

The destination defines the journey: an examination of the kinematics of hand-to-mouth movements

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Submitted 14 March 2016; accepted in final form 4 August 2016

Flindall JW, Gonzalez CL. The destination defines the journey: an examination of the kinematics of hand-to-mouth movements. *J Neurophysiol* 116: 2105–2113, 2016. First published August 10, 2016; doi:10.1152/jn.00222.2016.—Long-train electrical stimulation of the motor and premotor cortices of nonhuman primates can produce either hand-to-mouth or grasp-to-inspect movements, depending on the precise location of stimulation. Furthermore, single-neuron recording studies identify discrete neuronal populations in the inferior parietal and ventral premotor cortices that respond uniquely to either grasp-to-eat or grasp-to-place movements, despite their identical mechanistic requirements. These studies demonstrate that the macaque motor cortex is organized around producing functional, goal-oriented movements, rather than simply fulfilling muscular prerequisites of action. In humans, right-handed hand-to-mouth movements have a unique kinematic signature; smaller maximum grip apertures are produced when grasping to eat than when grasping to place identical targets. This is evidence that the motor cortex in humans is also organized around producing functional movements. However, in both macaques and humans, grasp-to-eat/hand-to-mouth movements have always been elicited using edible targets and have (necessarily) been paired with mouth movement. It is therefore unknown whether the kinematic distinction is a natural result of grasping food and/or is simply attributable to concurrent opening of the mouth while grasping. In *experiment 1*, we used goal-differentiated grasping tasks, directed toward edible and inedible targets, to show that the unique kinematic signature is present even with inedible targets. In *experiment 2*, we used the same goal-differentiated grasping tasks, either coupled with or divorced from an open-mouth movement, to show that the signature is not attributable merely to a planned opening of the mouth during the grasp. These results are discussed in relation to the role of hand-to-mouth movements in human development, independently of grasp-to-eat behavior.

grip aperture; grasp; hand; mouth; edible

NEW & NOTEWORTHY

Two experiments were performed, aimed at exploring a previously identified right-hand kinematic advantage for grasping movements whose end goal is to bring an item to the mouth. We provide evidence that this advantage for hand-to-mouth grasping movements is 1) nonspecific with respect to a target's edibility and 2) dependent on the concurrent opening of the mouth to accept the transported target.

THE PRIMATE MOTOR SYSTEM is organized around the production of complex coordinated behaviors rather than around specific muscle control (Graziano 2006). Several studies have shown

that long-train (500–1,000 ms) electrical stimulation of the motor and premotor cortices yields context-relevant reaching (Graziano et al. 2005), grasp-to-manipulate (Graziano et al. 2004), and hand-to-mouth grasping movements (Graziano et al. 2005). Additionally, single-neuron recording studies in macaques have identified task-specific neurons in both inferior parietal area PFG and ventral premotor area F5, which respond differentially to the purpose of a grasp. Neuronal populations in these regions respond selectively during grasping to place a target object, whereas other populations respond selectively to grasp-to-eat actions. These populations are sensitive only to the intent of the action, irrespective of the identity of the object to be grasped (Fogassi et al. 2005; cf. Bruni et al. 2015), induced reach-to-grasp kinematics (Bonini et al. 2010), or forced hand preshaping requirements (Bonini et al. 2012). Taken together, these results suggest that both grasp-to-manipulate and grasp-to-eat actions in macaques are supported by discrete neural networks [for review, see Kaas et al. (2011)]. It is yet unclear whether these actions are produced via a comparable framework in humans, although functional magnetic resonance imaging (fMRI) evidence shows that different neural networks are responsible for the planning of grasp vs. touch movements [for review, see Grefkes and Fink (2005) and Gallivan and Culham (2015)]. The superior parieto-occipital cortex has been shown to be uniquely activated during touch and pointing movements (De Jong et al. 2001; Kertzman et al. 1997), whereas the anterior intraparietal sulcus (IPS) has been linked to the planning of grasping actions (Cavina-Pratesi et al. 2007; Culham et al. 2006; Gallivan and Culham 2015). Still, the current limitations of fMRI technology, specifically with respect to head and arm movement (Culham et al. 2006), along with the invasive nature of direct electrical stimulation and single-neuron recording techniques, have limited the collection of direct evidence for task-based separation of grasping actions in humans. Instead, we look to kinematic differences in the execution of these two types of (mechanistically identical) grasps for evidence of their neural distinction.

In alignment with primate studies, researchers have recently identified behavioral evidence in humans supporting the neural division of “grasp-to-eat” and “grasp-to-place” movements (Ferri et al. 2010; Flindall and Gonzalez 2013). Specifically, when grasping a target with intent to eat, participants produce smaller maximum grip apertures (MGAs) than when grasping an identical target with intent to place it in a container near the mouth. This difference in the precontact phase of the grasp is exclusive to right-handed actions (Flindall and Gonzalez 2013), suggesting that not only are the grasp-to-eat and grasp-to-place movements distinct in their origins, but that the grasp-to-eat movement is left-hemisphere lateralized. This

