkeys in the PET older than 3 years cracked nuts (Mannu, 2002), so our study focused on nine individuals younger than 3 years (four females, four males, and a monkey that disappeared before we could know its sex). All but one adult female in the study group cracked nuts routinely during this study. We conducted naturalistic observations, that is, we did not provide any additional objects or food to the monkeys during the study.

Procedure

We used two separate protocols: (1) to compare frequency of manipulating stones and nuts and cracking nuts across different age classes, we used All Occurrences Sampling of activity by all animals in the group at nut-cracking sites (October 2000 to July 2002); (2) to evaluate the ontogeny of object manipulation and nut-cracking, we used Focal Animal Sampling of infants and juveniles younger than 36 months of age. We recorded object manipulation using 10-min focal samples (Altmann, 1974) on audio tape for approximately 4 hours per day, 12 to 20 days per month, for 29 months (March 2000 to July 2002). The order of observing focal individuals was randomly predefined before each day of data collection. The monkeys were equally sampled during mornings (600–1200 hr) and afternoons (1201–1900 hr), and sampling efforts were uniformly distributed throughout these periods. Table 1 displays the number of males and females and the distribution of the Focal Samples throughout the blocks of 6 months of age used for the longitudinal analysis (described below). Manipulative behavior was coded during focal sampling protocols using the categories listed in Table 2. Social behaviors

Table 1 *Number of males and females at each age block, and number of focal animal samplings, with the range in parenthesis. Block 1: zero to 6 months; Block 2: 6 months and 1 day to 12 months; Block 3: 12 months and 1 day to 18 months; Block 4: 18 months and 1 day to 24 months; Block 5: 24 months and 1 day to 30 months; Block 6: 30 months and 1 day to 36 months*

Blocks (months)	Males	Females	Unknown sex	Focal animal samples (range)
1 (0–6)	1	4	1	14–73
2 (6–12)	3	4	1	08–112
3 (12–18)	2	4		42–123
4 (18–24)	3	3		20–65
5 (24–30)	3	0		48–75
6 (30–36)	3	0		57–112

(Play, Grooming, Food Sharing and Agonism) were also recorded and are reported elsewhere (Ottoni, Resende & Izar, 2005; Resende, Izar & Ottoni, 2004). Data collection took an average of 4 hours/day. When all focal samplings scheduled for the day (one for each subject) were completed (which took around 3 hours), all-occurrences sampling was performed. Data from these two protocols were analyzed separately.

We subsequently pooled frequency data for manipulation of objects from the focal sampling into the following four categories:

Simple Manipulation (SM): Direct manipulation of objects or the substrate (for example: holding leaf or twig).
Combinatorial Manipulation 1 (C1): Bringing one object into contact with a surface (for example: rubbing stick against tree trunk; banging an object against a surface).
Combinatorial Manipulation 2 (C2): The simultaneous manipulation of two detached objects (for example: hold one stone in each hand and clack them).
Combinatorial Manipulation 3 (C3): The sequential or concurrent manipulation of two objects, related to the same activity, one of which is in contact with the substrate (for example, nut, stone, and substrate) or of three objects (for example, banging two nuts against a stone).

When a monkey pounded an object on an anvil, whether or not another object had been previously placed on the anvil surface, we coded 'Pounding at Nut-cracking Sites' (PNS) for focal and all-occurrences samplings. Data from both schedules were analyzed separately. We subdivided PNS into the following rank order of categories, scoring the highest ranked category observed in a given episode:

Simple Pounding is a subset of C1 and includes episodes in which the monkey pounded any object at a nut-cracking site except for Non-effective and Effective Nut-cracking (see below).
Non-effective Nut-cracking includes episodes in which monkeys struck the hammer against a nut placed on the anvil, but did not succeed in cracking the nut.
Effective Nut-cracking includes episodes in which monkeys struck the hammer against a nut placed on the anvil, opening the nut, and ingesting the endosperm. These latter two categories are types of combinatorial actions C3.

We also included the behavioral category *Place Nut* on an anvil surface (another subset of C1), whether or not the monkey subsequently struck the nut with an object.

An episode of PNS started when a monkey struck an object (usually a stone) against an anvil, whether or not another object had been placed on the anvil beforehand. The episode ended when the subject stopped banging, did not look for other nuts and started performing activities unrelated to nut-cracking. Brief interruptions associated with moving from one anvil site to another, looking for nuts, or observing other monkeys cracking nuts were included within an ongoing episode.

Focal data were collected by BR for the first 10 months of the study, and by BR and another observer for the last 19 months. To check inter-observer reliability, filmed focal samples were coded independently by both observers at three time points: May 2001 (range of reliability: 77 to 89%), December 2001 (76 to 83%), and June 2002 (78 to 90%). 'Pick' was eliminated from quantitative analysis because it could not be reliably scored. All-occurrence samples were all collected by BR.

Analysis

Cross-sectional analyses

All-occurrences data were used to compare the frequency of various forms of manipulation across age classes in a cross-sectional design. We divided the monkeys into three age classes: Infants (from birth to 1 year; $N = 4$), Juveniles (from 1 year to 5 years old; $N = 8$) and Adults (older than 5 years; $N = 7$). Each subject contributed data to a single age class. If a monkey appeared in two age classes during data collection (e.g. an infant became a juvenile), we used all-occurrences data from the age class in which it appeared longer. As monkeys were born, died or left the group during the study, we standardized the data by dividing the individual frequency scores by the number of months that each individual was present in the group during data collection, to arrive at a monthly rate. To test if age classes exhibited different frequencies of the three types of pounding at nut-cracking sites (simple, ineffective, and effective), we used Mann-Whitney tests for two-way comparisons of adults and juveniles (infants did not display these behaviors) and Kruskal-Wallis tests, followed by Dunn's *post hoc* tests for three age classes for Simple Pounding and Place Nut.

