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

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Abstract – The details of the evolutionary steps in the transition from nonvisual guidance of hand movements for feeding, as displayed by many non-primate species, to visual guidance of hand movements in primates are sparse. Contemporary theory holds that a small-bodied stem primate evolved visual control of the reach to guide a hand to obtain small insects and fruit items from the terminal branches of trees. The subsequent evolution of the visual control of hand and finger shaping movements of the grasp of anthropoids is uncertain. The present study finds that Balinese long-tailed macaques (*Macaca fascicularis*), video recorded while spontaneously eating at the Sacred Monkey Forest Sanctuary in Ubud in Indonesia, displayed two types of hand movements associated with two types of withdraw movements to place food items in the mouth. Small food items were brought directly to the mouth with hand supination, often with no visual monitoring after grasping. Large food items that protruded from the hand were visually monitored to orient the food item on the initial part of the withdraw but visually disengaged with a head movement and often a blink before the item was placed in the mouth. The results are discussed in relation to the idea that visual information related to orientating food items of varying sizes to an appropriate position in the mouth contributed to the evolution of the visual control of hand shaping skills in anthropoid primates.

Keywords – Hand posture, Feeding, Hand withdrawal, Long-tailed macaques, Visual engagement, Grasping, Primate vision

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Animals have evolved a remarkable number of ways to get food into the mouth, and among them, skilled hand use is a formidable asset used by many species of terrestrial vertebrates (Bels & Whishaw, 2019). The act of using a hand to eat consists of at least three movements: a reach that takes the hand to a food item, a grasp that adjusts the orientation of the hand/digits to purchase/manipulate a food item, and a withdraw that brings a food item to the mouth (Karl & Whishaw, 2013; Whishaw & Karl, 2014). These movements are used in different ways by animals in the many orders of vertebrates that use their hands to assist in feeding (Iwaniuk & Whishaw, 2000; Sustaita et al., 2013; Whishaw & Karl, 2019). Cartmill's (1972, 1974, 1992, 2012) visual-predation theory and Sussman's (1991; Sussman & Raven, 1978; Sussman et al., 2013) primate-angiosperm theory propose that visual guidance of the reach evolved 65 mya in a stem

primate foraging on the terminal branches of trees. The visual control of hand and finger shaping movements used in precision grasping likely evolved in stem anthropoids much later, about 37 mya (Bishop, 1964; Christel, 1993; Christel & Fragaszy, 2000; Macfarlane & Graziano, 2009; Marzke et al., 2015; Peckre et al., 2019; Pouydebat et al., 2008; Scott, 2019). The influences that shaped the evolution of this ability are unknown. The act of withdrawing food to the mouth may have contributed to the visual control of hand shaping but little research has been directed to describing the visual control of the withdraw. The aim of the present study is to fill this gap, especially focusing on the contribution of the withdraw in orienting food items of varying sizes toward the mouth.

The ability of animals to withdraw food items to the mouth by using their hands poses challenges in terms of sensorimotor coordination. Because humans can hold small food items between the fingers, it is likely that somatosensory guidance can accurately direct these items to the mouth. For example, experimental studies with humans show that the fingers can be accurately directed without vision to various parts of the body (Edwards et al., 2005) as well as to the mouth (de Bruin et al., 2008; Karl et al., 2012; Sacrey et al., 2011). If a food item is large and protrudes from the hand, however, and if the distal portion of the food is to be placed in the mouth, somatosensory information from the hand is likely insufficient to direct the distal end of the food item to a mouth target. Animals solve the problem of getting large items of food into the mouth in different of ways. Among marsupials, gray short-tailed opossums (*Monadelphis domestica*) use a wide-open mouth to receive large prey (Ivanco et al., 1996), whereas tree kangaroos (*Dendrolagus*) use tactile cues on the mouth in conjunction with head movements to assist their hands in positioning vegetation accurately to the mouth (Iwaniuk et al., 1998). Rodents that eat food items that protrude from the hand use vibrissae cues and head movements to assist in bringing food to the mouth (Whishaw & Coles, 1996; Whishaw et al., 1998, 2018, 2020). To date, there has been no study of how humans or other primates solve the large food size withdraw problem. Here we describe that in macaques, vision plays a role in the appropriate positioning of large food items that protrude from the hand so that they can be directed to the mouth. Our description of how vision guides the withdraw also provides insights into how vision may have evolved to control the skilled movements of the hands and fingers in anthropoid primates.

A free-ranging population of long-tailed macaques (*Macaca fascicularis*) was videorecorded as they ate both large and small food items. These macaques are an anthropoid member of the subfamily *Cercopithecinae* that display excellent visual control of hand movements for manipulating objects (Pouydebat et al., 2008). In this study, the food items were provisions that the macaques received from caretakers to keep them from pillaging crops. Variables of interest were obtained from a frame-by-frame analysis of video records of the withdraw movements used to bring food to the mouth after it had been grasped. The results provide a detailed description of two types of withdraw movements used by the macaques and the contribution of vision to getting the large food items into the mouth.

Materials and Methods

Ethics Statement

This study was a purely observational study of wild, free-ranging long-tailed macaques. Research permission was given by the management and staff of the Ubud Monkey Forest.

Animals

Eating behavior was filmed in 63 long-tailed macaques (26 males, 37 females) ranging in age from juvenile (i.e., no longer carried by the mother; $n = 20$) to adult ($n = 43$). The animals are part of a population of free-ranging, urban-dwelling, habituated and provisioned Balinese long-tailed macaques. The macaques live in and around the Sacred Monkey Forest Sanctuary in Ubud, central Bali, Indonesia. The study site, also known as the Ubud Monkey Forest, is a forested area surrounded by human settlements and Hindu temples. In 2019, when the data were collected, the study population totaled approximately 1,000

individuals and was comprised of seven neighboring groups with overlapping home range areas (Giraud, 2021). The group of macaques that were video recorded for the present study are provisioned at multiple feeding stations at least three times per day (i.e., early morning, midday, and end of afternoon) with fruits and vegetables by the temple staff.

