



Wild bearded capuchin monkeys (*Cebus libidinosus*) place nuts in anvils selectively

Qing Liu^{a,*}, Dorothy Frigaszy^a, Barth Wright^b, Kristin Wright^b, Patricia Izar^c, Elisabetta Visalberghi^d

^a Department of Psychology, University of Georgia, Athens, GA, U.S.A.

^b Department of Anatomy, Kansas City University of Medicine & Biosciences, MO, U.S.A.

^c University of São Paulo, Brazil

^d Institute of Science and Technology of Cognition, CNR, Rome, Italy

ARTICLE INFO

Article history:

Received 11 May 2010

Initial acceptance 4 August 2010

Final acceptance 18 October 2010

Available online 26 November 2010

MS. number: A10-00328

Keywords:

affordance

anvil use

capuchin

Cebus libidinosus

embodied cognition

nut cracking

perception–action

selectivity

social influence

tool use

Are wild bearded capuchin monkeys selective about where they place nuts on anvils, specifically the anvil pits, during nut cracking? In the present study, we examined (1) whether capuchins' preferences for particular pits are influenced by the effectiveness of the pit in cracking the nut and/or by the stability of the nut during striking, (2) how capuchins detect the affordances of novel pits and (3) the influence of social context on their selections. Anvil pits varied in horizontal dimension (small, medium and large) in experiment 1 and in depth (shallow, medium and deep) in experiment 2. In both experiments, three different pits were simultaneously presented, each on one anvil. We coded the capuchins' actions with the nut in each pit, and recorded the outcome of each strike. In both experiments, capuchins preferred the most effective pit, but not the most stabilizing pit, based on the number of first strikes, total strikes and nuts cracked. Their choice also reflected where the preceding individual had last struck. The capuchins explored the pits indirectly, placing nuts in them and striking nuts with a stone. The preference for pits was weaker than the preference for nuts and stones shown previously with the same monkeys. Our findings suggest that detecting affordances of pits through indirect action is less precise than through direct action, and that social context may also influence selection. We show that field experiments can demonstrate embodied cognition in species-typical activities in natural environments. © 2010 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Humans are selective when choosing a tool for the job at hand, as when seeking a hammer of the right weight, or a rake of the right length. This trait was present as early as 2.6 million years ago, when our ancestors selectively used particular materials for processing animal flesh and bones (Semaw et al. 2003). Nonhuman animals may also be selective. Darwin's (1881) work on how earthworms explore and select different leaves or paper triangles to pull into their burrows is a classic example illustrating how widespread selectivity is across the animal kingdom. Among others, chimpanzees, New Caledonian crows and capuchin monkeys have been studied for their selectivity in tool use (Boesch & Boesch 1983; Chappell & Kacelnik 2002; Visalberghi et al. 2009). For example, recent studies have shown that wild bearded capuchin monkeys select hammer stones to crack nuts and seeds with respect to stone weight and friability (tendency to crumble) (Visalberghi et al. 2009;

Ferreira et al. 2010). Frigaszy et al. (2010b) further report that wild bearded capuchin monkeys select heavier stones to crack larger, more resistant nuts, and prefer nuts that are easier to crack (i.e. of low resistance) over nuts that are harder (i.e. of high resistance). Thus, bearded capuchin monkeys are selective about tools and the objects they process with tools.

Selectivity rests upon perception of affordances. In his ecological approach to perception and action, Gibson (1979) used the term 'affordance' to label properties of the relationship between actor and environment (here, objects and surfaces) that the actor needs to perceive in order to generate effective actions. Action is used to generate these perceptions, which in turn will guide future actions. In other words, perception and action are inextricably linked. In tool use, actors need to detect the affordances of surfaces and objects and the relations between them.

Applying this framework to nut cracking with a stone percussor, the tool user needs to detect affordances of the nut, stone and the anvil in combination with each other. Explicitly interpreted, the affordance of the nut is the ease of cracking it on the anvil with the stone. The affordance of the hammer stone is its suitability to strike

* Correspondence: Qing Liu, Department of Psychology, University of Georgia, Athens, GA 30602, U.S.A.

E-mail address: freycall@gmail.com (Q. Liu).

the nut open when the nut is placed on the anvil. Previous studies have shown that bearded capuchin monkeys attend to these affordances in their selection of nuts and stones (Visalberghi et al. 2009; Fragaszy et al. 2010b). Our concern in this report is the affordance of the anvil in its quality as a striking platform for the nut and stone. A good platform should (1) provide high reactive force (i.e. transmit the force of impact to the nut) so that the nut cracks in fewer strikes than on an anvil with low reactive force, (2) keep the nut in place following striking and (3) provide easy accessibility to the capuchins and good stability.

The current study addresses the first two aspects of the affordance of anvils: their effectiveness for cracking the nut with a stone, and their relation to displacement of the nut after a strike. Wild bearded capuchin monkeys (hereafter, capuchins) in Fazenda Boa Vista, Piauí, Brazil, put a whole nut in a pit on the anvil before striking the nut, and frequently reposition the nut in the same pit or move the nut to a different pit on the same anvil between strikes (Fragaszy et al. 2010a). These behaviours suggest to us that the capuchins may be evaluating the affordance of the anvil, and more specifically, the pit in the anvil in which they place the nut. Capuchins prefer some anvils to others (D. Fragaszy & Q. Liu, personal observation), which may reflect perception of differential affordances of the anvils as sites to crack nuts.

In order to detect affordances of an object, the actor must act on the object when visual perception does not provide sufficient information. Bodily action, haptic exploration and feedback are all important in organizing actions with tools. The perception–action perspective that we adopt here is congruent with the increasingly prominent theory in studies of human cognition that cognition is ‘embodied’ (e.g. Barsalou 2008; Chemero 2009), in that cognition is shaped by the body and bodily actions. We propose that the same principles apply to nonhuman species. Visalberghi et al. (2009) and Fragaszy et al. (2010b) showed that capuchins handled and tapped stones when selecting between two hammer stones of equal volume and appearance, a circumstance in which the capuchins could not judge the mass of the stones by visual cues. In the current study, we expected that capuchins would generate behaviours to detect affordances of anvils, as they do for stones when they cannot judge affordances by vision, and we expected that they would prefer the anvils that provided certain affordances.