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finding was originally framed as evidence that the right-handed grasp-to-eat movement, by using a smaller, more quick-to-close (and thus, quick to capture) hand shaping strategy, could have served as a driving force behind the evolution of right-hand dominance in humans. Such a strategy would have the combined benefits of potentially being both more successful and more energetically efficient (Flindall and Gonzalez 2013; Harris 1995). However, a subsequent investigation into the grasp-to-eat movement revealed that target consumption is not required for the above kinematic advantage (Flindall and Gonzalez 2014), prompting questions related to the application of the “grasp-to-eat” label. In that study, participants were asked to grasp small food items and 1) eat them, 2) place them in a small container near the mouth, or 3) place them in the mouth briefly before then “spitting” them into a nearby trash receptacle. MGAs were significantly smaller in the “eat” condition than in the “place” condition (replicating the results of Flindall and Gonzalez 2013), but interestingly, the “spit” condition generated MGAs identical to those in the “eat” condition; thus the “grasp-to-eat advantage” described previously was found to be present even when consumption did not occur (Flindall and Gonzalez 2014). Perhaps the grasp-to-eat movement identified may be part of a larger class of hand-to-mouth actions, examples of which may or may not end in consumption. Alternatively, the grasp-to-eat effect in the “spit” condition may have been triggered by the target itself, i.e., a small item that serves no other purpose than to be eaten. It is possible that when bringing such obviously edible targets to the mouth, participants will automatically and subconsciously initiate a grasp-to-eat motor plan that may be adapted into a grasp-to-place movement later if required. Another confound in these studies is that all movements in which smaller MGAs were observed required simultaneous opening of the mouth to accept the target, regardless of end goal of the movement, whether it be eating (e.g., “grasp-to-eat;” Flindall and Gonzalez 2013, 2015; Flindall et al. 2015) or temporary placement in the mouth (e.g., “grasp-to-spit;” Flindall and Gonzalez 2014). Given that electrically induced hand-to-mouth movements in macaques were at all times paired with simultaneous mouth opening (Graziano 2006), it is possible that simply opening one’s mouth during grasping movements will prompt smaller MGA production, independent of the actor’s final intent. To address these concerns, we conducted two experiments with methods similar to those employed by Flindall and Gonzalez (2013, 2014), one controlling for item type and one controlling for mouth movement.

Experiment 1 was designed to test whether MGA differences between hand-to-mouth and grasp-to-place movements are dependent on the edibility of a target. Participants grasped edible items (Cheerios, Froot Loops) to either eat them (mouth condition) or place them in a container hanging just below the mouth (container condition). In addition, participants grasped inedible, nonfood items (nylon hex nuts) of similar sizes, again to either place them in the mouth or in a container near the mouth. We hypothesized that if a grasp-to-eat motor-plan is initiated when one is grasping food items, then such a plan would be inhibited when one is grasping unmistakably inedible nonfood items. If this is the case, then MGAs should only differ between task conditions when participants grasp those items that are edible; MGAs should not differ between mouth and container conditions when participants grasp nonfood

items, because a grasp-to-eat action would be precluded by the inedibility of the target.

Experiment 2 was designed to test whether concurrent mouth movement leads to smaller MGAs during grasping movements, irrespective of movement end goal. As in *experiment 1*, participants were asked to grasp food items and bring them either to the mouth or to a container near the mouth. During both end-goal conditions, however, participants either opened their mouths concurrently (open-mouth conditions) or kept their mouths closed throughout the entire movement (closed-mouth conditions). If planned concurrent mouth movement is responsible for smaller MGAs, then a difference between open- and closed-mouth conditions should be apparent regardless of movement end goal.

MATERIALS AND METHODS

For both *experiments 1* and 2, the equipment used matched that of Flindall and Gonzalez (2013). Briefly, three infrared light-emitting diodes (IREDs) were placed on the participant’s hand: two on the distal phalanges of the thumb and index finger, slightly proximal to the nails, and one on the wrist at the medial aspect of the styloid process of the radius (proximal and medial to the anatomical snuff box). An Optotrak Certus sensor (Northern Digital, Waterloo, ON, Canada) recorded IRED positions during the outward grasping movement at 200 Hz for 4 s. Vision was restricted between grasps via Plato Liquid-crystal glasses (Translucent Technologies, Toronto, ON, Canada), worn by the participant throughout the testing session. All experimental equipment was controlled using SuperLab 4.5 (Cedrus, San Pedro, CA) and NDI First Principles (Northern Digital) software.

Targets to be grasped consisted of both inedible (*experiment 1*) and edible objects (*experiments 1* and 2). Inedible targets were nylon hex nuts in both small (3/8-in. nylon 10-32, diameter 9.53 mm; B&F Fastener Supply, Ramsey, MN) and large varieties (nylon 6/6 hex nut, diameter 14.29 mm; McMaster-Carr Supply, Elmhurst, IL). Nylon hex nuts are nontoxic, tasteless, and colorless; they were chosen both for their small size (which was roughly comparable to that of the edible targets) and for their familiarity to the participants as inedible, nonfood objects. Edible targets were small (General Mills Cheerios; average diameter 11 mm) and large cereal (Kellogg’s Froot Loops; average diameter 15 mm), chosen both for their familiarity to participants and for their hypoallergenic nature (Flindall and Gonzalez 2014). Materials and equipment used in *experiment 2* were identical to those of *experiment 1*, save that only edible target objects were presented.

Participants

Participants in both experiments volunteered to take part in the study in exchange for course credit. All participants gave written informed consent on admission to the study, in accordance with the principles expressed in the Declaration of Helsinki and with the approval of the University of Lethbridge Human Subjects Research Committee (protocol no. 2011-022). Handedness was determined via self-report and confirmed using a modified Edinburgh/Waterloo handedness questionnaire (Cavill and Bryden 2003; Oldfield 1971; Stone et al. 2013) given to each participant following data collection. Participants were excluded from analysis if they were left-handed, if they had suffered neurological damage or recent mechanical injury affecting the dominant limb, or if they had received specific training encouraging nondominant hand use for 1 mo or more. Twenty volunteers were originally recruited for each experiment. Three participants from *experiment 1* and two from *experiment 2* were excluded for one or more of the above reasons, leaving 17 (mean age 20.1 yr,

11 women) and 18 participants (mean age 24.1 yr, 13 women) available for analysis in *experiments 1* and 2, respectively.