Table 2 *Description of manipulative categories. Although monkeys could theoretically perform additional combinations of actions with objects in C2 and C3 than are listed here, they did not do so*

	Description			
Actions	Simple Manipulation (SM)	Combinatorial Man. 1 (C1)	Combinatorial Man. 2 (C2)	Combinatorial Man. 3 (C3)
Pick	Pick an object, food or substrate using hands, feet or mouth.			
Bite	Bite objects, substrate or food.			
Lick	Put the tongue on the object, food or substrate.			
Smell	Smell object, food or substrate.			
Explore/Handle	Examine object, substrate or food, using the hands or mouth.			
Spread	Spread object or food using hands or feet.			
Hit	Hit object, substrate or food with hands or feet.	Hit object, substrate or food against a substrate.	Hold two objects, one in each hand, and, simultaneously, bang them.	More common: Strike one object placed against a substrate. Less common: Hold two objects, one in each hand, and, simultaneously, bang them against a third one.
Poke	Poke object, substrate or food using finger tips.			
Rub	Rub substrate using the hands.	Rub an object or food against a substrate.		
Insert	Insert hands or fingers inside the substrate.	Insert an object or food inside the substrate.		
Place (PNS)		Any placement of objects (usually the nut) on the substrate used as anvil for pounding with continuing monitoring of the object.		
Hit C1 + Place				Place an object (nut, fruit, chow, twig, corn, stone) on the anvil (any substrate used as support) and pound it with a hammer (stone, piece of wood).

Manipulative development

We noted the first appearance of each form of combinatorial manipulation and each form of action at nut-cracking sites, to establish a timeline of appearance of these behaviors for each monkey. To look for age-related changes in the frequencies of manipulative behaviors, we assigned the focal data for monkeys younger than 3 years to blocks of 6 months of age ('Age Blocks'): Block 1 (zero to 6 months), Block 2 (6 months plus 1 day to 1 year) and so on up to Block 6. As total focal sampling time differed for each subject, a manipulation rate (MR) was calculated for each subject in each block, for each category of manipulation (MR = *n* events/minutes of focal sampling). A Mixed Effects Model was developed to test for changes in manipulative frequency with age. For analyses of Simple Manipulation and C1, age was a fixed, continuous factor and subject was a random factor. To achieve normality and homogeneity of variance, manipulative frequencies (Simple Manipulation and C1) were square-root transformed before analyses.

To examine the relation between the monthly rates of different forms of manipulation, we calculated Spearman correlations using monthly rates from individuals presenting sufficient monthly records for these analyses.

The software EthoLog 2.2 (Ottoni, 2000) was used to transcribe Focal Animal samples, SPSS 10.0 for the ANOVA Repeated Measures tests, Biostat 3.0 for non-parametric tests (Spearman, Kruskal-Wallis, Dunn, Mann-Whitney, Wilcoxon), and Minitab for Mixed Effects Model tests.

Results

During 1420.45 hours of observation, we recorded 530 episodes of pounding at nut-cracking sites (Focal Animal Sampling: 147; All-Occurrences Sampling: 423; rate of approximately one episode to each 2.5 hours). During focal sampling (193 hours), we recorded 12,429 events of manipulation involving biting, rubbing, exploring, inserting, hitting and placing (rate of approximately 1 manipulation episode each minute).

Cross-sectional comparisons

We observed 325 events of Pounding at Nutcracking Sites (Adults = 70, $N = 8$, range = 0–20; Juveniles = 234, $N = 8$, range = 1–56; Infants = 21, $N = 4$, range = 0–14) (Figure 2). Using All-Occurrences data, we tested if monkeys from different age classes differed in their rates of Simple Pounding and Effective Nut-cracking. Juveniles exhibited more Simple Pounding than Adults or Infants [Kruskal-Wallis: $\chi^2(2, N = 20) = 99{,}521$, $p = .0069$; Average Ranks: Adults = 6.933; Juveniles = 15.53; Infants = 7.50; Dunn: ($p_{\text{adults×juveniles}}$) < .05]. There was no significant difference between Adults and Juveniles in rates of Effective Nut-cracking.

Table 3 *Range of emergence (Blocks of age) of Rub, Hit and Insert during Focal Sampling. SM: simple manipulation; C1: combinatorial manipulation involving using an object to act upon another object or substrate; C3: combinatorial manipulation involving the simultaneous or sequential use of two objects in relation to another object or substrate. PO: Place fruit, corn, object; PN: Place Nuts; NN: Non-Efficient Nut-cracking; EN: Efficient Nut-cracking*

		Blocks
Rub	SM	2
	C1	1–2
Hit	SM	2
	C1	1–2
	C3	3–5
Insert	SM	1–3
	C1	–
PO		1–4
PN		4
NN		4–5
EN		5

Manipulative development

Simple Manipulation appeared during the first months of life (range 2 to 3 months), when infants prehended small objects such as flowers or twigs. Table 3 presents the range of the Blocks of age when the monkeys started hitting, rubbing, inserting, and placing objects and pounding objects at nut-cracking sites. Of the four monkeys observed from birth, three were seen performing C1 before SM. These four monkeys started rubbing and hitting objects against substrates almost simultaneously (range 5 to 8 months), with the exception of a female that rubbed a twig against a tree when she was 4 months old, but only hit an object against the ground when 17 months old, and her younger sister, who rubbed a twig against the substrate when she was 7 months old, but did not hit any object until the end of data collection, when she was 14 months old. Some monkeys first hit ($N = 5$) and rubbed ($N = 2$) using objects (C1) and only later hit or rubbed their hands against substrates. Inserting and placing were rarer behaviors. With the exception of an infant who inserted a twig inside a tree hole, the monkeys inserted their hands or fingers, but not objects.

Although Simple Manipulation appeared early in life, Simple Manipulation of stones and nuts (or nutlike objects, i.e. other fruits or objects with the same size and shape of a nut) was first observed at least 4 months later (first seen between 6 and 12 months of life) in the monkeys who were born during data collection. All these monkeys exhibited C1 manipulation with stones (except for the youngest, who was 14 months old at the end of the study). C1 manipulation with nuts was never seen before C1 manipulation with stones, but it could occur concurrently.