In principle it should be easier to detect affordances when the actor acts on an object or surface directly with his or her body (Bernstein 1967; Pick & Lockman 1981) rather than indirectly, through an intermediary object. In nut cracking, the affordances of the stone and the nut are relatively easy for capuchins to detect because they handle the stone and nut directly (e.g. tapping, pushing or lifting stone, and tapping or sniffing the nut). In contrast, the capuchins usually act on the anvils indirectly by placing the nut in various positions on the anvil and striking it with the stone. Therefore, we expect that detecting affordances of the anvil is not as clear-cut as detecting affordances of the nut and stone. Our predictions in this study were that the capuchins would be selective about pits and that they would continue exploring pits across the testing period. We also wanted to document explorative actions by the capuchins that could provide information about the affordances of novel pits. For example, they could feel the pits directly with fingers, move nuts in and out of pits or strike the nut in the pit with a stone.

In this study, we provided novel anvils containing ellipsoid pits of different horizontal dimensions and different depths. We reasoned that the horizontal dimensions and depth of a pit could influence two aspects of affordances in nut cracking. One aspect is the probability that the strike will displace the nut (termed ‘fly-off’ hereafter). For a human, striking the nut in a pit significantly reduced the rate of fly-offs compared to striking the nut on a flat surface (Fragaszy et al. 2010a). We hypothesized that the capuchins

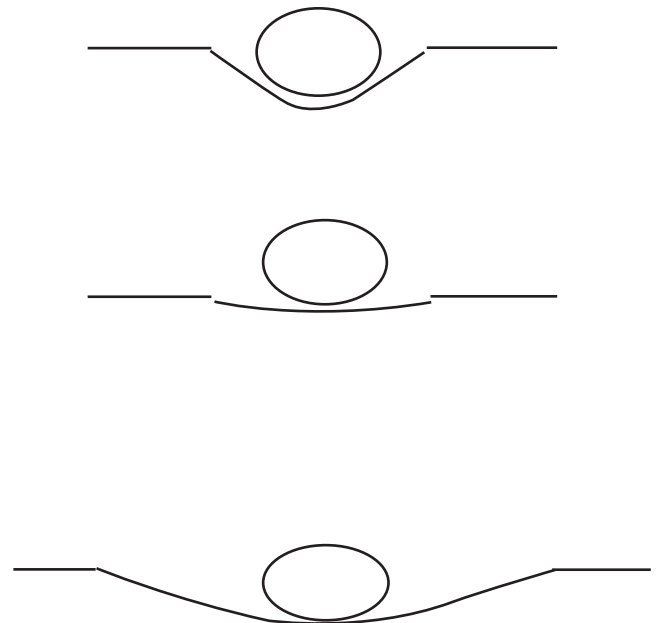


Figure 1. Sagittal view of a medium (6 cm wide, 2 cm deep), shallow (6 cm wide, 1 cm deep) and large (9 cm wide, 2 cm deep) pit, respectively.

use the pits in the anvils for the same reason, because displacing the nut off the anvil costs time of retrieval and risks losing the nut or the anvil site to a competitor while the animal attempts to retrieve the nut. A very shallow or a very large pit that approximates a flat surface would increase the probability that the nut would fly off (see Fig. 1 for illustration). A very small pit poses a similar risk. The second aspect is the effectiveness of the pit as a striking platform. We observed that capuchins stopped using pits when the pits became very deep (>3 cm) (D. Fragaszy & Q. Liu, personal observation). We further reasoned that the capuchins avoid striking a nut where little of the nut shell is exposed above the rim of the pit, because these strikes are ineffective. Therefore, we further predicted that the capuchins would prefer the pits associated with lowest fly-off rate and/or highest effectiveness (lowest number of strikes to success) and that they would avoid using the least effective (i.e. small and/or deep) pits.

We further recognized that nut cracking occurs in a social setting and that the capuchins' use of pits might be influenced by the choices of other individuals. In other settings group members have a strong effect on youngsters' choice of foraging sites. For example, young wild brown capuchins (*Cebus apella*) in Suriname were attracted to inspect and handle bamboo stalks previously opened by conspecifics (Gunst et al. 2008) even though those sites no longer contained prey. In this study, we examined how social influence plays a part in the choice of location and the enhancement of interest in a location in nut cracking.

METHODS

Site and Subjects

The study site (9°39'S, 45°25'W, altitude approximately 420 m above sea level) is located on private property (Fazenda Boa Vista) in a dry woodland plain in Piauí, Brazil (Fragaszy et al. 2004; Visalberghi et al. 2007). A group of wild bearded capuchin monkeys (*Cebus libidinosus*) routinely comes to an area where there are anvils and stones. This is the area where we carried out the field experiments. The monkeys are habituated to human observers.

Nine capuchins (six males: Chicao, Mansinho, Dengoso, Tucum, Teimoso and Jatoba; three adult females: Chuchu, Dita and Piaçava) from a group of 15 individuals participated in this study on a voluntary basis.

Materials

We used palm nuts of one species collected from the area. The nuts the capuchins cracked in this study (*Orbignya* sp.) have an ellipsoid shape and average 4 cm in diameter and 6 cm long (Visalberghi et al. 2008). Nuts of this species were commonly cracked by the capuchins at the study site outside of the experimental period as well as during the experiment. We supplied the capuchins with a single stone (1.46 kg) that was regularly used by these monkeys at this cracking site. We only used one species of nut and one stone as efficiency of cracking is related to the weight of the stone and the species and size of the nuts (Fragaszy et al. 2010b; Q. Liu, E. Visalberghi & D. Fragaszy, unpublished data).

