

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/263745725>

Eating interrupted: The effect of intent on hand-to-mouth actions

Article in *Journal of Neurophysiology* · July 2014

DOI: 10.1152/jn.00295.2014 · Source: PubMed

CITATIONS

19

READS

58

2 authors:



Jason Flindall

University of Lethbridge

20 PUBLICATIONS 130 CITATIONS

SEE PROFILE



Claudia L R Gonzalez

University of Lethbridge

83 PUBLICATIONS 1,842 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Multisensory integration effects on visual awareness [View project](#)



Visual Field Advantage: Redefined by Training? [View project](#)

Eating interrupted: the effect of intent on hand-to-mouth actions

Jason W. Flindall and Claudia L. R. Gonzalez

J Neurophysiol 112:2019-2025, 2014. First published 2 July 2014; doi:10.1152/jn.00295.2014

You might find this additional info useful...

This article cites 66 articles, 11 of which can be accessed free at:

</content/112/8/2019.full.html#ref-list-1>

Updated information and services including high resolution figures, can be found at:

</content/112/8/2019.full.html>

Additional material and information about *Journal of Neurophysiology* can be found at:

<http://www.the-aps.org/publications/jn>

This information is current as of October 17, 2014.

Eating interrupted: the effect of intent on hand-to-mouth actions

Jason W. Flindall and Claudia L. R. Gonzalez

The Brain in Action Laboratory, Department of Kinesiology, University of Lethbridge, Lethbridge, Alberta, Canada

Submitted 17 April 2014; accepted in final form 30 June 2014

Flindall JW, Gonzalez CL. Eating interrupted: the effect of intent on hand-to-mouth actions. *J Neurophysiol* 112: 2019–2025, 2014. First published July 2, 2014; doi:10.1152/jn.00295.2014.—Evidence from recent neurophysiological studies on nonhuman primates as well as from human behavioral studies suggests that actions with similar kinematic requirements but different end-state goals are supported by separate neural networks. It is unknown whether these different networks supporting seemingly similar reach-to-grasp actions are lateralized, or if they are equally represented in both hemispheres. Recently published behavioral evidence suggests certain networks are lateralized to the left hemisphere. Specifically, when participants used their right hand, their maximum grip aperture (MGA) was smaller when grasping to eat food items than when grasping to place the same items. Left-handed movements showed no difference between tasks. The present study investigates whether the differences between grasp-to-eat and grasp-to-place actions are driven by an intent to eat, or if placing an item into the mouth (sans ingestion) is sufficient to produce asymmetries. Twelve right-handed adults were asked to reach to grasp food items to 1) eat them, 2) place them in a bib, or 3) place them between their lips and then toss them into a nearby receptacle. Participants performed each task with large and small food items, using both their dominant and nondominant hands. The current study replicated the previous finding of smaller MGAs for the eat condition during right-handed but not left-handed grasps. MGAs in the eat and spit conditions did not significantly differ from each other, suggesting that eating and bringing a food item to the mouth both utilize similar motor plans, likely originating within the same neural network. Results are discussed in relation to neurophysiology and development.

kinematics; asymmetries; right hand; grasping; left hemisphere

DESPITE THE WELL-DOCUMENTED lateralization of hand preference for reach-to-grasp actions, many studies have shown that, unlike the lateralized preference for reaching and pointing actions, this preference for grasping is not coupled with kinematic advantage. Studies comparing right- and left-hand kinematics for grasping movements have shown few, if any, asymmetries between the hands (e.g., Grosskopf and Kultz-Buschbeck 2006; Tretriluxana et al. 2008). These studies used placement tasks in which participants were asked to pick up a solid geometric shape and place it in a nearby location, an action which, one might argue, has little ecological relevance. If instead participants are asked to perform an action with more ethological significance, for example, eating or drinking, kinematic asymmetries become more evident. Studies investigating right- and left-handed movements for such tasks have revealed a right-hand advantage wherein participants produce smaller and/or less variable maximum grip apertures (MGAs) when grasping to eat or drink with their right hands (Flindall et al. 2014; Flindall and Gonzalez 2013). Smaller grip apertures may be considered advantageous, because peak grip closing veloc-

ity, grip closing time, and metabolic energy requirements are reduced when MGA more closely matches absolute target size (Bootsma et al. 1994). Because there are no obvious differences in the mechanical requirements for grasping items to eat versus place, it is likely that these kinematic differences stem from the neural circuits in which they originate.

This inference, based on behavioral reports, is also supported by electrophysiological data. Studies on nonhuman primates have shown that distinct neural circuitry is differentially responsible for the production and control of mechanically similar movements. Long-train electrical stimulation of different locales on the motor cortex of an anesthetized macaque, for example, has been shown to produce behaviorally relevant movements, including reach-to-grasp, grasp-to-inspect, and hand-to-mouth actions (Graziano 2006; Graziano et al. 2002, 2004, 2005). Interestingly, these movements are firmly goal oriented in the sense that an evoked hand-to-mouth movement, for example, will present with the same end point regardless of initial limb position (Graziano et al. 2002). In other words, although activation of different muscle groups may be required to complete two separate hand-to-mouth movements (depending on initial hand location), these mechanically distinct but functionally equivalent movements are evoked from stimulation of the same neural circuit.

Support for task-specific organization of neural circuitry can be found in single-neuron recording studies as well. Researchers have shown that the firing rate of certain neuronal populations depends on the goal of a reach-to-grasp task (Bonini et al. 2011, 2012; Fogassi et al. 2005). In several studies, macaques were taught to grasp food items to either eat them or place them into containers located near their mouth, as well as to grasp nonfood items to place them into the same containers. While the macaques performed these actions, researchers recorded the firing rate of grasping neurons in the ventral premotor cortex (area F5) and the convexity of the inferior parietal area PFG, because these regions have been implicated in the organization of goal-directed reach-to-grasp actions (Bonini et al. 2010, 2011; Fogassi et al. 2005). The researchers observed no difference in the firing rate of grasping neurons in response to changes in the item to be grasped, but a significant proportion of neurons in both PFG and area F5 showed a selectivity for grasp-to-eat actions, firing more rapidly when an item was grasped with the intent to eat. This finding reinforces the notion that movements which share similar mechanics but differ in terms of their end goals are supported by separate and distinct neural networks. That is to say, the motor cortex is organized not around controlling individual muscles, but rather around producing functionally relevant actions.