During focal sampling, there were 178 events in which the monkeys placed nuts, and 61 events in which they placed corn, fruit, leaves, small stones or pellets of monkey

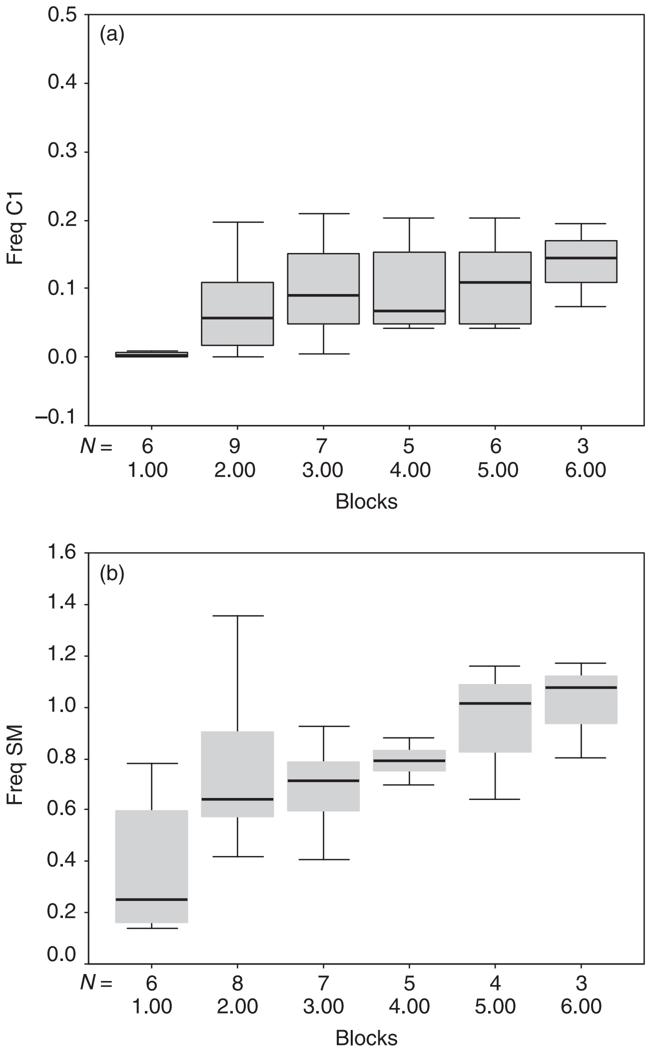

Figure 1 *Box Plot (median and quartiles) (a): Frequency of Combinatorial Manipulation 1 per minute. (b) Frequency of Simple Manipulation per minute. Note that the scales in the ordinate are different in (a) and (b).*

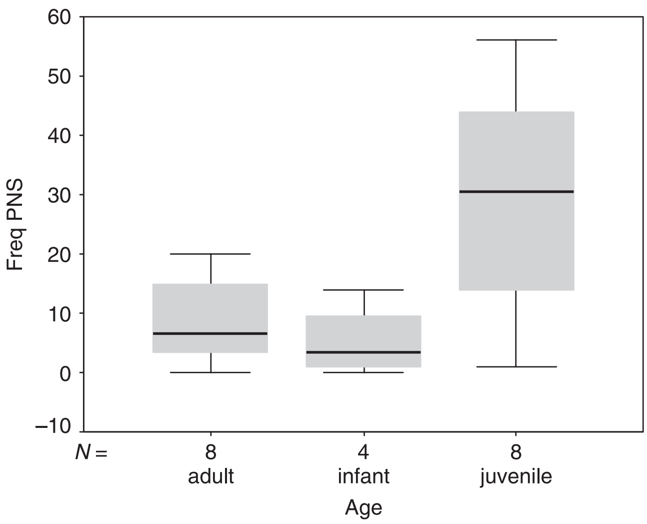

Figure 2 *Distribution of PNS (Pounding at Nut-cracking Sites) among age classes (median and quartiles).*

chow on the anvil (not considered in the quantitative analyses). The four monkeys who placed objects other than nuts were older than 1 and younger than 5 years, and two of them, the same who started cracking nuts effectively during data collection, were responsible for 98% of the placing events (Darwin = 56%; Químico = 42%). Before Effective Nut-cracking, they had placed only nuts, chow and corn (Darwin: 19 to 24 months old = 2 events; Químico: 24 to 28 months old = 5 events). The frequency of placing increased after the monkeys succeeded in nut-cracking (Darwin: 25 to 38 months old = 134 events; Químico: 29 to 37 months old = 96 events), and nuts were the main object placed (Darwin = 93; Químico = 85). Adults placed and struck only nuts.

Combinatorial Manipulation Level 2 (C2) was the least frequently observed form of manipulation. C2 was observed 17 times over the entire study, in just two monkeys (ages: 35 and 37 months). It appeared only in the context of what we labeled ‘stone (or nut) clacking’: the monkey held two small stones (or nuts), one in each hand, and beat one against the other.

Combinatorial Manipulation Level 3 (C3) was performed by monkeys older than 1 year. This type of manipulation includes Non-effective and Effective Nut-cracking. The three young monkeys who performed C3 used stones and nuts. C3 with objects other than stones and nuts (or nutlike objects) was observed only once.

Once these actions appeared, they remained in the monkey's repertoire. Actions in which subjects manipulated objects in relation to the substrate, to other objects or to their own body (the ‘combined actions’ of Fragaszy & Adams-Curtis, 1997) corresponded to 17% of total manipulatory activities registered through Focal Animal Sampling.

