ON ACTION INTENT: BEHAVIOURAL CORRELATES OF REACH-TO-GRASP ACTIONS

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MANUAL ASYMMETRIES IN THE KINEMATICS OF REACH-TO-GRASP ACTIONS

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Abstract

Evidence from electrophysiology suggests that non-human primates produce reach-to-grasp movements based on their functional end-goal rather than on the biomechanical requirements of the movement. However, the invasiveness of direct-electrical stimulation and single-neuron recording studies have precluded analogous investigations in humans. In this thesis, I present behavioural evidence in the form of kinematic analyses suggesting that the cortical circuits responsible for reach-to-grasp actions in humans are organized in a similar fashion. Grasp-to-eat movements are produced with significantly smaller and more precise maximum grip apertures (MGAs) than are grasp-to-place movements directed toward the same objects, despite near identical mechanical requirements of the two subsequent (i.e., -eat and –place) movements. Furthermore, the fact that this distinction is limited to right-handed movements suggests that the system governing reach-to-grasp movements is asymmetric. I posit that this asymmetry may be responsible, at least in part, for the preponderance of right-hand dominance among the global population.

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Outline

The dual visuomotor channel theory of grasping states that prehension movements are composed of distinct, temporally integrated components: a reach component, programmed in the dorsomedial reach channel of the occipitoparietal cortex, and a grasp component, programmed in the dorsolateral grasp channel, also in occipitoparietal cortex (Karl & Whishaw, 2013). The traditional view concerning kinematic execution of prehensile actions is that the reach is affected by extrinsic target parameters (e.g., location, both relative to the body and other objects in the environment), whereas the grasp is influenced by intrinsic target parameters (e.g., size, and shape) (Jeannerod, 1986a, 1986b). Thus, the theory implies that grasp execution is based entirely on the needs of the immediate environment.

Recent evidence from kinematic studies contradicts this view. By comparing execution of grasp-to-eat and grasp-to-place movements directed toward identical targets in identical environments, Flindall and Gonzalez have shown that movements with identical biomechanical requirements (e.g., reach-to-grasp actions directed towards targets that may have multiple affordances) differ based on the ultimate purpose of the grasp. The grasp-to-eat action (along with other hand-to-mouth movements) demonstrates a robust kinematic signature in the form of smaller maximum grip apertures (MGA; the widest aperture between forefinger and thumb during precision grasps) when executed with the right hand, whether that hand is dominant or non-dominant (Flindall & Gonzalez, 2013[1], 2014[2], 2015[3], 2016[4], 2017[5]; Flindall, Stone, & Gonzalez, 2015[6]).

This review will begin with an overview of the dual visuomotor channel theory for grasping, and present evidence in support of the theory from electrophysiology, psychophysics, and neuroimaging. We present a meta-analysis of data reported by Flindall, Gonzalez and colleagues, showing that the kinematic signature is not only exceptionally robust, but that it is alone in terms of kinematic asymmetries between left- and right-handed grasping movements. Finally, we will present evidence in support of an addendum to the dual visuomotor channel theory of grasping; namely, that it is more likely that grasps are produced not based solely on their mechanistic requirements, but that the appropriate grasp is instead chosen from a repertoire of actions (or, a vocabulary of movements), and that those grasps are then adapted to the intrinsic and extrinsic target parameters as needed. Based on our kinematic evidence, we posit that the motor plan controlling the hand-to-mouth movement is lateralized to the right-hand/left-hemisphere system, and speculate that this kinematic advantage for self-feeding may be at least partially responsible for right-hand dominance in humans.

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[1] Appendix 1: On the Evolution of Handedness: Evidence for feeding biases. *PLoS ONE*, 2014.

[2] Appendix 2: Eating Interrupted: The effect of intent on hand-to-mouth actions. *J Neurophysiol*, 2014.

[3] Appendix 3: Evidence for Right-hand Feeding Biases in a Left-handed Population. *Laterality*, 2015.

[4] Appendix 5: The Destination Defines the Journey: An examination of the kinematics of hand-to-mouth movements. *J Neurophysiol*, 2016.

[5] Appendix 6: The Inimitable Mouth: Task-dependent kinematic differences are independent of terminal precision. *Exp Brain Res*, 2017.

[6] Appendix 4: Children's Bilateral Advantage for Grasp-to-eat Actions becomes Unimanual by Age 10 Years. *J Exp Child Psych*, 2015.