During both experiments, participants sat before a self-standing height-adjustable triangular pedestal. The distance to the pedestal was normalized to each participant's reach distance (100% of length from shoulder to index finger with elbow at full 180° extension). The height of the pedestal was adjusted for each participant such that the target was at a comfortable reach height (approximately level with the base of the sternum of the seated participant), but also such that the edge of the pedestal did not act as a direct obstacle during the reach-to-grasp movement (Flindall and Gonzalez 2013; Whishaw et al. 2002).

Procedure

Experiment 1. Participants were presented with target items individually in 4 blocks of 20 trials each. Blocks were defined by a 2 (item type: edible, inedible) × 2 (end goal: mouth, container) factorial design. Large and small targets (10 of each) were pseudorandomly presented in each block. Block order was counterbalanced between participants.

Each trial began with the participant seated behind the pedestal with the right hand (thumb and index finger together) placed comfortably on the lap (rest position). The liquid crystal occlusion goggles worn by the participant remained in an opaque state between trials, meaning the participant was naive to the size and precise location of the target until the beginning of the trial. The researcher placed the large and small targets on the pedestal, one per trial, in a pseudorandom order in an effort to prevent the participant from preplanning movements. Trials began when the occlusion goggles transitioned to a transparent state, allowing the participant an initial view of the target. An auditory tone sounded 1,000 ms later; this indicated that the participant was to reach out and grasp the target, and either place it in the container or place it in the mouth, depending on block condition. If edible, the participant was instructed to eat the target after placing it in the mouth. In the case of inedible targets, the participant returned the right hand to the rest position before removing the target from the mouth with the untracked left hand; the target was then dropped in a trash receptacle. Note that the mouth conditions for both target types differed with respect to consumption requirements; nevertheless, they are assumed to be equivalent on the basis of results from Flindall and Gonzalez (2014). Participants were instructed to perform each grasp at a comfortable, natural pace, with an emphasis on accuracy over speed of movement.

Experiment 2. Participants were presented with target items individually in 4 blocks of 16 trials each. Blocks were defined by a 2 (goal: mouth, container) × 2 (mouth state: open, closed) factorial design. Eight food items of two sizes (small, large) were pseudorandomly presented within each block. The same food items from *experiment 1* (i.e., Cheerios, Froot Loops) were used in *experiment 2*. Block order was counterbalanced between participants. Goal conditions were similar to those in *experiment 1* in that participants were instructed to grasp an item to bring it either to the mouth or to a container hanging beneath the chin. During open-state trials, participants were instructed to open their mouths after grasping the target "as if [they] were about to eat the item." During closed-state trials, participants were instructed to keep their mouths closed (i.e., "teeth together but not clenched, and lips touching") throughout the movement. Note that "open-mouth" and "closed-container" conditions resulted in the production of "grasp-to-eat" and "grasp-to-place" movements as defined by Flindall and colleagues during previous experiments (Flindall and Gonzalez 2013; Flindall et al. 2015). During closed-mouth trials, participants briefly touched the grasped food item to their closed lips (Fig. 1A) before placing the item in a nearby trash receptacle. Participants were specifically instructed not to purse their lips as if kissing the item. During the open-container condition, participants were given special instruction to place the item directly into the container, without first moving toward the mouth

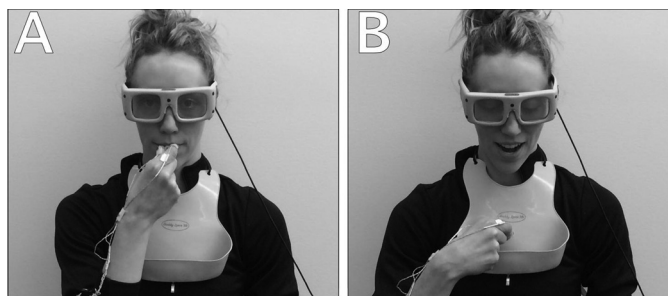


Fig. 1. Closed-mouth (A) and open-container conditions (B) used in *experiment 2*.

(Fig. 1B). If participants brought an item toward the mouth during the closed-container condition, that trial was removed from analyses and instructions were repeated. Participants were instructed to perform each grasp at a comfortable pace, with an emphasis on accuracy over speed of movement.

Data Analysis

Data were collected via NDI First Principles motion capture software, with kinematic calculations performed on unfiltered data using Microsoft Excel 2010. MGA was measured as the peak resultant distance between the thumb and index finger before the time of target contact. This value was obtained by averaging the resultant at rest (when fingertips were touching) across all of a participant's trials and subtracting that constant from the peak resultant between IREDs for each trial (Flindall and Gonzalez 2013, 2014). Note that, for both experiments, all statistical tests were simultaneously run on uncorrected MGA values and that results of these tests were consistent between both data sets. Aside from our main dependent variable of interest (MGA), we also report movement time (MT), peak resultant velocity of the wrist (PV), and relative time of MGA (MGAT). Movement time (in ms) describes the speed at which a participant completes the required action; it is measured as the time between reaction time (when the instantaneous velocity of the wrist marker exceeds 5% of the PV of the outgoing movement) and time of grasp onset (when instantaneous wrist velocity reaches a minimum before the beginning of the return/transport phase of the action). MGAT typically occurs after PV (within the deceleration phase of the approach) and is reported as a percentage of total movement time.

