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Withdraw-to-Eat Movements of the Platyrrhine *Sapajus libidinosus* to the Changing Affordance of Tubers with Eating

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Abstract – The evolution of hand ability in primates is staged, with the visual control of hand shaping likely originating in Platyrrhine primates, members of a monophyletic primate suborder whose stem group diverged from catarrhines about 40 million years ago. Platyrrhine hand shaping may have evolved in relation to visually mediated inhand food manipulation and hand withdraw to the mouth for eating movements. The present study examines this hypothesis in the Platyrrhine *Sapajus libidinosus,* the bearded capuchin monkey. These monkeys include the tuber *raiz de macaco*, or monkey's root, in their diet, a food item that poses challenges in handling, peeling and eating. Analysis of video recordings show that the capuchins used vision to render the tuber into fibers and roots that could be chewed and ingested. Visual engagement was initiated as each rendering/eating sequence began and visual disengage, with a blink and head raise, occurred just before a tuber reached the mouth. Two-handed withdraws mainly brought intact tubers to the incisors for peeling and shredding and one-handed withdraws mainly brought tuber fibers and roots that protrude from the hand to the premolars for chewing. The capuchins made use of novel power hand grasps, featuring the digit tips pressing food items against the interdigit pads and palm. They displayed individual but not group preference in pulling and holding the tubers with one hand and manipulating the tuber at the mouth with the other hand. The results are discussed in relation to the idea that the evolution of the visual and cognitive skills associated with inhand food handling to the changing affordance of food facilitates its management by the mouth. This visuomanual skill could be applied to other functions including tool use.

Keywords – Gaze with hand withdraw, Gaze for eating in *Sapajus*, Gaze for food eating by *Sapajus*, *Sapajus* eating, Tuber eating by *Sapajus*, Hand use by *Sapajus*

Insights into the skilled hand movements in vertebrates can contribute to understanding of the staged evolution of the visuomotor control of the hands in primates including humans (Iwaniuk & Whishaw, 2000; Sustaita et al., 2013). The visual control of reaching in primates may have had its origins in stem primates who foraged for insects or fruit in the terminal branches of trees (Cartmill, 1972, 2012; Scott, 2019; Sussman & Raven, 1978; Sussman et al., 2013), but the hand shaping abilities of contemporary catarrhines likely occurred later in primate evolution. Furthermore, the component movements of reaching in catarrhines, the reach, grasp and withdraw-to-eat movements, may each have had their own evolutionary history (Grant & Conway, 2019; Jeannerod, 1981; Jeannerod et al., 1995; Jeannerod et al., 1998; Karl & Whishaw, 2013; Sartori et al., 2015; Whishaw & Karl, 2014; Whishaw & Karl, 2019). There are two types of withdraw-to-eat movement: a ground withdraw, in which a food item is picked up by hand and brought directly to the mouth for eating, and an inhand withdraw-to-eat, in which a food item is held in hand and often manipulated before being presented to the mouth for eating. Among hand-related eating movements, the withdraw-to-eat may have had a central role in contributing to the origin of hand shaping. Platyrrhine and catarrhine, but not strepsirrhine, primates visually engage the food inhand as they manipulate it for presentation to the mouth (de Bruin et al., 2008; Hirche et al., 2022; Peckre et al., 2023; Whishaw et al., 2024). The affordances offered by inhand food items, including the affordances as the food is altered by its eating, can be challenging in terms of handling duration and complexity. The handling movements are also purposeful, as they aid in food management by the mouth. The cognitive skills associated with visuomotor handling could be related to, or could be the origin of, the hand shaping movements used for food grasping and other hand-related behaviors including tool use.

Capuchin monkeys (*Sapajus* spp.) display a wide variety of object grasping abilities in laboratory tasks (Spinozzi et al., 2004; Truppa et al., 2016). On the basis of the two general classes of grasps of humans defined by Napier (1956) as power and precision, capuchins have been reported to use power grasps, grasping between the digits and the palm, and precision-like grasps, grasping between the digits, usually the lateral aspects of digit I and II (Christel & Fragaszy, 2000; Costello & Fragaszy, 1988; Fragaszy et al., 2004; Pouydebat et al., 2009; Spinozzi et al., 2004; Truppa et al., 2019; Truppa et al., 2016; Whishaw et al., 2024). Capuchins also use objects as tools (Falotico et al., 2019; Fragaszy et al., 2004; Moura & Lee, 2004; Salmi et al., 2023; Spagnoletti et al., 2012; Visalberghi & Trinca, 1989). Their hand skills assist them in foraging and eating relatively difficult to access food. For example, in a study with *Sapajus libidinosus*, Truppa et al. (2019) described their extractive foraging for the tuber *raiz de macaco*, or monkey's root. The capuchins use their hands to dig up the tubers, clean sand from them by running their palm and wrist over the tuber and use their hands and mouth to remove the tuber shell and to tear off fibers of the meat for eating. The tubers are oblong in size, usually longer than the width of the capuchin's hands, and have many roots extending some distance from the tuber body. The affordance presented by tuber eating thus present a natural study opportunity to examine the capuchin's use of gaze for identifying portions of the tuber, especially portions of the tuber extending from the hand, that may assist the mouth in eating. This was the objective of the present study.

The study used video recordings of *Sapajus libidinosus* whose *raiz de macaco* extractive behavior that had filmed previously (Truppa et al., 2019). For each animal, relatively close-up videos of eating one tuber were obtained and subjected to frame-by-frame analysis. The objective of the analysis was to describe the use of vision for tuber eating and to describe the component movements and the mouth targets of tuber eating. Of special interest was how the capuchins responded to the affordance of tubers as they were changed into shreds, fibers and roots as they were consumed.

Method

Ethics Statement

This research was approved by IBAMA SISBIO 28689-3 and CNPq 002547/2011-2 (approvals granted to P. Izar, University of São Paulo, Brazil).

Subjects

Twenty wild bearded capuchin monkeys (*Sapajus libidinosus*), members of a group of 23 individuals consisting of 13 adults (≥5 years) and 10 immatures (<5 years) of both sexes were video recorded for the study (Truppa et al., 2019). They were habituated to human observers at close range, thus allowing close-up recording. Three females (two peripheral adults and a 5-month-old infant) were never observed to exploit the target food item during data collection. Accordingly, data are reported from 20 individuals (see Table 1). Body mass for these individuals was collected by Fragaszy et al. (2016). Ages of adults older than 89 months were estimated from body mass and behavior when they were first encountered by the researchers.

Table 1

Sex, Age, Body Mass, and Class of Age of Capuchin Monkeys in the Study Group

Subjects	Sex	Age (months)	Body mass (g)	Class of age
1. Mansinho	M	180*	3440	A
2. Piaçava	F	180*	1730	A
3. Jatobá	M	168*	4200	A
4. Teimoso	M	168*	3540	A
5. Chuchu	F	156*	2000	A
6. Dita	F	132*	2040	A
7. Tomate	M	89	2530	A
8. Catu	M	87	2730	A
9. Doree	F	78	1690	A
10. Pamonha	F	64	1730	A
11. Paçoca	F	64	1810	A
12. Coco	M	58	1880	I
13. Chani	F	39	1250	I
14. Taís	F	39	1480	I
15. Presente	M	36	1670	I
16. Cachaça	M	26	1290	I
17. Divina	F	18	980	I
18. Donzela	F	16	1050	I
19. Patrícia	F	16	980	I
20. Titia	F	16	1210	I

Note. * estimated age on the basis of body mass and behavior when they were first encountered by the researchers; A = adult (≥5 years); I = immature (<5 years).

Study Site

The study site is located at Fazenda Boa Vista (FBV), 21 km northwest or the town of Gilbués (9°39’36’’S, 45°25’10’’W), in the North-Eastern Brazilian state of Piauí. FBV is privately owned and is about 13 km sq situated in the ecotone between Cerrado (an area of open woodland) and Caatinga (an area that is semi-arid) biomes (Oliveira & Marquis, 2002). The field site is located on a sandy plain at approximately 420 m above sea level (for a description of the site see Spagnoletti et al., 2012). The area is characterized by low-nutrient sandy soils, seasonal climate, having a dry season from April to September and a rainy season from October to March. Interannually variable precipitation is 800–1,600 mm (Oliveira & Marquis, 2002). FBV is an ideal site to film capuchins' manipulative behavior because the vegetation allows good visibility and the animals spend about 30% of their active time on the ground (Wright et al., 2019). These capuchin monkeys have recently come under anthropogenic threat from land use changes (Presotto et al., 2020; Roncero et al., 2023).

Food

Capuchins living in FBV often eat the underground part of plants. The most frequently consumed food is the *raiz de macaco*, also called monkey's root by the local people (species not yet identified). *Raiz de macaco* is a relatively small tuber with a diameter of 1–2.5 cm and a length of 5–8 cm (Truppa et al., 2019). The morphological features of *raiz de macaco* suggest that they are tuberous roots, that is, thickened secondary roots modified for the storage of water and nutrients. In FBV, *raiz de macaco* is present in the flat, sandy plain area and consumption of the plant occurs mainly in the dry season (Santos, 2015). Nutrient content analysis carried out on about 100 g (dry matter with husk included), shows that *raiz de macaco* is a good source of carbohydrates (80.52%), nonstructural carbohydrates (starches and sugars: 50.05%), mineral salts/ash (11.72%), and crude protein (6.86%) (Santos, 2015). With respect to its mechanical properties, *raiz de macaco* has high toughness and resistance to deformation; i.e., elastic modulus (Chalk et al., 2016). The body of the tuber is encased in a husk and roots of varied thickness protrude from the body, often for many cm.

Video Recording

Data were collected during the dry season, from May to August 2014, by two observers (May–June: LAM and VT, July–August: LAM and MJFO), who followed the capuchins during their daily activities for approximately 600 hr (6:30–16:30, 5 days per week). Cameras used were HD digital camcorder (JVC GC-PX100) with a 10x zoom lens and a digital reflex camera (Canon EOS 600D Full HD) with an EF-S 55–250 mm f/4–5.6 IS zoom lens. Videos were recorded with a resolution of 1080p at 60 fps in MOV digital format. These settings allowed high resolution pictures with ample frames for behavioral coding. Videos were recorded at 2–5 m from the subject, with the capuchins seemingly ignoring the observers at this distance.

