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Gaze Audits Food Items for Bite Points During Human Withdraw-To-Eat Movements: Two Modes of Vision for Anthropoid Primate Withdraw-To-Eat

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Abstract – A distinguishing feature of anthropoid primates is the significant contribution of vision in influencing hand movements, particularly those involved in eating. However, the hand movements of eating are complex, and vision contributes differently to their components: the reach, grasp, and withdraw-to-eat actions. This suggests that these components are controlled by distinct visuomotor networks that likely have unique evolutionary histories. An additional puzzling aspect of gaze-related eating behavior is that gaze durations vary with differences in food items. Due to the technical challenges of monitoring food-related gaze in nonhuman anthropoids, the present analysis investigated the use of gaze with human participants. Eye-tracking and frame-by-frame video analyses were used to examine gaze patterns, gaze duration, gaze disengagement, eye blinking, and hand preference used in eating various food items. The results show that gaze identifies points on a food item that the dominant hand can grasp and then locates points on the food item that the mouth can engage to grasp or bite. Hand and finger shaping movements during both the initial grasp and subsequent food handling help expose targets for hand grasping and mouth biting. A comparison of real and pantomime eating suggests that only some real food items possess the affordance necessary to elicit gaze patterns for identifying targets for hand grasps and mouth bites. These findings are discussed in relation to the idea that there are two modes of visual control of withdraw-to-eat action, with peripheral vision providing guidance to the mouth and foveal vision auditing food for effective mouth biting.

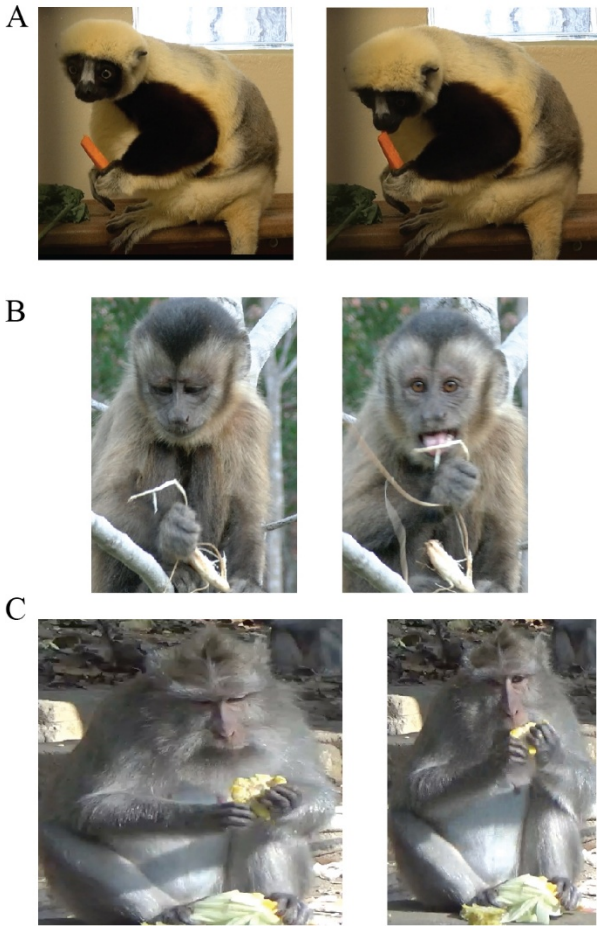
Keywords – Bite points for withdraw-to-eat, Gaze and blink to reach, Gaze and pantomime reach, gaze and real reach, reach and food audit, gaze and human food eating, visual attention for biting

The evolution of vision's association with hand reach and grasp in anthropoid primates, including humans, underlies their ability to exploit a variety of foods, (Castiello, 1997; Castiello & Dadda, 2019; Churchill et al., 1999; 2006; Karl & Whishaw, 2013; Mitchell et al., 2024; Quinlan & Culham, 2015; Whishaw & Karl, 2019). Accordingly, there is a long history of investigating the evolutionary origins of this visual control beginning with a debate on whether it was associated with the harvesting of insects or fruit on the distal branches of trees (Cartmill, 1972, 2012; Scott, 2019; Sussman & Raven, 1978; Sussman et al., 1978; 2013). One contemporary approach to understanding the visual control of hand movements divides reaching movements into components that including a reach, a grasp and a withdraw-to-eat. Each component is proposed to be mediated by a different visual neural network (An et al., 2022; Graziano, 2016; Milner & Goodale, 2006; Jennerod, 1999; Karl & Whishaw, 2013; Whishaw et al., 2016). For

example, for reaching, visual control is distinctive in that it is online and is not associated with reaching for pantomime objects and so is applied only to real target objects (Goodale et al., 1994; Kuntz et al., 2020). Recent work on the visuomotor adaptions in the feeding behavior of representative members of the three suborders of extant primate suggests that gaze also contributes to two types of withdraw-to-eat movements, the movements that bring a food item to the mouth once it grasped. A grasp-related withdraw-to-eat movement directly transports a food item to the mouth from the location where it was grasped, e.g., from a substrate, such as the ground or a tree branch. An inhand-withdraw movement involves holding and manipulating a food item in the hand before bringing it to the mouth. All members of the three primate suborders gaze towards food items to grasp them but, as illustrated in Figure 1, only members of the platyrrhine and catarrhine suborders additionally use gaze to mediate withdraw-to-eat movements (de Bruin et al., 2008; Hirsche et al., 2022; Peckre et al., 2023; Whishaw, 2024a,b).

Figure 1

Withdraw to Eat in Three Suborders of Primates



Note. A. A strepsirrhine primate *Propithecus coquerel,* holds a food item inhand, reaches for it with its mouth and obtains bite points using nonvisual cues (Peckere et al, 2023). B. A platyrrhine primate, *Cebus imitator*, directs gaze to a food item held in the hand before and during the initial portion of a withdraw-to-eat movement (Whishaw et al, 2024a). C. A catarrhine primate, *Macaca fascicularis,* directs gaze to a food item held in the hand before and during the initial portion of a withdraw-to-eat movement (Hirsche et al, 2022). Whereas *Propithecus* directs its mouth to the food, *Cebus* and *Macaca* withdraw the mouth away from the food to a horizontal position where the mouth receives the food from the hand.

Nevertheless, there are puzzling aspects of the gaze contribution to withdraw-to-eat movements. It might be expected that it could be more difficult both to grasp and then to target a small food item to the

mouth (Napier, 1933). Although, both nonhuman anthropoids and humans visually engage a target during the reach, if it is small they may disengage gaze from the target before, or as, the grasp is completed and so they often bring the item to the mouth without gaze (de Bruin et al., 2008; Hirsch et al., 2022; Sacrey, 2009, 2011; Whishaw et al., 2024). One explanation of why small food item withdrawal may not require foveal visual guidance lies in the observation that a finger can be directed to touch different parts of the body including the mouth using the guidance of body senses (de Bruin et al., 2008; Goodman & Tremblay, 2018; Hall et al., 2014; Karl et al., 2012; Edwards et al., 2005). So presumably, a finger contacting a small food item can serve as a guide to convey the item accurately to the mouth. Another explanation is that this is a function of peripheral vision. By contrast, larger food items are often held in hand and are visually engaged as eating progresses. This visual engage continues in association with the first portion of the withdraw to the mouth but disengagement occurs as the withdraw is completed (de Bruin et al., 2008; Hirsch et al., 2022; Sacrey, 2009, 2011; Whishaw et al., 2024). These observations suggest that some aspects of size, food identification, and/or manipulation of larger food items is dependent on foveal gaze.

We hypothesized that a portion of food protruding from the hand might require vision for guidance to the mouth as its location could not be easily signaled in the absence of foveal gaze. This hypothesis guided the present study's examination of the relation of gaze to withdraw-to-eat movement with food items of various sizes, including candy, donuts, carrots, bananas, and apples. Because of the many difficulties that would be related to conducting this study with nonhuman primates, including the use of eye tracking glasses, human participants were used. In some experiments, the participants were asked to pantomime the grasp and withdraw-to-eat movements with a pretend food item, an act that requires both reach and withdraw movements but may not be accompanied by online gaze (Davarpanah et al., 2016; Kuntz et al., 2020; Goodale et al., 1994).

The experiments were performed with adult female and male human participants who were video recorded in all experiments and wore eye-tracking glasses during some of the experiments. We used the frame-by-frame video inspection method of Karl et al. (2018) to analyze gaze direction and duration, movement duration, and eye blinks with respect to reach-to-grasp movements and withdraw-to-eat movement. The experiments indicated that the use of gaze during food handling and the withdraw-to-eat movement contributes to determining a bite point on a food item.

General Methods and Materials

Ethics Statement

The University of Lethbridge, University of Alberta and Thompson Rivers University Human Subject Research Ethics Committees approved the studies.

Participants

Participants were 71 right-handed young adults (mean age 20 ± 9 months) recruited from undergraduate and graduate psychology and neuroscience classes at Thompson Rivers University and the University of Lethbridge, Canada (see experiments for details). Undergraduate students received 1% bonus class credit for their participation. Participant handedness was determined by asking each participant which hand they wrote with. Each participant gave informed consent, authorized use of photos or videos for the experimental analyses, self-reported as having no history of neurological, sensory, or motor disorders as well as normal, or corrected-to-normal, visual acuity.

Experimental Setup

In Experiments 1 and 2, participants wore eye tracking glasses and were tested in a normally lit room with a self-standing height-adjustable pedestal placed in front of them. The pedestal was placed at a horizontal reach distance normalized to the participant's arm length and the height of the pedestal was

adjusted to the participant's sitting trunk height. When a participant reached with an outstretched arm while seated, they could comfortably grasp an object from the top of the pedestal (Whishaw et al., 2002). In Experiment 3, participants took a seat in a comfortable position on a chair, selected a food item from a tray, and proceeded to eat the food item.