Vision-for-Action in the Parietal Cortex

The parietal cortex's role in transforming vision into action is well-known (Goodale, 2011; Goodale & Milner, 1992; Milner & Goodale, 2008). Visual information, beginning in primary visual centers in occipital cortex, branches into two visual streams that differ in terms of their functional utility; a ventral visual stream, in the temporal cortex, and a dorsal visual stream, in the parietal cortex (Goodale & Milner, 1992). The ventral visual stream adapts visual information into a conscious representation of the world; responsible for our perception of relative size, colour, shape, luminance, and identity, the ventral stream represents what we first think of when considering "vision." The ventral stream is responsible for the formation of memory, and exemplifications of everyday objects are represented within ventral stream regions. In contrast, dorsal stream processing is unconscious, short-term, and functions solely to facilitate interaction with the world around us; an object's absolute size and egocentric location are processed by the dorsal visual stream to enable quick and efficient action toward that object.

The distinct functions of these visual centers have long been established with evidence from neuropsychology (Heider, 2000; Karnath, Rüter, Mandler, & Himmelbach, 2009; Milner et al., 1991), neuroimaging (Cavina-Pratesi, Goodale, & Culham, 2007; Culham, Cavina-Pratesi, & Singhal, 2006; Culham et al., 2003; Gallivan, Cavina-Pratesi, & Culham, 2009; Gallivan & Culham, 2015; Pettypiece, Goodale, & Culham, 2010), and behavioural studies (Bradshaw & Watt, 2002; Flindall, Doan, & Gonzalez, 2014; Franz, Hesse, & Kollath, 2007; Hu, Eagleson, & Goodale, 1999; Hu & Goodale, 2000; Whitwell, Striemer, Nicolle, & Goodale, 2011). These streams do not act in isolation, but rather in concert to quickly generate functionally relevant actions in our everyday lives (Hesse, Lane, Aimola, & Schenk, 2012; Schenk & McIntosh, 2010). Nevertheless, the critical role played by parietal cortex in the transformation of vision into action is well recognized, particularly in terms of reaching and grasping. Damage to parietal cortex, or to primary visual centers that feed parietal cortex, often results in reaching and grasping deficits, including an inability to move the hand efficiently through space toward a target or to appropriately shape the fingers to match the size of a to-be-grasped item (L. S. Jakobson, Archibald, Carey, & Goodale, 1991; Perenin & Vighetto, 1988). Thus, both the acts of reaching (the transport of the hand from a proximal location to a distal one), and grasping (the appropriate shaping of the hand and fingers to acquire a target object) can be traced to an origin in parietal cortex. Ostensibly, these actions are themselves produced and controlled within distinct parietal circuits that integrate temporally to generate smooth reach-to-grasp actions. The dorsomedial reach channel is responsible for the reach, whereas the dorsolateral grasp channel produces the grasp (Davare, Kraskov, Rothwell, & Lemon, 2011).

The Dual Visuomotor Channel Theory of Reaching and Grasping

The dual visuomotor channel theory of grasping posits that reach-to-grasp actions are comprised of distinguishable components arising from distinct visuomotor circuits (Jeannerod, 1981). The reach and grasp components may be distinguished based on their function, mechanisms of control, and environmental influences. The reach component transports the hand to the target, whereas the grasp component appropriately shapes the hand for target acquisition and control. With respect to biomechanics, the reach is controlled via the proximal musculature of the torso, shoulder, and upper arm, whereas the grasp is accomplished through skillful control of the distal musculature of the forearm, wrist, and hand (Jeannerod, 1984, 1986a). Reach and grasp components of prehension are also distinguishable in terms of the target properties to which they respond; reach kinematics are adjusted praimrily based on a target's extrinsic properties such as location, whereas the mechanics of the grasp respond mainly to intrinsic target properties like size and shape (Jeannerod, 1984, 1986a).