Behavioral Scoring

Capuchin tuber excavation from the soil, transport to a different location, the removing of the soil and removing of the husk and breaking of the tuber meat for ingestion has been described by Truppa et al. (2019). The present study used one video from each participant in which an entire sequence of handling and consuming the tuber was visible in close-up, from mainly a front view. The eating of a tuber provided many sequences of a capuchin looking at the tuber, manipulating it, and bringing it to the mouth to remove its husk and consume its fibrous flesh and roots.

Time Measurement

Time was measured by counts of video frames using the formula Time in seconds = number of video frames / 60.

Kinematic Measures

Kinematic analyses were made using the open-source software Tracker (https://physlets.org/tracker/). Kinematic analysis of the withdraw-to-eat movement were made from the first frame as the hand began to move toward the mouth to the point that the hand stopped at the mouth. A point centered on the 5th knuckle was digitized to track the hand movement. Kinematic measures were also made of head movements associated with a withdraw-to-eat movement by digitizing the tip of the nose. Eye blink movement was measured by digitizing at the middle edge of the upper eyelid.

Gaze Measurement

With a tuber held in hand, if the head of an animal was oriented toward the tuber at the time that the grasp occurred, that was taken as a sign that the animal was looking at some part of the tuber; i.e., visually engaged or gaze anchored as defined by Posner et al. (1987). The following head/eye orienting behaviors were quantified by counts of incidence and measures of duration by frame counting:

1. Gaze time: gaze time was the time between the video frame of the first movement that resulted in the face/eyes being directed toward the food item held in the hands to the video frame in which the face/eyes were disengaged (turned away) from the food item, often with a blink.

2. Gaze food handling time. Gaze food handling time was time from the video frame in which the head/eyes were first directed to a tuber held in the hands to the video frame in which the hand began to withdraw the tuber to place it in the mouth.

3. Gaze-hand carry time: gaze-hand carry time was the time between the video frame featuring the first hand movement directed toward the mouth to the video frame in which the gaze was disengaged from the tuber by head raising or a blink.

4. No-gaze hand carry time. No-gaze hand carry time was the time during which gaze was not directed to the tuber as it was carried to be placed in the mouth to the video frame in which the tuber reached the mouth.

5. Eye blink: Eye blinks were rapid closing then opening of the eyelid. The occurrence of a blink, and its duration was measured in video recordings in which a view of the eyes was adequate (de Bruin et al., 2008; Whishaw et al., 2024).

Hand Movements Descriptions

Each tuber eating event was associated with many hand movements of holding, manipulating, and carrying the tuber to the mouth with one or both hands. Once they grasped a tuber by mouth, capuchins pulled on the tuber to remove the husk or strip the meat fibers for eating. The following movements are described:

1. *One-hand food holding*. One-hand food holding was defined as a single hand holding the tuber, either as the capuchin was or was not looking at the tuber.

2. *Two-hand food holding*. Two-hand food holding was defined as both hands grasping the tuber body or tuber roots, either as the capuchin was or was not looking at the tuber.

3. *One-hand carry-to-mouth*. A one-hand carry-to-mouth was defined as a tuber that was being held in one hand being brought to the mouth by that hand. (One hand could also reach for and take a tuber from the mouth).

4. *One-hand reach to the mouth*. A one-hand reach to the mouth was defined as a hand reaching to take or to adjust a tuber portion held in the mouth.

5. *Two-hand carry-to-mouth*. A two-hand carry-to-mouth was defined as tuber held by both hands as it was brought to the mouth by both hands.

6. *Reach and grasp*. Reach and grasp movements were those in which a hand that was not holding the tuber, reached to additionally grasp the tuber body or its roots.

7. *One-hand pulls*. One-hand pulls were defined as hand pulls on a tuber as it was grasped by the teeth.

8. *Two-hand pulls*. Two-hand pulls were defined as both hands pulling a tuber held in the teeth.

9. *Asymmetrical two-hand-pulls*. If during a pull, one hand was observed to make most of the pull, the pull was classified as an asymmetrical two-hand pull. The hand engaging in most of the pull would pull further forward than the other hand or twist during the pull whereas the other hand remained adjacent to the mouth.

Mouth Grasps

Bringing a tuber to the mouth engaged the mouth in preparation in a variety of ways to take the tuber for eating. The following mouth grasps were identified:

1. *Incisor bite*: an incisor bite occurred when a tuber was presented to the front of the mouth and was grasped by the incisors.

2. Incisor bite duration: incisor bite duration was obtained by counting the number of frames beginning with the tuber first touching the mouth as it was brought to the mouth by the hands to the point that the tuber was pulled free of the mouth leaving a portion in the mouth.

3. *Premolar bite*: a premolar bite occurred when a tuber was presented to the side of the mouth and was grasped with the premolars.

4. *Premolar bite duration*: premolar bite duration was obtained by counting the number of frames beginning with the frame in which the tuber first touched the mouth as it was brought to the mouth by the hands to the frame in which the tuber was pulled free of the mouth leaving a portion in the mouth.

Statistical Analysis

Statistical analyses were performed using the software IBM SPSS Statistics (v28.0.1.1). The data are presented as mean ± standard error of mean (mean ± sem). For statistical comparisons, a mixed model ANOVA was used for within and between subject measures. A p-value of <.05 was defined as statistically significant. Power was measured by eta-squared (η^2), a descriptive measure of the strength of association between independent and dependent variables. Power analysis was used to estimate the minimum sample size observed for a conclusion. Follow-up tests were Newman-Keuls tests with significance level set at <.05. Pearson product-moment correlations were used for data fits and Pearson product correlations were expressed as *r*.

Results

Inhand Withdraw-to-Eat

The challenge in eating a tuber is that the tuber is progressively changed by rendering and eating, requiring ongoing modifications in each subsequent withdraw-to-eat movement. Tuber eating consists of many movements of grasping and handling that bring the tuber to the mouth for peeling and eating. An inhand withdraw-to-eat act is defined as instance in which a tuber held inhand is brought to the mouth for a bite. A total of 398 inhand withdraw-to-eat acts were obtained from the 20 capuchins, giving a mean ± sem of 19.9±2.0 (range 6-37) inhand withdraw-to-eat acts per capuchin. The time taken to eat a tuber by a capuchin was 3.14±0.38 min (mean ±sem).

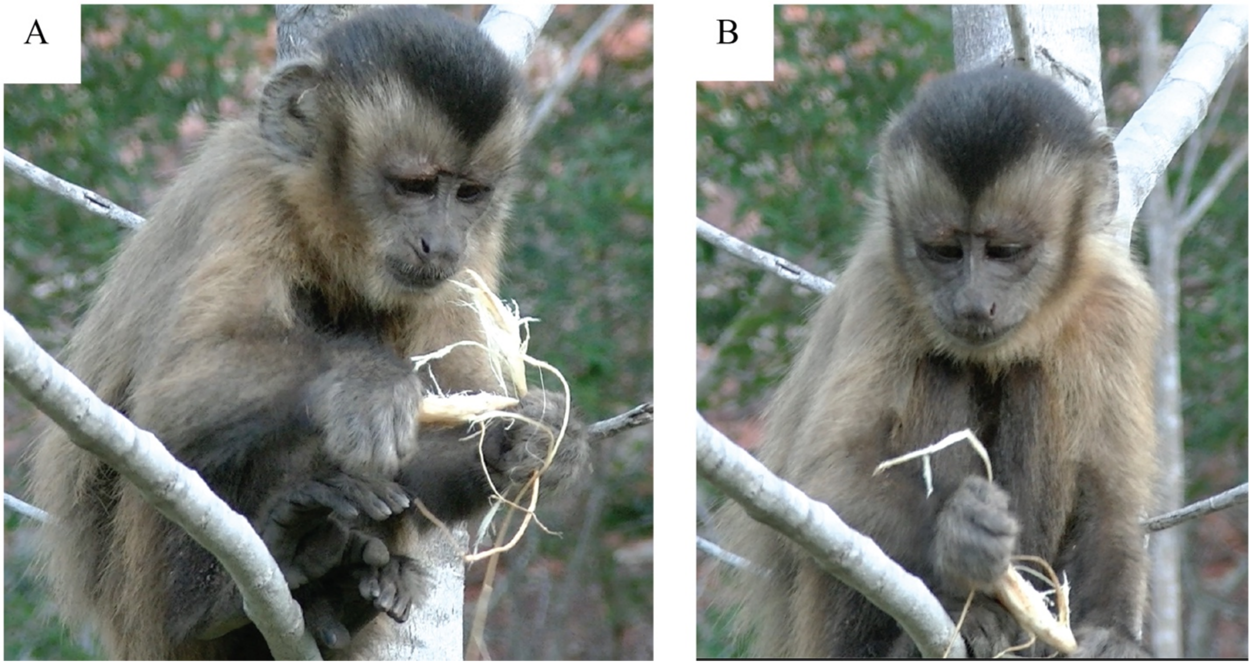
As the following sections describe, tuber-eating is guided by vision and is organized. There were two main types of withdraw-to-eat movement sequences, one bringing the tuber to the incisors and the other bringing the tuber to the premolars. Bringing a tuber to the mouth could be made with one hand or with two hands. Video S1 shows a withdraw-to-eat sequence in which a capuchin reaches with a free hand to grasp a tuber body for a two-hand carry to the incisors for rendering. Video S2 shows a withdraw-to-eat sequence in which a capuchin uses one hand to bring a tuber root to the premolars for chewing. These movements are described in more detail in the following sections.

Gaze Engages the Tuber for Withdraw-to-Eat

Withdraw-to-eat, consisting of handling and carry to the mouth sequences, with only a few exceptions, were made with gaze concurrently directed toward the tuber. If the tuber was held in two hands, with the hands on either side of the tuber, gaze was usually directed at the portion of the tuber located between the two hands (Figure 1A). If a portion of the tuber extended from the hands, gaze was usually directed at the protruding portion of the tuber (Figure 1B). Only seven instances of bringing a tuber to the mouth without first visualizing it were observed. All involved roots that protruded from the hand and for all, the placement with respect to the mouth was not accurate. As is illustrated in Video S3, after an inaccurate no-look attempt, a capuchin repeated the withdraw act with gaze, first looking at the tuber root and then placing it accurately in its mouth.

Figure 1

Tuber Directed Gaze by the Capuchin Taís.