Evidence for an action-oriented motor cortex organization in humans can be found from various behavioral studies. Specifically, it has been demonstrated that kinematics of reach and

Address for reprint requests and other correspondence: J. Flindall, Dept. of Kinesiology, Univ. of Lethbridge, 4401 Univ. Ave., Lethbridge, AB, Canada T1K 3M4 (e-mail: jason.flindall@uleth.ca).

grasp actions vary not only between grasp-to-eat and grasp-to-place movements (Ferri et al. 2010; Naish et al. 2013) but also between grasp-to-lift, grasp-to-place, and grasp-to-throw actions (Ansuini et al. 2008; Armbrüster and Spijkers 2006; Marteniuk et al. 1987). None of these kinematic studies have investigated asymmetries in these types of movements, nor have the electrophysiological stimulation or recording studies discussed above. One study investigating asymmetries demonstrated that kinematic differences in grasp-to-place and grasp-to-eat actions are limited to right-handed movements (Flindall and Gonzalez 2013). In that study, Flindall and Gonzalez argued that smaller peak grip apertures while grasping-to-eat constitute a right-hand advantage for feeding and as such may be particularly important to the evolution of right-handedness in humans. If early hominids grasped food with greater precision when using their right hand, then a preference to use that hand would have led to greater success in terms of food retrieval and consumption. What is not known is if the later mastication and consumption actions embedded in the task of eating are necessary components of the right-hand grasp-to-eat advantage, or if a hand-to-mouth movement, sans ingestion, is sufficient to activate the asymmetry.

To test this possibility, we analyzed the kinematics of three reach-to-grasp tasks. The first two tasks were identical to those described by Flindall and Gonzalez (2013), where each participant was asked to reach to grasp small food items to either 1) eat them or 2) place them in a bib hanging below the participant's chin. Our third task required participants to place the item between their lips for a brief moment before removing it with their opposite hand and placing it in a nearby trash receptacle (i.e., grasp to spit). To address the possibility that intent to eat will influence the hand-to-mouth movement during the eat task, the spit task was designed to be mechanically identical to the eat task, up to the final point in the motor chain involving the grasping limb. In this regard, any kinematic dissimilarities between the two movements may be ascribed to differences in actor intent. These tasks were performed in counterbalanced blocks with both the dominant (right) and nondominant (left) hands. We predicted that, as Flindall and Gonzalez have previously reported, participants would produce smaller MGAs in the eat than in the place task, but only during right-handed movements; however, MGAs produced in the spit task could resemble either movement. If the neural networks that support the grasp-to-eat action are unique to this behavior, then we expect MGAs for the spit task to resemble those of the grasp-to-place task. If instead the grasp-to-spit and grasp-to-eat tasks are found to share similar kinematics, then this right-hand advantage may perhaps be resultant from the hand-to-mouth nature of both movements.

METHODS

Participants. Twelve undergraduate participants (7 right-handed women, average age 20.4 yr; 4 right-handed men, average age 21.8 yr; 1 left-handed man, age 19 yr) participated in exchange for course credit. Handedness was determined by self-report and confirmed via a modified Waterloo/Edinburgh Handedness Questionnaire (Oldfield 1971; Stone et al. 2013). Participants were excluded if they had suffered from neurological damage or mechanical injury or had received specific training encouraging nondominant hand use for 1 mo or more. Participants were not excluded on the basis of reported hand preference, since many previous investigations on grasping and pre-

hension have shown comparable results between left- and right-handers (Boulinguez et al. 2001b; Flindall JW, Stone K, Gonzalez C, unpublished observations; Gonzalez et al. 2007; Stone et al. 2013). All participants gave written informed consent upon 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). Participants were able to withdraw from the study at any time without consequence.

Materials. Materials and methods were similar to those of Flindall and Gonzalez (2013). Three infrared light-emitting diodes (IREDs) were placed on the participant's hand: two on the distal phalanges of thumb and index finger, slightly proximal with respect to the nails, and one on the wrist at the medial aspect of the styloid process of the radius (proximal and medial with respect to the anatomic snuff box). An Optotrak Certus camera bar (Northern Digital, Waterloo, ON, Canada) recorded IRED position during each trial at 200 Hz for 5 s. Vision was restricted between trials using 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).

Participants were seated before a self-standing height-adjustable triangular pedestal. The pedestal held cereal food items of different sizes, presented individually. Both small (Cheerios, mean diameter 11 mm) and large (Froot Loops, mean diameter 15 mm) targets were used. These targets were chosen on the basis of their familiarity to the participants and their distinct sizes (Flindall and Gonzalez 2013). 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 food 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. Participants were seated behind the pedestal with their reaching hand (thumb and index fingertips together) placed comfortably on their lap (Fig. 1A). Plato liquid-crystal goggles, worn by the participant, remained in an opaque (closed) state between trials. Targets were placed on the pedestal in a pseudorandom order such that participants were naive to the target item's size before the beginning of each trial. Trials began with the Plato goggles transitioning to a transparent state (opening), at which point the participants became aware of the size of the target food item. An auditory tone (beep) sounded 1,000 ms following the opening of the goggles, indicating to the participants that they should begin the reach-to-grasp movement and subsequently eat the target (Fig. 1B), place the target in a bib hung snugly under their chin (Fig. 1C), or place the item between their lips, return their reaching hand to the start position, and then remove the item from between their lips (spit) with their other, untracked hand and place it into a trash receptacle at their side (Fig. 1D). Each condition (eat, place, and spit) was carried out in separate blocks of 20 grasps (10 small, 10 large, pseudorandomized order), with initial task and subsequent order counterbalanced between participants. Hand-start order was also counterbalanced, but all three tasks were completed with the starting hand before IRED markers were transferred to the other hand, at which point the three tasks were completed again in the same order.