Early support for this theory of reach and grasp distinction came almost entirely from observations of stable temporal coupling between the otherwise distinct kinematics of the reach and grasp (Jeannerod, 1984, 1986a, 1986b; Jeannerod & Biguer, 1982). Jeannerod noticed that while the reach and grasp kinematics responded to different aspects of the target and environment, these influences were not independent. An increase in maximum grip aperture (MGA) was usually accompanied by a lengthening of the reach's overall movement time (MT), with the end result being that MGA was reliably achieved at approximately 75% of MT (Jeannerod, 1984). More recently, support for the dual visuomotor channel theory stems from neuroimaging (Culham et al., 2006; Grol et al., 2007), electrophysiology (Bonini et al., 2012; Bonini et al., 2011; Graziano, Aflalo, & Cooke, 2005; Graziano, Taylor, & Moore, 2002), and neurophysiological studies (Davare, Andres, Cosnard, Thonnard, & Olivier, 2006; Davare et al., 2011; Olivier, Davare, Andres, & Fadiga, 2007). Neuroimaging evidence suggests that the reach and grasp are governed by distinct networks in the occipitoparietal cortex (Culham et al., 2006; Davare et al., 2011), the dorsomedial reach pathway and the dorsolateral grasp pathway, which together make up the cortical grasping network (Grafton, 2010). The dorsomedial reach pathway connects area V3A in the occipital cortex to the parietal reach region in posterior parietal cortex. The parietal reach region, which includes the superior occipitoparietal complex (SPOC) and medial intraparietal sulcus (mIPS) projects to the dorsal premotor cortex (PMd) before connecting to primary motor cortex (M1). The dorsolateral grasp pathway also starts in V3A, but passes through the anterior intraparietal sulcus (aIPS; a.k.a. area AIP in humans) on its way to ventral premotor cortex (PMv) and M1 (Davare et al., 2006; for review, see Karl & Whishaw, 2013). These circuits integrate in M1 to produce the temporally consistent reach-to-grasp movement that we perform dozens if not hundreds of times per day.

When investigating the kinematic components of prehension, researchers have had a tendency to separate the reach from the grasp by comparing the reach-to-grasp movement (which by definition incorporates both the outward movement of the reach and the hand-shaping of the grasp), to reach-to-point or reach-to-touch movements (e.g., Grol et al., 2007). This comparison ostensibly isolates the distal hand shaping of the grasp from the reaching action. The result is a series of studies conducted under the a priori assumption that the reach component of the reach-to-grasp action is the same reach component observed in reach-to-point actions. However, kinematic evidence from reach-to-point and reach-to-grasp studies imply that these movements, while functionally similar, may have entirely separate cortical and evolutionary foundations.

Hints of these distinctions can be found in landmark electrophysiological and neuroimaging studies; studies often cited in support of the dual visuomotor channel theory for grasping. In a series of ground-breaking papers, Graziano and colleagues described experiments wherein long-train electrical stimulation of the macaque motor and premotor cortex showed that, along with various other ecologically relevant movements, the reach, reach-to-grasp, and hand-to-mouth movements may be elicited by electrically stimulating distinct anatomical regions (Cooke & Graziano, 2004a, 2004b; Graziano, 2006; Graziano et al., 2005; Graziano et al., 2002). Generally, stimulation of precise sites within anterior premotor cortex results in an outward movement of the hand combined with relaxed, open posture of the fingers (i.e., a reach), and stimulation of precise sites within posterior premotor cortex results in movement of the hand to a central location and a manipulation-like shaping of the fingers (i.e., a precision grasp). Through these experiments, Graziano and colleagues showed that not only were reach and grasp movements elicited by stimulation of distinct regions, but that that stimulation resulted in consistent movements regardless of the proximal or distal muscle recruitment required for their execution. For example, when a hand-to-mouth movement was elicited, that movement was performed regardless of the starting posture of the hand. Whether that movement required an extension or a flexion of the shoulder, the hand was always brought to the mouth. This shows that, contrary to both popular belief and longstanding interpretation of early stimulation experiments (see

Penfield & Boldrey, 1937), the macaque motor cortex is organised around the production of functionally-relevant movements, rather than around the specific activation of individual muscles or muscle groups. An often-overlooked corollary of this finding, however, is that movements that appear similar in their execution may have entirely distinct neural origins; this in turn implies a possible distinction in terms of end-goal or functional relevance.