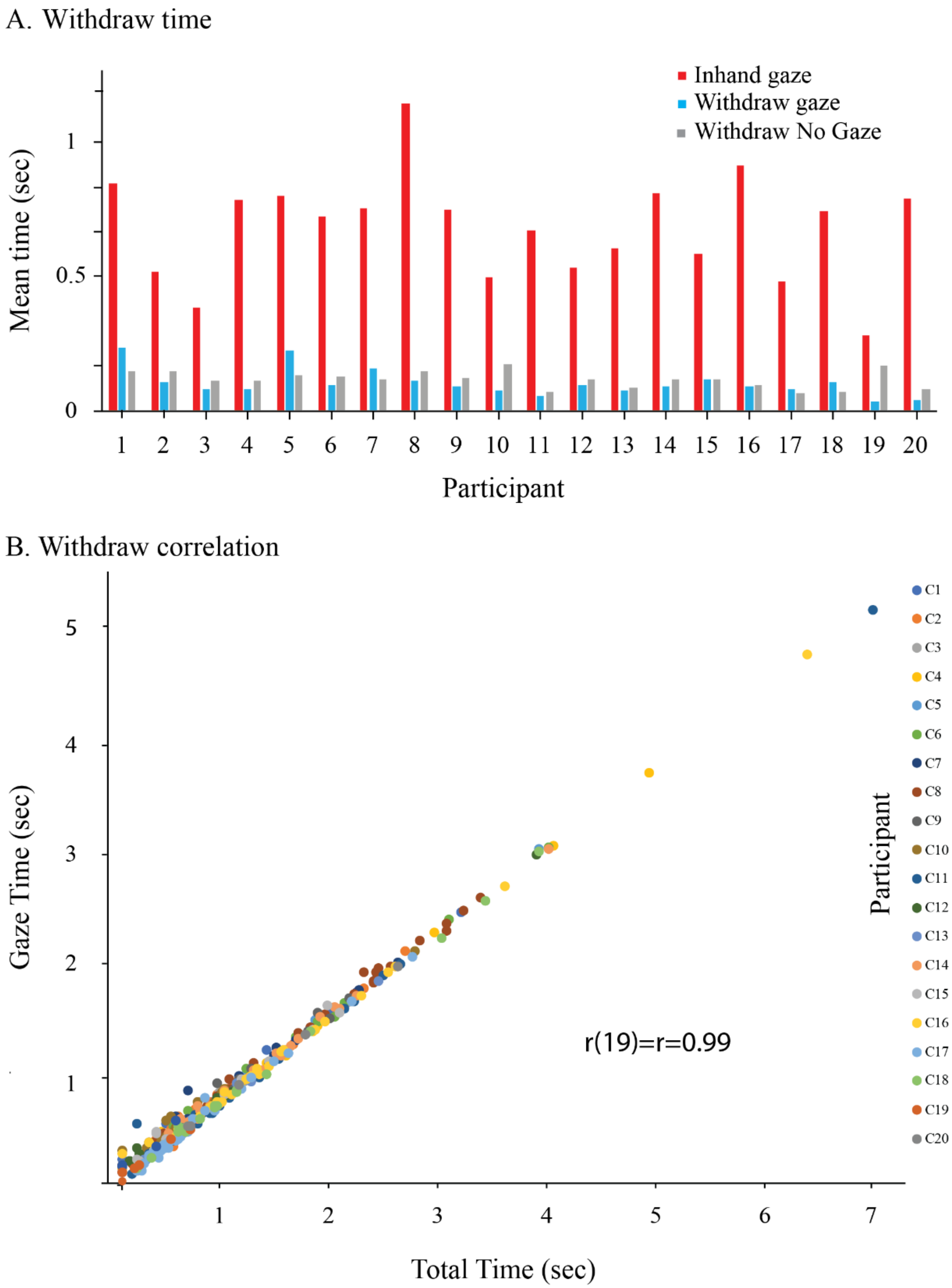
Note. A. The capuchin looks at the middle of body of a tuber that is held by both hands in a parallel grip. B. The capuchin looks at the root of a tuber that extends from a hand, with the tuber held in a tandem grip by both hands.

On the basis of gaze, a tuber eating sequence could be divided into three successive components: manipulation inhand with gaze, carry to the mouth with gaze, and carry to the mouth without gaze. Figure 2A gives a summary of the durations of these three components for each capuchin. The figure shows that for all capuchins, most gaze time is associated with looking at the tuber during food handling, with a brief period of gaze associated with looking at the tuber as the hand approached the mouth, and a similar brief period in which gaze was disengaged as the hand completed its movement to the mouth. An ANOVA comparing the three durations gave a significant effect, $F(2,38) = 38.3$, $p < .001$, $\eta^2 = 0.94$, observed power =1.0. The duration of gaze during food handling was longer ($p < .001$) than the duration of carry to the mouth with gaze and longer than the duration of carry to the mouth without gaze ($p < .001$), with the latter two not differing. Group average times (mean±sem) were: (1) food handling with gaze, = .68±0.37, carry with gaze .10±0.01 and carry without gaze 0.11±0.01 sec respectively. A comparison of duration between adult and juvenile participants did not give a significant effect, $F(2,40) = 2.07$, $p = .08$, $\eta^2 = 0.94$, observed power = 1.0.

Figure 2B illustrates the relationship between total gaze time and total time to complete a withdraw-to-eat act. The mean±sem of the average correlations for the 20 participants was $r = 0.99±0.002$. The relationship shown in Figure 2B. Because handling time was variable whereas withdraw time was relatively constant, the high correlation indicates that almost all variation in gaze time was associated with looking at the tuber during the period of food handling.

Figure 2

Gaze Duration Associated with Inhand Withdraw



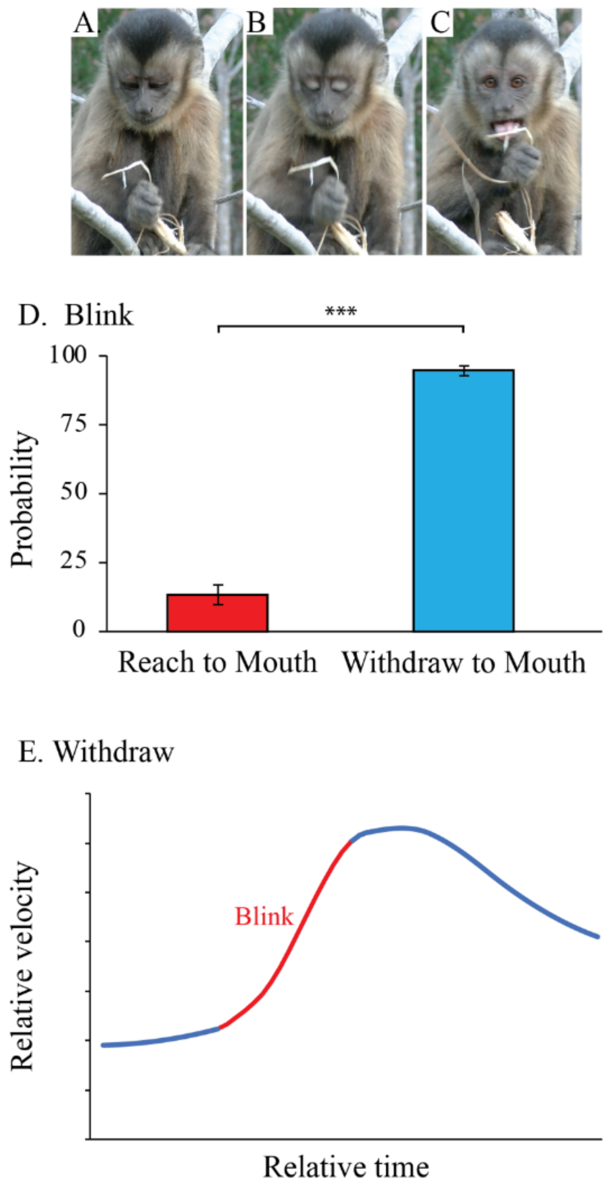
Note. A. Tuber handling and carry to the mouth time (mean±sem) divided into three components based on gaze: handling time with gaze, carry to the mouth time with gaze and carry to the mouth time after gaze disengage. B. The correlation between the average gaze related withdraw-to-eat time plotted against total time for each capuchin. The high correlation occurs because most variation in time involves gaze directed to the tuber during tuber handling.

Blinks with Head Movement Contribute to Gaze Disengage

The onset of gaze directed toward a tuber held in the hand was associated with a head movement that directed the face toward the tuber as illustrated in Figure 3A. Gaze disengagement was associated with raising the head and this movement was accompanied by a blink, as illustrated in Figure 3B. At the completion of the head raise, the mouth was in a relatively horizontal position to accept the tuber as is shown in Figure 3C.

Figure 3

Relation Between Hand Carry to the Mouth and a Blink in the Capuchin Taís



Note. A. The capuchin directs gaze to a tuber root that protrudes from its hand. B. The capuchin blinks as tuber is carried to the mouth. C. The head is raised and the eyes open after a blink, and the mouth accepts a tuber root. D. Blink incidence (mean±sem) with movements of hand to the mouth to take food vs movement of the hand to the mouth carrying food. E. Blinks occur during the acceleration of hand movement as the hand brings a tuber to the mouth. Note: the blink subdivides the carry of the tuber to the mouth into an initial portion with gaze and a terminal portion without gaze.

The capuchins made two kinds of hand movements directed toward their mouth. With one, they would reach to take food from the mouth and with the other would reach to place food in the mouth. The incidence of blinks associated with each type of movement is shown in Figure 3D. There were 102 reaches to take food from the mouth and only 13 (12.7%) of these reaches were associated with a blink. On a total of 338 out of 377 (89.6%) withdraw-to-eat movements, a blink occurred in association with head disengage. For most instances when a blink was not observed during the withdraw-to-eat, it was because the capuchin looked away or the video lighting was too poor to score the eyes. In summary, there were very few hand-to-mouth movements with food that were not associated with a blink. The probability of blink in no food vs food related hand movement to the mouth gave a significant effect, t-test for correlated groups $t(19) = 22.03$, $p < .001$. Frame counts to determine blink durations were made for all blinks in all capuchins and these gave a duration of .098±.004 (mean±sem) sec, a similar duration to that described for humans (Willett et al., 2023).