Video Recording

Video recording (30 fps) provided *ad libitum* samples of eating behavior of the macaques during food provisioning. In all, 44 video samples totalling 1h 45 m were collected by CC and two research assistants at the feeding stations during the three feeding times, between 8:00 hr and 17:00 hr, and across four days of observation. CC named each macaque on the soundtrack of the video recording to supplement chest tattoos that identified some of the animals. Because the macaques were habituated to tourists walking about the feeding stations, the observers were able to walk around and film the individual animals from within 3 to 5 meters as they sat and ate. Video-recorded data were collected by using handheld Sony Handycam cameras, model HDR-CX675, model HDR-PJ670, and model HDR-PJ540.

Food Items

The large food items were cut up corn cobs, sweet potatoes and bananas and the small food items were nuts, pieces of corn, pieces of sweet potatoes and pieces of fruit. In Balinese long-tailed macaques, the size of the palm of the hand ranges between 3 and 5 cm, from juveniles to adults, respectively, with no marked differences between males and females (Cenni et al., 2021). The small food items could be held in a pincer grasp while not protruding whereas large food items protruded from the hand.

Behavioral Analysis

Video Analysis

The video recordings of macaques eating were examined frame-by-frame using *Quicktime 7.7* (https://support.apple.com/en-ca/guide/quicktime-player/welcome/mac) on an Apple computer. The macaques were only observed to pick up food with one hand (see Regaiolli et al., 2016). The unstructured eating environment and the variable number of reaches obtained from different animals precluded an analysis of handedness. LAH and IQW developed the scoring systems and performed the frame-by-frame video analyses with an inter-scorer reliability coefficient of 0.96. Discrepancies in scoring were reconciled by rescoring (Hallgren, 2012). Every eating event in which a macaque was clearly visible from a front or side view was analyzed. Sometimes a macaque would withdraw a food item to the nose to sniff, and this behavior was analyzed separately from eating behavior. The events in which there were disturbances associated with feeding, including the "threatening" movement of one macaque to another and the movement of tourists and caretakers in the feeding area that interrupted feeding were discarded from the analysis. This selection left the large sample of eating behaviors analyzed here from macaques that ate while being relatively undisturbed (see below). We quantified the following variables from the video recording:

Body Posture. A macaque could adopt various postures when initially picking up a piece of food or when placing a food in the mouth. Posture was scored with each reaching and withdraw movement as:
(1) Sit: a macaque sat on its haunches when it reached for a food item with a single hand or when it withdrew a food item to the mouth with one or both hands.
(2) Stand: the macaque was standing when it reached for a food item with a single hand or when it withdrew a food item to the mouth with a single hand.

Withdraw-to-Mouth Movements. Two types of withdraw movement were recorded:

(1) Ground-withdraw: a food item was picked up from the ground and brought directly to the mouth without pause. Ground-withdraws were observed as happening with small or large food items.

(2) Inhand-withdraw: a food item that had previously been picked up and was being held in a hand, was brought to the mouth. Inhand-withdraws were observed as happening with small or large food items, and we documented whether they were made with one hand or two hands.

Hand Grasps. The macaques made different types of hand grasps when initially grasping and handling food items. Hand posture was recorded both when a food item was picked up and when a food item was transferred to the mouth as:

(1) *Pincer grasp*: a food item was grasped or held between the first two fingers (pollex and index finger).

(2) *Whole hand grasp*: a food item was grasped or held between the pollex and two or more of other fingers. Whole hand grasps can be subdivided into precision grasps in which an item is held with the digit tips and whole hand grasps in which the item is also held against the palm (Felix et al, 2015; Fragaszy, 1968), but because use of the palm was difficult to identify this distinction was not made here.

Head Posture for Taking Food from the Hand and Mouth Bites. When the macaques grasped the food with the mouth, they could do so with the mouth front (incisors) or the mouth side (molars). When grasping or biting a piece of food from a larger food item they could do so with a single bite or with more than one bite. Head posture in taking food was rated as *front* (incisors) or *side* (molars) and the number of bites associated with taking each food item were counted.

Visual Attention. When food items were grasped, if the head of the macaque was oriented toward the food at the time that the grasp occurred, that was taken as a sign that the macaque was looking at the food; i.e., visually engage as defined by Posner et al. (1987). The following orienting behaviors were quantified:

(1) *Head-engage*: a movement that resulted in the face being directed toward the food item before or as it was grasped.

(2) Head-disengage: a movement that resulted in the face being directed away from the food item that had been grasped.

(3) Eye blink: Eye blinks were rapid closing and opening of the eyelid. The occurrence of a blink was noted for those video recordings for which a view of the eyes was adequate and as a proportion of all withdraw movements (cf. de Bruin et al., 2008).

(4) Eye-disengage: an eye-disengage was scored if upon head-disengage a macaque was observed to be looking toward a location other than the food item that was being brought to the mouth.

Behavior Duration. Movement duration was obtained by counts of video frames (30 fps) converted to seconds for the following behaviors:

(1) Withdraw time. For each withdraw movement, the first video frame in which the hand grasping the food began to move toward the mouth was designated as the "0" frame for withdraw initiation. Withdraw time was the number of frames taken from the "0" frame of withdraw initiation to the frame at which the hand stopped moving as it reached the mouth.

(2) Disengage time. The video frame at which the first movement associated with head -disengage occurred was identified in relation to the "0" frame of withdraw (cf. de Bruin et al., 2008).

Withdraw-to-Sniff. Withdraw-to-sniff movements were movements associated with the withdraw of a food to the nose to sniff. Head orientation during sniffing movements were scored in the same way as were eating movements.