Data from neuroimaging studies implies a similar distinction. Grol et al. (2007) conducted an imaging study investigating the neuroanatomical underpinnings of reach-to-grasp movements. Consistent with the dual visuomotor channel theory, they found that reach-to-touch and reach-to-grasp actions were associated with increased neurovascular activity within the dorsomedial and dorsolateral channels, respectively. Interestingly, they also showed that the type of grasp one performed (precision vs. whole hand grasp) influenced the strength of the coupling between areas within the dorsolateral grasp channel. They interpreted this as evidence that the difficulty of the movement (i.e., the degree to which the movement requires online control) directly influences the recruitment of grasp related neurocircuitry; the amount of information available for planning the grasp naturally depends on the intrinsic qualities of the target (Grol et al., 2007). However, an alternate interpretation is that the differential activity within the dorsolateral channel reflects activation of distinct circuits – circuits that are recruited based on the function of the movement, and potentially difficult to distinguish given the limited biological resolution[7] of fMRI (Özcan, Baumgärtner, Vucurevic, Stoeter, & Treede, 2005; Yoo, Talos, Golby, Black, & Panych, 2004).

Human neurophysiology experiments also imply a neural distinction between the reach and grasp actions. Davare et al (Davare et al., 2006) showed that aspects of the grasp and aspects of the reach could be differentially disrupted by "virtual lesions," administered via transcranial magnetic stimulation (TMS) to ventral premotor cortex (PMv) or dorsal premotor cortex (PMd), respectively. Virtual lesions of PMv impaired hand pre-shaping during a reach-to-grasp action, altering the contact position of the fingertips when grasping to lift a small object. Conversely, a virtual lesion delivered to PMd altered the coupling between the grasp and lift components of that same action (Davare et al., 2011). In another TMS study, Davare's team demonstrated that interactions between PMv and M1 are context specific; during whole hand grasping, the net effect PMv has on M1 is inhibitory, whereas during precision grasping the relationship is one of facilitation (Davare, Lemon, & Olivier, 2008). Once again, the authors interpret this distinction in terms of the type of grasp being performed, and ignore the implications of grasp selection with respect to the functional goal of a movement. After all, one might grasp an apple to either pass it to a companion or to take a bite, and clues to these intentions may be found in the type of grasp the actor chooses.

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[7] Unlike the spatial resolution of MRI, which is largely limited by technology (e.g., by the strength of the magnetic field, or the versatility of signal processing software), biological resolution of fMRI is limited by neuroanatomy. Because fMRI measures changes in blood oxygenation level as an indicator of neural activity, the vascular architecture of the brain imposes a physical limit on the possible resolution of the BOLD signal.

Thus, there is convergent evidence from electrophysiology, neuroimaging, and psychophysical studies that the reach-to-point and reach-to-grasp actions are produced from distinct neurocircuitry. Perhaps the strongest evidence for this theory, however, comes from behavioural studies. The following sections discuss how kinematic asymmetries (or the lack thereof) present a strong case not only for distinction between these movements, but for a lateralization of the networks responsible for their production.

Kinematic Asymmetries in Pointing and Aiming

As early as 1899, researchers were investigating the accuracy, timing, and kinematics of reach-to-point and reach-to-aim movements. In an age before recorded video, Woodworth (1899) devised an ingenious method of measuring pointing and aiming efficiency; by having participants trace a line on a paper attached to a rotating drum, Woodworth was able to not only assess the end-point accuracy of goal-directed movements, but temporal and spatial parameters related to their execution as well. When participants reciprocally pointed to two laterally-separated end-points on the drum, Woodworth noticed that their movements were characterised by two phases; an initial, ballistic phase that was quick and relatively uniform between movements, and a comparatively slower approach phase characterized by fine adjustments toward the target goal (Elliott, Helsen, & Chua, 2001). Of particular relevance to the current review were performance asymmetries; Woodworth noticed that the dominant hand of right-handed participants was both more uniform and more accurate than the non-dominant left, especially in conditions of speed imperatives and reduced visual feedback availability – a finding that has been echoed in numerous studies conducted since (Carnahan, 1998; Carson, Chua, Elliott, & Goodman, 1990; Carson, Chua, Goodman, Byblow, & Elliott, 1995; Carson, Goodman, Chua, & Elliott, 1993; Elliott & Allard, 1985; Elliott & Chua, 1996; Elliott et al., 1993; Mieschke, Elliott, Helsen, Carson, & Coull, 2001; Roy & Elliott, 1986, 1989; Roy, Kalbfleisch, & Elliott, 1994). In the modern age of high-speed video and motion capture, studies show that right-hand aiming (relative to left-hand aiming) also shows advantages in terms of higher peak velocities (Carnahan, 1998; Roy et al., 1994), shorter movement times (Barthélémy & Boulinguez, 2002; Boulinguez, Nougier, & Velay, 2001; Boulinguez, Velay, & Nougier, 2001; Carnahan, 1998; Elliott et al., 1993; Maruff et al., 1999; Mieschke et al., 2001; Roy et al., 1994; van Doorn, 2008), and more efficient deceleration/approach phases (Lavrysen, Elliott, Buekers, Feys, & Helsen, 2007; Mieschke et al., 2001; Roy et al., 1994) regardless of handedness (Boulinguez, Velay, et al., 2001; Lavrysen et al., 2007). Conversely, the left-hand appears to show an advantage in reaction time: where the right-hand is almost inevitably faster to complete a pointing movement, the left-hand is quicker to initiate a movement (Barthélémy & Boulinguez, 2002; Boulinguez, Nougier, et al., 2001; van Doorn, 2008), especially when that movement is goal-oriented and/or spatially complex (Mieschke et al., 2001).