To further identify the timing between blinks and carry to the mouth movement, sample kinematic measures were made of the movement of the hand, head and blink. An example is shown in Figure 3E. The velocity of the hand movement to the mouth had a bell-shaped profile in which hand movement accelerated during the first portion of the movement and then slowed down to stop as the hand reached the mouth. The duration of the blink, when superimposed on the hand velocity profile (the red portion of the velocity curve in Figure 3E), showed that the blink occurred during the acceleration of the jerk of the hand movement. Thus, the blink is completed before the hand begins to slow down to present the tuber to the mouth. Not shown is the head raise movement, but it was concurrent with the blink.

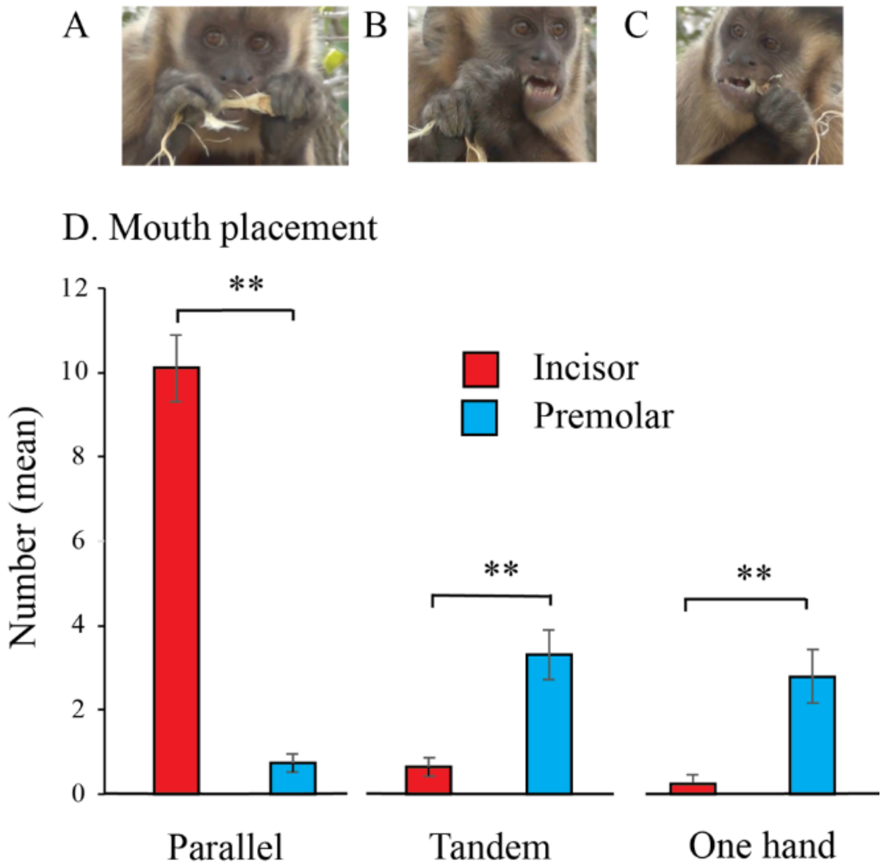
Hand Holding Configuration

The capuchins used three main hand-holding configurations as they brought a tuber to the mouth (Figure 4). (1) They held the tuber in one hand (Figure 4A). (2) They held the tuber with two hands, with the hands in a parallel orientation, one each side of the tuber (Figure 4B). They held the tuber with the hands in tandem, with an end of the tuber projecting from one hand (Figure 4C). For one hand and tandem hand holding, the tuber projecting from the hands was the tuber portion presented to the mouth. For two-hand parallel holding, the portion of the tuber between the hands was presented to the mouth.

Analysis of the mouth target of each of the hand-holding strategies indicated that the one-hand and tandem-hand strategies mainly brought the tuber to the side of the mouth to be grasped by the premolars. The parallel-hand strategy mainly brought the tuber to the front of the mouth to be grasped by the incisors (Figure 4D). The frequency with which each hand holding strategy brought the tuber to either the front of the mouth (incisor) or to the side of the mouth (molar) target was significant, $F(1,18) = 18.9$, $p < .001$, $\eta^2 = 0.51$, observed power = 0.98. The parallel-hand hold strategy brought a tuber to the incisors, whereas the tandem-hand or one-hand strategy brought a tuber to the premolars. The analysis hand holding strategy showed that there were more parallel-hand hold types than one or tandem hold types $F(2,36) = 38.4$, $p < .001$, $\eta^2 = 0.83$, observed power =1.0. In addition, the analysis of mouth use showed that tubers were more frequently taken to the incisors than to the premolars., $F(2,36) = 17.81.9$ $p < .001$, $\eta^2 = 0.82$, observed power = 1.0.

Figure 4

Targets of Withdraw-to-Eat in the Capuchin Paçoca



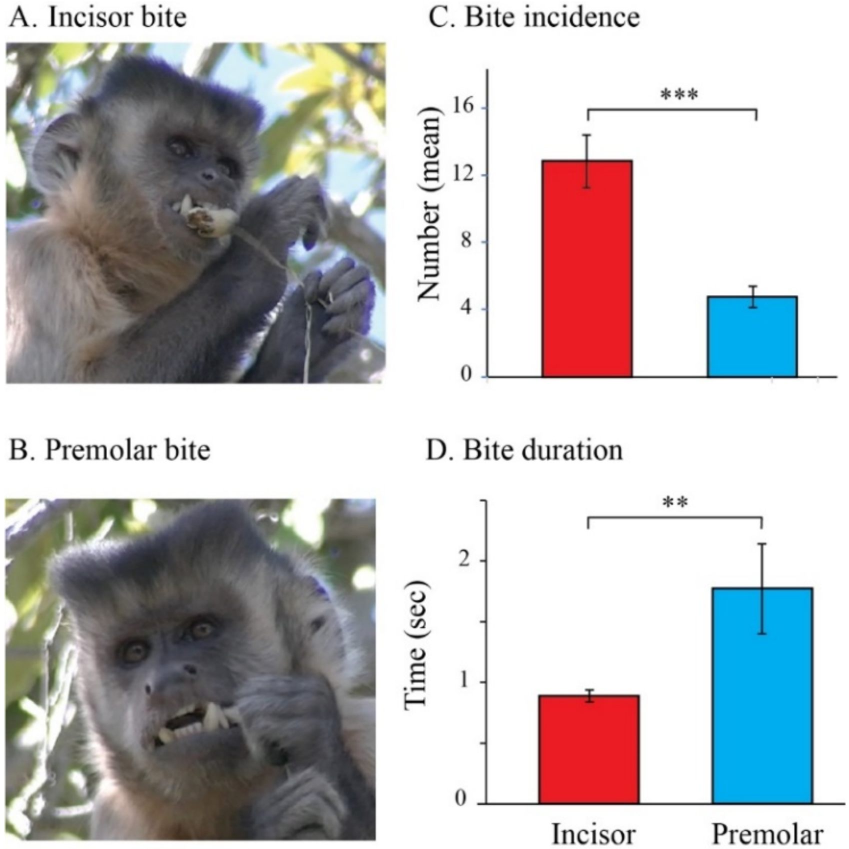
Note. A. Parallel two-hand withdraw holds the tuber on each of its ends and brings the tuber to the incisors. B. Tandem two-hand holds brings a tuber projecting from the proximal-to-mouth hand to the premolars. C. One-hand holds brings the tuber projecting from the hand to the premolars. Note: for all withdraw types, the thumbs are adjacent to the mouth for food transfer to the mouth. D. The incidence (mean±sem) of parallel, tandem and one hand withdraw-to-eat movements. Note: two-hand parallel holds bring tubers to the incisors and tandem and one hand holds bring tubers to the premolars.

Biting with Incisors and Premolars

The number of times that tubers were brought to the incisor teeth or the premolar teeth and the duration of biting at each location were different as were biting strategies (Figure 5). A tuber body was usually brought to the incisors by both hands and almost as soon as the tuber was grasped by the incisors, a capuchin pulled on it with both hands to remove its husk, after which it spat out the husk and ate the meat fibers. Tuber roots or fibers were more frequently brought to the premolars with one hand (see above), and they were frequently chewed on and often moved around by the hand in relation to the mouth, even being carried from one side of the mouth to the other. Accordingly, counts of the frequency with which tubers were brought to the incisors vs premolars gave a significant effect, $F(1,18) = 35.4$, $p < .001$, $\eta^2 = .66$, observed power = 1.0, with tubers more frequently taken to the incisors than the premolars. There was no significant effect of incisor vs premolar grasp as a function of capuchin age, $F(1,18) = 0.52$, $p = .82$, $\eta^2 = .003$, observed power = .005, and no interaction between incisor vs premolar use as a function of capuchin age, $F(1,18) = .19$, $p = .75$, $\eta^2 = .12$, observed power = .34.

Figure 5

Bite Times by Incisors and Premolars by the Capuchin Tomate



Note. A. A tuber is grasped by the incisors and the hands pull to assist the bite. B. A tuber is brought to the premolars and the hands hold the tuber for chewing before the pull to assist the bite. C. The incidence (mean±sem) of incisor and premolar bites. D. The duration (mean±sem) of incisor and premolar bites. Note: most carries to the mouth go the incisors and premolar bites take longer than incisor bites.

Bite durations, the length of time that a hand held a tuber for incisor vs premolar bite, were significantly different, F(1,18) = 6.76, p = .02, η^2 = 0.27, observed power = .69. When a hand held a tuber for the premolars, the duration was longer than when it held a tuber for the incisors. There was no significant effect of capuchin age in bite duration, F(1,18) = 0.53, p = .48, η^2 = 0.27, observed power = .13, and no interaction of bite location and age, F(1,18) = .11, p = .75, η^2 = .74, observed power = .006.

In summary, the parallel two-hand strategy was usually used at the beginning of tuber eating, when the body of the tuber was largely intact. Once the tuber was grasped by the incisors there was an almost immediate hand pulled to leave a portion of the husk or meat in the incisors. If that portion was husk, it was ejected from the mouth but if it was the meat, it was eaten. When the tuber protruded from the hands, with both hands in a tandem orientation, or protruded from the hands and was withdrawn with one hand, the end that protruded was most frequently brought to the side of the mouth and grasped with the premolars. The premolar grasping strategy was mainly used when the capuchin was eating tuber fibers and tuber roots, and usually resulted in prolonged chewing on the tuber before the portion of the tuber being chewed on was separated by pulling. If held in one hand, a tuber root or fiber could be moved from the premolars on one side of the mouth to the premolars on the other side of the mouth, but vision was not involved in mouth-related tuber manipulation.

Hand Preference for Pull and Holding vs Reach

The capuchins displayed preferences of hand use in three tuber manipulating behaviors.

