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

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 grasp-to-inpect, 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.

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 eat them or place the item 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 stop, such that participants would produce 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-sip 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 andprehension 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
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 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) × task (eat/place/spit) × 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 $\eta^2$.

### 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 [$F(1, 11) = 85.393, P < 0.001, \eta^2 = 0.886$]. 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

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

Values are means ± SE of movement time (MT), peak velocity (PV), deceleration phase duration (DP; calculated as %MT), maximum grip 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 those produced in the place task (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 \([F(2, 22) = 2.022, P = 0.004, \eta^2 = 0.396]\). 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) \([t(11) = -3.14, P = 0.009]\). 

Task interactions were observed for any other variable.

Size \times task. An interaction between hand and size was observed for PV \([F(1, 11) = 7.202, P = 0.035, \eta^2 = 0.343]\). 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 1.47 m/s, SD 0.30 m/s) than they did with their right hands (mean 1.50 m/s, SD 0.33 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 MGA \([F(1, 11) = 5.749, P = 0.035, \eta^2 = 0.343]\). Follow-up t-tests revealed this interaction was due to a significantly larger MGAs \([t(11) = 3.54, P = 0.005]\) 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 squat (mean 25.71 mm, SD 5.76 mm), but only during right-handed grasps. Right-handed eat and squat grasps were not significantly different from each other \([t(11) = 0.09, P = 0.929]\). No significant differences were observed between tasks \([t(11) \leq 1.01, P \leq 0.203]\) 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. Kine-
matic 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
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 deprecate the evolutionary significance of their findings, because the primary purpose (that is to say, original, or even primate 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 μA 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 Kuhtz-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


J Neurophysiol • doi:10.1152/jn.00295.2014 • www.jn.org

Downloaded from http://jn.physiology.org/ on September 24, 2016