We manufactured three log anvils cut from fallen candeia trees (*Piptocarpha rotundifolia*, Compositae), the wood of which is moderately heavy (density 0.65 g/cm³), hard, moderately durable, with thick rough texture and good mechanical resistance (Lorenzi 1992). The capuchins use anvils of this species of tree in other areas of our study site (Visalberghi et al. 2007). The anvils were 75 cm long and had similar cross-sections (range 15–23 cm). We smoothed the logs by peeling them and then made pits in the centre of each log with chisel, hammer and Dremel tool™ (Dremel, WI, U.S.A.). The pits varied in horizontal dimensions and depths. To determine the various horizontal dimensions and depths of the pits used in this study, we started with the average size of the nuts (4 × 4 × 6 cm). We assumed that a medium-size and medium-depth pit, corresponding to average nut size (4 cm wide, 6 cm long and 2 cm in depth) would fit the average nut snugly and thus provide the optimal horizontal dimensions for minimizing nut fly-off and maximizing effectiveness of each strike.

Design

In experiment 1, we presented pits of large (9 × 6 × 2 cm), medium (6 × 4 × 2 cm) and small (4 × 3 × 2 cm) horizontal

dimensions. We determined the horizontal dimensions of the pits as 1.5 times greater or smaller than the average size of the nuts, rounded to the nearest 1 cm (e.g. small pits were 1.5 times smaller than 4 cm, or 2.7 cm, rounded to 3 cm).

In experiment 2, we presented pits of shallow (6 × 4 × 1 cm), medium (6 × 4 × 2 cm) and deep (6 × 4 × 4 cm) depths. We determined the depth as 2 times greater or smaller than the average size of the nuts. The medium pits in both experiments had the same dimensions and depth. Pits of different horizontal dimensions and depths are shown in Fig. 2.

We made one pit on two opposite sides of each log (six pits total). A pit of each horizontal dimension or depth appeared on two different logs (see Fig. 3). We did this to ensure that the capuchins' use of different pits would not be affected by unknown properties of a specific pit (e.g. minor differences in rebound properties of different logs).

Procedure

As illustrated in Fig. 4, the three anvils were presented in an equilateral triangle. The logs were partially buried in the ground, so that the height above ground of the top surface was approximately 10 cm (similar to that of other log anvils the capuchins use) and the logs did not wobble when struck. Since we made two pits of each size on different logs, we rotated the logs daily to get a different combination of three pits (always one pit of each size).

At the beginning of each testing day, and periodically throughout testing, we rubbed all the pits with fresh cracked nut kernels to ensure they all had the same odour and oiliness so that these cues would not influence the monkeys' use of pits. A stone and a whole nut were presented in the centre of the log triangle before each trial. A trial began when a capuchin picked up the stone and a nut and brought them to an anvil to begin cracking. A trial ended when the capuchin cracked the nut, gave up the nut or was displaced by another individual. When the trial ended, we put the stone back in the centre ground of the anvil triangle and swept off the abandoned nut pieces from the anvils. All trials were recorded using a Canon™ GL2 miniDV camcorder.



Figure 2. Photographs of (a) small, (b) medium and (c) large pits used in experiment 1, and (d) shallow, (e) medium and (f) deep pits used in experiment 2.

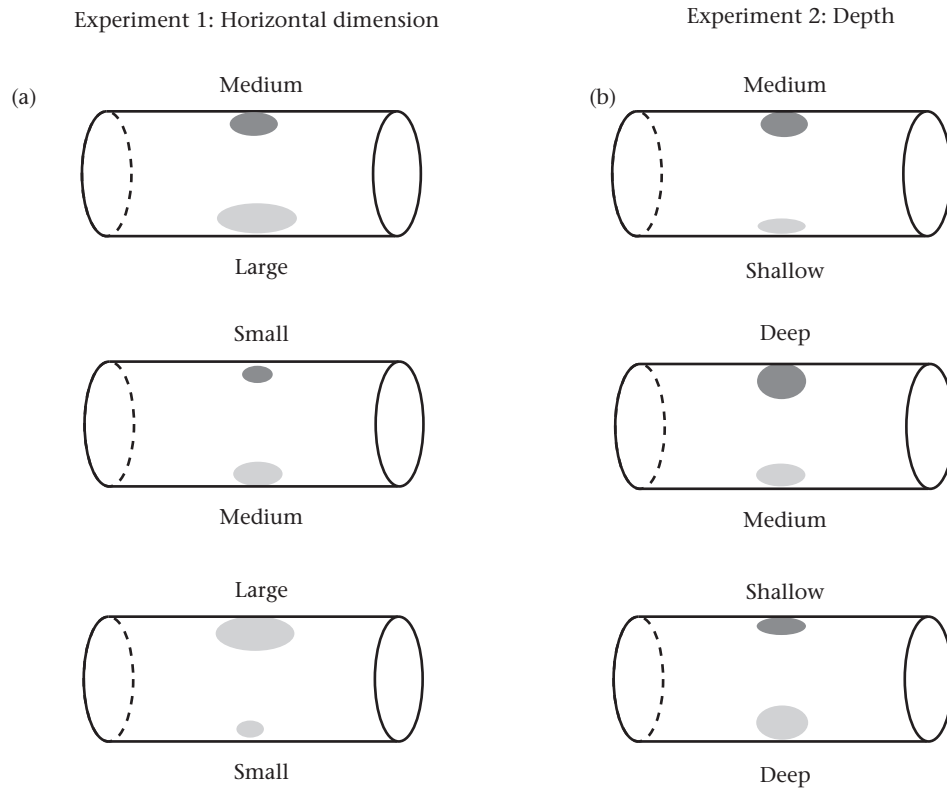


Figure 3. Illustration of two pits made in each anvil in (a) experiment 1 and (b) experiment 2.

Coding

All occurrences of four associated actions (touching pit with hand, positioning nut in pit, striking nut in pit, and switching from one pit to another) were coded for every trial. We also recorded the location of these actions with the nuts (i.e. the pit in which the subject positioned and struck the nut, and the pits to and from which the subject switched). Two outcomes, fly-off (nut bounced out of the pit and off the anvil, or nut remained in place) and success (cracked or not cracked) were also recorded.

We recorded the time interval (to the nearest minute) elapsed between successive subjects using the experimental anvil site by using the minutes displayed on tape. For example, if the previous subject finished cracking and left the anvils at 00:20, the next one



Figure 4. Experimental set-up, in which three logs were arranged in a triangle with a 1.46 kg stone and a nut in the centre.

arrived at the anvils at 00:22, the interval was recorded as 2 min. The time interval was recorded as zero when the next subject came to the anvil within 1 min after the previous subject left.