(1) *Pull/hold*. A main tuber eating strategy was to bring the tuber to the mouth with two hands, bite it, and then twist off a piece of the tuber by pulling it with one hand (Figure 6A). One hand exerted most of the pull whereas the other held the tuber adjacent to the mouth. The capuchin was usually successful in pulling off a piece but when it was not successful, it repeated the action. If successful, the hand that exerted the pull then continued to hold the tuber while the removed tuber piece was chewed. The other hand, which had held the tuber adjacent to the mouth, was freed.

(2) *Reach to mouth*. With its freed hand, a capuchin might reach to the mouth to adjust the tuber fragment in the mouth (Figure 6B).

(3) *Reach to tuber*. To obtain/regain a two-hand purchase, a capuchin might reach for the tuber to grasp it with a free hand for the next carry to the mouth (Figure 6C).

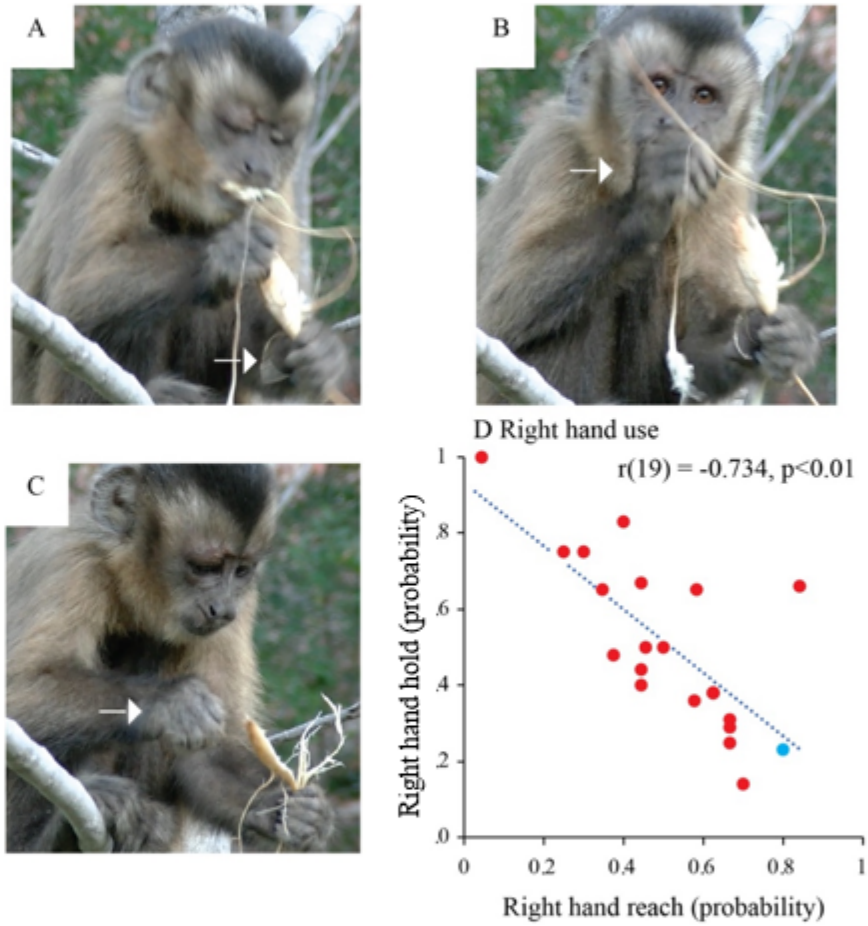
Vision was not directed to the hand that pulled/held the tuber (302 observations), or to the hand that reached to adjust a tuber fragment in the mouth (102 observations). Vision was nearly always directed to the tuber when the capuchin reached to grasp it, (225 of 251) reach observations.

Identification of hand use for pulling and then holding the tuber, vs the hand that manipulated the tuber at the mouth, indicated that although individual capuchins had hand preferences, there was no group preference for the hand used for pulling/holding and the hand used for manipulation at the mouth. Analysis with t-tests that compared hand preference to chance (0.5) gave no significant group effect for holding, $t(19) = 0.3$, $p = .74$, reaching for the mouth, $t(19) = 0.4$, $p = .48$, or reaching for the tuber $t(19) = 0.46$, $p = .92$.

If the capuchins had a hand preference for pulling/holding the tuber with one hand, they would also show a preference for reaching to the mouth or reaching to grasp the tuber with the other hand. Figure 6D gives a scatter plot showing a negative correlation between right hand pull/hold vs right hand reaching for the tuber, $r(19) = -.73$, $p < .01$. Similarly, there was a negative correlation between right hand pull/hold and right hand reach to the mouth, $r(19) = -0.54$, $p < .05$.

Figure 6

Incidence of Right-Hand Use for Reaching and Holding by the Capuchin Taís



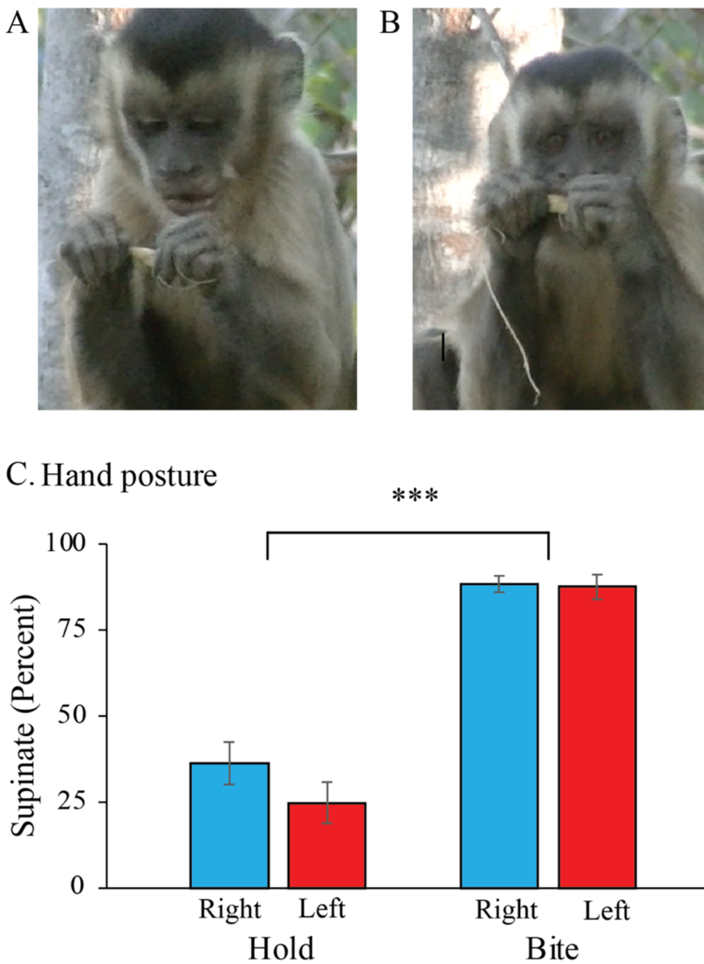
Note. A. The capuchin uses its left hand (arrow) to apply torque to a tuber held in the mouth by the right hand. B. The capuchin brings its right hand (arrow) to its mouth to adjust a piece of the tuber while holding the tuber in the left hand. C. The capuchin reaches with its right hand (arrow) for a tuber held with its left hand. D. A scatter plot of right-hand reaching vs left-hand holding for all of the capuchins gives a negative correlation, suggesting that each capuchin has preferred reaching and holding hands, with no group asymmetry. The blue dot in the scatter plot is the capuchin Taís illustrated in the pictures, who had a strong right-hand bias for reaching vs a strong left-hand bias for holding.

Hand Positioning for Tuber Manipulation and Biting

In previous study, the capuchin *Cebus imitator,* when eating fruit*,* has been found to present the fruit to the mouth with the hand oriented so that the thumb (digit I) is adjacent to the mouth (Whishaw et al., 2024). To determine whether *Sapajus libidinosus* uses a similar hand posture for mouth presentation, palm posture was rated for both hands as being largely horizontal (fully pronated or supinated) or largely vertical (the palm half supinated) when tuber holding and when the tuber was presented to the mouth. The palm was found to be in a more horizontal position prior to the initiation of carrying the tuber to the mouth (Figure 7A) and in a more vertical position with the thumb adjacent to the mouth when the hands reached the mouth (Figure 7B). The incidence of hand posture when holding at the mouth is shown in Figure 7C. An ANOVA on hand posture at the two locations gave a significant effect, $F(1,19) = 120.8$, $p < .001$, $\eta^2 = .86$, observed power =1.0. The relative posture, in which there was hand rotation to obtain a palm-vertical thumb-in posture at the mouth, was a feature of both hands, as there was no significant effect of hands, $F(1,19) = 1.66$, $p = .21$, $\eta^2 = .02$, observed power = .23.

Figure 7

Hand Rotation to Present Tubers to the Mouth by the Capuchin Coco



Note. A. Hands in pronated orientation while holding a tuber. B. Hands in supinated orientation with digit I adjacent to the mouth for tuber presentation to the mouth. C. Percent of supinated hand orientations (mean±sem) when holding a tuber and when presenting it to the mouth. Note: the hands rotate to take a supinated thumb to the mouth posture when presenting food to the mouth.

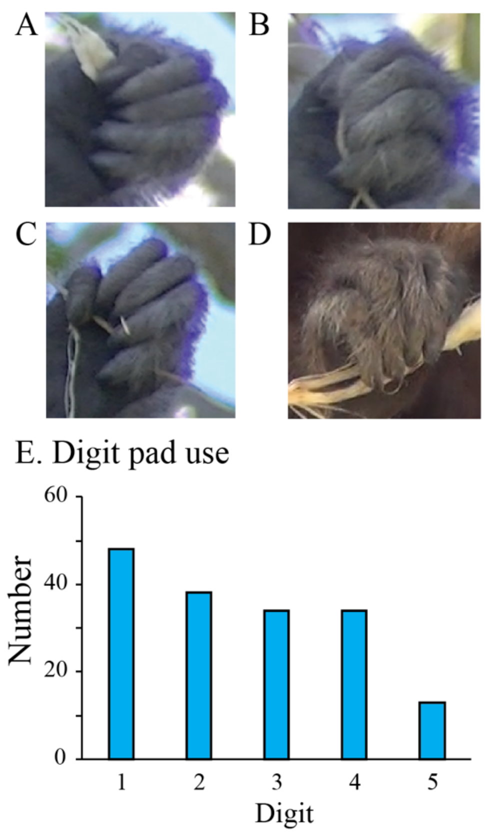
Capuchins Perform Digit Tip to Palm Grips with All Fingers

The use of precision and power grip has been described for tuber eating by Truppa et al. (2019). In that study, precision grips for tuber eating were rare and included holding a food item between the distal phalanges of the thumb and the index finger and between the distal phalanges of the index finger and the middle finger, whereas power grips were common and included holding a food item between digits I-V and the palm with digit I (the thumb) wrapping the food in the same or in the opposite direction with respect to digits II-V (Truppa et al., 2019).