Kinematic variables were averaged by condition, and statistical analyses were performed on condition means. Note that all reported kinematic variables are limited to the outward phase of the reach-to-grasp movement; the return (i.e., placement, or hand to mouth) phase of each trial was not analyzed, because Optotrak/IRED line-of-sight limitations within our data collection area prohibit the consistent collection of both the outward and inward phases. If participants failed to successfully grasp the target item during a trial (either by missing or anticipating the go signal or by accidentally knocking the target to the floor), that trial was removed from analysis and not repeated. In *experiment 1*, an average of 1.05 trials per participant (1.3%; range 0–6.25%) were removed due to these types of error, with 0.56 trials per participant (0.8%; range 0–4.7%) removed per participant in *experiment 2*. Data from *experiment 1* were initially subjected to a three-way repeated-measures ANOVA [size (small, large) × goal (mouth, container) × type (edible, inedible)]. *Experiment 2* variables were also subjected to a three-way repeated-measures ANOVA [size (small, large) × state (open, closed) × goal (mouth, container)]. Alpha significance for the ANOVAs was set at $P < 0.05$, with Bonferroni correction applied to post hoc comparisons as necessary. Estimates of effect size are reported using partial eta-squared (η_p^2).

Table 1. Between-participant means and SE for reach and grasp kinematics in experiment 1, averaged by condition

Type	Goal	Size	MGA, mm	MT, ms	PV, m/s	MGAT, %MT
Edible	Mouth	Small	20.42 ± 0.9	928 ± 43	0.65 ± 0.03	57.8 ± 2.2
		Large	24.13 ± 1.0	872 ± 39	0.65 ± 0.03	61.1 ± 2.3
	Container	Small	22.42 ± 1.2	926 ± 44	0.64 ± 0.03	56.7 ± 2.6
		Large	26.20 ± 1.4	882 ± 41	0.64 ± 0.03	61.6 ± 2.3
2-way ANOVA results			G, S	S		S
Inedible	Mouth	Small	18.52 ± 1.1	1097 ± 56	0.68 ± 0.03	48.0 ± 2.6
		Large	28.16 ± 1.4	856 ± 36	0.67 ± 0.03	65.3 ± 1.7
	Container	Small	20.51 ± 1.2	1153 ± 59	0.64 ± 0.03	44.7 ± 2.6
		Large	30.31 ± 1.5	871 ± 40	0.64 ± 0.03	61.4 ± 1.7
2-way ANOVA results			G, S	S	G	S
3-way ANOVA results			T, S, G, T × S	T, S, T × S	G, T × G	T, S, T × S

Variables reported are maximum grip aperture (MGA), movement time (MT), peak resultant velocity (PV), and time of MGA (MGAT, expressed as a percentage of MT). Significant within-subject ANOVA results by main effect (G, goal, S, size; T, type) and interaction are listed below kinematic values for the edible and inedible targets.

RESULTS

Experiment 1

Significant main effects and interactions are reported below. Between-subject means and SE for reach and grasp kinematics in experiment 1 are reported in Table 1.

Results of the three-way ANOVA revealed a main effect of target type on MGA [$F(1,16) = 5.315, P = 0.035, \eta_p^2 = 0.249$], where edible targets elicited smaller MGAs (23.4 ± 1.11 mm) than did inedible targets (24.4 ± 1.27 mm). A main effect of size was observed [$F(1,16) = 160.274, P < 0.001, \eta_p^2 = 0.909$], where small targets elicited smaller MGAs (20.47 ± 1.08 mm) than did large targets (27.20 ± 1.31 mm). A main effect of goal on MGA was also observed [$F(1,16) = 14.147, P = 0.002, \eta_p^2 = 0.469$], with smaller MGAs being produced for mouth-directed movements (22.81 ± 1.09 mm) than for movements directed toward the container (24.86 ± 1.30 mm). Finally, a size × type interaction was also observed [$F(1,16) = 87.300, P < 0.001, \eta_p^2 = 0.845$]. Post hoc paired-sample *t*-tests revealed that this interaction is due to the direction of differences between edible and inedible targets within each size category. When targets were small, edible targets elicited larger MGAs (21.42 ± 1.07 mm) than did inedible targets [19.52 ± 1.17 mm; $t(16) = 3.283, P = 0.005$], whereas the reverse was true for large targets, with inedible targets eliciting significantly larger MGAs (29.23 ± 1.48 mm) than did edible targets [25.22 ± 1.19 mm; $t(16) = -6.921, P < 0.001$]. However, this interaction is unsurprising given the discrepancies between edible and inedible targets within each size category.¹

¹Whereas size differences between small items in each category (~11- and 9.53-mm diameters for edible and inedible items, respectively) preclude relevance in our 3-way ANOVA, the more analogous size between Froot Loops and large hex nuts (~15 and 14.29 mm, respectively) allow a 2-way ANOVA with target type (edible, inedible) and goal (mouth, container) as factors. This comparison showed a main effect of goal (consistent with the results of the combined and individual ANOVAs), but interestingly, it also showed a main effect of target type [$F(1,16) = 48.068, P < 0.001, \eta_p^2 = 0.750$], with Froot Loops (25.2 ± 1.19 mm) generating smaller MGAs than comparably sized nylon hex nuts (29.2 ± 1.48 mm). This suggests that target type may indeed play some role in determining kinematics of the reach-to-grasp action, outside of that role played by actor intent. This finding must be explored in future studies within our laboratory but is beyond the scope of the current report.

A significant main effect of goal was found for PV [$F(1,16) = 9.946, P = 0.006, \eta_p^2 = 0.383$], where movements reached a higher PV when the grasped item was to be placed in the mouth (1.32 ± 0.1 m/s) than when the item was to be placed in the container (1.28 ± 0.1 m/s). A type × goal interaction was also observed in PV [$F(1,16) = 6.339, P = 0.023, \eta_p^2 = 0.284$]. Post hoc paired-sample *t*-tests revealed that this effect was due to a significant difference in PV between goal conditions for inedible items only, with grasps toward inedible targets achieving higher PVs when the target was to be brought to the mouth (1.35 ± 0.1 m/s) than when the target was to be brought to the container [1.28 ± 0.1 m/s; $t(16) = 3.828, P = 0.001$].