Data Collection

Video Recordings

Video cameras were Sony camcorders (HDRCX405) with variable shutter speed or an Apple iPhone 11. Filming was performed at a sampling rate of 30 Hz (1/1000 shutter speed on the camcorders and with the default recording mode on the iPhone), with the cameras placed to capture frontal views. In Experiment 2, the frontal eye tracking camera also recorded the participant's reflection in a mirror, which provided a participant side view. Inspection of the video was performed with Quick time v7.7.7 (https://quicktime.en.softonic.com/mac) or Adobe Premier Pro (2024, https://www.adobe.com/ca) software. The zoom function on Adobe Premier Pro was used to confirm eye blinks associated with reaching. The methodology used for video analysis was mainly frame-by-frame video inspection using the method of Karl et al. (2018).

Eye Movement Recordings

Participant gaze and blinks were recorded using a ViewPoint EyeTracker® (Arrington Research, Inc.), a monocular, scene-based, eye-tracking device. Participants wore the eye-tracking glasses for the entirety of the experiment and data was collected at a sampling rate of 30 Hz. A sixteen-point eye calibration was performed prior to data collection with each participant and was occasionally adjusted, if necessary, during the experiment if a drift developed between the participant's gaze-point (the point projected onto the video record to indicate gaze location) and the target to be fixated. Visual disengage events were determined by inspecting movements of the participant's gaze-point within the scene view from the eye-tracking glasses and blinks were determined by inspecting the eye view from the eye-tracking glasses, which recorded the participant's eye directly.

Movement Kinematics

Kinematic analyses of participants' arm, hand, and eye movements were conducted using the open access software program Tracker (https://physlets.org/tracker/). Event times and body and hand coordinates were transferred from Tracker to Microsoft Excel (https://www.microsoft.com/en-ca/microsoft-365/mac/microsoft-365-for-mac) to generate graphical representations and figures in Adobe Illustrator (https://www.adobe.com/ca/products/illustrator.html).

Behavioral Measures

General Measurement

1. *Total eating time.* Total eating time was the time taken to eat a food item, after an experimenter instructed the participant to begin the task, to the time that the participant indicated that they were finished eating.

Gaze Measures

1. *Number of gaze events*. A gaze event was defined as a movement of the head to direct the eyes to a food item or was indicated by the gaze point engaging the food item on the eye tracker (Posner et al., 1987).

2. *Number of ground-withdraw gaze events*. A ground-withdraw gaze event was one in which gaze was directed to the target during the reach-to-grasp.
3. *Number of inhand-withdraw gaze events*. Inhand-withdraw gaze-related events were gaze events directed to a food item that was being held in the hand before being brought to the mouth.
4. *Vicarious gaze events.* Vicarious gaze events were those that were directed to a food item held in the hand that ended with visual disengagement but no withdraw of the hand with the food item to the mouth.
5. *Gaze onset*. Gaze onset was defined as the first video frame on which the participant's gaze-point fixated on the pedestal/target, indicating that the participant was looking at the target.
6. *Gaze disengage.* Gaze disengage was defined as the first video frame on which the participant's gaze-point moved away from the target or failed to follow the target as the hand moved to bring a food item to the mouth.
7. *Gaze duration*. Gaze duration was the time between gaze onset and gaze disengage as measured in video frames converted to seconds.

Reach Measures

1. *Reach*. A reach was a movement of the hand directed to picking up a food item.
2. *Withdraw-to-eat*. Withdraw-to-eat events were defined as individual forearm and/or hand movements that brought a food item to the mouth so that a piece of the food item could be taken by the mouth.
3. *Reach duration.* Reach duration was the time from the first video frame that the hand moved to initiate a reach movement to the frame on which the fingers closed to grasp a food item.
4. *Withdraw-to-eat duration.* The duration of the withdraw-to-eat movement was defined as the time from the frame of the first movement of the hand after it grasped the food item to the frame that the food item first touched the mouth.

Hand and Arm Postures

1. *Grasp.* A grasp was a hand movement that purchased a food item. Hand grip postures were scored as precision grips, in which an item is usually held by the distal segment or pulp of the thumb and one or more of the other fingers, including the phalanx pads or the side of the distal segments of the fingers. Alternatively, they could be scored as power grips, in which an item is held against the hand palm, as defined by Napier (1956). Standard notation of the fingers is used as they are numbered from digit 1 to 5, beginning with the thumb, collectively or as thumb and fingers individually.
2. *Arm posture.* Arm postures when holding a food item were defined with respect to the degree of opening of the elbow. In a hand-up posture, the elbow is flexed, and the forearm and hand are held up and toward the mouth, with the elbow clear of the body or resting on the thigh. In a hand-down posture the elbow and forearm are extended and the hand is resting on the thigh or knee.
3. *Handedness.* When the participant was introduced to the task, they were asked which hand they wrote with, as a measure of self-declared handedness (Corey et al., 2001). When they were holding a food item to bring it to the mouth for eating, the hand used was recorded as either the left or right hand.
4. *Food manipulation events*. A food manipulation event is defined as a change in hand grip on a food item or a change in the hand that held the food. The specific strategy used to orient the food to the mouth, defined by particular changes in grip or handedness, were also scored.

Blink Counts

1. *Disengage blinks.* Disengage blinks were eye blinks that occurred just as the participant's gaze shifted from a food item, as indicated by the participant's gaze-point on the eye-tracker, or via inspection of the videos (Willettet et al., 2023). For experiments in which the eye-tracker was not used, blink occurrence was defined by video inspection, including inspection using the zoon function in Adobe Premiere Pro, which permitted a close-up, frame-by-frame inspection of the eye. Blinks were also associated with biting, but this relationship is not further reported here.

Statistical Analyses

The data were analyzed using a general linear model repeated-measures analysis of variance (RM-ANOVA) with the statistical program SPSS (v.29.0.1.1). A p value of $< .05$ was defined as significant. Group comparisons were made using t-tests or LSD tests. The strength of relationships between independent and dependent variables were indicated by SPSS eta-squared (η^2) and the strength of main effects was assessed with the SPSS power function. Pearson product-moment correlations were used for data fits and correlations were expressed as r values with associated statistical values. In the experiments, group differences were evaluated for sex differences, which are additionally reported in the experimental results if they occurred.

Experiment 1: The Relation of Gaze to Reaching for a Skittle or Donut Ball

Experiment 1 Procedure

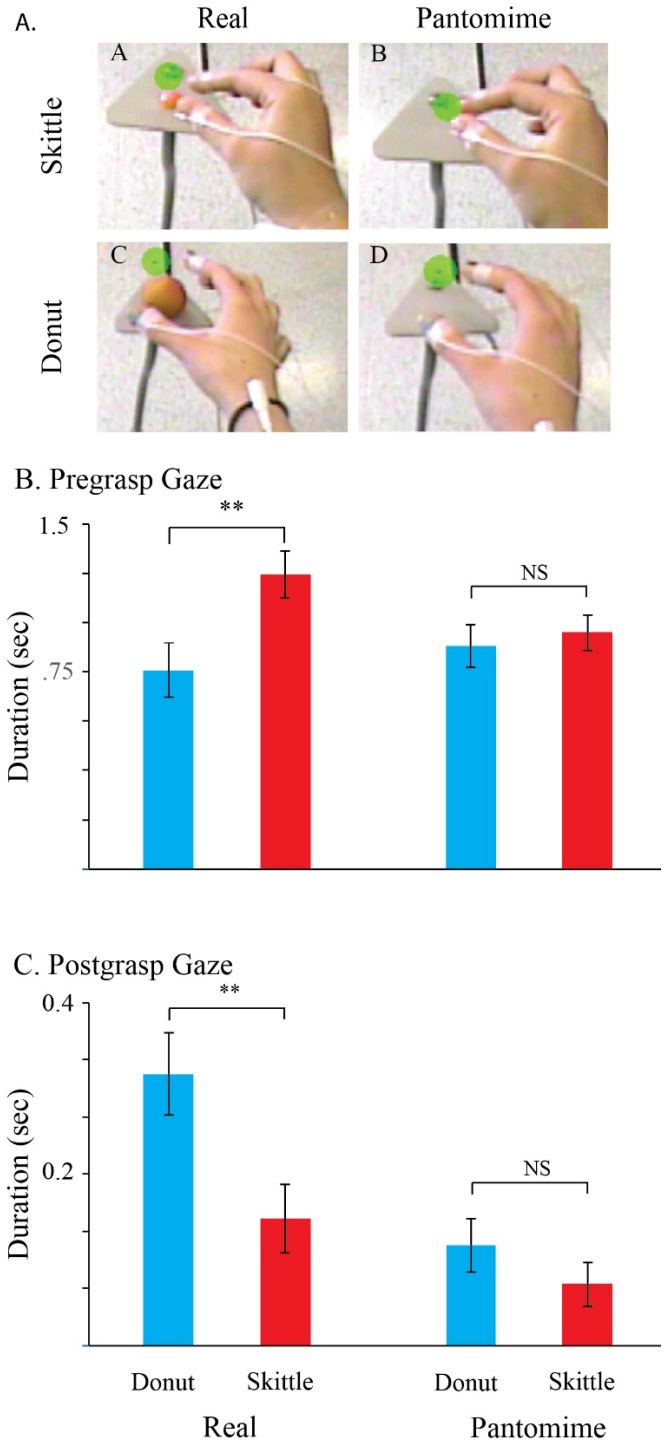
In Experiment 1, participants reached-to-eat two food items, a skittle or a donut ball (Figure 2A). The 17 participants, (all right-handed, 6 female), were drawn from an initial cohort of 23 (12 female), but 6 participants were removed from the analysis due to faulty video recording or eye tracking (Kuntz et al., 2020). Participants reached for a round donut ball with a diameter of approximately 29 mm or reached for skittles, a candy with an approximate diameter of 8 mm. Participants were seated in a comfortable upright position with feet flat on the floor and their hands placed in the start position. The start position for the right hand was marked on the dorsum of the right thigh, and participants started with their right thumb and index finger in opposition. The left hand rested in an open and relaxed position on the dorsum of the left upper thigh. Participants then completed a set of practice trials where they reached out and grasped an object and brought it back to their chest. This was done so that participants would be accustomed to the task and to ensure that the recording equipment would not interfere with their reach-to-grasp movements. Participants adopted the start position between trials and waited for a start prompt which was a soft verbal "GO" command from the experimenter. Participants reached-to-eat the food item under two reach conditions, real and pantomime.