Analyses. Kinematic comparisons were made between reach-to-grasp phases of each movement. Movement time (MT) represents the span during which the participant reached outward toward the target. MT was calculated as the difference between reaction time (defined as the time following the go signal at which a participant achieved a resultant equal to 5% of their peak velocity) and time of grasp contact. Grasp contact was defined as the point at which 1) the subject's outward speed dropped below 0.02 m/s and 2) the subject's corrected

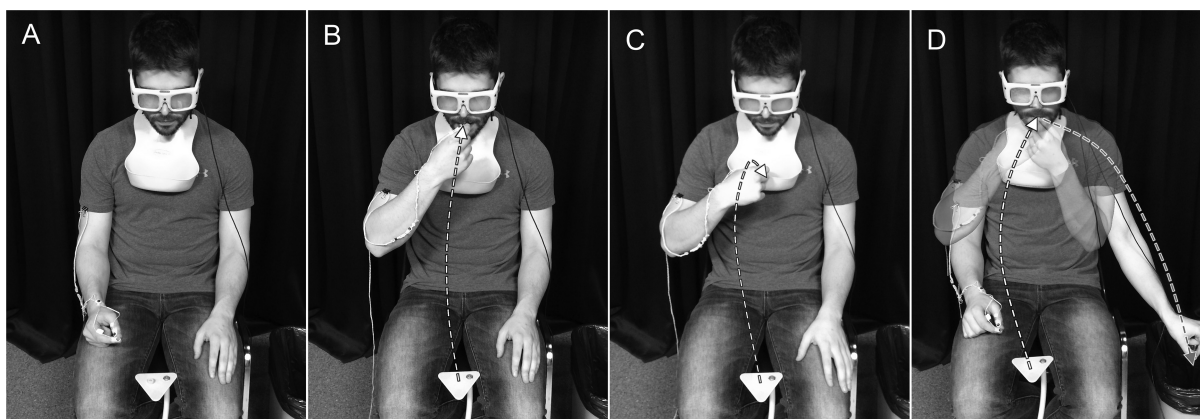


Fig. 1. Experimental procedure. *A*: participants began each trial in a rest position with their thumb and forefinger together. Subsequent actions varied by condition. *B*: the eat condition required participants to pick up the target and eat it. *C*: the place condition required participants to pick up the target and place it in a bib hanging below their chin. *D*: the spit condition required participants to pick up the food item, place it between their lips, remove it from their mouth with their other (untracked) hand, and deposit it into a trash receptacle. The bib and trash receptacle were present during all conditions. Dotted lines denote the path of the food item following initial grasp in each task.

grip aperture plateaued at the approximate diameter of the target. Peak velocity (PV) was defined as the maximum resultant velocity the participant achieved during outward movement toward the target, measured from the wrist marker. Deceleration phase duration (DP) was calculated as the time during which the participant was decelerating while still reaching outward toward the target (time of grasp contact minus time of PV). Because DP is reported as a percentage of total movement time, time of peak velocity and acceleration phase durations can be calculated by $1 - DP$. Because statistical analyses on these three variables (acceleration phase duration, time of PV, and DP) would return identical results, only DP means and analyses are reported in this article. MGA was measured as the peak resultant distance between the thumb and index finger before the time of grasp contact. Because grip aperture was calculated by measuring distance between IREDS, rather than actual distance between forefinger and thumb, variations in the IRED placement could potentially introduce error into our analyses. For this reason, participants were asked to grasp a rectangular block along its long axis (62.5 mm) with each hand at the beginning of data collection. A correction factor, calculated from IRED separation distance during this grasp, was applied to all MGA measurements to compensate for IRED placement variability (Tang et al. 2014). Variability of MGA (vMGA) was calculated as the standard deviation of the MGAs of each hand/task/size grouping.

Data processing. Data were collected via NDI First Principles, with kinematic calculations performed on unfiltered data using Microsoft Excel 2010. Statistical analyses were completed using PASW Statistics 18.0.0. If a participant moved to grasp the target before the go

signal, or if he/she failed to grasp the target on his/her first attempt (e.g., accidentally knocking the target to the floor), the offending trial was removed from analysis and not repeated. As a result of these types of error, an average of 3.3% of trials were removed per participant (range: 0–7.5%). Remaining trials were averaged by condition, with three-way within-subject repeated-measures analyses of variance [hand (left/right) \times task (eat/place/spit) \times size (small/large)] run on condition means. Alpha significance for initial ANOVA results was set at $P < 0.05$. Post hoc comparisons were conducted via paired-sample *t*-tests, with Bonferroni corrections applied where appropriate. Estimate of effect size is reported using partial η^2 .

RESULTS

Significant main effects and interactions are reported below. Between-subject means and standard errors of all measurements are reported in Table 1. Significant results are grouped by independent variable.

Hand. No main effects of hand were observed for any variable.

Size. Main effects of size were observed for MT [$F(1, 11) = 7.949, P = 0.017, \eta^2 = 0.420$], DP [$F(1, 11) = 6.023, P = 0.032, \eta^2 = 0.354$], and MGA [$F(1, 1) = 85.393, P < 0.001, \eta^2 = 0.886$]. Movement times toward large food items (mean 761 ms, SD 173 ms) were shorter than those toward small food items (mean 786 ms, SD 168 ms), as participants spent a larger