Significant main effects of item type [$F(1,16) > 12.231, P < 0.003, \eta_p^2 > 0.433$] and size [$F(1,16) > 89.631, P < 0.001, \eta_p^2 > 0.849$] and type × size interactions [$F(1,16) > 39.093, P < 0.001, \eta_p^2 > 0.710$] were observed for MT and MGAT. These effects are consistent with a strong main effect of size manifesting for both item types, with smaller items being associated with longer MTs and earlier relative MGATs than larger items. Again, these effects are complicated by differences in actual size of small and large items between types.

Given these complications, we split our data by target type (edible, inedible) and subjected each set to a two-way repeated-measures ANOVA [size (small, large) × goal (mouth, container)] to provide a clearer representation of our findings. The results of these ANOVAs are reported below.

MGA. A main effect of size was observed for both edible [$F(1,16) = 101.531, P < 0.001, \eta_p^2 = 0.864$] and inedible targets [$F(1,16) = 149.557, P < 0.001, \eta_p^2 = 0.903$]. MGAs scaled for target size during grasps directed toward both edible (small: 21.4 ± 1.07 mm; large: 25.2 ± 1.19 mm) and inedible targets (small, 19.5 ± 1.17 mm; large, 29.2 ± 1.48 mm). A main effect of goal was observed on MGAs for both edible [$F(1,16) = 9.390, P = 0.007, \eta_p^2 = 0.370$] and inedible targets [$F(1,16) = 8.716, P = 0.009, \eta_p^2 = 0.353$]. In both cases, mean MGAs were smaller when an item was to be placed in the mouth (edible: 22.3 ± 0.99 mm; inedible: 23.3 ± 1.28 mm) than when an item was to be placed in the container (edible: 24.3 ± 1.31 mm; inedible: 25.4 ± 1.36 mm; Fig. 2). No goal × size interactions were observed for either target type ($P > 0.7$).

MT. A significant main effect of size was found for both edible [$F(1,16) = 33.7, P < 0.001, \eta_p^2 = 0.678$] and inedible

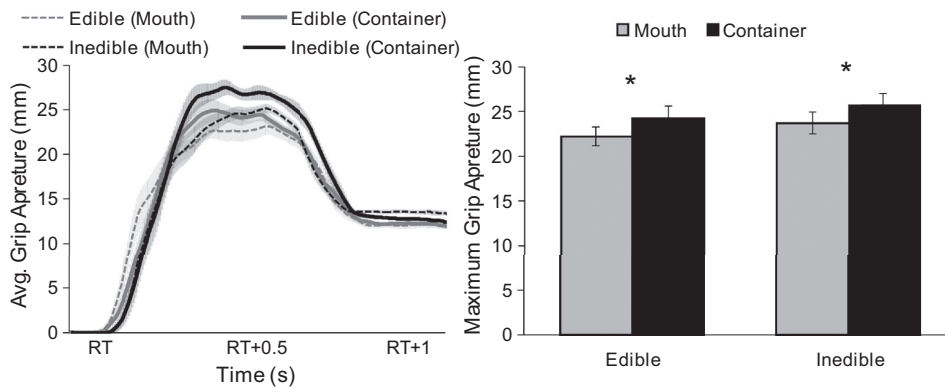


Fig. 2. Grip aperture differences between conditions in *experiment 1*. *Left*, average grip aperture over time for grasps directed toward large targets for a typical participant (participant TFO). Trials have been reaction time (RT)-aligned to best show differences in maximum grip aperture (MGA) between conditions. *Right*, MGAs (means and SE), collapsed across target size (small, larger), in the mouth and container goal conditions for edible and inedible objects. Difference between goal conditions was significant for both target types ($*P < 0.01$). Avg., average.

targets [$F(1,16) = 76.7, P < 0.001, \eta_p^2 = 0.827$]. MT was significantly longer for smaller items (edible: 927 ± 44 ms; inedible: $1,125 \pm 55$ ms) than it was for larger items (edible: 878 ± 40 ms; inedible: 863 ± 37 ms). No other main effects or interactions were observed.

PV. A significant main effect of goal was found for inedible objects [$F(1,16) = 13.565, P = 0.002, \eta_p^2 = 0.459$], where grasps achieved larger PVs when a hex nut was to be placed in the mouth (0.675 ± 0.03 m/s) than when it was to be placed in the container (0.638 ± 0.03 m/s). No other main effects or interactions were observed.

Relative time of MGA. A significant main effect of size was found for both edible [$F(1,16) = 17.6, P < 0.001, \eta_p^2 = 0.606$] and inedible targets [$F(1,16) = 105, P < 0.001, \eta_p^2 = 0.868$]. MGA occurred significantly earlier relative to total movement time during grasps toward smaller items (edible: $57.3 \pm 2.3\%$; inedible: $46.4 \pm 2.5\%$) than during grasps toward larger items (edible: $61.4 \pm 2.2\%$; inedible: $63.3 \pm 1.6\%$). Thus participants spent relatively more time closing their fingers around small items than they did around large items, regardless of item type. No other main effects or interactions were observed.

Experiment 2

Significant main effects and interactions are reported below. Between-subject means and SE for reach and grasp kinematics in *experiment 2* are reported in Table 2.