1. *Real reach*. In the real reach condition both the pedestal and the food item were present such that the participant reached for a real skittle or donut ball. Participants were instructed to "reach out and grasp the target and bring it back up to your mouth either to eat it or as if you were to eat it."
2. *Pantomime reach*. In the pantomime reach condition, the pedestal was present, but the food item was not. The participant was instructed to "pretend to reach out and grasp the target object as you did when the target was present and bring it to your mouth for eating."

In each context, each participant performed 10 real reaches and 4 pantomime reaches (Karl et al., 2013). The pantomime reaches were always conducted after the participants had completed the real reaches to ensure that all participants were familiar with the real reach condition before they performed the corresponding pantomime movement.

Figure 2

The Skittle and Donut Task



Note. A. Examples of hand shapes at maximum pregrasp aperture (MPA) in the real (left) and pantomime (right) variations of the reaching task. The green dot represents the gaze point provided by eye tracking. B. Gaze duration associated with reaching for the skittle is longer than that for reaching of reaching for the donut. C. Gaze duration associated with withdraw of the donut is longer than that for withdraw of the skittle. Comparable measures on pantomime reaches gave no similar food-item scaling difference (B,C, Left).

Experiment 1 Results

When reaching for real targets, the participants' gaze duration varied according to the movement they were performing and the type of food they were eating. During the reach movement, gaze durations were longer for the small skittle than for the larger donut. In contrast, during the withdraw movement, gaze durations were longer for the large donut than for the small skittle. There were no comparable differences in gaze durations in the pantomime condition.

Gaze Duration for the Reach

Figure 2B shows that a participant's gaze duration during the reach was influenced by the type of food item they were reaching for, but only when performing real, but not pantomime, movements. For reach movements, there was a significant interaction between condition and food type, $F(1,15) = 8.0$, $p = .013$, $\eta^2 = 0.39$, power = 0.49. Follow-up tests revealed that participants displayed longer gaze times when reaching for a skittle than a donut ball in the real condition ($p = .004$), but there was no comparable difference in gaze times relative to food items during the pantomime condition, ($p = .780$). A comparison of reach durations from the beginning of the hand movement to the grasp for the donut and for the skittle showed that reach duration to the donut was significantly shorter than the reach duration for the skittle, $t(15) = 3.4$, $p = .004$. The main effect of condition was trending towards significant, $F(1,15) = 4.3$, $p = .060$, $\eta^2 = 0.22$, power = 0.5. The main effect of food type (donut vs skittle gaze time), $F(1,15) = 3.96$, $p = .700$, $\eta^2 = 0.21$, power = 0.46 was not significant.

Gaze Duration for the Withdraw

Figure 2C shows that a participant's gaze duration during the withdraw movement was influenced by the type of food item they were reaching for, but only when performing real, not pantomime, movements. For withdraw movements, there was a significant main effect of food type, as gaze duration was longer for the donut ball than for the skittle, $F(1,15) = 7.2$, $p = .020$, , $\eta^2 = 0.3$, $p = .700$. There was also a significant main effect of condition as the gaze durations were significantly longer for the real compared to the pantomime condition, $F(1,15) = 16.3$, $p < .001$, $\eta^2 = 0.52$, power = 0.960. Follow-up tests showed that the longer gaze duration was only significant for the real-reach condition ($p = .016$) and not the pantomime-reach condition ($p = .290$). The interaction of condition by food item was trending towards significant, $F(1,15) = 3.27$, $p = .090$, $\eta^2 = 0.18$, power = 0.4. Movement duration for the withdraw-to-eat were not measured because the eye tracking glasses could not follow the hand as it approached the mouth.

Experiment 2: Small and Large Carrots

Experiment 2 Procedure

In Experiment 2, 16 participants (all right handed, 8 female) were fitted with the eye tracking glasses and reached-to-eat a small piece of carrot or a complete carrot using the right hand (Figure 3A). The small piece of carrot was cut from the butt end of a full carrot and had a diameter and length of about 2 cm. The butt end was used so that when oriented to the right side of the pedestal, the grasp size on the carrot piece and the full carrot would be equivalent. The length of the full carrot was about 15 cm, so that when grasped on its butt end, most of the carrot extended away from the hand. The remainder of the experimental procedure was the same as in Experiment 1. Participants reached-to-eat the food item under two reach conditions, real and pantomime (as described above for Experiment 1).

Experiment 2 Results

During real reach movements participants initially directed their gaze to the butt end of both the small and large carrot. Upon grasping the small carrot, they disengaged their gaze as they began the withdraw-to-eat movement. When reaching for the full carrot, participants shifted their gaze - before the grasp was completed - from the butt end to the far end of the carrot. Gaze remained on the far end of the carrot as the withdraw-to-the mouth movement began. In the pantomime condition, participants only directed their gaze to the end of the carrot that they grasped.

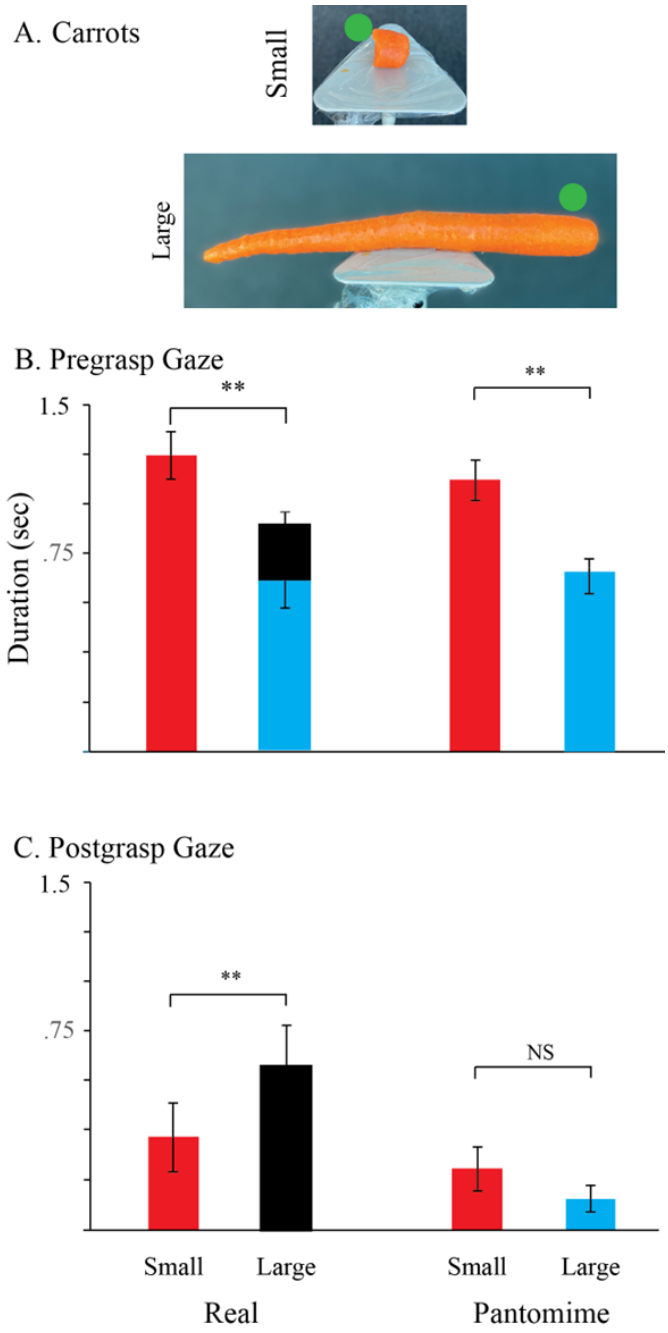
Pregrasp Gaze Duration

A summary of real gaze durations when reaching to the carrot butt vs a full carrot is shown in Figure 3B. There was a significant effect of carrot size on gaze duration during real reach-to-grasp movements, as the participants visually fixated on the small piece for longer compared to the full-sized carrot, $F(1,14) = 7.0$, $p = .019$, $\eta^2 = 0.21$, power = 0.08. There was no effect of the test condition (real *vs.* pantomime), $F(1,14) = 0.280$, $p = .160$, $\eta^2 = 0.21$, power = 0.08 and the interaction between test conditions and food size was not significant, $F(1,14) = 2.17$, $p = .160$, $\eta^2 = 0.13$, power = 0.30.

The differences in gaze duration related to the size of the target items likely influences reaching time, as the participants reached more quickly for the large carrot in both the real and pantomime conditions. This reach duration difference was likely due to the fact that the full carrot was easier to grasp because its end protruded from the pedestal; i.e., the participants did not have to modify their reach in relation to both the pedestal surface and the target, Size $F(1,14) = 7.02$, $p = .019$, $\eta^2 = 0.33$, power = 0.7. There was no significant effect related to the real vs pantomime conditions and no interaction between size and real *vs.* pantomime condition.