As can be seen in Figure 1, the rates of C1 and Simple Manipulation increased over age blocks. Longitudinal analyses indicated that the frequency of Combinatorial Manipulation varied significantly across Blocks [C1: $F = 6.12$, df = (8,5), $p < .01$, $r^2_{adj} = +0.74$]. Tukey's pair-wise post-tests revealed that C1 scores in Block 1 differed from C1 scores in the other Blocks ($p < .05$). Monkeys in Block 1 (up to 6 months) seldom exhibited any events of C1 manipulation (0.003 per min). The rate of C1 increased to almost one event per minute in Block 2 (7 to 12 months) (Figure 1). Individuals differed significantly in rates of performing C1 and Simple Manipulation [C1: $F = 5.44$, df = (8,5) $p < .05$; SM: $F = 3.02$, df = (8,5), $p < .05$].

The frequencies of Simple Manipulation exhibited by four monkeys correlated or tended to correlate positively with their frequencies of C1 (Químico: $r_s = +0.35$, $N = 29$, $p < .05$; Darwin: $r_s = +0.41$, $N = 29$, $p < .05$; Ada: $r_s = +0.74$, $N = 19$, $p < .05$; Janeiro: $r_s = +0.61$, $N = 13$, $p < .05$]. Although correlations between Simple Manipulation and C1 for the other subjects were also positive (except for one juvenile male), they were not significantly above chance level.

Emergence of nut-cracking

Effective Nut-cracking (EN) was registered only for Darwin (success: 25 months) and Químico (success: 29 months). Químico placed corn on an anvil stone when he was 24 months old, placed a nut for the first time at 26 months, and at 28 months, used a hammer stone to hit small stones he had placed on the anvil. When he was 29 months old, he placed fruits and nuts on the anvil and hit them using a hammer stone, and he succeeded at opening nuts later in this same month. Darwin placed a nut on the anvil and hit it with a stone for the first time when he was 19 months old. He succeeded at cracking a nut 6 months later. Thus, the monkeys that succeeded at cracking nuts first placed a nut (or nutlike object) on an anvil at 19 to 26 months, months after the other elements of nut-cracking appeared in their repertoire.

We correlated Químico's and Darwin's rates per month of Placing objects on the anvil with the rates per month of Simple Manipulation and C1 with and without nuts. The rate of Placing for both monkeys correlated positively with rates of Simple Manipulation with stones and nuts [Químico: $r_s = +0.493$; $N = 28$, $p < .05$; Darwin: $r_s = +0.669$, $N = 28$, $p < .01$], and C1 with stones and nuts [Químico: $r_s = +0.597$, $N = 29$, $p < .05$; Darwin: $r_s = +0.662$, $N = 28$, $p < .01$]. For Químico only, the rate of placing correlated positively with the rate of performing C1 with other objects as well [$r_s = +0.413$, $N = 28$, $p < .05$].

Discussion

Our study concerned the link between the development of manipulation and the appearance of nut-cracking using stones as hammers, a common form of tool use among the capuchin monkeys ranging in Parque Ecologico Tietê (PET). We consider the developmental linkage between these behaviors from the perspective of Perception–action theory, which posits that skills such as tool-using are acquired through linked action and perceptual learning, and that the actions which support such learning are those that are commonly evident in the species-typical repertoire of exploratory behaviors (Lockman, 2000; Gibson & Pick, 2000). Thus we sought to characterize normal manipulative development in young capuchin monkeys, and to evaluate how nut-cracking appeared within this context.

Manipulative behavior of young capuchin monkeys in PET followed the same developmental trajectory and timeline as observed in captive monkeys of the same species (*Cebus apella*) with very different (and more varied) objects and surfaces available for exploration, suggesting that the developmental pattern is robust across a range of environments. We were able to observe manipulative development from birth in four infants born during the course of our study. Direct manipulation of objects and surfaces (Simple Manipulation, in our terminology) appeared between 8 and 12 weeks. Actions combining objects and substrates (C actions, in our terminology) appeared even before Simple Manipulation in three infants, and appeared in a variety of forms by 16 to 24 weeks of age. It is noteworthy that combinatorial actions appeared prior to or essentially concurrently with simple manipulation. This pattern is in accord with the prediction drawn from Perception–action theory that exploratory routines (which encompass combinatorial actions such as banging) appear as soon as motor coordination permits, and initiate subsequent actions. For all individuals, actions combining objects and substrates commonly included percussion of an object against a substrate (cf. Adams-Curtis & Fragaszy, 1994; Byrne & Suomi, 1995; Fragaszy & Adams-Curtis, 1991). Early manipulative activity took place while the infant clung to a carrier, and expanded in frequency and variety when the infant locomoted regularly on its own, beginning in the fourth or fifth month.

Individual variation in the timing of appearance and frequency of different categories of manipulation was substantial, as in captive individuals. In general, however, percussive actions appeared at the same time as other combinatorial actions. Manipulation of nuts and stones and percussive actions with these objects appeared somewhat later (32 to 80 weeks of age in our sample) than similar manipulation of other objects such as twigs or pieces of food, except for infant Janeiro, who first combined an object with a surface when he hit a nutlike object against an anvil stone. Most likely this delay in the appearance of actions combining nuts and stones, compared to actions combining other objects and surfaces, is due in part to the preference of infants in the first year of life to remain with their mothers. Except for Janeiro's mother, adult females in this study exhibited low rates of cracking nuts (Resende, 2004). Therefore, other infants up to 12 months of age rarely encountered stones and nuts. We come back to the influence of social context of nut-cracking on young individuals' actions with nuts and stones later in the discussion (see also Ottoni *et al.*, 2005).