Kinematic Measures. Selective kinematic reconstructions of head and hand movements associated with eating were made using *Physics Tracker* (https://physlets.org/tracker/), an open-source program for

video analysis. Head movement was recorded by digitizing the tip of the nose and hand movement was digitized at the first knuckle of the first finger (the joint between the distal and proximal phalanges of the pollex). Every frame of a measured behavior was digitized, and the results were transposed to produce a velocity graph of movement. Video samples were used for which both body points were visible throughout the withdraw movement. Relative measures of hand and head movement distances were obtained using *PixelStick* (https://plumamazing.com/product/pixelstick/), a pixel-based measuring tool.

Statistical Analyses

We tested the effect of withdraw movements, duration, and visual attention according to the food item size, subject age and sex using repeated ANOVAs and t-tests for paired samples using the program SPSS (v.24.0.0). Results are reported as mean ± standard error. A *p* value of < .05 was considered statistically significant and a partial eta squared (ηp^2) was used to measure the effect size (Kelley & Preacher, 2012). Counts of behaviors including posture, grasping type, and food size, engage and disengage, blinking and eye direction are reported as the percent of the number of observations that were made. The relationship between the duration of the ground-withdraw and in hand-withdraw movements to head-engage and disengage duration were assessed using the Pearson product-moment correlation.

Results

When reaching for food, holding food, and withdrawing food to the mouth, the macaques were in a sit posture on 96.5% (*n* = 1,085 of 1,124) of the observations. Of the remaining occasions, a macaque was standing on three legs (*n* = 38) or was standing on two hind legs (*n* = 1). Figure 1 illustrates individual macaques in sitting postures as they engaged eating related behaviors including reaching, holding, and bringing food to the mouth and sniffing.

Figure 1

Members of a Group of Macaca fascicularis Eating Corn at a Provisioning Station.

Note. The different feeding activities: (1) "Lard" reaching for a large food item, (2,3) "S-7" and a juvenile female sniffing a food item, (4) "Batsy," a juvenile female looking a corn cob, (5) "Temple" bringing a food item to the mouth, and (6) "Lookout" holding a cob of corn in the mouth and manipulating another cob of corn in its hand. Also note the eating posture of sitting with elbows resting on the knees.

Ground-Withdraw Movements

Ground-withdraws were obtained from 26 macaques that made a ground-withdraw with one or more small food items and 46 macaques that made ground-withdraws with one or more large food items. Video 1 (Appendix) illustrates a representative ground withdraw that brought the hand holding a food item directly, without a pause, to the mouth. Before making a ground-withdraw movement, the macaques made a head-engage movement that consisted of turning their face toward the target item on 100% (206 of 206) of the movements and then made a head-disengage movement before the food item contacted the mouth on 96.8% (200 of 206) of the movements.

For ground-withdraw movements with small food items, the macaques appeared to display head-disengage at any point during the withdraw, including at about the point of grasping (Figure 2). With larger food items head-disengage occurred only during the last portion of the withdraw movement. These observations were confirmed by statistical analyses on frame by frame counts of the ground-withdraw and head-engage behaviors. The duration of head-engage was shorter than ground-withdraw time for both small and large food items, Movement duration ($F(1,70) = 206.61$, $p < .001$, $\eta p^2 = .75$). Follow-up tests on the significant finding of an interaction between Food size and Movement duration, $F(1,70) = 36.10$, $p < .001$), showed that head-engage duration was shorter for ground-withdraw movements with small food items than with large food items (Figure 3).
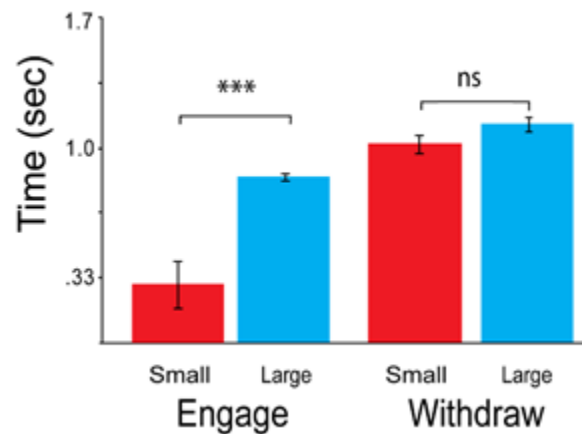
Figure 2

A Long-tailed Macaque Named "Langur" Reaching for a Small Food Item.

Note. A. The food item is visualized for grasping. B. As grasping is complete, vision is disengaged by looking away. C. Most of the withdraw is completed without vision directed toward the food.

Figure 3

Time (Mean and Standard Error) of Engagement After Grasping for Small and Large Food Items and Total Time to Withdraw to the Mouth


Note. The earlier disengage is related to small food items vs large food items. ***$p < .001$

A correlation between the duration of the ground-withdraw movement and the duration head-engage with small food items was not significant, $r(23) = .30$, $p > .05$ (Figure 4A). A correlation between the duration ground-withdraw movements and the duration of head-engage with large food items was significant, $r(66) = .967$, $p < .001$ (Figure 4B). Thus, head-engage duration appeared more important to the withdraw of large vs small food items.

Figure 4

*Relations Between Head-Disengage and Food Size*
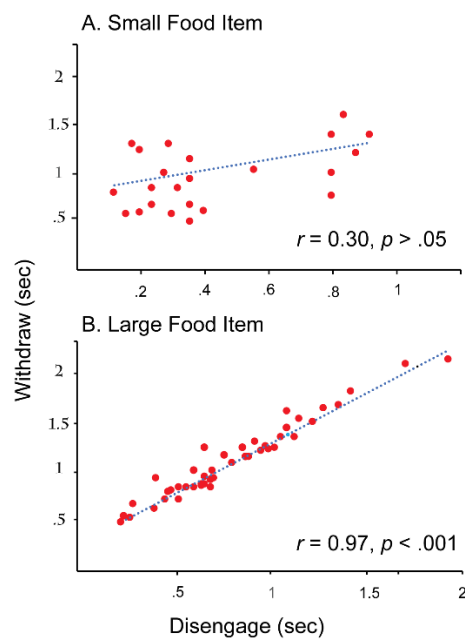
Note. A. Relation between ground-withdraw time and head-disengage time for small food items. B. Relation between ground-withdraw time and head-disengage time for large food items.