The use of these grip patterns was confirmed by the present study. In addition, we observed power grips in which the pads of only some digits or even a single digit might press a food item, especially the thin roots of the tuber, against the interdigital or palm pads. Figure 8A illustrates a grip in which digit I holds a piece of a tuber against the interdigital pads. Figure 8B shows digit II and digit V pressing a piece of tuber against the interdigital pad and palm respectively. Figure 8C illustrates digit I and digit IV pad contact with a tuber fiber against the palm. Figure 8E illustrates a number of digits holding a tuber part against the interdigital pads or palm with the digit pads. These observations were made from a relatively small number of instances of food holding (n=63) during which the hand was oriented such that it allowed a view of finger positioning. The count likely underestimates the frequency of these types of individuated pad-to-pad power grips.

Figure 8

Digit Pad Use for Holding Tuber Fibers or Roots



Note. A. The thumb holds a tuber fiber against the thenar pad. B. Digit II and digit V pads hold a tuber root against the palm. C. Digit I and digit IV pads hold a tuber root against the interdigit pads. D. Digits II to digit V pads hold a tuber adjacent to the palm. E. The number of observations made of digit pad I-V being used to hold tuber parts against the interdigit pads or other parts of the palm.

Discussion

We investigated the visual control of food handling and eating movements by the platyrrhine *Sapajus libidinosus* as it ate the tuber *raiz de macaco*, or monkey's root. With a tuber held inhand, vision was engaged at the onset of tuber manipulation and disengaged as the tuber was presented to the mouth, with variation in the duration of visual attention related to the duration of tuber handling. Tuber manipulation was directed either toward presenting the tuber body to the incisor teeth for husk or fiber removal or presenting fibers and roots to the premolar teeth for chewing. Torque on a tuber, for husk or fiber removal, when held between the hand and the incisors, was obtained with a preferred hand that continued to hold the tuber in inter handling intervals. Concomitantly, the other hand was free to adjust the tuber in the mouth or renew purchase by again reaching for the tuber. Although capuchins had hand preferences, there was no group asymmetry in torque application/holding, reaching, or hand to mouth movements. Tuber holding featured a variety of power grips with various novel digit pad to palm grip variations. The organization of visually guided behavior in relation to the changing affordance of tubers undergoing eating, is cognitively rich, assists the mouth in managing the food, and could be considered as a candidate behavior that contributes to hand skill more generally.

Three aspects of handling of tubers for eating are noteworthy with respect to visual control. First, tuber handling offers many instances of visually related hand interactions with the tuber. These handling movements position a tuber for an average of about 20 presentations of the tuber to the mouth to complete its consumption. Second, the process of handling/eating changes the tuber and its orientation and so presents continuously changing target for subsequent handling. Comparatively, the visuocognitive challenges presented by inhand withdraw-to-eat movements related to the eating of tuber far exceed the number and the demands that would be related to simply picking up a food item by hand. For this reason, it is relevant to consider inhand manipulation of food as having contributed to the evolution of the visuocognitive control of skilled hand movements more generally (Hirche et al., 2022; Peckre et al., 2023; Whishaw et al., 2024). Once evolved, inhand visual control could be applied to the management by the mouth of many different food types and could also be directed toward other hand use functions, including visually guided reaching and tool use.

An organizational feature of tuber handling was whether a tuber was to be presented to the front of the mouth to be grasped by the incisors or to the side of the mouth to be grasped by the premolars. Rosenbaum et al. (1990; 2012) propose that the way that an object is initially grasped/handled is determined in part by the disposition of the object in the interest of end-state comfort. Here the end-state comfort of bringing a tuber to the mouth appeared to be related to whether it was to be de-husked/shredded or whether it was to be chewed. De-husking/shredding involved grasping the tuber in the incisors and applying torque on the tuber body, whereas chewing involved bringing the ends of roots and fibers that extended from the hands to the premolars where it was held for chewing. The present study was not directed to classifying the many hand-shaping movements made by the capuchins, as has been done with Macaques (Macfarlane & Graziano, 2009; Mangalam & Singh, 2013), but rather to examine visual control of hand movements in relation to end-state function. An attractive feature of an end-state analysis of tuber manipulation is that it highlights the affordance presented by a tuber in relation to the cooperative movements of the hands and mouth that may be mediated by common neural control (An et al., 2022).

Although tuber handling appears to involve an array of complex movements, the behavior is simplified in relation to a limited number of affordances. A classic proposal, suggests that serial actions, including those involved in reaching, are related to the translation of visual plans to action plans (Lashley, 1951; Rosenbaum et al., 2012). The relation between gaze and tuber handling, however, suggests that the serial actions of tuber-eating lie in part in tuber affordances (Gibson, 1977; Withagen et al., 2012), such as “peelable” vs “chewable”. The ability to perceive the affordance of complex food items likely depends upon visual object working memory for tuber size and shape and spatial working memory related to orienting tuber parts relative to the mouth. These cognitive processes are proposed to be mediated by separate areas of prefrontal cortex (Cruz-Rizzolo et al., 2011; Goldman-Rakic, 1992; Kaas, 2019; Preuss & Goldman-Rakic, 1991; Williams et al., 2010), which are well developed in capuchins. The visuomotor skills for tuber handling may be additionally mediated by the penetration of the direct projection of the corticospinal tract to cervical motor neurons, which is also reported to be dense in capuchins (Bortoff & Strick, 1993; Strick et al, 2021). It seems likely that the evolution of visuomotor systems sensitive to affordances of food could be applied in other ways including to tool use ability. Studies have reported on a variety of tool use skills in capuchins (Falotico et al., 2019; Moura & Lee, 2004; Salmi et al., 2023; Spagnoletti et al., 2012; Visalberghi & Trinca, 1989). The relationships between eating and other manipulatory skills such as those involved in tool-use could be furthered by investigating the inhand eating and hand use behavior of other platyrrhine primates.

Although a different capuchin species, *Cebus imitator,* manipulates fruit that is relatively small and symmetrical using both hands, for the withdraw to the mouth, it preferentially holds the fruit and presents it to the mouth with one hand in a capuchin-precision grip involving the thumb and index finger (Whishaw et al., 2024). *Sapajus libidinosus* is here found to more frequently bring tubers to the incisors using both hands, but the animals still display specialization in hand use. One hand was favored in applying torque to the tuber when shredding it and this hand then continued to hold the tuber during chewing periods. The other hand was concomitantly used to manipulate portions of the tuber near the mouth and to reach for the tuber to regain a two-hand grasp. A comparison of the hand used for holding and for reaching revealed individual preferences in the capuchins, but no group preference. This observation is in line with findings that visually guided unimanual grasping-for-food actions performed by capuchins standing in a stable posture induced individual but not group-level asymmetries (Spinozzi et al., 2004; Truppa et al., 2016). The absence of a group asymmetry in two handed eating contrasts with a bimanual asymmetry reported in *Sapajus libidinosus* tool use (Salmi et al., 2023), suggesting that if handedness is lateralized in capuchins, lateralization might characterize only some hand-use actions.

As has been reported previously, precision grips involving interdigital grasping were not a feature of tuber eating as most tuber handling involved power grips in which the tuber was held by the fingers against the palms (Spinozzi et al., 2004; Truppa et al., 2016). Here we made the novel observation that the capuchins used a variety of power grips, especially when holding tuber roots and fibers. The capuchins held these relatively thin items between one or more distal phalanx pads and interdigital or palm pads; e.g., pad-to-pad grips. Other studies have shown that capuchins use the distal phalanx pads in locating fruit for grasping as well as for assessing its ripeness (Melin et al., 2022; Whishaw et al., 2024) and these pads are richly innervated by Meissner corpuscles (Melin et al., 2022) Possibly because string-like target objects have not been provided to the capuchins in studies of hand grip (Christel & Fragaszy, 2000; Costello & Fragaszy, 1988; Fragaszy et al., 2004; Mangalam and Fragaszy, 2015; Pouydebat et al., 2009; Spinozzi et al., 2004; Truppa et al., 2019), the capuchins' ability to hold such items between the distal phalanx pads and palm has not been previously observed. It is noteworthy that Spinozzi et al. (2004), in *Sapajus libidinosus,* and Nelson et al. (2023), in the spider monkey *Ateles fusciceps rufiventris,* have observed that monkeys pick up small food items from a table surface using a palm-down power grasp with flexed digits. Possibly, in making this grasp, the monkeys are making a distal phalanx pads-to-pad grasp. Digit tip to palm grasping is not noteworthy in humans (Wong & Whishaw, 2004), possibly because the behavior requires long fingers. Thus, the grasps displayed by the capuchins argues for an expansion of the definition of power grips to include various distal phalanx pads to palm grasps, a suggestion consistent with the idea that there are variations in power grips (Elliott & Connolly, 1984; Feix et al., 2016). Of special interest is the possibility that the ability to grasp an object between a finger distal phalanx pad and the palm may be an evolutionary precursor to precision grasping using the opposition of a pollex distal phalanx pad to finger pads.

The association of eye-disengage with an eye blink as food is brought to the mouth observed here in *Sapajus* is consistent with similar findings in humans, macaques and *Cebus* (de Bruin et al., 2008; Hirche et al., 2022; Karl & Whishaw, 2013; Sacrey et al., 2011; Whishaw et al., 2024). Here we found that gaze-related behavior subdivides withdraw-to-eat movements into three sequential parts. These include gaze associated food handling, gaze associated carry to the mouth, and gaze disengage carry to the mouth. The blink subdivides the gaze associated carry and gaze disengage associated carry movements. Suggested explanations for blinks include adjustments to the stress of accommodation, a protective response for the eyes, and an eye response for facilitating focus elsewhere (Ang & Maus, 2020; Jaschinski et al., 1996; Kiorpes, 2019). We favor the idea that blinks may augment a brain network change (Brych & Handel, 2020; Nakano et al., 2013). The visual demands of assessing the affordance of an uneaten tuber may be relieved by a blink, thus facilitating the somatosensory mediated carry that presents the tuber to the mouth for hand/mouth manipulation.