The pattern of manipulative development observed in young capuchins largely follows the pattern observed in other young primates, including chimpanzees and humans (Inoue-Nakamura & Matsuzawa, 1999; Gesell & Thompson, 1938; Lockman, 2005; Takeshita *et al.*, 2005; see Table 4), with some important exceptions that we discuss below. The timeline for each species is in accord with the development of postural stability and locomotor ability for that species, as these support reaching out, grasping, and handling objects, and movement to objects that interest the individual. For capuchin monkeys, this is apparent in the appearance of manipulation when the infant can first reach out while clinging to a carrier, and the appearance of more vigorous and varied actions from 5 months onward, when locomotion

Table 4 *Age ranges (chimpanzees and capuchins) or norms (humans) (in months) for the appearance of key elements in manipulation and nut-cracking**

Species	Simple manipulation	Combinatorial manipulation	Percuss with nuts or stones	Succeed at cracking a nut
Chimpanzees (*Pan troglodytes*)	3–4	12–17	18	30–42
Capuchins (*Cebus apella*)	2–3	4–8	6–12	≥25
Humans (*Homo sapiens*)	6[+]	6[@]	7[#]	NA[^]

* Data for chimpanzees are taken from Takeshita, 1999; Brakke, 1989; and Inoue-Nakamura and Matsuzawa, 1997. Data for capuchins are from this study. Data for humans are taken from Gesell and Thompson, 1938 (p. 102, Table VII.4, Consecutive Cubes). Ages for humans are those where 50% or more of children exhibited the behavior.
[+] Children grasped a wood cube, 2.5 cm^2.
[@] Children pushed or pulled a wood cube on a table top.
[#] Children banged one wood cube against a table top.
[^] NA = Not applicable.

and postural stability reach sufficient maturity (Fragaszy, 1989; Fragaszy & Adams-Curtis, 1997). As in captive monkeys (Fragaszy & Adams-Curtis, 1997), juvenile capuchins in PET engaged in manipulatory activities with inedible objects frequently and for extended periods, apparently for the intrinsic pleasure of acting with objects.

Two out of four monkeys that were observed from birth manipulated stones and nuts during this study. At first, the monkeys manipulated stones and nuts directly, and percussed them against a substrate. Direct percussion appeared at the same time as first manipulation of stones and nuts. Often the monkeys struck a nut against a stone. However, nut-cracking requires one more step, and this element was the last to appear in our capuchins: placing the nut on an anvil surface, and releasing it, leaving it on the anvil. Non-effective nut-cracking emerged when the monkeys began to release the nut and continue to direct actions towards it, and particularly, to place the nut on an adequate anvil. Two juveniles in this study passed from non-effective to effective nut-cracking. Darwin first placed nuts on the anvils at 19 months, and executed Effective Nut-cracking 6 months after that. Químico was 26 months old when he started placing nuts on the anvils. He achieved Effective Nut-cracking 1 month after first placing nuts on an anvil.

Once they began to pound at nut-cracking sites, juveniles pounded more frequently than adults. However, the form of their activity still differed from adults' for some period after they began to use nut-cracking sites. The two juveniles that became effective nut-crackers during this study (Darwin and Químico) continued Simple Pounding and other exploratory activity such as pounding other things on the anvils besides nuts or stones, even after they opened nuts. These monkeys also placed objects other than nuts on the anvil around the same time that they achieved success in nut-cracking, suggesting that practice involved placing as well as pounding actions. Eventually Simple Pounding and placing objects other than nuts disappear: when adults used anvil sites, they immediately placed a nut and began to crack it with a stone.

Young capuchins in PET followed the same global developmental pattern as captive adult capuchins learning to crack nuts with a percussive tool (Visalberghi, 1987): (1) simple pounding of both the stone and the nut appeared first; (2) the monkeys eventually placed nuts (and other objects) on the anvil, and struck them with a stone, but were not effective at opening them; (3) eventually, they became effective at opening the nuts by placing them on an appropriate substrate and striking them with a stone. Improving effectiveness takes varying degrees of practice depending on the toughness of the nut, the size and hardness of the percussor, the hardness of the anvil, the size of the individual trying to crack the nut, etc., as Boesch and Boesch (2000) describe also for chimpanzees in the Taï Forest. Skilled percussion with a hammer to break an object requires more than the proper sequence of actions; it also requires refinement of the actions, and this takes much practice (years, for skilled human hammering to produce fluted glass beads; Bril, Roux & Dietrich, 2006).

This global description omits one very important aspect, which we have noted in our results: Placing the nut on an anvil, and releasing it, is a late-appearing element in capuchins' acquisition of nut-cracking. For our subjects, placing the nut and releasing it in such a way that it does not move when released seemed to pose one of the main difficulties for nut-cracking. Producing the correct sequence of actions (placing followed by striking) was not difficult for them once they were able to place the nut.

In normal circumstances, capuchin monkeys do not release an object that they are trying to open. They may bang, bite, and pull on it for many minutes, but they do not release it until they succeed at breaking it open or lose interest in it. Releasing an object in which they are still interested requires over-riding a strong proclivity to maintain a secure grip on it. Thus the last appearing element in the sequence of actions needed to crack nuts is the second in the sequence: placing the nut on the anvil. The finding that the last-appearing element, developmentally, is in the middle of the sequence of actions needed for effective nut-cracking suggests that releasing the nut to place it on the anvil may be the most challenging aspect of nut-cracking for the capuchin monkeys. Organizing percussive action with a stone against an anvil surface appears much earlier.

Contrasting this picture with the descriptions of nut-cracking in young chimpanzees is revealing, and suggests that the two species face quite different challenges in learning to crack nuts. Matsuzawa (1996) described the sequence of actions involved in nut-cracking with a hierarchical diagram in which the actions involved in this activity form a branching tree structure, noting the three objects involved as lines (nut, stone, and anvil) and connected via lines to two nodes representing actions with these objects: lower node 1: place the nut on the anvil; higher node 2, strike the nut (placed on the anvil) with the hammer stone. In his analysis and later work from the same laboratory (Inoue-Nakamura & Matsuzawa, 1997; Matsuzawa, Biro, Humle, Inoue-Nakamura, Tonooka & Yamakoshi, 2001), the organization of the hierarchical (i.e. ordered) sequence of actions with two objects and a substrate is considered the primary challenge faced by young chimpanzees. In more recent work, Hayashi *et al.* (2005) suggest that some adult captive chimpanzees face three principal difficulties in learning to crack nuts using a percussive tool: (1) they do not routinely percuss objects against a substrate (see also Takeshita *et al.*, 2005); (2) they do not display extended exploratory manipulation of stones, and (3) combining three objects in a sequence of two actions can be performed incorrectly in many ways (i.e. there are several degrees of freedom in the system). Thus, learning the correct sequence takes much practice. Chimpanzees and capuchins both face the last challenge, but they differ in the preceding two (exploration and percussion), and capuchins face one that chimpanzees do not (placement). Capuchins percuss objects against substrates from very early in life (this study and Fragaszy & Adams-Curtis, 1997), and they explore objects frequently in many ways. However, they rarely place and release an object on a substrate as part of exploration.