Inhand-Withdraw Movements

Inhand-withdraw movements were recorded from 61 macaques and gave a total of 918 movements (mean of 15 ± 5 per animal), and an example is shown in Video 2 (Appendix). Before making an inhand-withdraw movement, a macaque made a head-engage of the food item followed by a head-disengage before the food item was placed in the mouth (918 of 918 inhand-withdraws). A representative example of head-disengage is shown in Figure 5, in which the animal is first looking at a piece of corn cob held in the hand (Figure 5A), followed by a head-disengage as the hand begins to bring the food item toward the mouth (Figure 5B). Figure 5C illustrates the relative velocity of movement of the head and the hand. The hand follows the movement of the mouth and catches up to the mouth, both because hand velocity is faster than head velocity, and because the head stops moving.

Figure 5

Visual Disengage with Withdraw by a Long-Tailed Macaque Named "Mini Koba"
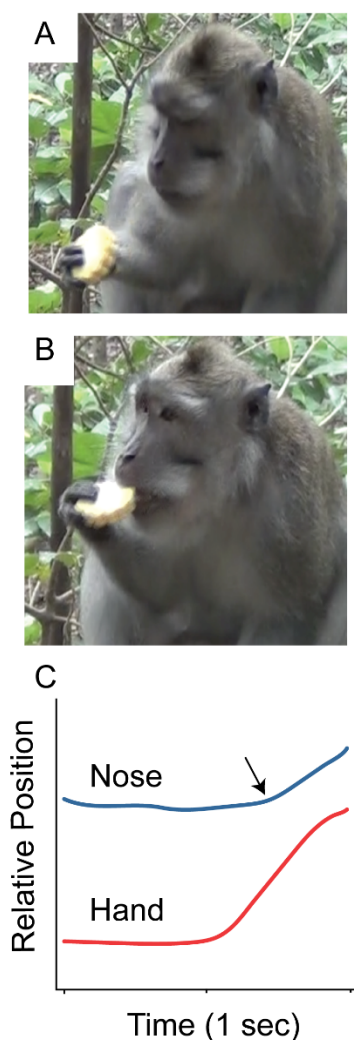

Note. A. The macaque visually inspects a piece of corn cob held in its hands. B. The macaque raises its head and visually disengages from the food during the withdraw. C. Relative position of the head and the hand during withdraw. The arrow marks the point of head-disengage.

That head-disengage always occurred before the food reached the mouth was confirmed by a statistical test on frame counts that revealed a shorter duration for head-engage vs the duration of the inhand-withdraw movement, $t(59) = 9.38$, $p < .001$. Figure 6 illustrates the point of head-engage and head-disengage and duration of 65 hand withdraws for the macaque "Serenade," a representative animal that also provided the largest number of withdraw movements. Figure 6A shows a starting point, with the forearm extended in a horizontal orientation with the food item positioned in a supinated hand at the time of head-engage. The red dot shows the average point in terms of hand movement time to head-disengage relative to the starting position. For this macaque, average head-disengage occurred 47% of the way through the withdraw. The correlation between head-disengage time and total withdraw time was significant for Seranade, $r(64) = .79$, $p < .001$, suggesting that head-engage was important for the initial part of the withdraw movement. That head-engage/inhand-withdraw relationship in this macaque was similar to that of the study group as confirmed by the finding of a significant correlation obtained from an analysis of the combined results of all of the macaques, $r(60) = .90$, $p < .001$.

Figure 6

Head-Disengage for Inhand-Withdraw by a Macaque Named "Serenade"
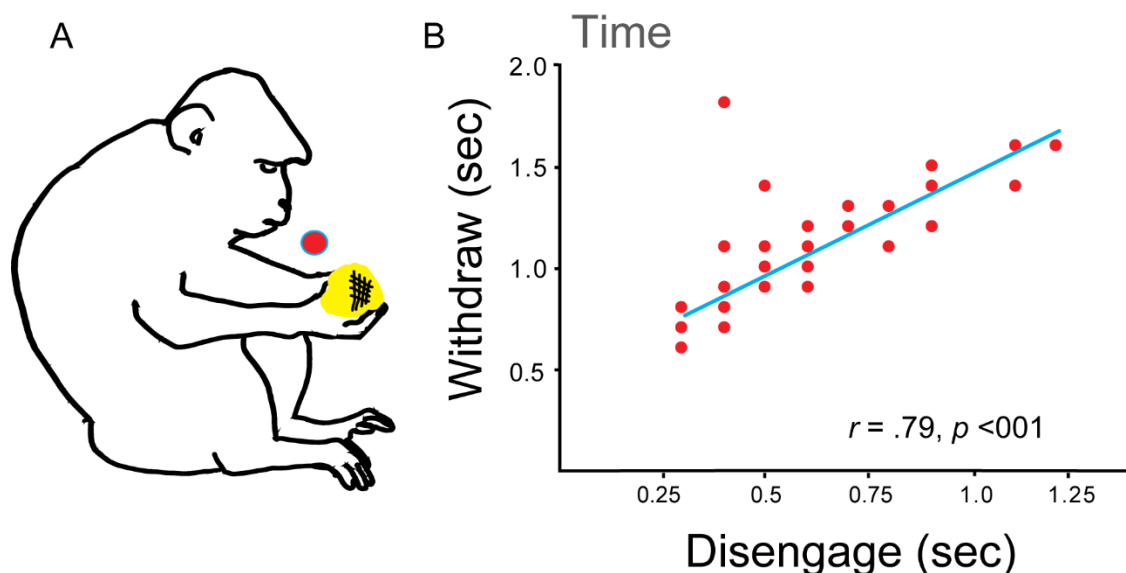
Note. A. Food eating posture with inhand food items with the elbow resting on the knee and the lower arm in a horizontal position. The red dot indicates the point of visual disengage relative to the start of the withdraw movement as determined by movement time. B. Relation between withdraw time and disengage time. The significant correlation suggests that although the withdraw time may vary, the withdraw is dependent upon vision.