The coder recoded 10 randomly selected trials from each experiment, and the intracoder agreement was 100% for all variables combined. Another coder who was blind to the design also coded 10 randomly selected trials from each experiment, and the intercoder agreement was 97% for all variables combined.

Analysis

We first evaluated the affordances of the pits, then analysed the capuchins' detection of affordances, based on their preferences and strategies of detection (feel the pit, position a nut in the pit, and strike a nut in the pit with a stone), using repeated *t* tests. We also examined patterns of switches to determine whether the capuchins used the more energy-conserving strategy (position only before switch) or the less energy-conserving strategy (position and strike before switch), and whether they switched from ineffective pits (termed 'self-correction', hereafter) more frequently than they switched from effective pits. For all of the above analyses, we used data from trials in which the subjects cracked a whole nut (422 trials for experiment 1 and 482 trials for experiment 2). Finally, we examined whether the monkeys were socially influenced by their choice of pits. For this purpose, we used the 'whole nut' trials during which the subjects worked on whole nuts, plus the trials during which subjects brought a piece of a nut (partial nut) from elsewhere to crack on the anvils, resulting in 446 trials in experiment 1 and 633 trials in experiment 2.

Affordances and capuchins' detection of affordances

We evaluated the affordances of each pit for each individual in terms of fly-off rate and effectiveness score. Then we examined each monkey's number of first choices, number of total strikes and

number of nuts cracked when using each pit. Lastly, we evaluated how the two aspects of affordances correlated with the three behavioural variables.

Fly-off rate was defined as the total number of fly-off events in that pit divided by the total number of strikes in that pit. Effectiveness of the pit was defined as the total number of nuts cracked divided by the total number of strikes multiplied by 100. For experiment 1, we predicted fly-off rate as medium < large < small, and effectiveness as medium > large or small. For experiment 2, we predicted fly-off rate as deep < medium < shallow, and effectiveness as medium or shallow > deep.

Next, we looked at the capuchins' behaviours with each pit. We expected their pattern of behaviours to reflect differences among pits in fly-off rate and effectiveness measures. Because we expected small pits to have the highest fly-off rate and deep pits to have the lowest effectiveness and because they were the most visually distinctive, we predicted that the capuchins would avoid them. We predicted that the capuchins would prefer the pit with highest effectiveness and/or the lowest fly-off rate in both experiments. Their preference would be evident in the following behavioural variables: number of first choices (defined as first strikes), number of total strikes and number of nuts cracked. This prediction was evaluated by repeated measures *t* tests comparing large and medium pits in experiment 1 and shallow and medium pits in experiment 2. The small sample of trials using shallow and deep pits precluded use of ANOVAs for these analyses.

Switches and self-correction

We assessed two behaviours through analysis of switches from one pit to another while cracking a single nut. First, we used a repeated measures *t* test to examine whether the subjects used the more energy-conserving strategy of switching (position only, then switch) more often than they did the less energy-conserving strategy (position, strike, then switch). Second, we used repeated measures ANOVA to examine whether the subjects made proportionally more switches from less effective pits (i.e. self-correction) than they did from effective pits. Data were arcsine transformed for these analyses. Effect size was calculated using Hedge's *d* (corrected for small sample size) for all pairwise comparisons.

Social influence

We examined whether social influence affected the capuchins' choice of each pit by comparing the relative frequency with which subjects used the same pit as the preceding individual to the overall frequency with which the subjects first positioned a nut in that pit.

RESULTS

General Results

In experiment 1, we collected 21–87 trials per subject, where the number of trials corresponds to number of nuts attempted (422 trials total, including 98 trials in which nuts were not cracked). Each subject cracked an average of 36 nuts. In 21.3% of trials (90 trials), the subjects switched from one pit to another at least once. The subjects produced a total of 2201 strikes, with 50.3% in large pits, 46.3% in medium pits and 3.4% in small pits.

In experiment 2, we collected 14–78 trials per subject (482 trials total, including 131 trials in which nuts were not cracked), with an average of 39 nuts cracked by each subject. The subjects switched at least once in 18.5% of these trials (89 trials). The subjects had a total of 2338 strikes, 75.4% in shallow pits, 24.1% in medium pits and 0.4% in deep pits.

Table 1
Number of trials and switches per testing day

Testing day	Total number of trials	Total number of switches
Experiment 1		
Day 1	40	12
Day 2	5	0
Day 3	56	6
Day 4	8	2
Day 5	96	24
Day 6	10	5
Day 7	51	16
Day 8	45	9
Day 9	69	7
Day 10	42	9
Total	422	90
Experiment 2		
Day 1	92	20
Day 2	64	15
Day 3	79	17
Day 4	88	14
Day 5	96	20
Day 6	63	3
Total	482	89

We observed no change in frequency of switching as a function of testing days (see Table 1). Regression analyses showed that testing day did not predict the frequency of switches in experiment 1 ($B = 0.005$, $t_8 = 0.32$, $P = 0.76$) or experiment 2 ($B = -0.028$, $t_4 = -2.29$, $P = 0.08$).

Across experiments, only two subjects directly touched the pit with their hand. In both cases, the subjects picked up nut pieces or dirt out of a medium pit. Smelling the pits or their hand following manual exploration was also not observed. Instead, capuchins routinely positioned the nut in the pit and struck the nut in the pit with a stone.

Affordances and Capuchins' Detection of Affordances

Experiment 1: horizontal dimension of the pit

Fly-off rate did not differ significantly between large (mean \pm SD = 0.34 ± 0.10) and medium (0.30 ± 0.09) pits (paired *t* test: $t_8 = 1.69$, $P = 0.13$); however, Hedge's effect size ($d = 0.40$) reflected a medium-sized difference. Fly-off rate for small pits (mean \pm SD = 0.74 ± 0.18) was excluded from the test because three subjects did not strike in small pits and three subjects struck but did not crack any nuts in them. Effectiveness of large pits (mean \pm SD = 19 ± 11) was significantly higher than that of medium pits (10 ± 4) (paired *t* test: $t_8 = 3.49$, $P = 0.008$; Hedge's effect size: $d = 1.04$). Effectiveness of small pits (mean \pm SD = 7 ± 9) was excluded from the test because of small sample size ($N = 3$).