Why might the action routines of the two species vary in this way? Here we suggest an ecological (functional) explanation. Wild capuchin monkeys feed routinely on hard-husked fruits and seeds. They process these by banging and biting them open to eat the digestible inner material (e.g. Izawa & Mizuno, 1977). Percussion is a characteristic element in their foraging behavior (see Fragaszy *et al.*, 2004, for review). They forage primarily above ground, where placing and releasing an object risks losing it. Chimpanzees, in contrast, feed primarily on fleshy fruits. These can require extensive processing (e.g. *Sabah* fruits; Corp & Byrne, 2002), but they do not require percussion to open them. Chimpanzees do not routinely feed on hard-husked seeds or fruits that must be broken open by percussion, although in some places they break open baobab fruits by smashing them (Marchant & McGrew, 2006). Also, chimpanzees commonly move on the ground, and may feed on the ground (Hunt, 1998). Placing an object on the ground does not risk losing it. Thus each species' action repertoire fits its foraging ecology. Capuchins are primarily arboreal, use vigorous actions in foraging, and are cautious about releasing food; chimpanzees are more terrestrial than capuchins, use less vigorous actions in foraging, and can be more relaxed about placing food on a surface and releasing it.

Researchers concerned with how humans learn to produce structured or hierarchical sequences of actions (as in language) have developed models of learning based on detection of the statistical temporal structure of events or stimuli to be learned (e.g. Cleeremans & McCelland, 1991; Cleeremans & Jimenez, 1998; Tubau, Hommel & Lopez-Moliner, 2007; Spiegel & McLaren, 2006). In statistical structural learning models, the relative frequency of encountering or producing specific sequences affects the ease of mastering production of these sequences (e.g. Soetens, Melis & Notebaert, 2004), even when the person is unaware of the structure of the actions, stimuli, or events which he or she must master (Whittlesea & Wright, 1997). We assume that monkeys and apes learning to crack nuts are learning a four-part sequence with additional internal spatial structure (collect nut, place nut [on anvil], collect stone, strike nut with stone), and that they, like humans learning an arbitrary sequence in a laboratory experiment, are not explicitly aware of the rules governing the task. Thus their performance should reflect similar processes of statistical learning. From this perspective, capuchins and chimpanzees face an equivalent problem, and their rates and patterns of learning should be equivalent. However, we have seen that they do not master the sequence of actions in the same way.

A Perception–action perspective can extend the concept of statistical learning by bringing particular attention to action biases that will impact learning action sequences. From a Perception–action perspective, an individual will perform species-typical exploratory routines more frequently than other actions. This bias in action, according to statistical models of sequence learning, should result in delays in learning a sequence in which less probable actions must appear before exploratory routines compared to learning a sequence of the reverse order (prepotent actions first; other actions second). In the case of capuchins learning to crack nuts, placing the nut and then striking it means altering the prepotent routine of striking the object of interest (the nut). Thus we predict that capuchins will require more experience manipulating nuts and stones to learn to produce the sequence of actions needed for effective nut-cracking (pick up the nut, place the nut, then pick up a stone and percuss the nut), than chimpanzees, who must append a less frequent action (percussion) to the end of a common sequence (pick up the nut, place the nut, pick up another object). Testing this prediction requires more detailed longitudinal data on individuals' experiences with nuts and stones than are currently available. Although collecting appropriate data from wild populations would be extremely challenging, collecting such data is feasible in laboratory settings, in which the experimenters can control individuals' opportunities to encounter nuts and stones.

In sum, the Perception–action perspective clarifies the role of species-typical exploratory activity, evident in spontaneous exploratory and playful activity with objects and substrates, in learning skilled action sequences, such as cracking nuts. It suggests that the challenges facing youngsters of two different species in learning the same skill are differently weighted, in accord with different predominant action routines present in each species: in this case, placing in chimpanzees and striking in capuchins. This analysis suggests a new direction for studies on the role of social influence on the emergence and refinement of nut-cracking and other forms of goal-directed manipulation of objects in these two taxa, a topic of considerable interest to students of cognition in nonhuman primates (e.g. Matsuzawa, Tomonaga & Tanaka, 2006; Ottoni *et al.*, 2005; Fragaszy & Visalberghi, 2004).

For chimpanzees, perhaps social influence supports organizing the sequence of actions, and perhaps also supports generation of percussive actions which are otherwise not prominent in their repertoire. Myowa-Yamakoshi and Matsuzawa (1999) show that, following observation of a familiar human's actions, chimpanzees are more likely to reproduce actions involving moving an object than other kinds of actions. Percussive actions are of this type: the actor moves the hammer stone toward the nut and anvil. It would be interesting to look at the kinematics of percussive actions in young chimpanzees and young capuchins to evaluate predictions drawn from Perception–action theory. In chimpanzees, we predict that early striking actions are very gentle, and that the force of the strike more than the accuracy increases with practice.