Because the macaque sample consisted of a mix of female and male animals of varying age, analyses of time to disengage vs total inhand-withdraw time were made as a function of age and sex. There was no significant age difference (juvenile vs adult) in time to disengage, $F(1,59) = 0.27$, $p = .60$, or total time to withdraw, $F(1,59) = 0.84$, $p = .36$. There was no significant effect of sex (male vs female) in time to disengage, $F(1.59) = 0.26$, $p = .61$, or total time to withdraw, $F(1,59) = 0.10$, $p = .74$.

Food Manipulation and Withdraw

Of the 1,124 withdraw movements, 323 were made with a single hand, 767 were made with two hands, and 34 were made with both hands and one foot.

For each withdraw, we examined the hand/food movement to determine whether there was a change in food position associated with head engage. Of the 1,124 withdraws, 896 were observed to be associated with changes in food position. For ground-withdraws, when the food was grasped, the hand was pronated and by the time the hand reached to the mouth it was supinated. Thus, food positioning was a part of the ground-withdraw movement. For inhand-withdraws, food positioning movements included those in which one or both hands might pronate or supinate, flex, or extend, or change relative orientation, thus changing the orientation of the food item before it was brought to the mouth. Changes in food orienting included those in which the food was moved further away or closer before the withdraw began, as if a macaque was focusing vision on some part of the food item. The food positioning movements were seemingly directed to positioning a protruding portion the held food item so that it could be presented to the mouth.

Figure 7

*Blink with Disengage by a Macaque Named "Connie"*
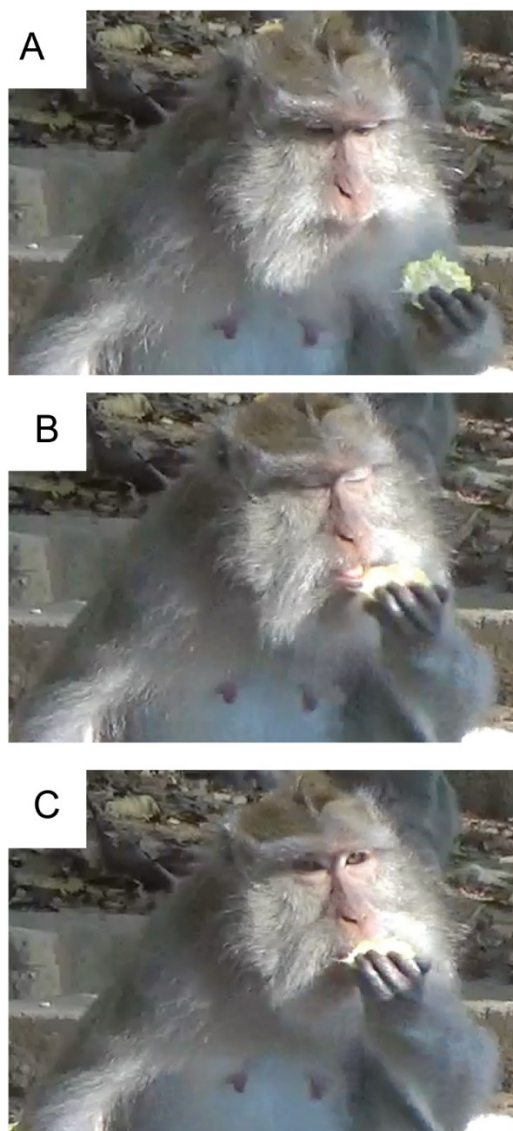
Note. A. She visually engages the kernels of a corn cob that she will bring to the mouth for eating. B. After she begins the withdraw, she head-disengages and blinks. C. When the food reaches the mouth, she is looking elsewhere.

Figure 8 shows two different food positioning movements by a macaque eating a slice of corn. In Figure 8A, as the macaque visually engages a corn cob, it supinates the hand so that an uneaten piece of corn (located on the left side of the cob) is oriented toward its mouth. In Figure 8B, that portion of the corn is placed in the mouth. In Figure 8C, as the macaque similarly engages the corn cob and begins the withdraw, it pronates its hand and orients an uneaten piece of corn (located on the right of the cob) to its mouth. In Figure 8D, that part of the corn cob is placed in the mouth. Note that for these examples the changes in food orientation are taking place at about the time of the initial portion of the withdraw during head-engage. Some of the inhand-withdraws were not associated with changes in food orientation and these instances were associated with large sweet potatoes ($n = 178$) and previously uneaten pieces of corn ($n = 44$). These were food items that were symmetrical and held in such a way that positioning change would likely not affect the way that the food was presented to the mouth for a bite.