MGA. A main effect of size was observed [$F(1,17) = 59.5, P < 0.001, \eta_p^2 = 0.778$], where participants produced smaller MGAs for smaller targets (21.2 ± 0.753 mm) than for larger ones (24.5 ± 0.629 mm). A main effect of state was observed [$F(1,17) = 10.2, P = 0.005, \eta_p^2 = 0.375$], where smaller

MGAs were produced when participants grasped items and then opened their mouths (21.9 ± 0.625 mm) than when their mouths remained closed throughout the movement (23.8 ± 0.807 mm). No main effect of goal was found; however, a significant state \times goal interaction was observed [$F(1,17) = 7.42, P = 0.014, \eta_p^2 = 0.304$]. Post hoc paired-sample *t*-tests revealed that this effect was due to a significant difference between open (21.2 ± 0.665 mm) and closed states (24.0 ± 0.806 mm) when the end goal of the movement was the mouth [$t(17) = 5.595, P < 0.001$; Fig. 3]. When the end goal of the movement was the container, there was no difference between open (22.6 ± 0.675 mm) and closed conditions [23.5 ± 0.906 mm; $t(17) = 1.161, P = 0.262$]. The difference between open-mouth and closed-container conditions was also significant [$t(17) = 3.017, P = 0.008$], replicating our results from *experiment 1*. Finally, the difference between open-mouth and open-container conditions was suggestive [$t(17) = 2.942, P = 0.011$]; however, this difference was not significant following Bonferroni correction ($\alpha = 0.0083$).

MT. A main effect of size was observed [$F(1,17) = 29.768, P < 0.001, \eta_p^2 = 0.637$], where grasps directed toward small targets (912 ± 42 ms) took significantly more time to complete than grasps directed toward large targets (857 ± 38 ms). A main effect of goal was observed [$F(1,17) = 9.647, P = 0.006, \eta_p^2 = 0.362$], where grasps whose ultimate end goal was the container (917 ± 45 ms) took significantly longer to complete than did grasps whose ultimate end goal was the mouth (852 ± 37 ms). Finally, a size \times state interaction was observed [$F(1,17) = 17.320, P = 0.001, \eta_p^2 = 0.505$]. Post hoc paired-sample *t*-tests revealed this effect was due to a significant difference between MTs when small (935 ± 47 ms) and large

Table 2. Between-participant means and SE for reach and grasp kinematics in *experiment 2*

State	Goal	Size	MGA, mm	MT, ms	PV, m/s	MGA _t , %MT
Open	Mouth	Small	19.39 ± 0.7	848 ± 33	0.72 ± 0.04	53.7 ± 2.8
		Large	22.98 ± 0.6	836 ± 42	0.70 ± 0.04	56.3 ± 2.1
	Container	Small	21.00 ± 0.7	929 ± 49	0.71 ± 0.04	54.5 ± 2.2
		Large	24.22 ± 0.7	883 ± 38	0.70 ± 0.04	57.9 ± 2.0
Closed	Mouth	Small	22.49 ± 0.9	893 ± 40	0.72 ± 0.05	53.2 ± 2.3
		Large	25.51 ± 0.7	830 ± 36	0.72 ± 0.04	56.5 ± 2.3
	Container	Small	21.88 ± 1.0	979 ± 55	0.70 ± 0.05	50.1 ± 2.7
		Large	25.15 ± 0.9	878 ± 47	0.70 ± 0.05	56.0 ± 2.8
ANOVA results			S, St, S \times G	S, G, S \times St	S	S

Variables reported are maximum grip aperture (MGA), movement time (MT), peak resultant velocity (PV), and time of MGA (MGA_t, expressed as a percentage of MT). Significant within-subject ANOVA results by main effect (S, size; St, mouth state; G, goal) and interaction are listed below kinematic values for the open- and closed-mouth states.

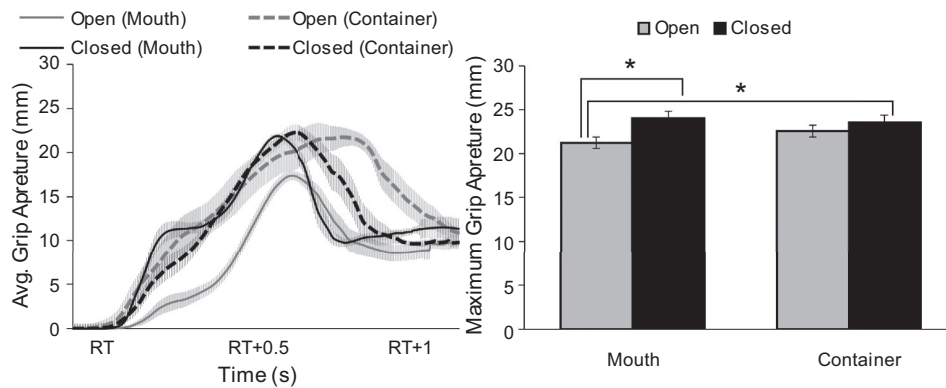


Fig. 3. Grip aperture differences between conditions in *experiment 2*. *Left*, average grip aperture over time during grasps directed toward large targets for a single typical participant (participant MMS). Trials have been RT-aligned to best show MGA differences between conditions. *Right*, MGAs, (means and SE), collapsed across size, for open- and closed-state conditions in mouth and container goal conditions. MGAs during the open-mouth condition (i.e., when participants ate the target) were significantly smaller than MGAs in both closed-mouth (* $P < 0.001$) and closed-container conditions (* $P < 0.008$). No other conditions were significantly different from one another following Bonferroni correction ($P > 0.0083$).

(854 ± 41 ms) targets were grasped when the mouth was to remain closed [$t(17) = 7.11, P < 0.001$]. The difference between MTs for small (888 ± 41 ms) and large targets (859 ± 39 ms) in the open-state conditions was not significant following Bonferroni correction [$t(17) = 2.392, P = 0.029$].

PV. A significant main effect of size was found [$F(1,17) = 7.339, P = 0.015, \eta_p^2 = .302$], where grasps directed toward small targets achieved larger PVs (0.714 ± 0.043 m/s) than did grasps directed toward large targets (0.706 ± 0.042 m/s). No other main effects or interactions were observed.