For capuchins, we predict the converse: that strikes are hard from the outset and that experience affects accuracy rather than the probability of striking with greater or lesser force. Moreover, we predict that social influence is more important for capuchins in learning to place the nut on the anvil while continuing to act towards it than for generating percussion. Human-reared capuchins show a strong interest in objects contacted by their human companions (Deputte & Busnel, 1997) and they are modestly able, with training, to reproduce familiar actions bringing one object into a specific spatial relation with a substrate or another object (Fragaszy *et al.* unpublished data; Hemery, Deputte & Fragaszy, 1998; reviewed in Fragaszy *et al.*, 2004). In PET, young monkeys are attracted to sites where others are cracking nuts (Ottoni *et al.*, 2005). Observers seem to have some understanding of the relative proficiency of their group mates, preferentially watching the more skilled nut-crackers. This preference for watching more skilled individuals enhances not only scrounging payoffs (e.g. obtaining bits of nuts from others' work), but also social learning opportunities. Young monkeys were more involved in the observation of nut-cracking events when they spent more time in proximity to other members of the group, especially juveniles, who were the major actors at the nut-cracking sites (Resende, 2004), rather than when they were younger and spent more time in proximity to or in contact with their mothers. Staying near individuals who spend time engaged in cracking nuts provides opportunities for the young monkey to encounter nuts, anvils and hammers, and, after the other individual leaves the anvil site, to manipulate these objects in species-typical (percussive) combinations in the same locations. It also affords opportunities to observe the action sequence of placing the nut followed by picking up a stone.

In view of capuchin monkeys' interest in watching others act with objects, especially during nut-cracking, and their tendency to position objects in the same place as others place them, it would be interesting to look more closely at the origins of placement of objects on anvils by young monkeys, and the temporal relation of this activity to observation of others and combination of placement with percussive action towards the placed object. We predict that young capuchins are more likely to place nuts on anvils while or shortly after observing others cracking nuts in species-typical social settings than when acting with nuts and stones by themselves. In other words, one particular benefit of social context for the young capuchin learning to crack nuts with a stone could be the facilitation of the action of placing the nut on the anvil; a second, related benefit could be the facilitation of the sequence of actions of placing the nut followed by striking with a stone.

In general, understanding the role of social context in the maintenance of skilled technological traditions is an important challenge facing contemporary primatology, and theoretically driven studies are needed for progress in this area (Fragaszy & Perry, 2003; Fragaszy, 2003; Mesoudi, Whiten & Laland, 2006). Perception–action theory can be of use here, because it can generate predictions about the aspects of learning a skill that are most challenging, and thus where social influence may be most helpful.

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References

Adams-Curtis, L., & Fragaszy, D.M. (1994). Development of manipulation in capuchin monkeys during the first 6 months. *Developmental Psychobiology*, **27**, 123–136.

Altmann, J. (1974). Observational study of behaviour: sampling methods. *Behaviour*, **49**, 223–265.

Boesch, H., & Boesch, C. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution*. Oxford: Oxford University Press.

Brakke, K. (1989). The comparative development of postural competence and object manipulation in bonobo (*Pan paniscus*) and chimpanzee (*Pan troglodytes*). Master's thesis, Georgia State University.

Bril, B., Roux, V., & Dietrich, G. (2006). Stone knapping: Khambat (India), a unique opportunity? In V. Roux & B. Bril (Eds.), *Stone knapping: The necessary conditions for a uniquely hominin behaviour* (pp. 530–572). McDonald Institute Monographs.

Byrne, G., & Suomi, S.J. (1995). Development of activity patterns, social interactions, and exploratory behavior in infant tufted capuchins (*Cebus apella*). *American Journal of Primatology*, **35** (4), 255–270.

Byrne, G., & Suomi, S.J. (1996). Individual differences in object manipulation in a colony of tufted capuchins. *Journal of Human Evolution*, **31**, 259–267.

Cleeremans, A., & Jimenez, L. (1998). Implicit sequence learning. In M.A. Stadler & P.A. Frensch (Eds.), *Handbook of implicit learning* (pp. 323–364). Thousand Oaks, CA: Sage.

Cleeremans, A., & McClelland, J.L. (1991). Learning the structure of event sequences. *Journal of Experimental Psychology: General*, **120**, 235–253.

Connolly, K.L., & Dalgleish, J. (1989). The emergence of tool using skills in infancy. *Developmental Psychology*, **25**, 894–912.

Corp, N., & Byrne, R.W. (2002). The ontogeny of manual skill in wild chimpanzees: evidence from feeding on the fruit of *Saba florida*. *Behaviour*, **139** (1), 137–168.

Deputte, B.L., & Busnel, M. (1997). An example of a Monkey Assistance Program: PAST – The French Project of simian help to quadriplegics – A response to Iannuzzi and Rowan's (1991) paper on ethical issues in animal-assisted therapy programs. *Anthrozoos*, **10** (2–3), 76–81.

Ferreira, R.G., Resende, B.D., Mannu, M., Ottoni, E.B., & Izar, P. (2002). Bird predation and prey-transference in Brown Capuchin Monkeys (*Cebus apella*). *Neotropical Primates*, **10**, 84–89.

Fragaszy, D.M. (1989). Activity states and motor activity in an infant capuchin monkey from birth to eleven weeks. *Developmental Psychobiology*, **22**, 141–157.

Fragaszy, D.M. (2003). Making space for traditions. *Evolutionary Anthropology*, **12**, 61–70.

Fragaszy, D.M., & Adams-Curtis, L.E. (1991). Generative aspects of manipulation in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, **105** (4), 387–397.

Fragaszy, D.M., & Adams-Curtis, L.E. (1997). Developmental changes in manipulation in tufted capuchins (*Cebus apella*) from birth through 2 years and their relation to foraging and weaning. *Journal of Comparative Psychology*, **111** (2), 201–211.

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

Fragaszy, D.M., & Cummins-Sebree, S. (2005b). Choosing and using tools: capuchins (*Cebus apella*) use a different metric than tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology*, **119**, 210–219.

Fragaszy, D.M., & Perry, S. (2003). Towards a biology of traditions. In D.M. Fragaszy & S. Perry (Eds.), *The biology of traditions* (pp. 1–33). Cambridge: Cambridge University Press.

Fragaszy, D.M., & Visalberghi, E. (2004). Socially-biased learning in monkeys. *Learning and Behavior*, **32** (1), 24–35.

Fragaszy, D.M., Visalberghi, E., & Fedigan, L. (2004). *The complete capuchin*. Cambridge: Cambridge University Press.