Figure 8

Positioning of the Food During Visual Inspection of the Food by a Long-Tailed Macaque Named "Connie"
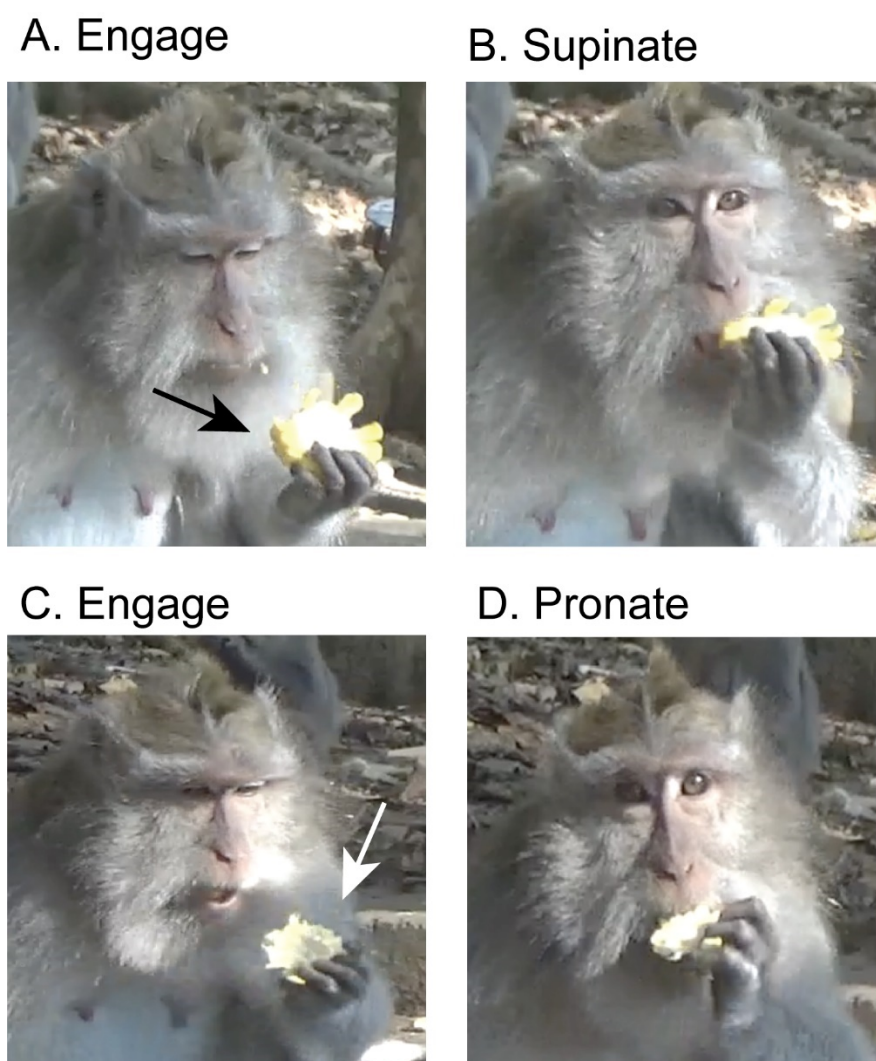

Note. A. She visually identifies some uneaten kernels of corn (arrow) on a corn cob and then (B) supinates the hand during withdraw to present the uneaten kernels to the mouth. C. She visually identifies some uneaten kernels of corn on a corn cob (arrow) and then (D) pronates the hand during withdraw to present the uneaten kernels to the mouth.

Head Posture for Taking Food from the Hand and Mouth Bites

Although every head-disengage consisted of an upward movement, the head orientation relative to the food as it was accepted by the mouth could vary depending on the terminal head angle and how the withdraw brought food to the mouth. On 89% (1,001 of 1,124) of withdraw movements, the food was grasped with front of the mouth and on 11% (123 of 1,124) of withdraw movements, the food was grasped with the side of the mouth. Figure 9A shows the mouth is raised relative to a hand so that a large food item could be grasped with the incisors. Figure 9B shows the head turned to the side relative to a hand so that the macaque could bite a large food item with its molars.

Figure 9

Head Position with Food Acceptance
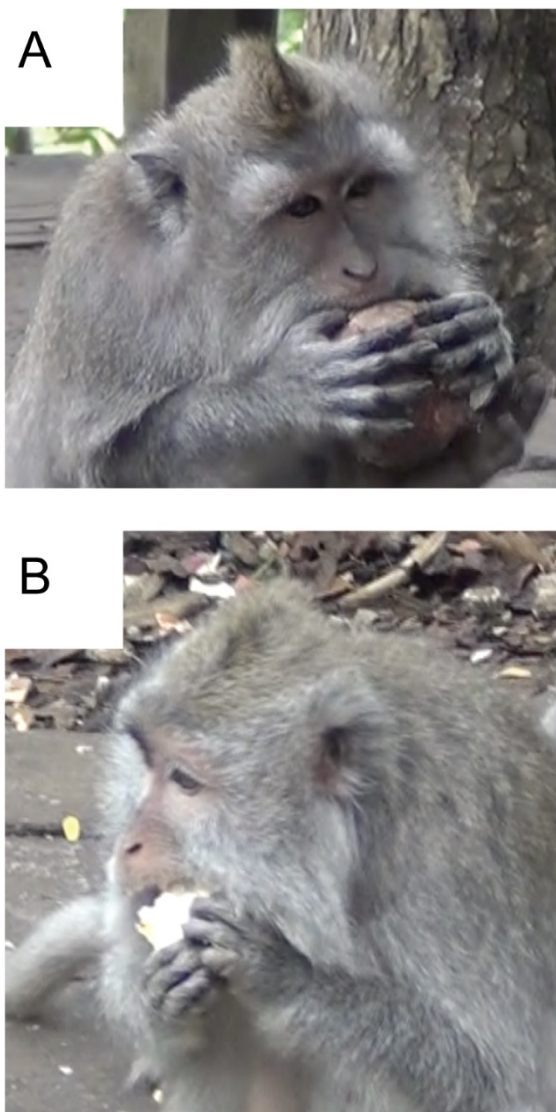
Note. A long-tailed macaque named "Yetta" presents a large food item to the front of its mouth with the head raised so that it can grasp the food with a single bite with the incisors. B. A long-tailed macaque named "Nancy" presents a large food item to the side of its mouth with the head raised and turned so that the food can be grasped with a single bite by the molars.

When a food item was brought to the mouth it was accepted with a single bite on 91% (1,024 of 1,124) of instances. These single bites accepted the entirety of 137 smaller food items and removed a piece of food from 987 large food items. On 9% (100 of 1,124) of occasions a macaque made as many as 2, 3, or 4 bites before removing a piece of food from a large food item. Some repeated bites were made with bananas (29 of 100) during which a macaque was attempting to remove the banana from the banana peel whereas the others (55 of 100) involved attempts to remove a piece of sweet potato from the whole potato. The remaining repeat bites may have occurred because a macaque did not obtain a bite on a first attempt.