Figure 3

The Carrot Shoulder and Whole Carrot Task



Note. A. Top: The shoulder end of the carrot on a pedestal. Bottom: the whole carrot extends from the pedestal and participants were asked to grasp its shoulder. B. Gaze duration prior to and following the real grasps when reaching for the carrot shoulder fragment and the whole carrot. The black portion of the bar for the whole carrot is associated with the gaze shift from the shoulder to which the participants were reaching to the far end of the carrot, which occurs before the carrot is grasped. C. Gaze duration following the grasps when reaching for the carrot shoulder and the whole carrot. The black bar represents gaze on the far end of the carrot from the shoulder end. In the pantomime condition the participants did not shift gaze to the far end of the full carrot.

Postgrasp Gaze Duration

A summary of real gaze durations when withdrawing-to-eat the carrot butt vs the complete carrot is shown in Figure 3C. There was a significant effect of carrot size on gaze duration during real withdraw-to-eat movements, as participants maintained their gaze on the small carrot for a short time after grasping. In contrast, they disengaged from the grasp point on the full carrot before the grasp was complete, $F(2,30) = 45.10$, $p < .001$, $\eta^2 = 0.73$, power = 1.0, by shifting their gaze to the other end of the carrot; i.e., to the end that they would bring to their mouth (the black bar in Figure 3C).

There was a significant main effect of condition, $F(1,14) = 18$, $p < .001$, $\eta^2 = 0.560$, power = 0.98. For the pantomime condition, participants maintained gaze on the pretend end of the butt of both the small and full-sized carrot after grasping. The longer duration of gaze directed to the full-sized carrot in the real vs. pantomime condition, result a significant condition by food type interaction, $F(1,14) = 15.8$, $p < .001$, $\eta^2 = 0.53$, power = 0.96.

Participant gaze on the butt end of the full-sized carrot was shorter than for grasping the small piece of carrot because they shifted gaze to the far end of the carrot before the grasp. Nevertheless, total gaze time during the withdraw movement (including the visual shift to the terminal end of the full carrot shown by the black bar in Figure 2B) was longer for the full carrot than for the small carrot, $t(14) = 9.3$, $p < .001$). In addition, the duration of gaze after the grasp was also longer for the complete carrot than the small carrot, $t(14) = 2.65$, $p = .019$.

Blink Associated with Visual Disengage

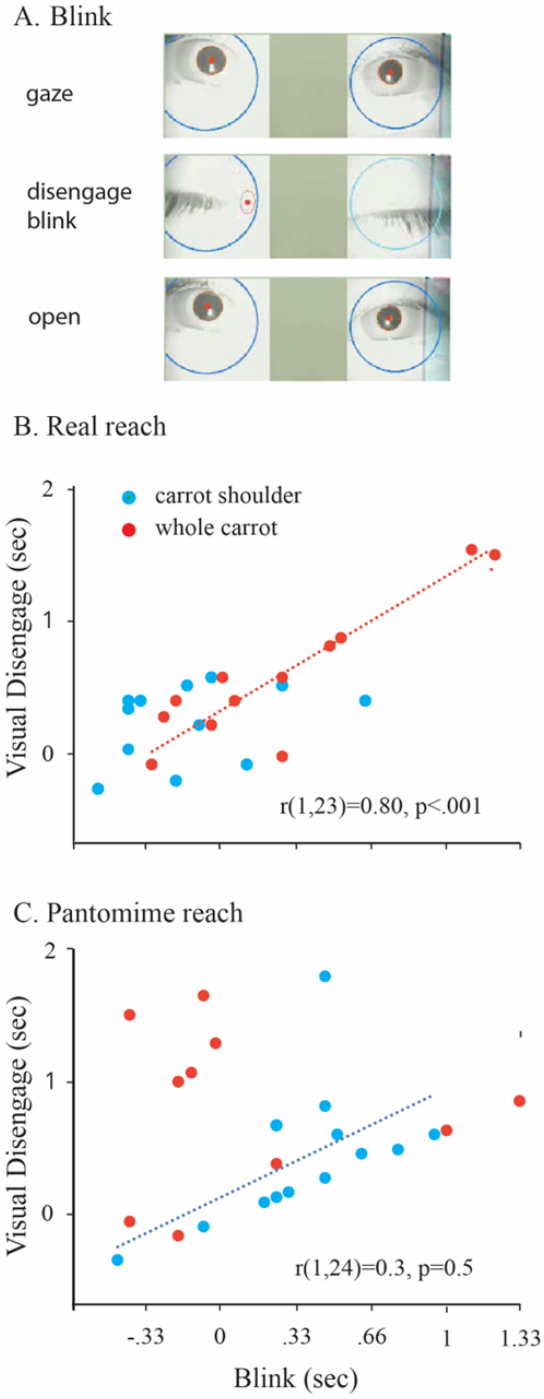
The eye-tracking glasses collect both the participant's gaze-point as well as a video of the participant's eyes, showing that they often blinked when they visually disengaged from the food item as they brought it toward the mouth. Participants blinked during the withdraw-to-eat movement in 81% of real reaches and 79% of pantomime reaches. Figure 4A, shows that there was a significant positive correlation between the time of gaze disengage and the time of a blink during real withdraw-to-eat movements, $r(38) = 0.860$, $p < .001$. That is, the participants blinked as they visually disengaged from target during real withdraw movement. Figure 4B shows that there was no significant correlation between the time of gaze disengagements and the time of blinks during pantomime withdraw movements, $r(37) = 0.220$, $p = .06$ In the pantomime condition, participants sometimes blinked as they visually disengaged from the pretend target, other times they simply directed their gaze elsewhere and blinked later.

Reach-to-Grasp and Withdraw-to-Eat Movement Duration

Measures associated with the reach movement are confounded by the placement of the food on the pedestal, as the carrot butt was completely on the pedestal while the full carrot butt extended beyond the pedestal. Measures associated with the withdraw-to-eat movement are also confounded because the full carrot extended beyond the hand, resulting in the hand moving a shorter distance when bringing the full carrot *vs*. the carrot butt to the mouth. The influence of target and placement were confirmed by a significant condition by movement type interaction, $F(1,14) = 4.8$, $p = .047$, $\eta^2 = 0.3$, power = 0.5. Follow-up tests indicated that the reach movement was significantly longer in the real compared to pantomime condition ($p < .021$. It was likely easier to grasp the real carrot because it extended away from the pedestal.

Figure 4

Relation Between Visual Disengage and Blinks in Real and Pantomime Reaches for a Carrot Shoulder Fragment and a Whole Carrot



Note. A. Eye view before during and after a blink. Top, gaze directed toward the full carrot end; Middle, blink; Bottom; gaze redirected away from the carrot. B. In the real condition, visual disengage was correlated with a blink. C. In the pantomime condition, the correlation was smaller and any correlation associated with the mime reach for the carrot shoulder was associated with gaze directed toward the pedestal.

Experiment 3: Carrots, Bananas, and Apples

Experiment 3 Procedure

In Experiment 3, 10 participants (5 female) ate a carrot (approximately 15 cm in length, 1 - 1.5 cm diameter), 11 participants (5 female) ate an apple (7 cm diameter), and 11 participants (5 female) ate a banana (17 cm length). Pantomime eating was assessed with 10 participants (5 female). The participants declared that they wrote with their right hand and all but one participant held the food item in their preferred-for-writing hand. One participant held the banana in their left hand and peeled it with their right hand. Participants brought a friend with them to the test room in order to produce test comfort. The participant was seated comfortably in a chair and took a food item that was offered on a tray. The participant was instructed to eat the food item in a relaxed and normal way, as they ordinarily might, and to freely engage in conversation with their friend or the experimenters while they ate. Participants that selected bananas were instructed to peel the banana as they ate it, rather than peeling it in its entirety first and then eating it. No instructions were given on how to eat the carrot or the apple. Pantomime eating assessment used apples. Participants were told that they would first eat part of and apple and then return it to a plate and then from another plate they would take a mime apple and eat it in the same way that they had eaten the real apple. Eating behaviors were filmed with an iPhone mounted on a holder on a table in front of the participant. A waste basket was placed near the participant's chair, where participants could place the remnants of the food items. Participants were told to begin eating when prompted by the experimenter with the verbal signal, "you can begin," which was given when they had the food item in hand.

Experiment 3 Results

Grip Patterns

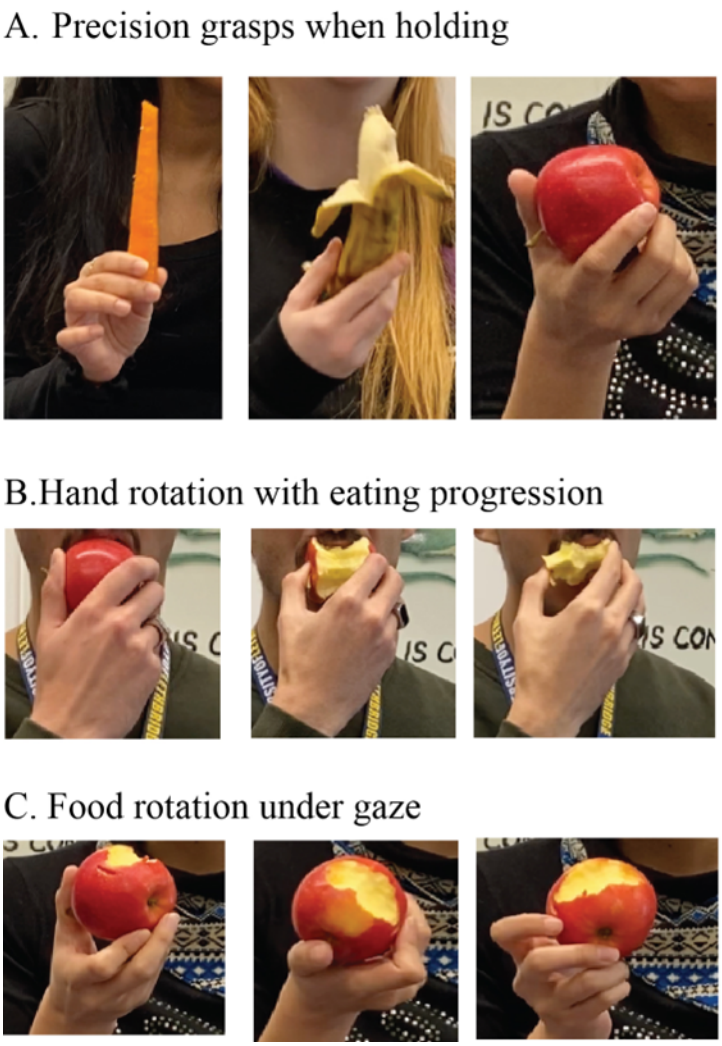
All participants held the food items using a precision grip in which the thumb tip was opposed to one or more of the fingertips. Participants gripped the food item with the distal phalanx or the sides of the distal portions of the fingers as shown in Figure 5A. Once a participant obtained a preferred grip, there was little change in the grip pattern that they used for the remainder of item eating, although they manipulated the food items by changing finger pressure and orientation as shown in Figure 5B. Only one participant was observed to change grip, and this was to eat the last portions of the apple, during which the participant used both hands to hold the core with pincer grips, between the distal phalanx of the thumb and that of the second finger. All but one participant held food items in the same hand throughout eating. That participant passed a banana from one hand to the other once during eating. Participants also looked at the food items between withdraw movements, during these vicarious gazes they often changed the orientation as illustrated for a participant holding an apple in Figure 5C.