Gesell, A., & Thompson, H. 1938. *The psychology of early growth*. New York: Macmillan.

Gibson, E., & Pick, A. (2000). *An ecological approach to perceptual learning and development*. Oxford: Oxford University Press.

Hayashi, M., Mizuno, Y., & Matsuzawa, T. (2005). How does stone-tool use emerge? Introduction of stones and nuts to naïve chimpanzees in captivity. *Primates*, **46**, 91–102.

Hemery, C., Deputte, B., & Fragaszy, D. (1998). Human-socialized capuchins match objects but not actions. *Abstracts of the XVII Congress of the International Primatological Society*, p. 45. University of Antananarivo, Madagascar.

Hunt, K. (1998). Ecological morphology of Australopithecus afarensis: travelling terrestrially, eating arboreally. In E. Strasser, J. Fleagle, A. Rosenberger, & H. McHenry (Eds.), *Primate locomotion: Recent advances* (pp. 397–418). New York: Plenum.

Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **111** (2), 159–173.

Izawa, K., & Mizuno, A. (1977). Palm-fruit cracking behavior of wild black-capped capuchins (*Cebus apella*). *Primates*, **18**, 773–792.

Lockman, J. (2000). A perception–action perspective on tool use development. *Child Development*, **71**, 137–144.

Lockman, J. (2005). Tool use from a Perception–action perspective: developmental and evolutionary considerations. In V. Roux & B. Bril (Eds.), *Stone knapping: The necessary conditions for a uniquely hominin behaviour* (pp. 319–330). McDonald Institute Monographs.

Mannu, M. (2002). *O uso espontâneo de ferramentas por macacos-prego (Cebus apella) em condições de semi-liberdade: descrição e demografia* [Spontaneous tool-use by semifree tufted capuchin monkeys: description and demography]. Master's thesis, University of São Paulo, Brazil.

Marchant, L., & McGrew, W. (2006). Percussive technology: chimpanzee baobob smashing and the evolutionary modeling of hominin knapping. In V. Roux & B. Bril (Eds.), *Stone knapping: The necessary conditions for a uniquely hominin behaviour* (pp. 341–350). McDonald Institute Monographs.

Matsuzawa, T. (1996). Chimpanzee intelligence in nature and in captivity: isomorphism of symbol use and tool use. In W.C. McGrew, L.F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 196–209). Cambridge: Cambridge University Press.

Matsuzawa, T., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R., & Yamakoshi, G. (2001). Emergence of culture in wild chimpanzees: education by master–apprenticeship. In T. Matsuzawa (Ed.), *Primate origins of human cognition and behavior* (pp. 557–574). Tokyo: Springer.

Matsuzawa, T., Tomonaga, M., & Tanaka, M. (2006). *Cognitive development in chimpanzees*. Tokyo: Springer Verlag.

Mesoudi, A., Whiten, A., & Laland, K.N. (2006). Towards a unified concept of cultural evolution. *Behavioral and Brain Sciences*, **29** (4), 329–347.

Myowa-Yamakoshi, M., & Matsuzawa, T. (1999). Factors influencing imitation of manipulatory actions in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **13** (2), 128–136.

Ottoni, E.B. (2000). EthoLog 2.2: a tool for the transcription and timing of behavior observation sessions. *Behavior Research Methods, Instruments, and Computers*, **32** (3), 446–449.

Ottoni, E.B., & Mannu, M. (2001). Semifree-ranging tufted capuchins (*Cebus apella*) spontaneously use tools to crack open nuts. *International Journal of Primatology*, **22**, 347–358.

Ottoni, E.B., Resende, B.D., & Izar, P. (2005). Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. *Animal Cognition*, **24**, 215–219.

Resende, B.D., Greco, V.L.G., Ottoni, E.B., & Izar, P. (2003). Some observations on the predation of small mammals by tufted capuchin monkeys (*Cebus apella*). *Neotropical Primates*, **11**, 103–104.

Resende, B.D., Izar, P., & Ottoni, E.B. (2003). Interaction between social play and nut-cracking behavior in semifree tufted capuchin monkeys (*Cebus apella*). *Revista de Etologia*, **5**, 198.

Resende, B.D., Izar, P., & Ottoni, E.B. (2004). Social play and spatial tolerance in tufted capuchin monkeys (*Cebus apella*). *Revista de Etologia*, **6**, 55–61.

Resende, B.D., Mannu, M., Izar, P., & Ottoni, E.B. (2004). Interaction between capuchin monkeys (*Cebus apella*) and Coatis (*Nasua nasua*): non-agonistic behaviors and lack of predation. *International Journal of Primatology*, **25**, 1213–1225.

Soetens, E., Melis, A., & Notebaert, W. (2004). Sequence learning and sequential effects. *Psychological Research*, **69**, 124–137.

Spiegel, R., & McLaren, I.P.L. 2006. Associative sequence learning in humans. *Journal of Experimental Psychology: Animal Behavior Processes*, **32** (2), 156–163.

Takeshita, H. (1999). *Kokoro to kotoba no shoki hattatsu – Reichorui no hikaku kodo hattatsugaku* [Early development of the human mind and language: Comparative study of behavioral development in primates]. Tokyo: Tokyo University Press.

Takeshita, H., Fragaszy, D., Mizuno, Y., Matsuzawa, T., Tomonga, M., & Tanaka, M. (2005). Exploring by doing: how young chimpanzees discover surfaces through actions with objects. *Infant Behavior and Development*, **28**, 316–328.

Tubau, E., Hommel, B., & Lopez-Moliner, J. (2007). Modes of executive control in sequence learning: from stimulus-based to plan-based control. *Journal of Experimental Psychology: General*, **136** (1), 43–63.

Visalberghi, E. (1987). Acquisition of nut-cracking behavior by two capuchin monkeys (*Cebus apella*). *Folia Primatologica*, **49**, 168–181.

Whittlesea, B.W.A., & Wright, R. (1997). Implicit (and explicit) learning: acting adaptively without knowing the consequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, **23**, 181–200.

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