To summarize, large and medium pits showed a large difference in effectiveness (large > medium) and a minimal difference in fly-off rate (medium < large). Therefore, if capuchins are sensitive to the affordances of the pits, they should prefer large pits.

We analysed capuchins' use of the pits with three variables: number of first strikes, number of total strikes and number of nuts cracked in each pit per subject. Capuchins made significantly more first strikes in large pits (mean \pm SD = 28.4 ± 15.3) than they did in medium (19.4 ± 14.0) or small (1.2 ± 1.1) pits (paired *t* tests: $t_8 = 3.43$, $P = 0.009$; Hedge's effect size: $d = 0.58$). Capuchins struck in medium (mean \pm SD = 113 ± 33) and large (123 ± 65) pits equally often (paired *t* test: $t_8 = 0.55$, $P = 0.60$; Hedge's effect size: $d = 0.18$). The average \pm SD number of total strikes in small pits was 8.2 ± 11.0 . Capuchins cracked significantly more nuts in large pits

Table 2

Affordances of pits (lowest fly-off rate, highest effectiveness) and three behavioural measures for monkey's preference for pits (highest number of first strikes, total strikes and nuts cracked per individual)

	Affordances of the pit		Highest number of		
	Lowest fly-off rate	Highest effectiveness	First strikes	Total strikes	Nuts cracked
Experiment 1: Horizontal Dimension (L=large, M=medium)					
Chicao	M	L	L	M	L
Chuchu	M	L	L	M	M
Dengoso	M	L	L	L	L
Dita	M=L	L	M	M	M
Jatoba	L	L	L	M	L
Mansinho	L	L	L=M	M	L
Piaçava	L	L	L	L	L
Teimoso	M	L	L	L	L
Tucum	M	L	L	L	L
Experiment 2: Depth (S=shallow, M=medium)					
Chicao	M	S	S	S	S
Chuchu	M	S	S	S	S
Dengoso	M	S	S	S	S
Dita	M	S	S	M	M=S
Jatoba	S	S	S	S	S
Mansinho	M	S	S	S	S
Piaçava	M	S	S	S	S
Teimoso	M	S	S	S	S
Tucum	M	S	S	S	S

(23 ± 16) than they did in medium pits (12 ± 8) (paired *t* test: $t_8 = 3.23$, $P = 0.012$; Hedge's effect size: $d = 0.83$).

Large pits had the highest effectiveness for all individuals and were preferred by four individuals for all three behavioural measures, and by another three individuals for two of the three measures (Table 2).

Experiment 2: depth of the pit

Fly-off rate was significantly higher in shallow pits (mean ± SD = 0.50 ± 0.11) than in medium pits (0.30 ± 0.21) (paired *t* test: $t_8 = 2.44$, $P = 0.04$; Hedge's effect size: $d = 1.13$). Fly-off rate for the deep pits could be calculated for only one subject that struck 10 times and produced one fly-off in a deep pit (fly-off rate = 0.1). Mean ± SD effectiveness of shallow pits (16 ± 8) was significantly higher than that of medium pits (12 ± 7) (paired *t* test: $t_8 = -4.02$, $P = 0.004$; Hedge's effect size: $d = 0.51$). Effectiveness of deep pits was zero for the one subject that struck in a deep pit.

To summarize, shallow and medium pits differed significantly in effectiveness (shallow > medium) and in fly-off rate (medium < shallow). Therefore, effectiveness alone predicted preference for shallow pits, and fly-off rate alone predicted preference for medium pits.

Capuchins made significantly more first strikes (mean ± SD = 41 ± 18) and total strikes (196 ± 78) in shallow pits than they did in medium pits (11 ± 6 and 63 ± 43, respectively; paired *t* test: first strikes: $t_8 = 5.72$, $P < 0.001$; Hedge's effect size: $d = 2.11$; total strikes: $t_8 = 4.81$, $P = 0.001$; Hedge's effect size: $d = 2.00$). Capuchins also cracked significantly more nuts in shallow pits (mean ± SD = 32 ± 19) than they did in medium pits (7 ± 5) ($t_8 = 4.81$, $P = 0.001$; Hedge's effect size: $d = 1.71$).

Shallow pits had the highest effectiveness for all individuals and were preferred by eight of nine individuals on all three behavioural measures.

Switches and Self-correction

In 52% of the trials in which the capuchins switched in experiment 1, they positioned the nut in a pit and switched to

another pit ('position only' switch); in the other 48% of trials in which the capuchins made a switch, they positioned the nut in a pit and struck it with the stone before switching ('position and strike' switch). The mean ± SD percentage of 'position only' switches (37 ± 34%) and 'position and strike' switches (63 ± 34%) did not differ significantly (paired *t* test on arcsine transformations: $t_8 = -0.83$, $P = 0.43$). Four of nine subjects used the more energy-conserving strategy (position only) more often than they did the less energy-conserving strategy (position and strike). In experiment 2, subjects made significantly more 'position only' switches (mean ± SD = 74 ± 20%) than they did 'position and strike' switches (26 ± 20%) (paired *t* test on arcsine transformations: $t_8 = 3.39$, $P = 0.009$; Hedge's effect size: $d = 2.28$). Seven of nine subjects used the more energy-conserving strategy more often than they did the less energy-conserving strategy.

To assess self-correction, we compared the percentage of switches (from all initial positions) for all three pits for both experiments. The mean ± SD percentage of switches from small (81 ± 8%), medium (24 ± 8%) and large (12 ± 5%) pits differed significantly (repeated measures ANOVA on arcsine transformations: $F_{2,12} = 69.37$, $P < 0.001$; effect size of partial $\eta^2 = 0.92$). Post hoc comparisons with Bonferroni correction revealed that subjects switched from small pits significantly more often than they did from large pits ($P < 0.001$; Hedge's $d = 9.82$) and medium pits ($P = 0.001$; Hedge's $d = 6.77$), and they showed a tendency to switch from medium pits more often than they did from large pits, but the difference was not significant ($P = 0.087$; Hedge's $d = 1.71$).