Eye Blinks and Eye Disengage

Eye blinks, a brief closure of the eyelids, were observed in association with head-disengage but were not observed at any other point of food grasping or food withdraw. Figure 7A illustrates a macaque that is looking at a food item held in the hand. Figure 7B illustrates an eye blink as the macaque makes a head-disengage during the withdraw. Figure 7C shows that the macaque's head and gaze are oriented elsewhere as the withdraw reaches the mouth. Eye blinks were recorded with 21% (43 of 206) of ground-withdraw head-disengage movements and 27% (251 of 918) of inhand-withdraw head-disengage movements. Because the macaques were video recorded from a vantage point that was somewhat above them, their eyes were frequently not fully visible on many of the withdraws. For all animals for which the video recording gave an adequate view of the face for judging eye blinks, blinks occurred on 43.7% of withdraw movements. Macaques for which the largest numbers of observations were obtained with the face in view, gave the following instances of blinks associated with head-disengage; "Connie": 22 of 50 (44%); "Wayan Flange": 23 of 25 (92%); "Yeti": 20 of 33 (61%).

At the completion of head-disengage, the macaques were observed to be looking away and not down toward the food item that was being brought to the mouth on 96.9% (1,090 of 1,124) of withdraw movements.

Figure 10

Comparison of Withdraw for a Sniff and Withdraw to Eat by a Long-Tailed Macaque Named "Ivan"
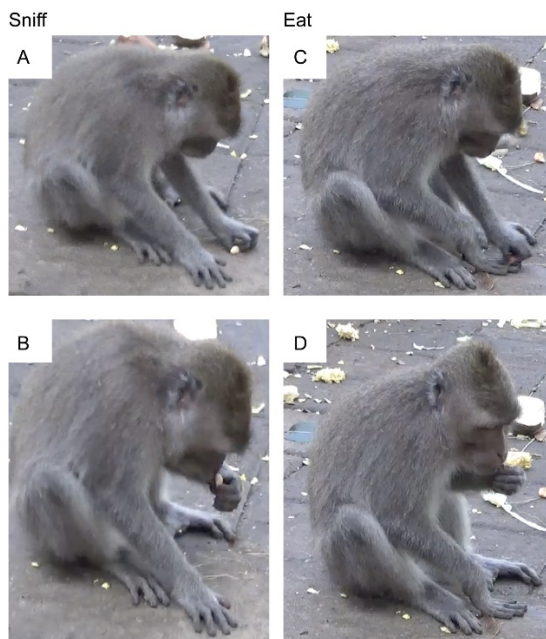
Note. A-B. Sniff: the head is down as he visualizes the food and grasps it with a precision grasp and the head maintains its position or even lowers slightly during the withdraw of the food item to the nose. C-D. Eat: the head is down as he visualizes the food and grasps it with a precision grasp, but the head is raised and disengages the food as he withdraws the food item to the mouth.

Withdraw to Sniff

There were occasions in which a macaque picked up both small or large food items and withdrew them directly toward its nose to sniff them, and 57 of these sniffs were observed. With sniffing, the head remained engaged and down, it was not possible to determine for how much of the withdraw was associated with visual engage. Figure 10 A-B shows a withdraw movement associated with sniffing a small object in which there is no head-disengage. Figure 10 C-D illustrates the head-disengage associated with bringing a small food item directly to the mouth.

Discussion

The objective of this study was to determine the sensory control used by macaques to bring small pieces of food held within the fingers vs large pieces of food that protruded from the hand to the mouth. Visual disengage from small food items held in the fingers could occur at any time during the withdraw, suggesting that small food items are not necessarily guided to the mouth using vision but are likely guided by somatosensation. A visual engage with larger food items as the withdraw was initiated and was associated with food positioning movements suggests a role for visual guidance. We propose that a longer visual inspection, longer holding, and associated food positioning of large food items may have played a role in the evolution of the visually dependent hand shaping movements displayed by anthropoid primates.

When reaching for food and when withdrawing food to the mouth, the macaques most often adopted a sitting posture. Sitting may have been the preferred posture for reaching for food because food was readily available but even when food was picked up by a macaque in a standing posture, sitting was quickly adopted for eating. A sitting posture for eating appears to be a featured posture in euarchontoglires, including rodents, strepsirrhines, and anthropoids (Reghem et al., 2011; Whishaw et al., 1988), even though the same species show large differences in how they withdraw food to the mouth for eating. As documented here for the macaques, a sitting posture may contribute to food visualization, manipulation and withdrawing to food for presentation to the mouth. Nevertheless, a more extensive analysis of eating postures in macaques in different feeding situations might suggest that sitting is useful but not essential for making a visually dependent withdraw.

Although the macaques visualized small food items to grasp them, visualization did not appear essential for the withdraw because the macaques often quickly visually disengaged the hand with a head movement making a withdraw without visual monitoring. Moreover, in some cases, visual disengagement occurred even before an object was fully grasped. A similar early disengage by head movement with an accompanying eye disengage and blink has been reported for human participants who are reaching for small pieces of food to withdraw to the mouth for eating (de Bruin et al., 2008; Sacrey et al., 2011). The human participants wore eye tracking glasses and so the documentation of visual disengage and blinking at about the time that grasping took place could be monitored. This methodology could be useful for the future study of the withdraw movement in macaques. The early disengage for small food items suggests that somatosensation provided by finger contact with the food item is sufficient to accurately bring a small item of food to the mouth (Karl et al., 2012). This conclusion is supported by visual occlusion experiments with human participants. Visual occlusion does disrupt the reach for a small food item but does not disrupt the withdraw of the same item (de Bruin et al., 2008; Sacrey et al., 2011).

The early head-disengage from a small item of food may occur for a number of ancillary reasons. First, once the grasping movement is initiated, it is likely that any error in the grasp would then occur so quickly that it could not be corrected by visual feedback (Hayashi et al., 2020). Second, disengage may allow a shift in visual attention from the food to the surroundings of the animal, perhaps to search for the next food item or to monitor a competitor (Raffi et al., 2020; Vieweg & Müller, 2020). In our study, we noted that there were frequent interruptions of eating by a macaque in relation to the approach of other macaques and people. Eating macaques did seem attentive to and monitored the movements of their congeners and people.