Arm Posture when Holding

Figure 6 illustrates postures of the arm used during eating. In one posture, the arm flexed at the elbow with the elbow held up or resting on the lap and the forearm and hand oriented up toward the mouth as shown in Figure 6A. In the other posture the elbow is extended with the forearm resting on the lap and the food item held near the lap. For all participants, the respective postures were used throughout the eating sequences (Figure 6B). More female participants used the elbow flexed posture, whereas more male participants used the elbow extended posture (Chi-square 5.12, $p = .024$).

Figure 5

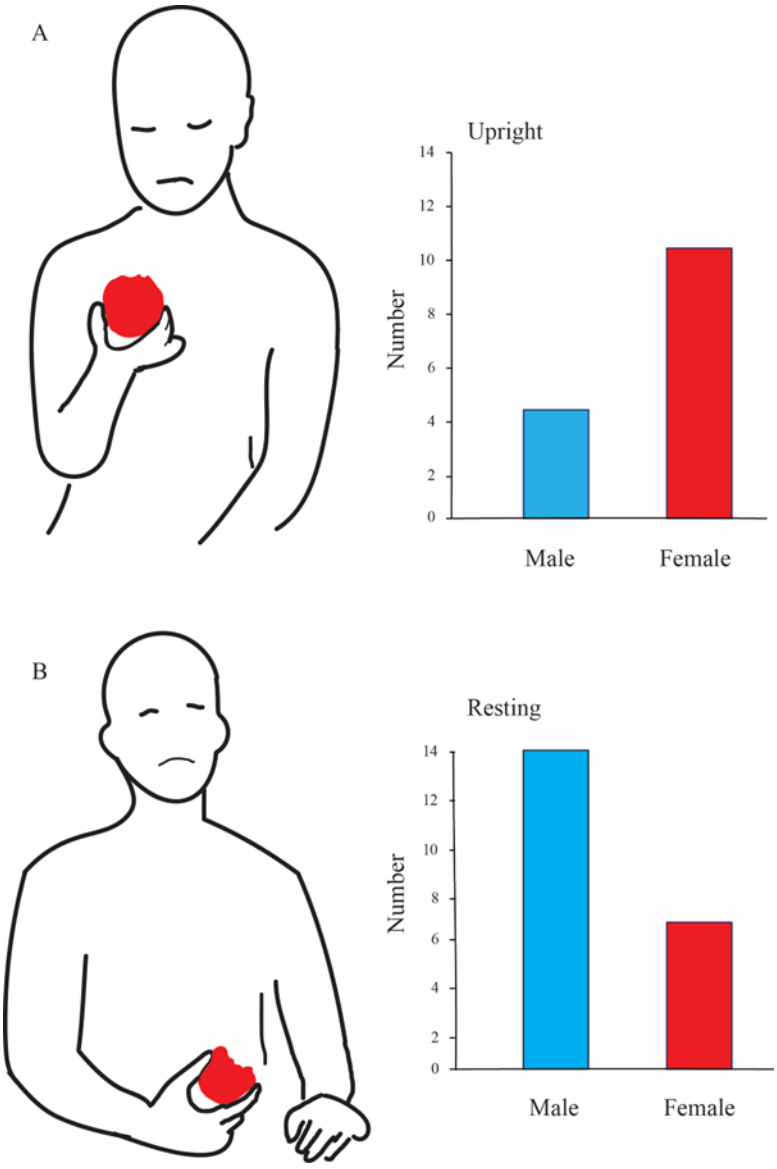
Grasp Patterns Associated with Eating a Carrot, Banana or Apple



Note. A. Precision grasps, involving opposition between the distal thumb pad (pulp) and the distal pads of the other fingers, were always used for holding the food items. B. Adjustments of the precision grasp pattern as well as wrist rotation are used to position the food objects for mouth placement as eating progresses, as is illustrated for eating an apple. C. With vicarious gaze directed to an apple, a participant rotates the apple to expose target points for biting before the apple is withdraw to the mouth.

Figure 6

Arm Posture for Holding a Food Item



Note. A. The elbow flexed arm posture has the lower arm directed to toward the mouth with the elbow free or resting on a thigh. B. The elbow extended arm posture has the lower arm resting on the lap. Note: more female participants used the flexed arm posture and more male participants used the extended arm posture.

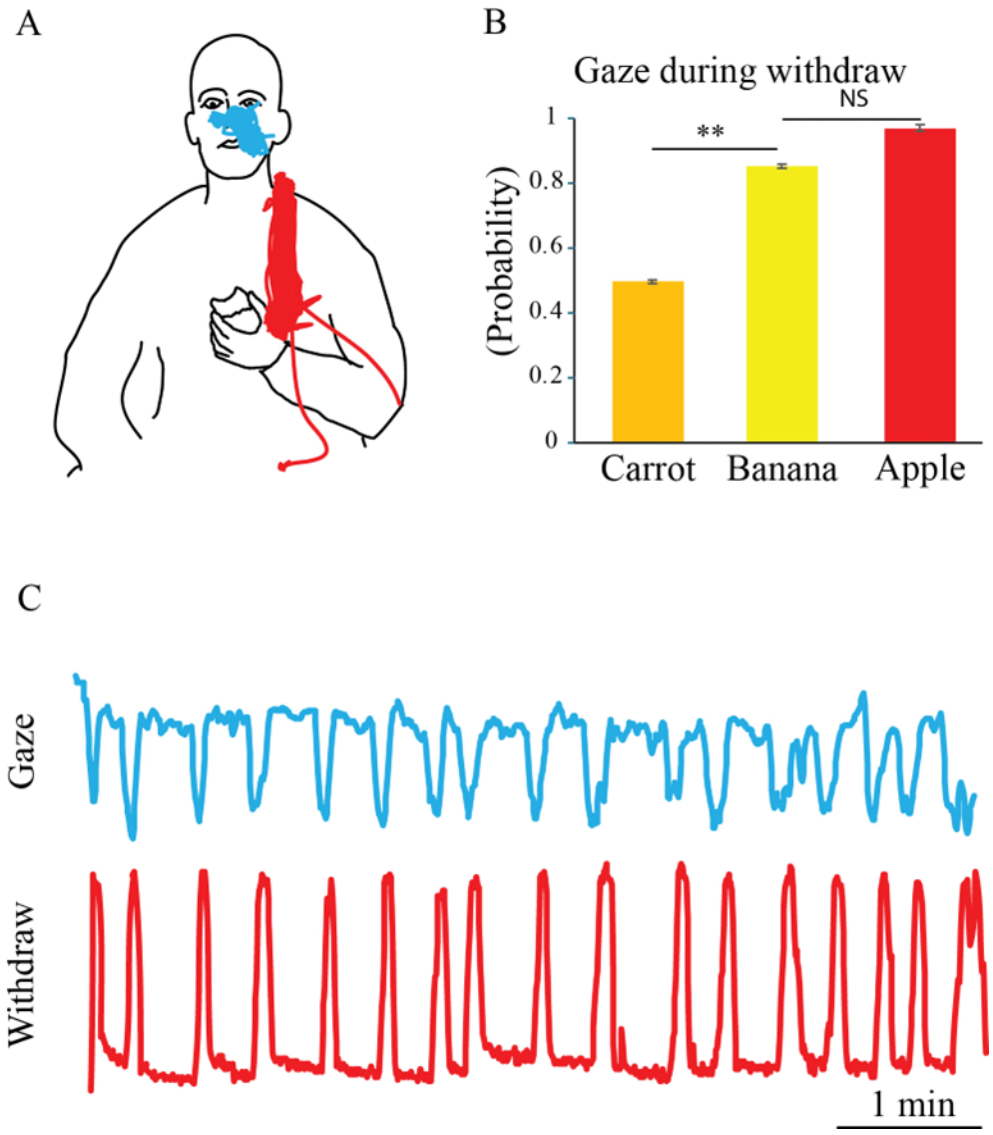
Gaze-Related Withdraw-to-Eat

An example of gaze behaviour associated with withdraw-to-eat movements in one participant eating an apple is shown in Figure 7. Figure 7A illustrates the kinematic measures associated with 17 withdraw-to-eat arm movements, with the apple repeatedly brought to the mouth from a holding position with the arm in an elbow-flexed posture. Figure 7B shows the continuous record of gaze movements (red trace) and withdraw-to-eat movements (blue trace), which were closely related and similar for each withdraw-to-eat movement. Figure 7C shows that there were differences in the probability that the participant's gaze was directed to the food item during a withdraw-to-eat movement depended on the food

item that they were eating. When eating carrots, only half of the withdraw-to-eat movements associated were associated with a gaze event. In contrast, when eating a banana or an apple nearly every withdraw-to-eat movement was associated with a gaze event.