Table 1. Reach and grasp kinematics

| Hand | Size | Task | MT, ms | PV, m/s | DP, %MT | MGA, mm | vMGA, mm SD |
|-------|-------|-------|--------------|----------------|-----------------|-----------------|----------------|
| Left | Small | Eat | 776 \pm 53 | 1.48 \pm 0.1 | 67.77 \pm 0.8 | 26.53 \pm 2.1 | 3.28 \pm 0.4 |
| | | Place | 771 \pm 45 | 1.41 \pm 0.1 | 66.70 \pm 1.0 | 25.62 \pm 1.8 | 3.33 \pm 0.5 |
| | | Spit | 770 \pm 48 | 1.58 \pm 0.1 | 67.69 \pm 0.9 | 26.65 \pm 2.3 | 3.40 \pm 0.5 |
| | Large | Eat | 751 \pm 53 | 1.50 \pm 0.1 | 67.28 \pm 1.1 | 31.57 \pm 2.2 | 3.27 \pm 0.5 |
| | | Place | 741 \pm 48 | 1.42 \pm 0.1 | 65.39 \pm 1.2 | 30.46 \pm 1.9 | 3.27 \pm 0.4 |
| | | Spit | 734 \pm 53 | 1.56 \pm 0.1 | 66.58 \pm 1.1 | 30.70 \pm 2.3 | 2.98 \pm 0.4 |
| Right | Small | Eat | 803 \pm 43 | 1.49 \pm 0.1 | 68.13 \pm 1.2 | 23.54 \pm 1.6 | 2.73 \pm 0.4 |
| | | Place | 816 \pm 59 | 1.48 \pm 0.1 | 67.43 \pm 1.3 | 25.93 \pm 1.7 | 2.98 \pm 0.5 |
| | | Spit | 779 \pm 52 | 1.56 \pm 0.1 | 66.90 \pm 1.3 | 23.63 \pm 1.5 | 2.84 \pm 0.3 |
| | Large | Eat | 771 \pm 41 | 1.44 \pm 0.1 | 65.88 \pm 1.3 | 27.96 \pm 1.8 | 2.99 \pm 0.3 |
| | | Place | 788 \pm 65 | 1.45 \pm 0.1 | 66.33 \pm 1.3 | 30.31 \pm 2.0 | 3.07 \pm 0.5 |
| | | Spit | 779 \pm 59 | 1.52 \pm 0.1 | 67.35 \pm 1.0 | 27.76 \pm 1.5 | 2.43 \pm 0.2 |

Values are means \pm SE of movement time (MT), peak velocity (PV), deceleration phase duration (DP; calculated as %MT), maximum grasp aperture (MGA), and variability of MGA (vMGA; calculated as the SD of MGAs for each group).

portion of the movement decelerating toward small food items (mean 67.4%, SD 3.0%) than they did toward large food items (mean 66.5%, SD 3.4%). As expected, participants also opened their hands wider when grasping large food items (mean 29.8 mm, SD 5.7 mm) than they did when grasping small food items (mean 25.3 mm, SD 6.2 mm).

Task. A main effect of task was observed for PV [$F(2, 22) = 7.202, P = 0.004, \eta^2 = 0.396$]. Follow-up *t*-tests revealed that participants achieved higher peak velocities when grasping to spit (mean 1.56 m/s, SD 0.31 m/s) than when grasping to place (mean 1.44 m/s, SD 0.31 m/s) [$t(11) = -3.14, P = 0.009$]. *t*-Tests revealed that grasp-to-spit PVs were also higher than grasp-to-eat PVs (mean 1.48 m/s, SD 0.31 m/s); however, this effect was not significant following Bonferroni correction [$t(11) = -2.75, P = 0.019$]. The difference between eat and place PVs was not significant ($P > 0.05$).

Hand \times size. An interaction between hand and size was observed for PV [$F(1, 11) = 5.749, P = 0.035, \eta^2 = 0.343$]. Follow-up *t*-tests revealed this interaction was due to a significant difference between left- and right-handed PVs achieved while reaching for large food items [$t(11) = 3.54, P = 0.005$]. Specifically, participants reached higher PVs with their left hands (mean 1.50 m/s, SD 0.33 m/s) than they did with their right hands (mean 1.47 m/s, SD 0.30 m/s). No other significant hand \times size interactions were observed.

Size \times task. No interactions between size and task were observed for any variable.

Hand \times task. An interaction between hand and task was observed for MGA [$F(2, 22) = 6.236, P = 0.007, \eta^2 = 0.362$]. Follow-up *t*-tests revealed that this interaction was due to significantly larger MGAs [$t(11) \geq 2.82, P \leq 0.016$] when grasping to place (mean 28.12 mm, SD 6.33 mm) than when grasping to eat (mean 25.75 mm, SD 5.76 mm) or spit (mean 25.71 mm, SD 5.06 mm), but only during right-handed grasps. Right-handed eat and spit grasps were not significantly different from each other [$t(11) = 0.09, P = 0.929$]. No significant differences were observed between tasks [$t(11) \leq 1.01, P \geq 0.203$] during left-handed movements (Fig. 2). No significant hand \times task interactions were observed for any other variable.

Hand \times size \times task. A significant hand \times size \times task interaction was observed for DP [$F(2, 22) = 4.261, P = 0.027, \eta^2 = 0.279$]. Follow-up *t*-tests revealed that this effect was due to a significant difference between the left and right hands when grasping large food items with the intent to eat [$t(11) = 3.64, P = 0.004$]. Participants spent relatively more of the movement decelerating during left-handed actions (mean 67.3%, SD 3.86%) than they did during right-handed actions

(mean 65.9%, SD 4.46%). No other comparisons were significant following Bonferroni correction [$t(22) \leq 2.57, P \geq 0.03$].