A number of theories have been put forward to explain these asymmetries in terms of cerebral organization (for a brief review, see Grouios, 2006). The precise parametrization of force theory posits that the right-hand benefits from a more effective and consistent capacity for movement programming in the left-hemisphere (Roy & Elliott, 1986, 1989). In other words, the left-hemisphere/right-hand system exhibits less variability in force production during the initial ballistic phase of a movement, and therefore requires fewer adjustments during the approach phase of aiming and pointing movements (J. Annett, Annett, Hudson, & Turner, 1979; Schmidt, Zelaznik, Hawkins, Frank, & Quinn Jr, 1979). In simplest terms, this theory states that the right-hand advantage stems from a left-hemisphere specialization in motor output accuracy. Conversely, the feedback processing theory posits that the asymmetries in manual aiming stem not from motor-output asymmetries, but rather from a left-hemisphere advantage for the processing of visual feedback relating to the ongoing movement (Flowers, 1975). An advantage of this theory over the precise parametrization of force theory is that it accounts for the reduced kinematic and accuracy asymmetries observed when vision of the moving limb is occluded (Foley, 1975), and that it is parsimonious with right-hand advantages in response to target perturbations during aiming movements (Boulinguez, Nougier, et al., 2001; Boulinguez, Velay, et al., 2001; Carnahan, 1998). Third, the lateralized attention theory states that manual kinematic asymmetries observed in right handers is simply due to an attentional bias favouring the dominant hand (Peters, 1981). That is, because right-handers pay more attention to their right hands, they are more effective when translating that visual and haptic input into appropriate motor output (Helsen, Starkes, Elliott, & Buekers, 1998).

Finally, the dynamic dominance hypothesis (Sainburg, 2002) explains manual asymmetries not in terms of a general hemispheric dominance, but in terms of hemispheric specializations for various aspects of movement. In contrast with previously discussed theories, Sainburg hypothesizes that both cerebral hemispheres have evolved distinct but complementary mechanisms for control of movement (Mutha, Haaland, & Sainburg, 2013). Rather than simply being a weaker analog for movement (in comparison to the “dominant” left hemisphere), the right hemisphere has its own advantages and contributions to motor control. Evidence of these contributions comes directly from Sainburg’s own research. In a series of complimentary experiments, Sainburg and colleagues use a gravity-countering frictionless sled in which participants suspend their arms; the researchers may then alter the reach environment by adjusting the resistance or torque affecting the sled’s movement. They then measure how participants respond to these unexpected perturbations during left and/or right-handed reaches. Sainburg establishes that the left hemisphere is optimized for the dynamic control of movement by demonstrating that participants are better able to correct directional/trajectory manipulations when pointing with their dominant right hands (Bagesteiro & Sainburg, 2002; Mutha, Sainburg, & Haaland, 2011; Sainburg, 2002; Schaefer, Haaland, & Sainburg, 2009). Meanwhile, participants are more efficient at correcting force-related end-point manipulations when using their non-dominant left hands (Bagesteiro & Sainburg, 2003; Duff & Sainburg, 2007; Wang & Sainburg, 2007). Thus, the left-hemisphere/right-hand system is optimized for maintaining consistent reach-path trajectories in the face of unanticipated torques, while the right-hemisphere/left-hand system is optimized for achieving stable postures at the end-point of a movement in spite of unexpected resistance (Mutha et al., 2013).

Clearly, there exist multiple hypotheses of cerebral organization that may explain kinematic asymmetries in reach-to-touch, -aim, or –point movements. One would expect that the reach-to-grasp movement, being a combination of reach and grasp components, would show the same kinematic asymmetries predicted by these hypotheses. As we are about to see, however, kinematic asymmetries in grasping actions are not nearly as robust as those in reach-to-touch movements; assuming, that is, that they are even found at all.