Figure 7

Association Between Gaze and the Withdraw-To-Eat Movement in a Participant Who Holds an Apple in the Elbow Flexed Position



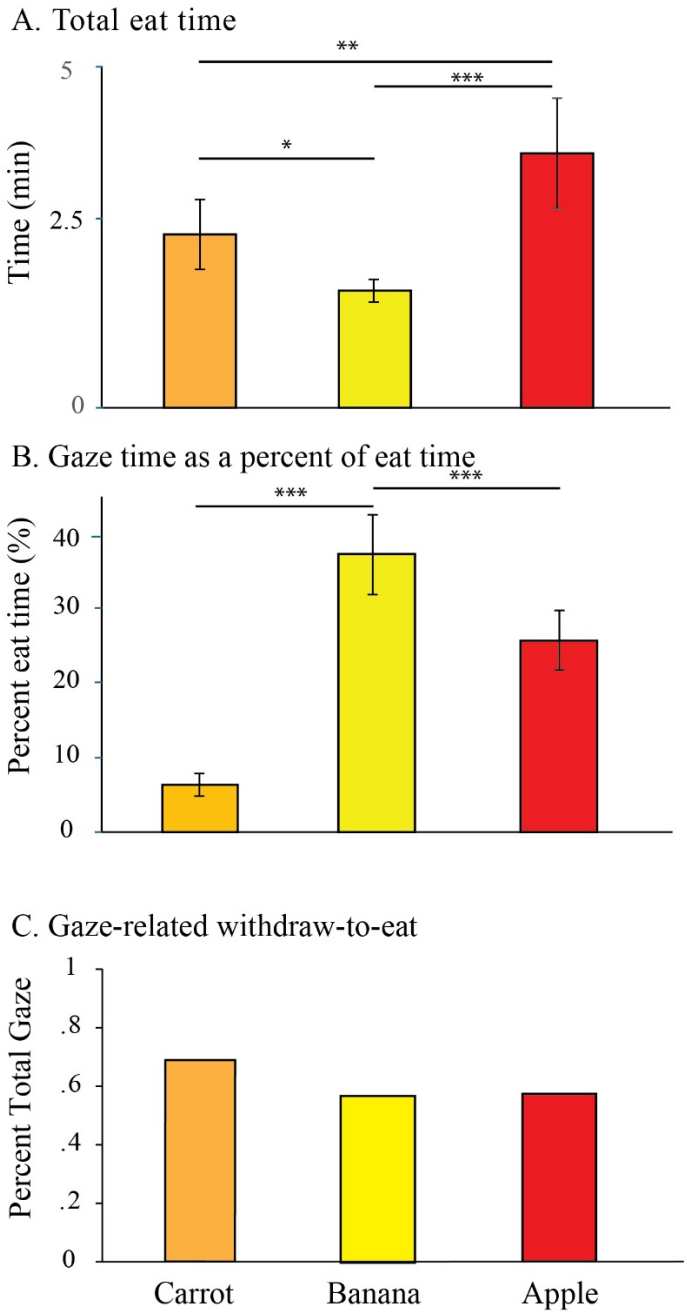
Note. A. Holding posture and kinematic representations of 17 successive head (blue, nose tip tracks) and hand (red, thumb knuckle tracks) of up-down movements taken to eat an apple. B. Relative movement associated with gaze (red, nose tip movement) and withdraw-to eat (blue, thumb knuckle movement) associated with 17 withdraw movements taken to complete apple eating. C. Relationship between the number of gaze events and withdraw-to-eat events in all participants when eating carrots, bananas or apples. Gaze is associated with less than half of carrot eating withdraw-to-eat movements but nearly every banana and apple eating withdraw-to-eat movement.

Eating Duration, Gaze Duration, and Gaze Type

Figure 8 provides a summary of total eating time, percent of eating time associated with gaze, and percent of gaze events associated with withdraw-to eat movements.

Figure 8

Eating Time, Gaze Times and Gaze Related Withdraw-to-Eat Probability



Note. A. Total eating time (mean ± se) to eat carrots, bananas, or apples indicates that it took longer to eat the apple than the other food items. B. Total gaze time as a percent of eating time to eat carrots, bananas, or apples. The long gaze times for the banana were related to peeling. C. About half of all gaze events directed to food items occurred during withdraw-to-eat. The remaining gaze events were vicarious gazes that were not associated with withdraw-to-eat.

Total Eating Duration. A summary of total eating duration for the three different food items is shown in Figure 8A. An ANOVA revealed a significant main effect of food type on total eating duration, $F(2,29) = 0.850$, $p < .001$, $\eta^2 = 0.4$, power = 0.97. Follow-up pairwise comparisons revealed that participants took longer to eat the apple than the carrot ($p = .003$) and the banana ($p < .001$) and longer to eat the carrot than the banana ($p = .043$).

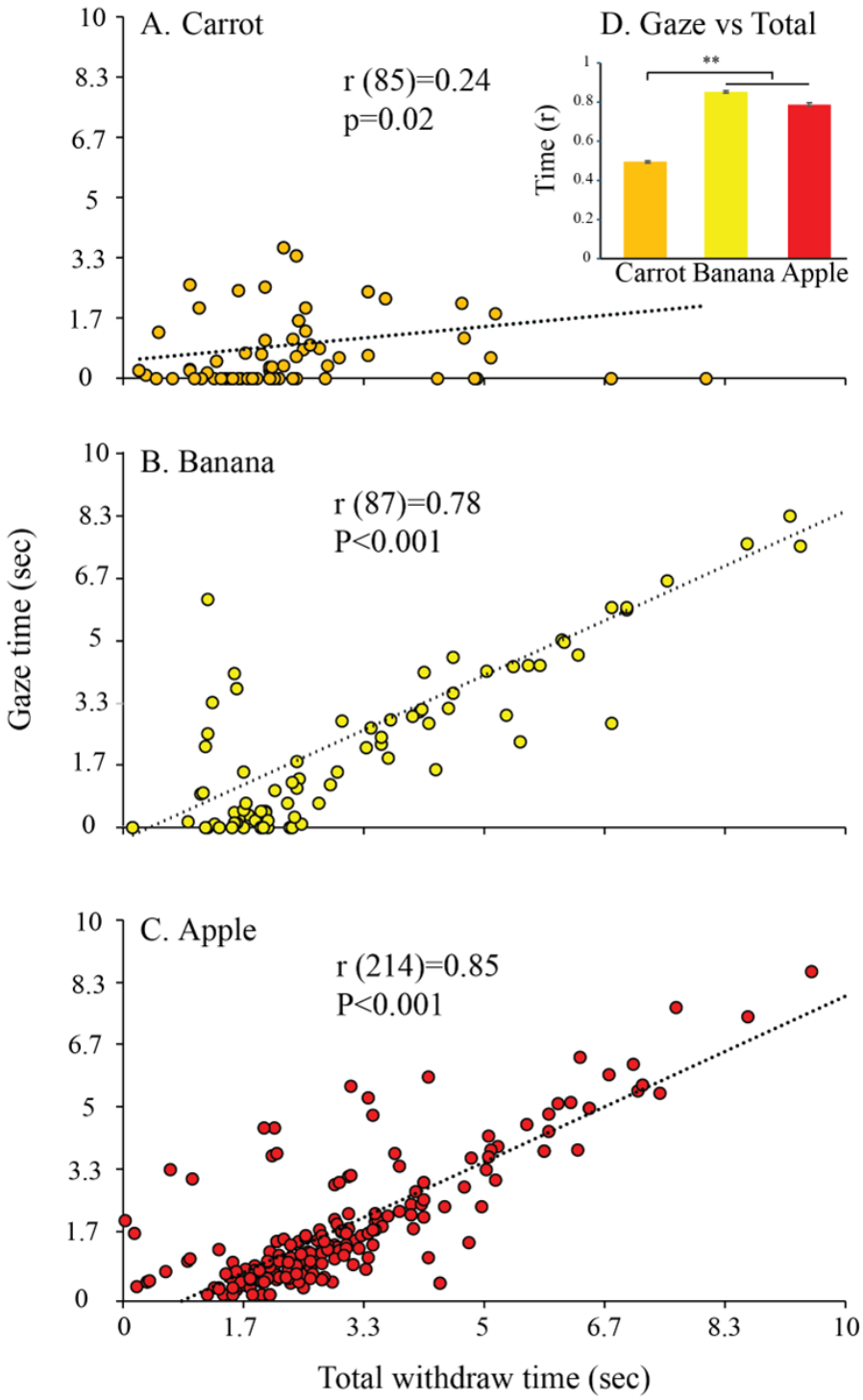
Total Gaze Duration. A summary of total gaze duration as a percentage of total eating duration is shown in Figure 8B. An ANOVA revealed a significant main effect of total gaze duration, $F(2,29) = 14.15$, $p = .001$, $\eta^2 = 0.5$, power = 1. Follow-up pairwise comparisons showed that participants spent a significantly greater proportion of time visually fixating on the banana relative to the carrot ($p = .001$) and apple ($p = 003$). This is most likely related to the time spent peeling the banana, an activity that was performed almost entirely under gaze. Participants also spent a significantly greater proportion of eating time visually fixating on the apple relative to the carrot ($p = .001$), likely reflecting the fact that some participants seldom looked at the carrot during eating.