DISCUSSION

Previous research has shown that there are differences in the kinematics of the grasp-to-eat and grasp-to-place movements and that these differences are limited to movements performed with the right hand (Flindall and Gonzalez 2013). Specifically, right-handed grasp-to-eat MGAs are produced with a smaller margin for error than are right-handed grasp-to-place MGAs, suggesting that grasp-to-eat movements are produced with more precision and control. The significance of this finding is twofold: first, the kinematic disparity, in the absence of any obvious difference in mechanical requirements between the tasks, points to separate neural origins for these two types of movements. Second, the right-hand lateralization of task differences may be interpreted as a right-hand advantage for the grasp-to-eat movement. This advantage may have been a driving force behind the population-level right-handedness observed in humans. The purpose of the current study was to address the possibility that hand-to-mouth movements, decoupled from eating, and grasp-to-eat movements may share similar kinematics, suggesting a common neural origin. Kinematic data were collected while participants reached for, grasped, and transported food items to the self to either 1) eat them, 2) place them in a bib located just beneath their chin, or 3) place them briefly in their mouth before spitting them out. These tasks were performed in left- and right-hand blocks, with both small and large food items. Statistical analyses were conducted to determine the influence of these variables on MT, DP, PV, MGA, and vMGA. Consistent with previous research (Bootsma et al. 1994; Castiello et al. 1993; Flindall and Gonzalez 2013; Gentilucci et al. 1991; Kudoh et al. 1997; Marteniuk et al. 1990; Pryde et al. 1998; Zaal and Bootsma 1993), target size was observed to significantly influence MT, DP, and MGA, with smaller food items producing smaller MGAs and longer MTs with longer relative DPs. These findings have been discussed elsewhere in depth and are interpreted as a reach-to-grasp variation of the speed/accuracy trade-off described by Fitts' Law (Fitts 1954; e.g., Bootsma et al. 1994; Gentilucci et al. 1991). In the current study, however, our primary interest resides in the hand \times task interaction observed on MGA.

It has been shown that discrete actions embedded in a functional chain are influenced by the requirements of subsequent actions in that chain (Gentilucci et al. 1997; Hesse and Deubel 2010). That is to say, "discrete" actions, including grasping actions, are rarely discrete; their execution is influenced by the requirements of the movements that must follow. In the current study, when participants used their right hand to bring food to the mouth, they produced smaller MGAs regardless of their ultimate intent (i.e., eat or spit). In this effect, the right-hand advantage for grasp-to-eat movements found by Flindall and Gonzalez (2013) was replicated and extended to cover grasp-to-place-in-the-mouth movements. This suggests that the grasp-to-eat action may not be unique in its production or control and indicates that other self-directed tasks may share not only its kinematic pattern but also its locus of control. In the current study, both eat and spit conditions required participants to bring the food item to the mouth while simultaneously

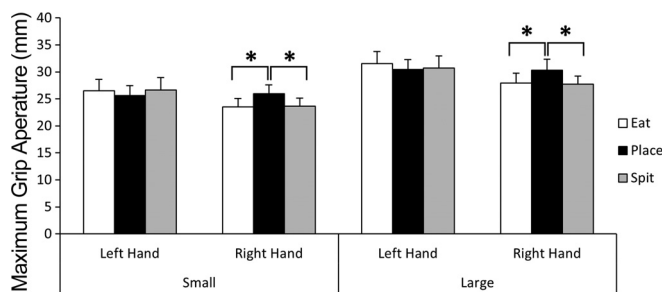


Fig. 2. Hand \times task interaction for MGA. MGAs produced in both the eat and spit tasks were significantly smaller than those produced in the place task ($P \leq 0.03$) when the right hand was used, for both small and large food sizes. No effect of task was observed during left-handed movements ($P \geq 0.203$).

opening the mouth to accept said item; they differed only in terms of ultimate goal (i.e., to eat vs. to spit). In both movements, the grasping hand's involvement in the motor chain ends when the food item is placed in the mouth. Because the grasping limb is no longer involved in the acts that follow, we may assume that this marks the end of the motor chain investigated in the current study. In effect, the current results broaden the label (i.e., grasp to eat) placed on the hand-to-mouth movement by Flindall and Gonzalez. Instead of grasp to eat, the movement may be better described as grasp to bring to the mouth; under these terms, our eat and spit tasks are, for all intents and purposes, the same movement. The kinematic similarities between these two tasks support this notion. The fact that Flindall and Gonzalez narrowly labeled the hand-to-mouth movement does not depreciate the evolutionary significance of their findings, because the primary purpose (that is to say, original, or even primal purpose) of the hand-to-mouth movement was almost certainly to facilitate consumption. Although modern hand-to-mouth movements make up nearly half of all object-oriented movements in primates (Graziano 2009) and may serve a near infinite variety of functions including feeding, manipulation (treating the mouth as a grasping appendage), and exploration, we find it difficult to imagine a scenario where hand-to-mouth movements evolved for non-feeding purposes. Because hand-to-mouth movements represent more than 20% of the total movement repertoire in primates (Graziano 2009), one might argue that a right-hand advantage for hand-to-mouth movements of any type may have influenced population-level hand preference in a rightward fashion. We suggest that a right-hand kinematic advantage leading to greater success in feeding would have quickly and directly led to greater rates of survival among early hominids.

In macaques, hand-to-mouth movements can be evoked by electrical stimulation of the ventral regions of the forearm representation area in the premotor cortex (Cooke and Graziano 2004a; Graziano et al. 2002). Specifically, 500-ms electrical stimulation (100 μ A at 500 Hz) of the anterior edge of the precentral gyrus, just posterior to arcuate sulcus, will induce a pincer-grasp movement, coupled with a forearm supination and elbow/shoulder rotation bringing the hand toward the face and an opening of the mouth (Graziano et al. 2002). This region is anteriorly adjacent to other areas of the precentral gyrus, which will, when stimulated, produce similar movements directed instead toward the macaque's chest (Cooke and Graziano 2004a, 2004b; Graziano et al. 2002). Although neither of these evoked actions were coupled with an outward reach (Graziano 2009), they both closely resemble the post-grasp movements produced by participants in the current study. While there is often considerable variability in brain architecture between individuals (Cabeza and Nyberg 1997, 2000; Culham and Kanwisher 2001; Johnson-Frey et al. 2003), researchers have suggested that the human homolog of this region lies within the primary motor cortex, in BA4 (Roland and Zilles 1996; Zilles et al. 1995). Indeed, studies have shown that hand-to-mouth movements may be evoked in humans through direct stimulation of motor (Desmurget et al. 2013) and premotor cortex (Desmurget et al. 2009). In one such direct electrical stimulation study involving human patients, Desmurget et al. (2014) found multiple locales on the precentral gyrus that evoked simultaneous movements of the mouth and upper limb. During stimulation of these sites, the mouth "gradually