MGA_t. A significant main effect of size was found [$F(1,17) = 14.2, P = 0.002, \eta_p^2 = 0.454$]. MGA_t occurred significantly earlier relative to total movement time during grasps toward smaller items ($52.9 \pm 2.2\%$) than during grasps toward larger items ($56.7 \pm 2.1\%$). No other main effects or interactions were significant.

DISCUSSION

In *experiment 1*, when grasping edible targets, participants produced significantly smaller MGAs when eating edible targets than when placing them into a container. Interestingly, the same task-dependent difference was observed during grasps directed toward inedible targets; again, when placing these inedible targets in the mouth, participants produced smaller MGAs than when placing those targets into the container. Indeed, main effects of goal and size were consistent between the two item types for all kinematic variables measured (except PV for edible items, although a consistent nonsignificant trend was observed, $P = 0.15$). Thus the task-dependent effect on MGA identified in previous studies (i.e., smaller MGAs when performing hand-to-mouth movements) is independent of target type. We suggest that the kinematic advantage identified in previous studies should be described as a result of hand-to-mouth movements, rather than grasp-to-eat movements.

In *experiment 2*, participants were asked to grasp small food items to bring them to the same goals as in *experiment 1*; however, now these goal conditions were further separated into two distinct mouth-state conditions. In the open-state conditions, participants opened the mouth either to eat the item (open-mouth condition) or “as if to eat the item” (open-container condition) while bringing the item directly to either the mouth or container, respectively. Conversely, in the closed-

state conditions, participants kept the mouth firmly closed (teeth together, lips touching) whether they were to bring the item to the mouth (closed-mouth condition) or place it in the container (closed-container condition). When participants brought the grasped items to the container, kinematics of the grasping actions did not differ between the open- and closed-state conditions. However, when bringing the item to the mouth, participants produced significantly smaller MGAs when they opened the mouth to accept the grasped item (open-mouth condition). When participants brought the item to a closed mouth (closed-mouth condition), MGAs were larger and not significantly different from either grasp-to-place action. These results are in contrast with those of previous studies, which found that opening the mouth during a grasping action results in significantly larger MGAs (Gentilucci et al. 2001; Gentilucci and Campione 2011). This may be explained by differences between the experiments; Gentilucci and colleagues instructed their participants to assume an open-mouth posture before initiating a grasp, whereas in the current experiment participants only opened the mouth during the transfer phase of the movement, after the object had successfully been acquired. It is possible that the delay between finger and mouth movement may have reduced or eliminated the reciprocal influence these movements have on one another (Gentilucci et al. 2001; Gentilucci and Campione 2011). Regardless, the current study shows that concurrent mouth movement alone is not responsible for the hand-to-mouth kinematic advantage that we have previously identified. Where previous studies showed that food-directed grasps demonstrated a kinematic advantage when the end-goal was to eat rather than place, both experiments in the current study show that intent to eat, whether conscious or unconscious, is not a necessary component of these kinematically distinct movements. We show that the grasped item must be placed in the mouth, versus simply being brought to the mouth (as in the closed-mouth condition in *experiment 2*); thus the MGA advantage appears to be generalized for hand-to-mouth grasping actions, rather than grasp-to-eat movements as previously presented (cf. Flindall and Gonzalez 2014).

With respect to other kinematics of the reach and grasp (namely, MT, PV, and MGA_t), main effects of size in both experiments point toward an overall longer, presumably more

careful approach phase of the movement toward smaller items, irrespective of the end goal of the movement or edibility of the target. This effect of size is in accordance with results reported in previous kinematic investigations (e.g., Bootsma et al. 1994; Chieffi and Gentilucci 1993). Interestingly, *experiment 1* showed that grasps directed toward inedible targets achieved higher peak velocities than grasps directed toward edible targets, suggesting that our perception of whether or not an item is edible may play a role in determining kinematics of the reach-to-grasp action. This is in accordance with findings from Bruni et al. (2015), who identified neurons within the macaque premotor cortex that respond selectively to the edibility of a target during visually cued grasping tasks. Unfortunately, meaningful comparisons between target types in *experiment 1* of the current study are hindered by the differences between edible and inedible targets within each size category; the main effects and interactions involving object type that we report may be due entirely to discrepancies in size, shape, and variability between our edible and inedible targets. Future studies in our laboratory aimed at investigating these identity-dependent differences will follow the example set by Bruni et al. (2015) and match target size, shape, and color as precisely as possible between target types.

The results of the current studies also align well with results from electrophysiological experiments. When hand-to-mouth movements were generated via long-train stimulation of the macaque motor cortex, researchers observed that such movements were always paired with a simultaneous opening of the mouth (Graziano et al. 2002, 2005). In the current study, we have shown that the kinematics of the hand-to-mouth grasping action are only significantly different from those of the grasp-to-place action when one not only brings the item to the mouth, but also concurrently opens the mouth to accept the transported item [see also Ferri et al. (2010)]. In the direct-stimulation studies, researchers naturally interpreted the evoked hand-to-mouth movement as a grasp-to-eat action; however, we have shown in the current study that one need not grasp the item with intent to eat for kinematics to be affected. As long as the item is grasped with intent to place it in the mouth, the movement is kinematically differentiated from grasping actions with different end goals but otherwise identical mechanistic requirements. This finding, along with those of electrophysiological (Bonini et al. 2012; Bruni et al. 2015; Fogassi et al. 2005; Graziano et al. 2005) and behavioral studies (Ferrari et al. 2003; Ferri et al. 2011), supports the theory of a primate motor system organized around the production of complete, purpose-driven actions differentiated by end goal, rather than one organized around simply satisfying the mechanistic requirements of a task within a given environment.