Gaze Related Withdraws. Gaze directed toward a food item could be divided into two types. Vicarious gazes were gazes directed toward a food item that was then not withdrawn to the mouth. Withdraw-to-eat gazes were directed toward a food item that was then brought to the mouth for eating. Figure 8C shows the proportion of withdraw-to-eat gazes as a percent of all gazes. About half of all gazes were withdraw-to-eat gazes and an ANOVA did not give a significant main effect of food type associated with the percent of gaze associated withdraw-to-eat events, $F(2,29) = 2.1$, $p = .06$, η^2

Gaze Withdraw Duration Related to Food Inspection. Figure 9 depicts the correlation between gaze duration and total withdraw-to-eat time for each of the food items. Gaze duration included time spent looking at the food item as it is held plus time spent looking at it as it is withdrawn to the mouth (the first portion of the withdraw movement). Total time of withdraw-to-eat included gaze time plus the period of withdraw after visual disengage during which a food item brought to be placed in the mouth and positioned for biting. The correlations in Figure 9 show that the variation in gaze time is due mainly to the time spent looking at the food item before the withdraw movement begins. As illustrated in the Figure 9A, the correlation for the carrot is relatively low, as gaze was not associated with many carrot withdraw-to-eat acts. The correlation for the banana (Figure 9B) and the apple (Figure 9C) are high as gaze was associated with most withdraw-to-eat acts. The insert in Figure 8 (top) depicts the mean ± se of the gaze time vs. total withdraw durations of each of the participant's correlation for each food item. A comparison of correlation for individuals as a function of food item was significant, $F(2,29) = 9.85$, $p < .001$. Pairwise comparisons confirmed that the strength of this relationship was weaker for the carrot, compared to the banana ($p = .016$) and apple ($p = .010$), which were not different.

Figure 9

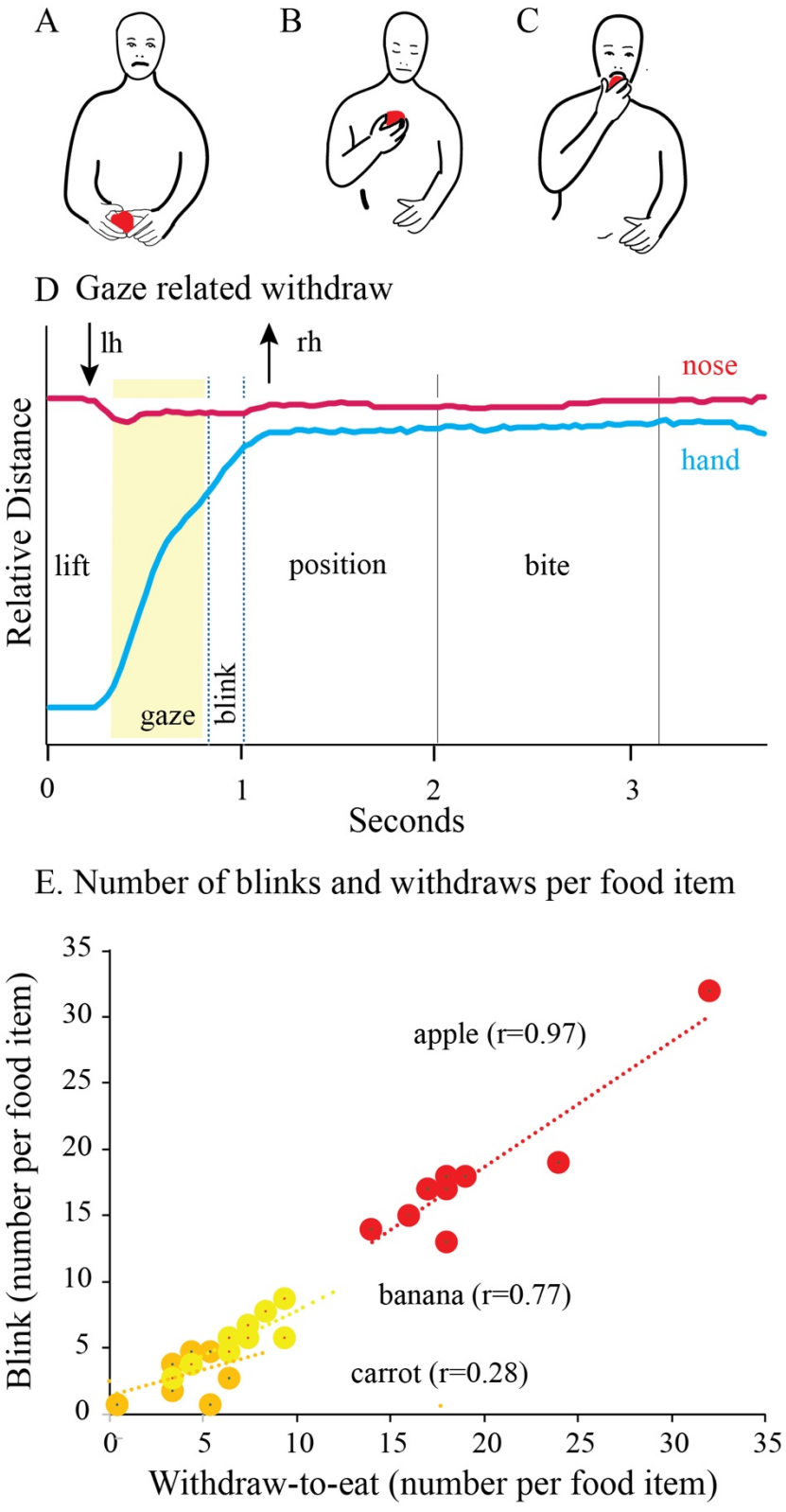
Correlations Between Gaze Duration and Total Withdraw-To-Eat Time



Note. A-C. Group results for participants eating carrots, bananas, or apples. D. Insert bar graph shows the correlations (mean±se) averages obtained from individual participants eating each food item. Positive correlations show that the duration of gaze on the food accounts for most of the variation in the total duration of withdraw-to-eat time. The nonsignificant result for the carrot results from many carrot withdraw-to-eat movements being made without associated gaze, but no withdraw-to-eat events associated with apple eating that were not associated with gaze, however brief.

Figure 10

Relation Between Visual Disengage and a Blink During Apple Eating



Note. A-C. For the withdraw; the apple rests in the hand in the elbow extended position, is withdrawn toward the mouth, and placed in the mouth. D. Kinematic trace of the nose tip (red) indicate head movement, to look toward or away from the food item, and the corresponding trace of the knuckle of the thumb (blue) represent hand movement to bring the apple to the mouth. Note: the withdraw is divided into three phases: the lift to bring the apple to the mouth, the positioning of the apple in the mouth, and then the bite, in which a piece of apple is taken. Gaze is associated with the lift. Disengage is associated with the blink and occurs before the apple reaches the mouth. E. Correlations between withdraw movement associated with gaze and the occurrence of a blink for participants eating a carrot, banana or apple. (lh - head lower, rh – head raise).

Blink Events Related to Gaze Disengage. When a participant who had directed gaze to a food item then brought the food item toward the mouth, the visual disengage was often associated with a blink. Figure 10 (top) illustrates this relationship. The participant first looks at a food item as it is held on the lap and then maintains gaze on the food item during the withdraw-to-eat until gaze disengage, which occurs before the food reaches the mouth (Figure 10 A-C). Figure 10D shows kinematic traces illustrating the timing and the duration of a blink in relation to the withdraw-to-eat movement. The blink occurs just before the hand reaches the mouth, at about the same time that gaze disengage occurs and about the same time that the head is raised so that the food can be accepted into the mouth.

Figure 10E shows the relationship between the number of blinks and the number of withdraw-to-eat movements associated with gaze. The correlation for the carrot was not significant, $F(1,8) = 2.3$, $p = .160$, as many carrot withdraw-to-eat movements were not associated with gaze directed to the carrot. Correlation were significant for the banana, $F(1,10) = 17.8$, $p = .002$, and the apple, $F(1,8) = 48.4$, $p < .001$. When participants made vicarious gazes to a food item, gaze disengage from that item was also associated with a blink. A correlation that included all vicarious gaze events to food items that did not involve a withdraw to the mouth, showed that the correlation ($r = .91$) between disengage and the occurrence of a blink, was significant $F(1,30) = 36.7$, $p < .001$.

Pantomime Apple Eating. After a participant had made a first withdraw-to-eat with a real apple or the pantomime apple, the next three withdraw-to-eat movements were examined for the presence of gaze associate with the withdraw-to-eat. For the real apple, gaze was directed to the apple on 29/30 withdraw-to-eat occasions *vs* 13/30 for the pantomime condition, a difference that was significant as shown by a t-test for paired samples, $t(9) = 3.1$, $p = .006$.

Discussion

The present study investigated the role of gaze during hand withdraw-to-eat movements in human participants as they brought food items of varying sizes and types to the mouth. The experiments were designed to clarify the use of gaze in anthropoid primates more broadly. Our hypothesis was that if food items are large and protrude from the hand, foveal gaze is employed to localize and guide the protruding portion of the food item to the mouth. The experiments showed, however, that foveal gaze is not engaged by food size, shape or protrusion *per se*, but by determining which part of the food is to be received by the mouth for biting. This result suggests that foveal gaze serves a feature-detection function, identifying the affordance offered by food—first to determine hand-grasp points to guide hand movements and then to identify and expose mouth-grasp points so that the food is accurately brought to the mouth for biting. For food that does not require the identification of bite points, peripheral vision likely guides the food to mouth. Clavagnier et al. (2007) have described separate visocortical networks for foveal and peripheral vision in guiding reaching movements. The present analysis of gaze in determining bite points and the assistance provided by the hands in exposing these points suggest that withdraw-to-eat movements are candidate behaviors for contributing to the evolution of visual control of hand skills in anthropoid primates more generally.