In experiment 2, the mean ± SD percentage of switches from deep (100 ± 0%), medium (25 ± 10%) and shallow (10 ± 4%) pits differed significantly (repeated measures ANOVA on arcsine transformations: $F_{2,14} = 64.77$, $P < 0.001$; effect size of partial $\eta^2 = 0.90$). Post hoc comparisons with Bonferroni correction showed that subjects switched from deep pits significantly more often than they did from shallow pits ($P < 0.001$; Hedge's $d = 30.23$) and medium pits ($P = 0.001$; Hedge's $d = 10.08$), and they showed a tendency to switch from medium pits more often than they did from shallow pits, but the difference was not significant ($P = 0.23$; Hedge's $d = 1.87$).

Social Influence

We examined whether the subject's initial choice of a pit (first positioning) was socially influenced by the preceding individual. Subjects often came to an anvil immediately after the preceding individual, resulting in an intersubject interval of 0 min (the median intersubject interval = 1 min, range 0–10 min for both experiments). In 72% of subject–pit combinations in experiment 1 and 86% in experiment 2, subjects first positioned the nut in the same pit where the preceding individual had last struck at a frequency that was higher than their own overall frequency of first positioning in that pit (Table 3). We had too few cases to run chi-square tests on each subject's use of each pit, with one exception. Piaçava had 39 trials where the preceding monkey had last struck in shallow pits in experiment 2 and she followed in 32 of those trials, which was more frequent than her own overall proportion of first positioning in shallow pits (57%; $\chi^2_1 = 9.99$, $N = 39$, $P = 0.002$).

Table 4 shows the frequency with which each monkey was followed, ranked by the individual's overall efficiency score in the study (efficiency = (total number of strikes/total number of nuts cracked) × 100). Less proficient individuals did not follow more proficient individuals more often than expected by chance.

Table 3

Number of subjects whose proportion of following the preceding monkey in using a given pit was higher than its own overall proportional use of that particular pit

Pit	Proportional use of pit
Experiment 1	
Small	5/7*
Medium	6/9
Large	7/9
Experiment 2	
Deep	2/4*
Medium	9/9
Shallow	8/9

* Sample sizes are smaller than 9 because some monkeys never followed another monkey that had struck in the small or the deep pit.

DISCUSSION

We adopted a Gibsonian perception–action perspective to examine the wild capuchin monkeys' detection of affordances of novel anvils. We predicted that the capuchins would prefer pits providing certain affordances, namely, effective cracking and secure positioning for the nut. We also predicted that they would be less selective about pits than they are about stones and nuts (Visalberghi et al. 2009; Fragaszy et al. 2010b), because it is easier to detect affordances of an object or surface directly with one's body than indirectly, as when cracking a nut through contact via intermediary object(s). We also predicted that the capuchins would prefer the most functional pits and that they would need to detect affordances of the pits through action (by positioning and striking the nuts in the pits).

Selectivity was confirmed by the capuchins' preference for the large and shallow pits. Our finding that capuchins preferred the two most effective pits (large and shallow, as measured by the effectiveness score) suggests that they were more sensitive to the effectiveness of the pit (namely, how easily they could crack a nut in the pit) than they were to the rate of nut fly-off, which favoured the medium pit in both experiments (although not significantly so in experiment 1). In experiment 2, when the difference in fly-off rate between the shallow pit and the medium pit was larger in magnitude (as reflected by effect size) than the

difference between large and medium pits in experiment 1, the capuchins still showed a stronger preference for the shallow pit.

We also confirmed that the capuchins' preference for pits is not as clear-cut as their preference for stones and nuts. The magnitude of their preference for a particular pit (50% of total strikes in the large pit in experiment 1 and 75% in the shallow pit in experiment 2) was not as large as their preference for heavier stones (94% of all conditions combined: Visalberghi et al. 2009; 78% of all conditions combined: Fragaszy et al. 2010b) or their preference for nuts that were easier to crack (96% of all conditions combined: Fragaszy et al. 2010b). This is in accordance with the notion that detecting affordances embodied by the relation between surface and object(s) is more difficult than detecting affordances of a single object. The most relevant aspect of affordances of a pit, its effectiveness, is not detectable solely by visual perception. Rather, it is discovered by positioning and/or striking a nut with a stone. This held true even in the case of the nonfunctional pits (small or deep). All subjects positioned the nut at least once in a small pit, and all but one subject positioned the nut at least once in a deep pit. Three subjects struck a nut in a small pit, and one subject struck a nut in a deep pit. Thus, even though the relevant dimensions of the small and deep pits may have readily been perceived by vision, subjects still occasionally used actions such as positioning and striking to detect their affordances.

The capuchins continued to explore all pits throughout the testing period. It is of note that they did not directly touch the pits on the anvils with their palms or fingers; instead, their actions with the pits were always indirect: they positioned nuts in the pits and struck the nuts in the pits with a stone. During nut cracking on a familiar anvil, capuchins often repeatedly reposition the nut in a pit, in quick succession, before releasing it and striking it with the stone. The final position of the nut is very specific, with the more spherical sides of the nut against the sides of the pit (D. Fragaszy, B. Wright, A. Allen & Q. Liu, unpublished data). The systematic final positioning of the nut suggests the capuchins attend to haptic information afforded by positioning the nut in the pit. Positioning the nut in the pit (without striking it) is a more energy-conserving way to explore different pits than positioning plus striking the nut. 'Position only' switches occurred significantly more often than 'position plus strike' switches in experiment 2 (where depth of the pits varied), but not in experiment 1 (where the horizontal

Table 4

Number of trials each subject ended in each pit and number of trials each subject was followed by others in that pit