started to open while the closing hand moved toward the face through contraction of upper limb flexor muscles" (Desmurget et al. 2014). Based on the work of Desmurget and colleagues, we contend that this region is likely to be the site of production for the hand-to-mouth movements produced in the current study (Desmurget et al. 2009, 2013, 2014). In addition to the well-documented role that BA4 plays in the production of precision grasps (Cavina-Pratesi et al. 2007; Ehrsson et al. 2000), BA4 has also been linked with the mirror neuron system by multiple studies (Cebolla et al. 2014; Gazzola et al. 2007; Hari et al. 1998; Järveläinen et al. 2004; Kessler et al. 2006). Because mirror neurons fire during both execution and observation of a movement, it has been suggested that these neurons are critical not only for understanding the movements of another but also in learning via imitation (Rizzolatti and Craighero 2004). While it is unlikely that mirror neurons are limited to grasping movements alone, the proximity of mirror neurons to the production site of hand-to-mouth movements may indicate a functional link between the two systems. This may present an explanation for the early development of a right-hand preference for grasp-to-eat actions observed by Sacrey and colleagues, who showed that preference for unimanual self-feeding develops several years earlier than hand preference for grasp-to-manipulate tasks (Sacrey et al. 2012a). It is possible to speculate that the mirror neuron system, being important for learning, should be particularly necessary and active during the period of time in which a child first gains control of distal movements (Fagard 2000; Fagard and Marks 2000; Sacrey et al. 2012b). If hand-to-mouth movements are different from grasp-to-place movements not as a result of practice, but rather because they are invaluable for development of dexterity, then this strengthens the evolutionary argument that lateralized hand-to-mouth movements are a driving force behind population-level handedness patterns (Flindall and Gonzalez 2013; Hopkins and Rönnqvist 1998; Hopkins et al. 2011).

Another significant point of discussion lies in the MGA differences identified in the current study. These differences between left- and right-handed reach-to-grasp actions are conspicuously absent in many previous grasping studies. Kinematic asymmetries favoring the dominant hand in reach-to-point actions are well documented (Boulinguez et al. 2001a; Carson et al. 1990, 1993; Elliott and Chua 1996; Elliott et al. 1993; Fisk and Goodale 1985; Roy and Elliott 1986, 1989; Velay et al. 2001), whereas multiple studies have demonstrated that manual asymmetries in the reach-to-grasp movement are subtle, if not altogether absent (Begliomini et al. 2008; Flindall 2012; Flindall et al. 2014; Grosskopf and Kuitz-Buschbeck 2006; Tretriluxana et al. 2008). The kinematic asymmetry recently identified during grasp-to-eat movements was interpreted as a right-hand/left-hemisphere advantage for eating, because participants produced smaller MGAs to eat while using their right hand only (Flindall and Gonzalez 2013). It is possible that the requirement to open the mouth to accept the item is a key factor in determining whether the previously labeled grasp-to-eat motor plan is recruited for the hand-to-mouth movement. This possibility would be supported by electrical stimulation studies in macaques, where evoked hand-to-mouth movements were always accompanied by a concurrent opening of the mouth (Graziano et al. 2002). It is also possible that the asymmetries in the current study were evoked

by our choice of target, given that participants were asked to grasp food items for all three tasks. Future studies will address these possibilities by including nonfood items as targets, as well as hand-to-mouth tasks disentangled from any simultaneous movement of the mouth.

In conclusion, the results of the current study find a kinematic dissociation between self-directed grasp-to-place and grasp-to-place-in-the-mouth actions performed with the right hand. These results are interpreted as a kinematic advantage for feeding during right-handed movements. Importantly, we have shown that this advantage does not require consumption, because similar kinematics were observed between grasp-to-eat and grasp-to-spit actions. This finding suggests a shared neural origin for these two hand-to-mouth movements, independent of the subsequent act of consumption.

GRANTS

We thank the National Science and Engineering Research Council of Canada, the Canada Foundation for Innovation, and the University of Lethbridge for generous support.

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. and C.L.G. analyzed data; J.W.F. and C.L.G. interpreted results of experiments; J.W.F. prepared figures; J.W.F. and C.L.G. 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.