In the study, human participants were asked to reach for food items of varying sizes and shapes, with the range of items designed to represent the sizes and shapes of food that would be eaten by many species of anthropoid primate. Because the tasks varied in design and eye movements were tracked using eye-tracking glasses, conducting a similar study with nonhuman anthropoid primates would be difficult. Nevertheless, knowing that gaze is directed toward determining both hand-grasp points and mouth-grasp

points on food in humans helps interpret the function of gaze during eating in nonhuman primate species, especially during natural foraging. The results also contribute to understanding behavioral differences between strepsirrhine and anthropoid primates, as the former likely use gaze to distinguish food identity but do not use gaze to identify hand-grasp and mouth-grasp points, as do anthropoid primates (Peckre et al., 2023). The hypothesis that foveal gaze functions to distinguish hand-grasp and mouth-grasp points could be further tested in future experiments examining the food-handling behavior of nonhuman primates.

Anthropoid primates employ two types of withdraw-to-eat movements to bring food grasped in the hand to the mouth (Hirsch et al., 2022). A grasp-withdraw movement directly transports and releases a food item into the mouth from the location where it is grasped, e.g., from a substrate such as the ground or a branch, including a pedestal as used in the present study. An inhand-withdraw movement involves holding and manipulating a grasped food item in the hand before bringing it to the mouth. The results of the first two experiments with our human participants seemingly support the idea that food size and the extent to which a food item protrudes from the hand engage foveal gaze. In the first experiment, the comparison of real and pantomime reaching conditions showed that gaze duration is scaled to the size of real food items, with smaller items invoking longer foveal gaze during the reach and larger items invoking longer foveal gaze during the withdraw. Similar scaling of movement speed and gaze duration did not occur in a pantomime conditions (see also Coats et al., 2008; Goodale et al., 1994; Jeannerod, 1991; Kennedy et al., 2015; Kuntz et al., 2020; Plamondon & Alimi, 1997; Quinlan & Culham, 2015). The second experiment investigated whether the extent to which a food item protruded from the hand influenced the use of foveal gaze. Participants reached for a carrot shoulder or a whole carrot. When grasped on its end, the whole carrot protruded appreciably from the hand, much more so than did the carrot shoulder. When reaching for the whole carrot, all participants shifted their gaze from the grasp point before the grasp was completed and directed their gaze to the far end of the carrot, the end that protruded from the hand and was to be placed in the mouth. A similar gaze shift was not associated with a pantomime reach for a whole carrot. The gaze shift directed to the end of the carrot that protruded from the hand was also associated with a longer gaze duration than for the carrot shoulder. These observations suggest that foveal gaze is used to identify the protruding portion for subsequent eating and they also seem to indicate that it is the extent of protrusion that determines the associated foveal gaze timing and duration.

The third experiment, in which participants spontaneously ate a carrot, banana, or apple—each of which protruded from the hand—suggests, however, that it is not the size, shape or protrusion of an item that engages foveal gaze. Rather, foveal gaze is engaged when a participant looks for a mouth related grasp point or in short, as measured in the study, a bite point. Participants were less likely to use foveal gaze to bring a carrot or banana as compared to an apple to their mouth, even though these items extended appreciably more than the apple from the hand. The progression of apple eating required continuous use of the hand to reorient the apple under foveal gaze, to determine the next bite point for the mouth. The carrot and banana present no similar ambiguity regarding how they are to be taken by the mouth. Although the participants did bite the carrot and banana, a bite was simply directed to the item's end and it is likely that peripheral vision sufficed. We found support for the relevance of bite points to the use of gaze in our video archive. For four participants eating popsicles—food items held by a stick, which also protrude from the hand—all participants gazed at the popsicle when picking it up. However, three of the participants never looked directly at the popsicle again, despite bringing it to their mouths many times. One participant looked at their popsicle once during eating. We also observed that when vision was obscured, they more frequently touched the popsicle with the lips and tongue and also used mouth reaching movements to grasp it, observations that support the idea that peripheral vision can guide food items to the mouth.

We observed that vicarious gazes were common during apple eating. As participants chewed the food after a bite, they made vicarious gazes at the food items they held, often manipulating the items as they did so. There were more vicarious gazes directed to the apple than to the carrot and banana, suggesting that these gazes are involved in planning biting actions for subsequent withdraw-to-eat movements. It is interesting that Redish (2016) has suggested that vicarious actions, more generally, are associated with assessing the possibilities of forthcoming action. Thus, these vicarious food-related gazes may comprise a nonconscious procedural audit of the item. The occurrence of vicarious gazes during food eating is a novel

observation that could be investigated to determine whether it occurs in other primate species during eating and to answer the question of whether they similarly make estimates for forthcoming action related to eating.

Previous studies have noted that humans and some other representative anthropoid primates blink at about the time they visually disengage, either when grasping a food item or during the withdraw-to-eat movement (de Bruin et al., 2008; Hirsch et al., 2022; Whishaw et al., 2024a,b). Causes of blinks have been proposed to include relief from the accommodation required to visualize the target, protecting the eyes from the item when bringing the hand to the mouth, switching from visual to somatosensory guidance, or reflecting a central network change such as alternating between an attention network and the default network (Ang & Maus, 2020; Brych & Handle, 2020; Jaschinski et al., 1996; Nakano et al., 2013; Willett et al., 2023). Here, we make a new observation about the relationship between blinks and gaze that eliminates one of these suggestions. Blinks occurred when the participant visually disengaged from vicarious gazes—gazes that were not associated with a withdraw-to-eat. This observation weakens the idea that the function of blinks is to protect the eyes from potential injury that could be inflicted by food items brought toward the face as the item is not withdrawn. This finding strengthens the suggestion that blinks are associated with an attentional shift or the removal of visual attention from a target (Daza et al., 2020; Sakai et al., 2017). In addition, it may be that visual attention directed at a food item inhibits blinking and the attentional shift associated with gaze disengagement provides an opportunity for a blink to occur (Irwin, 2011).

It is notable that there was a similarity in hand preference related to the eating of various types of food. Participants reached-to-grasp and withdrew-to-eat all food items predominantly using the hand with which they wrote. Only one participant was observed to eat a banana with their declared non-preferred hand. This finding is consistent with the strong relationship reported between handedness for eating and handedness more generally (Sacrey et al., 2013). The observation is relevant to the question of handedness in eating by nonhuman primates, in which only a small number of subjects are usually available for study (Fagot & Vauclair, 1991; MacNeilage et al., 1987; Salmi et al., 2023). The present results suggest that a small subject number should not be an obstacle to drawing inferences about hand preferences and laterality but comparatively presents the requirement that any hand preference be similarly pronounced.

Of the two types of grasp identified with primate hand use (Napier, 1933; 1956), precision grasps were used for all grasping, holding, and eating actions. The participants not only grasped and held small food items with various precision grips between the thumb and fingers (Wong & Whishaw, 2004), but they also primarily held the apples, which were the largest food items in terms of diameter, in a similar way. Most participants held the apple between the thumb and middle finger and rotated it to orient it for eating, using a combination of index finger manipulation and rotational movements of the hand. As a result, an entire apple was consumed with little to no change in grip, but with significant variations in the relative forces and angles applied by the grip to the item. Although there are descriptions of grip types used by nonhuman primates (Elliott & Connolly, 1984; Feix et al., 2016; Macfarlane & Graziano, 2009; Napier, 1956; Pouydebat et al., 2009; Spinozzi et al., 2004; Whishaw et al., 2024), their functions have not been thoroughly examined with respect to their purpose. The present results suggest that the function of grip selection and grip change is to cooperate with vision in determining bite points to be made by the mouth. The participants' predominant use of precision grips aligns with Napier's (1933;1956) suggestion that it is function, not size, of an object that determines grip choice.

We observed only one sex difference in our analysis of eating-related gaze behavior: female participants held food with a flexed elbow more frequently than with an extended elbow. This may exemplify one of many socially related sex differences in behavior (Becker et al., 2005; Wood & Eagly, 2007). Otherwise, the present results are consistent with numerous similar studies indicating that gaze-related hand movements are not distinguished by sex (de Bruin et al., 2008; Hirsch et al., 2022; Sacrey, 2009, 2011; Whishaw et al., 2024). In studies of eating behavior in nonhuman primates, we are unaware of reports identifying sex differences in the way food is consumed. However, there are reports of sex differences related to aspects of feeding such as food selection, metabolism, and aggression (Harrison, 1983; Rose, 1984; Schuppli et al., 2021).

In conclusion, the results of the present study suggest that there are two types of guidance for bring food to the mouth. Foveal gaze is used to determine bite points on food items as they are brought to the mouth for biting. Peripheral vision is sufficient for guidance to the mouth but not for identifying bite points. Thus, foveal gaze determines mouth-bite points on a food item as well as hand grasp points. Previous studies have noted that objects can be grasped in relation to their endpoint comfort or use (Martin, 1994; Rosenbaum, 2012), but the present study shows that for eating, further gaze analysis is necessary for the interactions that the mouth may have with food. In relation to hand-mouth grasping, the interdependence between gaze, hand movement, and mouth movement is consistent with the suggestion that these functions may be mediated by separate visual networks (Clavagnier et al. 2007) and frontal oromanual motor neocortex regions dedicated to food eating (An et al., 2022; Graziano, 2016; Karl & Whishaw, 2013). Finally, the results of this study with human subjects, and the similarities of the behavior of humans to other anthropoid primates, suggest that the feature-detector role of vision in identifying mouth-handling points on food is an anthropoid trait, providing an explanation for their withdraw-to-eat behavior vs that of strepsirrhines as describe in the introduction. Further study of nonhuman primates may clarify the evolution of visually related hand skills and perhaps even shed light on whether visually related handling movements originated in harvesting insects or fruit (see Introduction).

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Data Availability Statement: Videos are archived by Ian Q Whishaw.

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