In conclusion, the objective of the present study was to describe hand use in tuber eating by *Sapajus* capuchins and assess the idea that food-oriented gaze to food held inhand could require visuomotor skills that might in turn contribute to visuocognitive control of object manipulation movements more generally. The platyrrhine *Sapajus libidinosus* uses vision when orienting food for withdraw to the incisors for peeling/shredding and withdraw to the premolars for chewing. The visuomotor ability to respond to the changing affordances of food underlying these eating decisions is likely be exploited in many ways including for reach-to-grasp acts and for tool manipulation.

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Conflict of Interest: We have no conflicts of interest to disclose.

Data Availability Statement: Videos are archived by Valentina Truppa and data summary used in the present study is archived by Ian Q Whishaw

References

An, X., Matho, K., Li, Y., Mohan, H., Xu, X. H., Whishaw, I. Q., Kepecs, A., & Huang, Z. J. (2022). A cortical circuit for orchestrating oromanual food manipulation. *bioRxiv*, 2022.2012.2003.518964. https://doi.org/10.1101/2022.12.03.518964

Ang, J. W. A., & Maus, G. W. (2020). Boosted visual performance after eye blinks. *Journal of Vision*, *20*(10), 2. https://doi.org/10.1167/jov.20.10.2

Bortoff, G. A., & Strick, P. L. (1993). Corticospinal terminations in two new-world primates: further evidence that corticomotoneuronal connections provide part of the neural substrate for manual dexterity. *Journal of Neuroscience*, *13*(12), 5105-5118. https://doi.org/10.1523/JNEUROSCI.13-12-05105.1993

Brych, M., & Handel, B. (2020). Disentangling top-down and bottom-up influences on blinks in the visual and auditory domain. *International Journal of Psychophysiology*, *158*, 400-410. https://doi.org/10.1016/j.ijpsycho.2020.11.002

Cartmill, M. (1972). Arboreal adaptations and the origin of primates. In R. Tuttle (Ed.), *The functional and evolutionary biology of primates* (1 ed., pp. 97-122). Aldine-Atherton.

Cartmill, M. (2012). Primate origins, human origins, and the end of higher taxa. *Evolutionary Anthropology*, *21*(6), 208-220. https://doi.org/10.1002/evan.21324

Chalk, J., Wright, B. W., Lucas, P. W., Schuhmacher, K. D., Vogel, E. R., Fragaszy, D., Visalberghi, E., Izar, P., & Richmond, B. G. (2016). Age-related variation in the mechanical properties of foods processed by *Sapajus libidinosus*. *American Journal of Physical Anthropology*, *159*(2), 199-209. https://doi.org/10.1002/ajpa.22865

Christel, M. I., & Fragaszy, D. (2000). Manual Function in *Cebus apella*. Digital Mobility, Preshaping, and Endurance in Repetitive Grasping. *International Journal of Primatology*, *21*(4), 697-719. https://doi.org/10.1023/A:1005521522418

Costello, M. B., & Fragaszy, D. M. (1988). Prehension in *Cebus* and *Saimiri*: I. Grip type and hand preference. *American Journal of Primatology*, *15*(3), 235-245. https://doi.org/10.1002/ajp.1350150306

Cruz-Rizzolo, R. J., De Lima, M. A., Ervolino, E., de Oliveira, J. A., & Casatti, C. A. (2011). Cyto-, myelo- and chemoarchitecture of the prefrontal cortex of the *Cebus* monkey. *BMC Neuroscience*, *12*, 6. https://doi.org/10.1186/1471-2202-12-6 de Bruin, N., Sacrey, L. A., Brown, L. A., Doan, J., & Whishaw, I. Q. (2008). Visual guidance for hand advance but not hand withdrawal in a reach-to-eat task in adult humans: reaching is a composite movement. *Journal of Motor Behavior*, *40*(4), 337-346. https://doi.org/10.3200/jmbr.40.4.337-346

Elliott, J. M., & Connolly, K. J. (1984). A classification of manipulative hand movements. *Developmental Medicine and Child Neurology*, *26*(3), 283-296. https://doi.org/10.1111/j.1469-8749.1984.tb04445.x

Falotico, T., Proffitt, T., Ottoni, E. B., Staff, R. A., & Haslam, M. (2019). Three thousand years of wild capuchin stone tool use. *Nature, Ecology and Evolution*, *3*(7), 1034-1038. https://doi.org/10.1038/s41559-019-0904-4

Feix, T., Romero, J., Schmiedmayer, H. B., Dollar, A. M., & Kragic, D. (2016). The GRASP Taxonomy of Human Grasp Types. *IEEE Transactions on Human-Machine Systems*, *46*(1), 66-77. https://doi.org/10.1109/THMS.2015.2470657

Fragaszy, D. M., & Crast, J. (2016). Functions of the Hand in Primates. In T. L. Kivell, P. Lemelin, B. G. Richmond, & D. Schmitt (Eds.), *The Evolution of the Primate Hand: Anatomical, Developmental, Functional, and Paleontological Evidence* (pp. 313-344). Springer New York. https://doi.org/10.1007/978-1-4939-3646-5_12

Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). The Complete Capuchin: The Biology of the Genus Cebus.

Gibson, J. J. (1977). The theory of affordances. In J. B. Robert E Shaw (Ed.), *Perceiving, acting, and knowing: toward an ecological psychology* (pp. pp.67-82). Hillsdale, N.J.: Lawrence Erlbaum Associates. https://hal.science/hal-00692033

Goldman-Rakic, P. S. (1992). Working memory and the mind. *Scientific American*, *267*(3), 110-117. https://doi.org/10.1038/scientificamerican0992-110

Grant, S., & Conway, M. L. (2019). Some binocular advantages for planning reach, but not grasp, components of prehension. *Experimental Brain Research*, *237*(5), 1239-1255. https://doi.org/10.1007/s00221-019-05503-4

Hirche, L. A., Cenni, C., Leca, J.-B., & Whishaw, I. Q. (2022). Two types of withdraw-to-eat movement related to food size in long-tailed macaques (*Macaca fascicularis*): Insights into the evolution of the visual control of hand shaping in anthropoid primates. *Animal Behavior and Cognition*, *9*(2), 176-195. https://doi.org/https://doi.org/10.26451/abc.09.02.02.2022

Iwaniuk, A. N., & Whishaw, I. Q. (2000). On the origin of skilled forelimb movements. *Trends in Neurosciences*, *23*(8), 372-376. https://doi.org/Doi 10.1016/S0166-2236(00)01618-0

Jaschinski, W., Bonacker, M., & Alshuth, E. (1996). Accommodation, convergence, pupil diameter and eye blinks at a CRT display flickering near fusion limit. *Ergonomics*, *39*(1), 152-164. https://doi.org/10.1080/00140139608964441

Jeannerod, M. (1981). Intersegmental coordination during reaching at natural visual objects. In J. Long & A. Baddeley (Eds.), *Attention and performance IX* (pp. 153-168). Erlbaum.

Jeannerod, M., Arbib, M. A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends in Neurosciences*, *18*(7), 314-320. https://www.ncbi.nlm.nih.gov/pubmed/7571012

Jeannerod, M., Paulignan, Y., & Weiss, P. (1998). Grasping an object: one movement, several components. *Novartis Foundation Symposium*, *218*, 5-16; discussion 16-20. https://doi.org/10.1002/9780470515563.ch2

Kaas, J. H. (2019). The origin and evolution of neocortex: From early mammals to modern humans. *Progress in Brain Reerach*, *250*, 61-81. https://doi.org/10.1016/bs.pbr.2019.03.017

Karl, J. M., & Whishaw, I. Q. (2013). Different evolutionary origins for the Reach and the Grasp: an explanation for dual visuomotor channels in primate parietofrontal cortex. *Frontiers in Neurology*, *4*. https://doi.org/ARTN 20810.3389/fneur.2013.00208

Kiorpes, L. (2019). Understanding the development of amblyopia using macaque monkey models. *Proceedings of the National Academy of Sciences U S A*, *116*(52), 26217-26223. https://doi.org/10.1073/pnas.1902285116

Lashley, K. S. (1951). The problem of serial order in behavior. In *Cerebral mechanisms in behavior; the Hixon Symposium.* (pp. 112-146). Wiley.

Macfarlane, N. B., & Graziano, M. S. (2009). Diversity of grip in *Macaca mulatta*. *Experimental Brain Research*, *197*(3), 255-268. https://doi.org/10.1007/s00221-009-1909-z

Mangalam, M., & Singh, M. (2013). Flexibility in food extraction techniques in urban free-ranging bonnet macaques, Macaca radiata. Plos one, 8(12), e85497. https://doi.org/10.1371/journal.pone.0085497

Melin, A. D., Veilleux, C. C., Janiak, M. C., Hiramatsu, C., Sánchez-Solano, K. G., Lundeen, I. K., Webb, S. E., Williamson, R. E., Mah, M. A., Murillo-Chacon, E., Schaffner, C. M., Hernández-Salazar, L., Aureli, F., & Kawamura, S. (2022). Anatomy and dietary specialization influence sensory behaviour among sympatric primates. *Proceedings of the Royal Society B Biological Sciences*, *289*(1981), 20220847. https://doi.org/10.1098/rspb.2022.0847

Moura, A. C., & Lee, P. C. (2004). Capuchin stone tool use in Caatinga dry forest. *Science*, *306*(5703), 1909. https://doi.org/10.1126/science.1102558

Nakano, T., Kato, M., Morito, Y., Itoi, S., & Kitazawa, S. (2013). Blink-related momentary activation of the default mode network while viewing videos. *Proceedings of the National Academy of Sciences U S A*, *110*(2), 702-706. https://doi.org/10.1073/pnas.1214804110

Napier, J. R. (1956). The prehensile movements of the human hand. *Bone and Joint Journal*, *38-b*(4), 902-913. https://doi.org/10.1302/0301-620x.38b4.902

Nelson, E. L., Taylor, M. A., Del Valle, A., & Pavon, N. (2023). Reach-to-grasp kinematic signatures in Colombian spider monkeys (*Ateles fusciceps rufiventris*). *Journal of Comparative Psychology*. https://doi.org/10.1037/com0000355

Oliveira, P., & Marquis, R. (2002). *The Cerrados of Brazil*. Columbia University Press. https://doi.org/10.7312/oliv12042

Peckre, L. R., Fabre, A.-C., Wall, C. E., Pouydebat, E., & Whishaw, I. Q. (2023). Evolutionary history of food withdraw movements in primates: Food withdraw is mediated by nonvisual strategies in 22 species of Strepsirrhines. *Evolutionary Biology*, *50*(2), 206-223. https://doi.org/10.1007/s11692-023-09598-0

Posner, M. I., Inhoff, A. W., Friedrich, F. J., & Cohen, A. (1987). Isolating attentional systems: A cognitive-anatomical analysis. *Psychobiology*, *15*(2), 107-121.