The hand-to-mouth movement is evolutionarily significant in that mammalian grasping probably evolved for the purpose of self-feeding (Goodale 1990; Iwaniuk and Whishaw 2000; MacNeilage et al. 1987; Whishaw 2003). Although some have conversely proposed that the ancestral form of grasping in primates was primarily for arboreal locomotion (Szalay and Dagosto 1988), it is nevertheless significant that all modern animals that display grasping behavior do so for purposes of self-feeding (Iwaniuk and Whishaw 2000). However, primates also reach toward their mouths for other reasons, including to bite a grasped object or to push food from their cheek pouches (Graziano et al. 2004), or for sucking, breaking, or taking-away movements (Ferrari et al. 2003). Such movements, it may be

argued, are somewhat related to feeding but, nevertheless, do not directly result in ingestion. Grasps purposed to subsequently crack seeds, or arthropod shells, are still ethologically relevant movements for which a right-hand advantage could have exerted evolutionary pressure on our forebears, leading to a global tendency toward right-handedness in humans.

The hand-to-mouth movement is also one of the first movements performed by children in development; infants and even fetuses in the womb will perform hand-to-mouth movements, for which there is often a right-hand bias (De Vries et al. 1982; Hepper et al. 1998; Piaget and Cook 1953; Rochat et al. 1988). The purpose behind these movements is, again, not necessarily for self-feeding; after all, babies are not prepared to ingest solid (graspable) food for the first 4–6 mo of life (American Academy of Pediatrics and American College of Obstetricians and Gynecologists 2013). The prehension reflex in infants emerges at around the same time, at age 4–10 mo (Twitchell 1965), but still well before the infant is developmentally prepared to feed himself. Instead, grasping in infants is exploratory in nature; toys and other inedible objects are often brought directly to the mouth following a successful grasp (Butterworth 1992; Gibson 1988). Whereas some research has shown that a right-hand preference for hand-to-mouth grasps develops years earlier than does a right-hand preference for manipulation grasps (Sacrey et al. 2013), others have shown that handedness in infants is fluid, with hand preference (as measured during a single testing session) changing from one side to the other and back again throughout development into toddlerhood (Rönqvist and Domellöf 2006). Instead of measuring laterality through preference, some researchers suggest that kinematic proficiency may be a better predictor of lateralization into adulthood (Rönqvist and Domellöf 2006). Unfortunately, grasping kinematics among infants, especially those related to distal control, are notoriously unrefined and thus unsuited to analysis using current technology (Nelson et al. 2014). A task-dependent kinematic difference (as described in the current study), lateralized to one hand or the other, would be undetectable in infants until their grasping kinematics mature. The relationship between hand dominance and hand preference specifically for hand-to-mouth actions, however, has yet to be studied; this might serve as a better, more stable predictor of handedness in later years. Longitudinal data are necessary to address this speculation, but such data may be collected with relative ease, in open/unconstrained environments, perhaps even outside of the laboratory setting.

The kinematic signature for hand-to-mouth movements identified in the current study may be used to form a practical basis for such research. To assess hand-to-mouth movement development, we must first determine that which constitutes a hand-to-mouth movement: specifically, we must ascertain the maximum degree of separation in terms of distinct goals between reaction time and end goal. If a person grasps a grape with intent to eat but first brushes it off with the opposing hand before bringing it to the mouth, should the initial grasp be considered a grasp-to-eat action or a grasp-to-brush action? If an infant grasps a toy, one may predict with some certainty that the infant will eventually bring that toy to the mouth: but if the infant takes a detour to shake or pet the toy before bringing it to the mouth, can it still be considered a hand-to-mouth grasping action? The smaller MGA produced during hand-to-mouth actions may serve to identify these movements, and

indeed future research should be conducted to confront this question.

A significant limitation with this study concerns the differences in size between edible and inedible targets used in *experiment 1*. Although the results of our three-way ANOVA (and the 2-way ANOVA with goal and target identity as factors, see footnote) are suggestive, differences in size, shape, and variability between edible and inedible targets preclude any meaningful comparisons within the current data set, especially with respect to MGA. The nylon hex nuts used in the current study, though of comparable size to the cereal items, are not precisely the same; large hex nuts were 1 mm smaller along the small axis (and 2 mm wider along the long axis) than the average Froot Loop, and small hex nuts were at least 2 mm narrower than the average Cheerio. Additionally, edible targets were not perfectly consistent in size or shape, even after they were sorted to remove outliers in each size category; Froot Loops especially have significant variability in shape and depth, with one side often being a full millimeter wider/higher than the side opposite. Nevertheless, the data suggest that a significant difference in kinematics may exist between the two item types; such a finding would be consistent with the results of Bruni et al. (2015), who found neuron populations in area F5 of the macaque cortex that responded selectively to the identity of a target (i.e., edible or inedible) during visually cued grasp-to-eat or grasp-to-place actions. Future studies in our laboratory will investigate this possibility using targets matched for size, shape, and color (Bruni et al. 2015).

In conclusion, the current study shows that movements in which an item is brought to the open mouth, regardless of target edibility, are kinematically different from placing actions, suggesting different neural origins for hand-to-mouth and grasp-to-place movements with otherwise identical mechanistic requirements. This finding has important significance toward future research on the origin and development of handedness in humans.

GRANTS

This research was conducted with support from the Natural Sciences and Engineering Research Council of Canada (NSERC). Funding for J. W. Flindall was provided by an Alexander Graham Bell Canadian Graduate Scholarship (CGS-D). Funding for C. L. R. Gonzalez was provided by NSERC Discovery Grant 14367. Additional support was provided by the University of Lethbridge.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

J.W.F. and C.L.G. conception and design of research; J.W.F. performed experiments; J.W.F. analyzed data; J.W.F. and C.L.G. interpreted results of experiments; J.W.F. prepared figures; J.W.F. drafted manuscript; J.W.F. and C.L.G. edited and revised manuscript; J.W.F. and C.L.G. approved final version of manuscript.

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