Visual attention to large food items during inhand-withdraw movements appeared essential for the early portion of a withdraw. At this point in the withdraw, head-engage was associated with positioning the food item suggesting that food positioning required vision. Vision is also likely used to calculate the trajectory of a protruding part of the food item to an appropriate position in the mouth. When the food item reached the mouth, it was taken with a single precise bite suggesting that the target was precalculated. Nevertheless, because head disengage occurred before the food item reached the mouth, somatosensation likely contributes to the latter part of the withdraw movement. The visual engage described here, although specific for orchestrating the withdraw, likely also contributes to the many hand and finger shaping movements that can occur with manipulating a food item before the withdraw to the mouth (see Macfarlane & Graziano, 2009, for a description of some hand manipulation movements).

The use of vision to assist in determining an orientation and trajectory of a food item relative to the mouth may be an anthropoid innovation. As noted in the introduction, animals have evolved a remarkable number of ways to get food into the mouth and the results of the present study suggest that the macaques exhibit two strategies. For small food items that are enveloped in the fingers, they use somatosensation, whereas for large food items they additionally use vision. Preliminary observations on human children and adults show that they, like macaques, visualize large food items, including food items on a fork, more than small items (Whishaw et al., unpublished data, see also, de Bruin et al., 2008; Sacrey et al., 2011) suggesting that the behavior is widespread amongst anthropoids. In our repository of film of anthropoid eating, we have observed similar behavior in chimpanzees (*Pan troglodytes*), capuchin monkeys (*Cebus albifrons*) and squirrel monkeys (*Saimiri oerstedii*). Other non-primate species for which descriptions are available, including marsupials and rodents, use somatosensory information combined with head movements (Ivanco et al., 1996; Iwaniuk et al., 1998; Whishaw & Coles, 1996; Whishaw et al., 1998, 2018, 2020). An examination of the withdraw movement of strepsirrhines shows that they make extensive use of head movements to take food from the hand, do not monitor food during the withdraw and do not take the food with single precise bite (Peckre et al., unpublished manuscript).

The findings of the present study, related to the visual control of hand movements in early part of the withdraw, suggest that the hand shaping movement of the withdraw and the hand shaping movements of grasping are related. Jeannerod (1981; Jeannerod et al., 1995, 1998; see also Arbib, 1981; Grant & Conway, 2019; Karl and Whishaw, 2013; Sartori et al, 2015) posits that distinguishing features of the reach and the hand shaping associated with the grasp are their different visuomotor computations. One visuomotor channel directs the reach toward the extrinsic (spatial) features of a target and a different visuomotor channel directs the hand shaping of the grasp in relation to the intrinsic (size, shape) features of a target. Given that the withdraw using vision is directed toward the intrinsic properties of a food item so it they can be appropriately positioned for placement in the mouth, it is possible that the same visuomotor system concurrently became useful for the hand shaping of a grasp. The visual guidance of food orientation for the withdraw in anthropoids may have been enabled by some of the many changes that adapted them to a diurnal lifestyle (Kay et al., 1997; Ross & Kay, 2004; Smith et al., 2014; Williams et al., 2010). Featured amongst these changes was the evolution of a cone retina that enables fine grain visual discrimination and the many associated anatomical changes in visuomotor systems, including an enlarged granular frontal cortex mediating object location and object identity (Kaas, 2019; Preuss and Goldman-Rakic 1991; Goldman-Rakic 1992; Williams et al., 2010). Further insights into the origin of hand shaping movements could benefit from a more formal study of eating movements in strepsirrhines and other anthropoids as well as comparisons of the development of food related withdraw during infancy in nonhuman primates and humans (e.g., Sacrey et al., 2012).

An associated feature of the head-disengage movement was the presence of eye blinks. The distance to the food held inhand by a macaque in a sitting posture gave the appearance of being at the near point, or least distance of distinct vision, for relaxed vision, which in humans is about 25 cm (Kiorpes, 2019). One macaque ("S5") who was quite old and had no front teeth, held her food with a foot and used her hands to break off pieces of food to bring to the mouth, possibly displaying an example of macaque presbyopia (Kaufman et al., 1982). We also observed some of the macaques adjusting the distance that they held the food, as if to improve focus. These observations support the idea that the continued focus on a food item to

grasp it or position it require visual accommodation. Ang and Maus (2020) report that there is a boost in visual performance after a blink, and so blinks may represent release from the strain of accommodation. A blink may also facilitate focusing when looking elsewhere (Jaschinski et al., 1996). Blinks may also be related to a shift of attention from hand control by vision to hand control by somatosensation that would occur with disengage during a withdraw (Brych & Händel, 2020). In this respect, it is interesting that Nakano et al. (2013) reported the engagement of the default brain network following blinks. Here we suggest that visual disenge associated with the withdraw and blink may be associated with a shift from a visual network that orients the food item to a somatosensory network that completes the withdraw and bite.

In conclusion, the present findings show that macaques use vision in addition to somatosensation to direct their withdraw movements to bring food to the mouth. Visualization of food items that protrude from the hand during the early part of the withdraw is associated with hand movements that adjust the position of food items for presentation to the mouth where it is taken with precise bites. The results suggest that the visual control of hand shaping movements during the withdraw of anthropoid primates may have preceded or concurrently contributed to visual control of hand and finger shaping movements associated with reaching to grasp food items.

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Appendix

Video 1. A long-tailed macaque named "Flossey" reaching for a small food item. Note that Flossey visually disengages from the food item as soon as it is grasped: https://doi.org/10.6084/m9.figshare.19687950.v1

Video 2. Food inspection and positioning by a long-tailed macaque named "Connie." Note that Connie disengages with an upward head movement and blink as the food is withdrawn to the mouth from an inhand position: https://doi.org/10.6084/m9.figshare.19687953.v1