Pouydebat, E., Gorce, P., Coppens, Y., & Bels, V. (2009). Biomechanical study of grasping according to the volume of the object: human versus non-human primates. *Journal of Biomechanics*, *42*(3), 266-272. https://doi.org/10.1016/j.jbiomech.2008.10.026

Presotto, A., Remillard, C., Spagnoletti, N., Salmi, R., Verderane, M., Stafford, K., dos Santos, R. R., Madden, M., Fragaszy, D., Visalberghi, E., & Izar, P. (2020). Rare bearded capuchin (*Sapajus libidinosus*) tool-use culture is threatened by land use changes in northeastern Brazil. *International Journal of Primatology*, *41*(4), 596-613. https://doi.org/10.1007/s10764-020-00166-3

Preuss, T. M., & Goldman-Rakic, P. S. (1991). Myelo- and cytoarchitecture of the granular frontal cortex and surrounding regions in the strepsirhine primate *Galago* and the anthropoid primate *Macaca*. *Journal of Comparative Neurology*, *310*(4), 429-474. https://doi.org/10.1002/cne.903100402

Roncero, P., de Mendonça-Furtado, O., & Izar, P. (2023). Human-induced rapid environmental change: A case study showing negative impact on animal culture. *Journal for Nature Conservation*, *74*, 126424. https://doi.org/https://doi.org/10.1016/j.jnc.2023.126424

Rosenbaum, D. A., Chapman, K. M., Weigelt, M., Weiss, D. J., & van der Wel, R. (2012). Cognition, action, and object manipulation. *Psychological Bulletin*, *138*(5), 924-946. https://doi.org/10.1037/a0027839

Rosenbaum, D. A., Marchak, F., Barnes, H. J., Vaughan, J., Slotta, J. D., & Jorgensen, M. J. (1990). Constraints for action selection: Overhand versus underhand grips. In *Attention and performance 13: Motor representation and control.* (pp. 321-342). Lawrence Erlbaum Associates, Inc.

Sacrey, L. A., Travis, S. G., & Whishaw, I. Q. (2011). Drug treatment and familiar music aids an attention shift from vision to somatosensation in Parkinson's disease on the reach-to-eat task. *Behavioural Brain Research*, *217*(2), 391-398. https://doi.org/10.1016/j.bbr.2010.11.010

Salmi, R., Le, K., Silva, J. M., Conceição, D. P., Presotto, A., & Rodrigues Dos Santos, R. (2023). Hand preference in wild crab-eating capuchin monkeys (*Sapajus libidinosus*) in the coastal area of Northest Brazil. *American Journal of Primatology*, *85*(11), e23546. https://doi.org/10.1002/ajp.23546

Santos, L. P. C. d. (2015). Parâmetros nutricionais da dieta de duas populações de macacos-prego: *Sapajus libidinosus* no ecótono cerrado/caatinga e Sapajus nigritus na Mata Atlântica. *Biblioteca digitall*. https://doi.org/10.11606/T.47.2015.tde-10082015-110633

Sartori, L., Camperio-Ciani, A., Bulgheroni, M., & Castiello, U. (2015). Intersegmental coordination in the kinematics of prehension movements of macaques. *PLoS One*, *10*(7), e0132937. https://doi.org/10.1371/journal.pone.0132937

Scott, J. E. (2019). Macroevolutionary effects on primate trophic evolution and their implications for reconstructing primate origins. *Journal of Human Evolution*, *133*, 1-12. https://doi.org/10.1016/j.jhevol.2019.05.001

Spagnoletti, N., Visalberghi, E., Verderane, M. P., Ottoni, E., Izar, P., & Fragaszy, D. (2012). Stone tool use in wild bearded capuchin monkeys, *Cebus libidinosus*. Is it a strategy to overcome food scarcity? *Animal Behaviour*, *83*(5), 1285-1294. https://doi.org/https://doi.org/10.1016/j.anbehav.2012.03.002

Spinozzi, G., Truppa, V., & Laganà, T. (2004). Grasping behavior in tufted capuchin monkeys (*Cebus apella*): grip types and manual laterality for picking up a small food item. *American Journal of Physical Anthropology*, *125*(1), 30-41. https://doi.org/10.1002/ajpa.10362

Strick, P. L., Dum, R. P., & Rathelot, J. A. (2021). The cortical motor areas and the emergence of motor skills: A Neuroanatomical perspective. *Annual Review of Neuroscience*, *44*, 425–447. https://doi.org/10.1146/annurev-neuro-070918-050216

Sussman, R. W., & Raven, P. H. (1978). Pollination by lemurs and marsupials: an archaic coevolutionary system. *Science*, *200*(4343), 731-736. https://doi.org/10.1126/science.200.4343.731

Sussman, R. W., Tab Rasmussen, D., & Raven, P. H. (2013). Rethinking primate origins again. *American Journal of Primatology*, *75*(2), 95-106. https://doi.org/10.1002/ajp.22096

Sustaita, D., Pouydebat, E., Manzano, A., Abdala, V., Hertel, F., & Herrel, A. (2013). Getting a grip on tetrapod grasping: form, function, and evolution. *Biological Reviews*, *88*(2), 380-405. https://doi.org/10.1111/brv.12010

Truppa, V., Marino, L. A., Izar, P., Fragaszy, D. M., & Visalberghi, E. (2019). Manual skills for processing plant underground storage organs by wild bearded capuchins. *American Journal of Physical Anthropology*, *170*(1), 48-64. https://doi.org/10.1002/ajpa.23893

Truppa, V., Spinozzi, G., Laganà, T., Piano Mortari, E., & Sabbatini, G. (2016). Versatile grasping ability in power-grip actions by tufted capuchin monkeys (*Sapajus spp.*). *American Journal of Physical Anthropology*, *159*(1), 63-72. https://doi.org/10.1002/ajpa.22836

Visalberghi, E., & Trinca, L. (1989). Tool use in capuchin monkeys: Distinguishing between performing and understanding. *Primates*, *30*(4), 511-521. https://doi.org/10.1007/BF02380877

Withagen, R., De Poel, H. J., Araújo, D., & Pepping, G. J. (2012). Affordances can invite behavior: Reconsidering the relationship between affordances and agency. *New ideas in psychology*, *30*(2), 250-258. https://doi.org/10.1016/j.newideapsych.2011.12.003

Whishaw, I. Q., & Karl, J. M. (2014). The contribution of the reach and the grasp to shaping brain and behaviour. *Canadian Journal of Experimental Psychology-Revue Canadienne De Psychologie Experimentale*, *68*(4), 223-235. https://doi.org/10.1037/cep0000042

Whishaw, I. Q., & Karl, J. M. (2019). The evolution of the hand as a tool in feeding behavior: The multiple motor channel theory of hand use. In V. Bels & I. Q. Whishaw (Eds.), *Feeding in Vertebrates: Evolution, Morphology, Behavior, Biomechanics* (pp. 159-186). Springer International Publishing. https://doi.org/10.1007/978-3-030-13739-7_6

Whishaw, I. Q., Mah, M. A., Casorso, J. G., Chacon, E. M., Chalk-Wilayto, J., Laird, M. F., & Melin, A. D. (2024). The platyrrhine primate *Cebus imitator* uses gaze to manipulate and withdraw food to the mouth. *Animal Behavior and Cognition*, *11*(1), 1-23. https://doi.org/https://doi.org/10.26451/abc.11.01.01.2024

Willett, S. M., Maenner, S. K., & Mayo, J. P. (2023). The perceptual consequences and neurophysiology of eye blinks. *Frontiers in System Neuroscience*, *17*, 1242654. https://doi.org/10.3389/fnsys.2023.1242654

Williams, B. A., Kay, R. F., & Kirk, E. C. (2010). New perspectives on anthropoid origins. *Proceedings of the National Academy of Sciences U S A*, *107*(11), 4797-4804. https://doi.org/10.1073/pnas.0908320107

Withagen, R., de Poel, H. J., Araújo, D., & Pepping, G.-J. (2012). Affordances can invite behavior: Reconsidering the relationship between affordances and agency. *New Ideas in Psychology*, *30*(2), 250-258. https://doi.org/https://doi.org/10.1016/j.newideapsych.2011.12.003

Wong, Y. J., & Whishaw, I. Q. (2004). Precision grasps of children and young and old adults: individual differences in digit contact strategy, purchase pattern, and digit posture. *Behavioural Brain Research*, *154*(1), 113-123. https://doi.org/10.1016/j.bbr.2004.01.028

Wright, K. A., Biondi, L., Visalberghi, E., Ma, Z., Izar, P., & Fragaszy, D. (2019). Positional behavior and substrate use in wild adult bearded capuchin monkeys (*Sapajus libidinosus*). *American Journal of Primatology*, *81*(12), e23067. https://doi.org/10.1002/ajp.23067

Supplementary Materials

Video S1.

A two-hand hold and carry to the mouth of a tuber held by both hands in a parallel orientation by the capuchin Taís.

https://doi.org/10.6084/m9.figshare.26828263.v1

Note: the carry brings the central portion of the tuber to the incisors which bites off husk for ejection and meat for swallowing.

Video S2.

A one-hand hold and carry to the mouth of a tuber root that projects from the hand by the capuchin Taís.

https://doi.org/10.6084/m9.figshare.26828269.v1

Note: gaze is directed to the root extending from the hand and this portion of the root is brought to the premolars for chewing.

Video S3.

With no vision, a one-hand carry of a tuber root extending from the hand that misses the mouth by the capuchin Mansinho.

https://doi.org/10.6084/m9.figshare.26828272.v1

Note: the capuchin repeats the carry with gaze and is more accurate.