REFERENCES

- Ansuini C, Giosa L, Turella L, Altoè G, Castiello U.** An object for an action, the same object for other actions: effects on hand shaping. *Exp Brain Res* 185: 111–119, 2008.
- Armbrüster C, Spijkers W.** Movement planning in prehension: do intended actions influence the initial reach and grasp movement? *Motor Control* 10: 311–329, 2006.
- Begliomini C, Nelini C, Caria A, Grodd W, Castiello U.** Cortical activations in humans grasp-related areas depend on hand used and handedness. *PLoS One* 3: e3388, 2008.
- Bonini L, Rozzi S, Serventi FU, Simone L, Ferrari PF, Fogassi L.** Ventral premotor and inferior parietal cortices make distinct contribution to action organization and intention understanding. *Cereb Cortex* 20: 1372–1385, 2010.
- Bonini L, Serventi FU, Bruni S, Maranesi M, Bimbi M, Simone L, Rozzi S, Ferrari PF, Fogassi L.** Selectivity for grip type and action goal in macaque inferior parietal and ventral premotor grasping neurons. *J Neurophysiol* 108: 1607–1619, 2012.
- Bonini L, Serventi FU, Simone L, Rozzi S, Ferrari PF, Fogassi L.** Grasping neurons of monkey parietal and premotor cortices encode action goals at distinct levels of abstraction during complex action sequences. *J Neurosci* 31: 5876–5886, 2011.
- Bootsma RJ, Marteniuk RG, MacKenzie CL, Zaaf F.** The speed-accuracy trade-off in manual prehension: effects of movement amplitude, object size, and object width on kinematic characteristics. *Exp Brain Res* 98: 535–541, 1994.
- Boulinguez P, Nougier V, Velay JL.** Manual asymmetries in reaching movement control. I: Study of right-handers. *Cortex* 37: 101–122, 2001a.
- Boulinguez P, Velay JL, Nougier V.** Manual asymmetries in reaching movement control. II: Study of left-handers. *Cortex* 37: 123–138, 2001b.
- Cabeza R, Nyberg L.** Imaging cognition: an empirical review of PET studies with normal subjects. *J Cogn Neurosci* 9: 1–26, 1997.
- Cabeza R, Nyberg L.** Imaging cognition II: an empirical review of 275 PET and fMRI studies. *J Cogn Neurosci* 12: 1–47, 2000.
- Carson RG, Chua R, Elliott D, Goodman D.** The contribution of vision to asymmetries in manual aiming. *Neuropsychologia* 28: 1215–1220, 1990.
- Carson RG, Goodman D, Chua R, Elliott D.** Asymmetries in the regulation of visually guided aiming. *J Mot Behav* 25: 21–32, 1993.
- Castiello U, Bennett K, Stelmach G.** Reach to grasp: the natural response to perturbation of object size. *Exp Brain Res* 94: 163–178, 1993.
- Cavina-Pratesi C, Goodale MA, Culham JC.** fMRI reveals a dissociation between grasping and perceiving the size of real 3D objects. *PLoS One* 2: e424, 2007.
- Cebolla A, Palmero-Soler E, Dan B, Cheron G.** Modulation of the N30 generators of the somatosensory evoked potentials by the mirror neuron system. *Neuroimage* 95: 48–60, 2014.
- Cooke DF, Graziano MS.** Sensorimotor integration in the precentral gyrus: polysensory neurons and defensive movements. *J Neurophysiol* 91: 1648–1660, 2004a.
- Cooke DF, Graziano MS.** Super-finchers and nerves of steel: defensive movements altered by chemical manipulation of a cortical motor area. *Neuron* 43: 585–593, 2004b.
- Culham JC, Kanwisher NG.** Neuroimaging of cognitive functions in human parietal cortex. *Curr Opin Neurobiol* 11: 157–163, 2001.
- Desmurget M, Reilly KT, Richard N, Szathmari A, Mottolese C, Sirigu A.** Movement intention after parietal cortex stimulation in humans. *Science* 324: 811–813, 2009.
- Desmurget M, Richard N, Harquel S, Baraduc P, Szathmari A, Mottolese C, Sirigu A.** Neural representations of ethologically relevant hand/mouth synergies in the human precentral gyrus. *Proc Natl Acad Sci USA* 111: 5718–5722, 2014.
- Desmurget M, Song Z, Mottolese C, Sirigu A.** Re-establishing the merits of electrical brain stimulation. *Trends Cogn Sci* 17: 442–449, 2013.
- Ehrsson HH, Fagergren A, Jonsson T, Westling G, Johansson RS, Forssberg H.** Cortical activity in precision-versus power-grip tasks: an fMRI study. *J Neurophysiol* 83: 528–536, 2000.
- Elliott D, Chua R.** Manual asymmetries in goal-directed movement. In: *Manual Asymmetries in Motor Performance*, edited by Elliott D and Chua R. Boca Raton, FL: CRC, 1996, p. 143–158.
- Elliott D, Roy EA, Goodman D, Carson RG, Chua R, Maraj BK.** Asymmetries in the preparation and control of manual aiming movements. *Can J Exp Psychol* 47: 570–589, 1993.
- Fagard J.** Linked proximal and distal changes in the reaching behavior of 5- to 12-month-old human infants grasping objects of different sizes. *Infant Behav Dev* 23: 317–329, 2000.
- Fagard J, Marks A.** Unimanual and bimanual tasks and the assessment of handedness in toddlers. *Dev Sci* 3: 137–147, 2000.
- Ferri F, Campione GC, Dalla Volta R, Gianelli C, Gentilucci M.** To me or to you? When the self is advantaged. *Exp Brain Res* 203: 637–646, 2010.
- Fisk JD, Goodale MA.** The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral space. *Exp Brain Res* 60: 159–178, 1985.
- Fitts PM.** The information capacity of the human motor system in controlling the amplitude of movement. *J Exp Psychol* 47: 381–391, 1954.
- Flindall JW.** Manual asymmetries in the kinematics of reach-to-grasp actions. In: *Kinesiology*. Lethbridge, AB, Canada: University of Lethbridge, 2012, p. 135.
- Flindall JW, Doan JB, Gonzalez C.** Manual asymmetries in the kinematics of a reach-to-grasp action. *Laterality* 19: 489–507, 2014.
- Flindall JW, Gonzalez C.** On the evolution of handedness: evidence for feeding biases. *PLoS One* 8: e78967, 2013.
- Fogassi L, Ferrari PF, Gesierich B, Rozzi S, Chersi F, Rizzolatti G.** Parietal lobe: from action organization to intention understanding. *Science* 308: 662–667, 2005.
- Gazzola V, Rizzolatti G, Wicker B, Keysers C.** The anthropomorphic brain: the mirror neuron system responds to human and robotic actions. *Neuroimage* 35: 1674–1684, 2007.
- Gentilucci M, Castiello U, Corradini M, Scarpa M, Umiltà C, Rizzolatti G.** Influence of different types of grasping on the transport component of prehension movements. *Neuropsychologia* 29: 361–378, 1991.
- Gentilucci M, Negrotti A, Gangitano M.** Planning an action. *Exp Brain Res* 115: 116–128, 1997.
- Gonzalez C, Whitwell RL, Morrissey B, Ganel T, Goodale MA.** Left handedness does not extend to visually guided precision grasping. *Exp Brain Res* 182: 275–279, 2007.
- Graziano MS.** *The Intelligent Movement Machine*. Oxford, UK: Oxford University Press, 2008.