	Efficiency rank	Number of trials						Sum		Overall % followed
		Ending in			Followed in			Trials	Trials followed	
Experiment 1: Horizontal Dimension										
		Large	Medium	Small	Large	Medium	Small			
Mansinho	1	20	16	1	16	13	1	37	30	81
Dengoso	2	17	13	3	12	9	1	33	22	67
Chicao	3	6	9	1	3	6	0	16	9	56
Teimoso	4	17	12	4	8	8	2	33	18	55
Jatoba	5	9	3	0	5	1	0	12	6	50
Piaçava	6	19	12	1	15	10	1	32	26	81
Dita	7	7	20	1	3	14	0	28	17	61
Chuchu	8	15	12	0	11	10	0	27	21	78
Tucum	9	22	14	6	15	11	1	42	27	64
Experiment 2: Depth										
		Shallow	Medium	Deep	Shallow	Medium	Deep			
Mansinho	1	36	12	0	29	7	0	48	36	75
Dengoso	2	37	9	1	31	3	0	47	34	72
Chicao	3	30	7	0	21	1	0	37	22	59
Teimoso	4	29	9	0	24	5	0	38	29	76
Jatoba	5	15	3	0	12	0	0	18	12	67
Piaçava	6	32	12	1	25	5	0	45	30	67
Dita	7	16	9	0	14	5	0	25	19	76
Chuchu	8	41	7	0	30	2	0	48	32	67
Tucum	9	43	13	2	36	8	1	58	45	78

dimensions varied). Perhaps depth can be detected by positioning more effectively than can horizontal dimensions, or perhaps the capuchins learned to rely on positioning more over time. Our current design did not permit us to distinguish these alternative explanations.

In summary, the capuchins selected the novel pits in accord with the effectiveness of the pits for cracking nuts, where effectiveness was defined as the number of nuts cracked with 100 strikes in that pit. The capuchins detected the 'effectiveness' of the pits by positioning and striking nuts in them. This is similar to findings of Visalberghi et al. (2009) and Fragaszy et al. (2010b), who reported that capuchins gain information about stones through tapping and handling them. However, our findings differ from those of these previous studies in that the capuchins did not select the most effective pit from the first trial, as they did with nuts and stones. Nor did they consistently continue using the same pit after their first strikes, whereas the capuchins always (Visalberghi et al. 2009) or almost always (Fragaszy et al. 2010b) continued to use the same stone. In our study, the capuchins explored all the pits throughout the testing period, although their overall activity with pits correlated positively with the effectiveness of the different pits. Collectively, these findings support our prediction that detecting affordance of pits in the anvils is less precise than that for nuts and stones, even though the capuchins were equally experienced at cracking nuts in pits and at selecting nuts and stones. Thus, our present findings support the hypothesis that detection of affordances incorporating objects and surfaces is more difficult than detection of mass or composition of stones and resistance to cracking of the nuts, which are properties of single entities.

We also examined the role of social influence in the monkeys' selection of pits. Capuchin groups are relatively cohesive, with members usually staying within 10 m of another group member (Fragaszy et al. 2004). In our study group, members often waited in nearby trees for their turn to crack nuts. The visibility was good, with little or no obstruction from foliage between tree limbs and the anvil. This situation could set the stage for one individual's choice of pit to influence those that followed. Indeed, the pattern of results suggests that the capuchins were more likely to use the same pit where the preceding individual had last struck, compared to the overall frequency with which they initially used the pit, even when the pit was ineffective.

Therefore, social influence could be an alternative explanation for the lower magnitude of preference for pits in this study, compared to the magnitude of preference for stones and nuts in Visalberghi et al.'s (2009) and Fragaszy et al.'s (2010b) studies. However, we cannot draw the conclusion that social influence is more important for choice of pits than it is for choice of stones, because the design of the studies about choice of stones prevented social influence on choice. We counterbalanced the positions of three anvils across testing days, but the anvils had fixed positions across all trials on any given testing day. In the two studies mentioned above, the positions of stones and/or nuts were randomized in every trial. Therefore, their set-up prevented social influence from affecting choice of nuts and stones, whereas our set-up allowed social influence to affect choice of anvil pits. Future studies should investigate the extent to which social influence can change the magnitude of capuchins' preference for heavier stones or less resistant nuts.

Social influence in foraging has been observed in many animal species, but Clayton (1978) and Rapaport & Brown (2008) reported that more studies have focused on the choice of foraging item (the thing eaten) than on the choice of foraging location (where the food is found or processed). Social influence in the choice of foraging location, as documented in the current study, reflects the phenomenon of 'local enhancement', in which individuals are attracted to a place

associated with the behaviour of conspecifics in that place. Gunst et al. (2008) likewise documented local enhancement in foraging activity in another species of capuchin monkey, the brown capuchin (*Cebus apella*). We consider it likely that local enhancement is a common social influence on foraging in capuchins.

Ottoni et al. (2005) noted that capuchins watched and followed the most proficient nut-crackers more often than they did less proficient individuals. This outcome could occur either because the capuchins recognize proficiency in others, or because more proficient individuals are more likely to produce opportunities for the others to scrounge left-over pieces (Ottoni et al. 2005). However, individuals did not preferentially follow more proficient individuals in our study. Perhaps other characteristics of an individual, such as social rank and affiliation, play a larger role than proficiency in an individual's salience to others (Coussi-Korbel & Fragaszy 1995). Studies with birds (as reviewed by Tóth et al. 2009) show that observers' scrounging tactics are influenced by a variety of factors such as kinship with the provider birds, early social experience and social rank. The situation is likely to be equally nuanced in capuchin monkeys and in other animals. Thus, future studies will be necessary to unravel how social factors and foraging proficiency of all the individuals involved influence foraging behaviours in capuchins.

We now turn to the broader implications of our main finding, that capuchins are sensitive to certain properties of the pits they use in nut cracking, preferring to use pits that require the fewest strikes to crack nuts. Capuchins assessed the effectiveness of the pits either by positioning the nut, using the nut as an extension of their hand, or by striking the nut with the stone, thereby indirectly gaining information about the pit. In the latter situation, the stone serves as an extension of the hand, until the point of contact between the nut and the stone, when rebound, vibration, sound or other movement of the stone and the nut inform the body. This is a naturally occurring example in nonhuman animals illustrating that the boundary of the animal–environment system (what constitutes animal and what constitutes environment) shifts dynamically (i.e. when the nut or the stone becomes the vehicle by which affordances of the pit are perceived). By examining how the environment is incorporated into an animal's exploratory process as a result of the animal's own actions, thereby producing a boundary shift, we gain an ecologically relevant account of learning, perception and action.