- Graziano MS.** The organization of behavioral repertoire in motor cortex. *Annu Rev Neurosci* 29: 105–134, 2006.
- Graziano MS, Aflalo TN, Cooke DF.** Arm movements evoked by electrical stimulation in the motor cortex of monkeys. *J Neurophysiol* 94: 4209–4223, 2005.
- Graziano MS, Cooke DF, Taylor CS, Moore T.** Distribution of hand location in monkeys during spontaneous behavior. *Exp Brain Res* 155: 30–36, 2004.
- Graziano MS, Taylor CS, Moore T.** Complex movements evoked by microstimulation of precentral cortex. *Neuron* 34: 841–851, 2002.
- Grosskopf A, Kuitz-Buschbeck JP.** Grasping with the left and right hand: a kinematic study. *Exp Brain Res* 168: 230–240, 2006.
- Hari R, Forss N, Avikainen S, Kirveskari E, Salenius S, Rizzolatti G.** Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proc Natl Acad Sci USA* 95: 15061–15065, 1998.
- Hesse C, Deubel H.** Advance planning in sequential pick-and-place tasks. *J Neurophysiol* 104: 508–516, 2010.
- Hopkins B, Rönqvist L.** Human handedness: developmental, and evolutionary perspectives. In: *The Development of Sensory, Motor and Cognitive Capacities in Early Infancy: From Perception to Cognition*, edited by Simion F and Butterworth G. Hove, UK: Psychology, 1998, p. 189–233.
- Hopkins WD, Phillips KA, Bania A, Calcutt SE, Gardner M, Russell J, Schaeffer J, Lonsdorf EV, Ross SR, Schapiro SJ.** Hand preferences for coordinated bimanual actions in 777 great apes: implications for the evolution of handedness in hominids. *J Hum Evol* 60: 605–611, 2011.
- Järveläinen J, Schuermann M, Hari R.** Activation of the human primary motor cortex during observation of tool use. *Neuroimage* 23: 187–192, 2004.
- Johnson-Frey SH, Maloof FR, Newman-Norlund R, Farrer C, Inati S, Grafton ST.** Actions or hand-object interactions? Human inferior frontal cortex and action observation. *Neuron* 39: 1053–1058, 2003.
- Kessler K, Biermann-Ruben K, Jonas M, Roman Siebner H, Bäumer T, Münchau A, Schnitzler A.** Investigating the human mirror neuron system by means of cortical synchronization during the imitation of biological movements. *Neuroimage* 33: 227–238, 2006.
- Kudoh N, Hattori M, Numata N, Maruyama K.** An analysis of spatiotemporal variability during prehension movements: effects of object size and distance. *Exp Brain Res* 117: 457–464, 1997.
- Marteniuk R, MacKenzie C, Jeannerod M, Athenes S, Dugas C.** Constraints on human arm movement trajectories. *Can J Psychol* 41: 365, 1987.
- Marteniuk RG, Leavitt JL, MacKenzie CL, Athenes S.** Functional relationships between grasp and transport components in a prehension task. *Hum Mov Sci* 9: 149–176, 1990.
- Naish KR, Reader AT, Houston-Price C, Bremner AJ, Holmes NP.** To eat or not to eat? Kinematics and muscle activity of reach-to-grasp movements are influenced by the action goal, but observers do not detect these differences. *Exp Brain Res* 225: 261–275, 2013.
- Oldfield RC.** The assessment and analysis of handedness: the Edinburgh Inventory. *Neuropsychologia* 9: 97–113, 1971.
- Pryde KM, Roy EA, Campbell K.** Prehension in children and adults: the effects of object size. *Hum Mov Sci* 17: 743–752, 1998.
- Rizzolatti G, Craighero L.** The mirror-neuron system. *Annu Rev Neurosci* 27: 169–192, 2004.
- Roland PE, Zilles K.** Functions and structures of the motor cortices in humans. *Curr Opin Neurobiol* 6: 773–781, 1996.
- Roy EA, Elliott D.** Manual asymmetries in aimed movements. *Q J Exp Psychol* 41a: 501–516, 1989.
- Roy EA, Elliott D.** Manual asymmetries in visually directed aiming. *Can J Psychol* 40: 109–121, 1986.
- Sacrey LA, Arnold B, Whishaw IQ, Gonzalez C.** Precocious hand use preference in reach-to-eat behavior versus manual construction in 1- to 5-year-old children. *Dev Psychobiol* 55: 902–911, 2012a.
- Sacrey LA, Karl JM, Whishaw IQ.** Development of rotational movements, hand shaping, and accuracy in advance and withdrawal for the reach-to-eat movement in human infants aged 6–12 months. *Infant Behav Dev* 35: 543–560, 2012b.
- Stone K, Bryant D, Gonzalez C.** Hand use for grasping in a bimanual task: evidence for different roles? *Exp Brain Res* 224: 455–467, 2013.
- Tang R, Whitwell RL, Goodale MA.** Explicit knowledge about the availability of visual feedback affects grasping with the left but not the right hand. *Exp Brain Res* 232: 293–302, 2014.
- Tretriluxana J, Gordon J, Winstein CJ.** Manual asymmetries in grasp pre-shaping and transport-grasp coordination. *Exp Brain Res* 188: 305–315, 2008.
- Velay JL, Daffaure V, Raphael N, Benoit-Dubrocard S.** Hemispheric asymmetries and interhemispheric transfer depend on the spatial components of the movement. *Cortex* 37: 75–90, 2001.
- Whishaw IQ, Suchowersky O, Davis L, Sarna J, Metz GA, Pellis SM.** Impairment of pronation, supination, and body co-ordination in reach-to-grasp tasks in human Parkinson's disease (PD) reveals homology to deficits in animal models. *Behav Brain Res* 133: 165–176, 2002.
- Zaal FT, Bootsma RJ.** Accuracy demands in natural prehension. *Hum Mov Sci* 12: 339–345, 1993.
- Zilles K, Schlaug G, Matelli M, Luppino G, Schleicher A, Qü M, Dabringhaus A, Seitz R, Roland P.** Mapping of human and macaque sensorimotor areas by integrating architectonic, transmitter receptor, MRI and PET data. *J Anat* 187: 515, 1995.