A perception–action approach allows us to examine the perceptual processes that contribute to selectivity in behaviour in animals, including selection of objects for a specific goal, which is certainly not limited to tool use, or to primates. For example, nest-building behaviour has been widely studied in ornithology. As reviewed by Hansell (2000), birds are highly selective about nest materials and use different techniques with different materials in nest building. Early manipulative experience with materials is crucial for successful nest building in adulthood (Collias & Collias 1973), suggesting that manipulative actions are important in the development of selectivity. California sea otters, *Enhydra lutris*, which use stone anvils on their chest for pounding open mussels, crabs and urchins (Hall & Schaller 1964), provide another example. Hall & Schaller (1964) noted that the otters use stones of particular weight for pounding, suggesting selectivity. As far as we are aware, studies on material selection in animals have primarily focused on documenting selectivity but have largely ignored the exploratory behaviours that lead to selectivity. We propose that prospective studies should investigate the exploratory behaviours that support detection of affordances and lead to selectivity. Field experiments in which subjects have the full complement of experience with natural materials and activities (e.g. nest building) would be particularly beneficial. Such studies will enrich our understanding of embodied cognition across the animal kingdom.

Acknowledgments

Thanks to R. Greenberg for help with data collection and the Oliveira family for logistical assistance. Permission to work in Brazil was granted by IBAMA and CNPq to Q.L., D.F. and E.V. Funding was provided by IM-CleVer (No. FP7-ICT-IP-231722) and the National Geographic Society (CRE 8774-07).

References

- Barsalou, L. 2008. Grounded cognition. *Annual Review of Psychology*, **59**, 617–645.
- Bernstein, N. A. 1967. *The Coordination and Regulation of Movements*. Oxford: Pergamon.
- Boesch, C. & Boesch, H. 1983. Optimisation of nut-cracking with natural hammers by wild chimpanzees. *Behaviour*, **83**, 265–286.
- Chappell, J. & Kacelnik, A. 2002. Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). *Animal Cognition*, **5**, 71–78.
- Chemero, A. 2009. *Radical Embodied Cognitive Science*. Cambridge, Massachusetts: MIT Press.
- Clayton, D. A. 1978. Socially facilitated behavior. *Quarterly Review of Biology*, **53**, 373–392.
- Collias, E. C. & Collias, N. E. 1973. Further studies on development of nest-building behaviour in a weaverbird (*Ploceus cucullatus*). *Animal Behaviour*, **21**, 371–382.
- Coussi-Korbel, S. & Fragaszy, D. 1995. On the relation between social dynamics and social learning. *Animal Behaviour*, **50**, 1441–1453.
- Darwin, C. 1881. *The Formation of Vegetable Mould, through the Action of Worms with Observations on Their Habits*. London: J. Murray.
- Ferreira, R. G., Emidio, R. A. & Jerusalinsky, L. 2010. Three stones for three seeds: natural occurrence of selective tool use by capuchins (*Cebus libidinosus*) based on an analysis of the weight of stones found at nutting sites. *American Journal of Primatology*, **72**, 270–275.
- Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. B. & de Oliveira, M. G. 2004. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, **64**, 359–366.
- Fragaszy, D., Pickering, T., Liu, Q., Izar, P., Ottoni, E. B. & Visalberghi, E. 2010a. Bearded capuchin monkeys' and a human's efficiency at cracking palm nuts with stone tools: field experiments. *Animal Behaviour*, **79**, 321–332.
- Fragaszy, D., Greenberg, R., Visalberghi, E., Ottoni, E. B., Izar, P. & Liu, Q. 2010b. How wild bearded capuchin monkeys select stones and nuts to minimize the number of strikes per nut cracked. *Animal Behaviour*, **80**, 205–214.
- Gibson, J. J. 1979. *The Ecological Approach to Visual Perception*. Boston: Houghton Mifflin.
- Gunst, N., Boinski, S. & Fragaszy, D. M. 2008. Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artefacts as an indirect social influence. *Behaviour*, **145**, 195–229.
- Hall, K. R. L. & Schaller, G. B. 1964. Tool-using behavior of the California sea otter. *Journal of Mammalogy*, **45**, 287–298.
- Hansell, M. 2000. *Bird Nests and Construction Behaviour*. Cambridge: Cambridge University Press.
- Lorenzi, H. 1992. *Arvores Brasileiras. Manual de identificacao e cultivo de plantas nativas do Brasil*. Nova Odessa, São Paulo: Editora Plantarum.
- Ottoni, E. B., Resende, B. D. & Izar, P. 2005. Watching the best nut-crackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. *Animal Cognition*, **24**, 215–219.
- Pick, H. L. & Lockman, J. J. 1981. From frames of reference to spatial representations. In: *Spatial Representation and Behavior across the Lifespan* (Ed. by L. S. Liben, A. H. Patterson & N. Newcombe), pp. 39–61. New York: Academic Press.
- Rapaport, L. G. & Brown, G. R. 2008. Social influences on foraging behavior in young nonhuman primates: learning what, where, and how to eat. *Evolutionary Anthropology*, **17**, 189–201.
- Semaw, S., Rogers, M. J., Quade, J., Renne, P. R., Butler, R. F., Dominguez-Rodrigo, M., Stout, D., Hart, W. S., Pickering, T. & Simpson, S. W. 2003. 2.6-Million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *Journal of Human Evolution*, **45**, 169–177.
- Tóth, Z., Bókony, V., Lendvai, A. Z., Szabó, K., Péntzes, Z. & Liker, A. 2009. Effects of relatedness on social-foraging tactic use in house sparrows. *Animal Behaviour*, **77**, 337–342.
- Visalberghi, E., Fragaszy, D., Ottoni, E., Izar, P., de Oliveira, M. G. & Andrade, F. R. D. 2007. Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. *American Journal of Physical Anthropology*, **132**, 426–444.
- Visalberghi, E., Sabbatini, G., Spagnoletti, N., Andrade, F. R. D., Ottoni, E., Izar, P. & Fragaszy, D. 2008. Physical properties of palm fruits processed with tools by wild bearded capuchins (*Cebus libidinosus*). *American Journal of Primatology*, **70**, 884–891.
- Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P. & Fragaszy, D. 2009. Selection of effective stone tools by wild bearded capuchin monkeys. *Current Biology*, **19**, 213–217.