Kinematic Asymmetries in Reach-to-Grasp Movements

As might be expected, since the introduction of marker-based motion capture systems in the early 90s a great many studies on the kinematics of reach-to-grasp actions have been conducted. In addition to kinematics shared with reach-to-point actions (i.e., reaction time, movement time, peak velocity, and acceleration/deceleration phase duration), researchers are able to report and describe kinematics unique to the hand pre-shaping component of the grasping action; i.e., maximum grip aperture, timing of maximum grip aperture, and variability of maximum grip aperture (see Jeannerod, 1984, 1986a, 1986b for examples). Consistent with results from pointing studies, the reach-specific kinematics of reach-to-grasp actions are affected by such target-specific factors as distance (Chieffi & Gentilucci, 1993; Kudoh, Hattori, Numata, & Maruyama, 1997), size (Castiello, Bennett, & Stelmach, 1993; Kudoh et al., 1997), and location (Jackson, Jackson, & Rosicky, 1995; Paulignan, Frak, Toni, & Jeannerod, 1997), as well as extrinsic factors such as visual feedback availability (Chieffi & Gentilucci, 1993; Franz et al., 2007;

Goodale, 1990; Holmes, Mulla, Binsted, & Heath, 2011), and perceived fragility (Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987). However, somewhat unexpectedly, very few studies on reach-to-grasp kinematics attempt to validate the asymmetries described in the pointing/aiming literature by comparing kinematics of left and right handed grasping movements (Flindall et al., 2014; Grosskopf & Kuhtz-Buschbeck, 2006; Seegelke, Hughes, & Schack, 2011; Smeets & Brenner, 2001; Tretriluxana, Gordon, & Winstein, 2008). Those few studies that do compare left and right-handed grasps do not find the robust manual asymmetries that are so prevalent in the reach-to-point literature. The first such study (of which we are aware) comparing left- and right-hand kinematics, conducted by Smeets and Brenner (2001), monitored simple kinematics of the index finger, thumb, and wrist while participants grasped a small disk with either the left hand, the right hand, or bimanually (between the index fingers of both hands). Amazingly, the authors reported that the grasps in all three conditions were “remarkably similar,” in that the kinematic parameters of grip aperture and movement time did not differ as a function of hand(s) used. In another early study comparing kinematics between the left and right hands of right-handed participants, Grosskopf and Kuhtz-Buschbeck (2006) asked participants to grasp a peg and fit it snugly into one of several holes in a board extending perpendicularly from the participants midline. Participants completed this task in a closed-loop condition, where they were able to complete the grasp with full visual feedback of the target and moving limb throughout the reach, and in an open-loop condition, wherein the lights were extinguished upon movement initiation, and participants completed the movement in the dark. While minor kinematic asymmetries were present in the open-loop condition (specifically, smaller early grip apertures in left-handed movements), participants performed this task equally well with their dominant and non-dominant hands when visual feedback was available. Absolutely no asymmetries were observed in reaction time, movement time, peak velocity, average velocity, maximum grip aperture, or any of the other pre-contact kinematics measured. In yet another study, when Seegelke et al. (2011) asked participants to grasp a cylinder to either transport it laterally to a nearby pedestal or flip it over (adopting an awkward wrist position in the process), they observed no main effect of hand on any kinematic measures within the pre-contact phase of the movement; again, left and right handed grasps were symmetrical. When Tretriluxana et al. (2008) asked participants to grasp and lift small cylinders of various sizes while vision of the moving limb was occluded, they found minor asymmetries in terms of higher peak velocities and shorter movement times in the right hand, but again, only when visual feedback was restricted. Flindall et al. (2014) asked participants to grasp a small drinking glass that was either nearly full or almost empty; aside from differences in inter-trial consistency of MGA, the only asymmetry between left and right-handed movements (a tendency for longer movement times in left-handed grasps) was found only when vision was restricted during both the immediate preparation and execution phases of the movement.

A common thread throughout these studies is that when simple reach-to-grasp movements are performed within normal, everyday conditions, asymmetries between the kinematics of left- and right-handed movements are all but absent. This raises two important questions: first, if right- and left-handed reach-to-grasp movements are kinematically identical (i.e., equal in terms of performance), why then do humans overwhelmingly prefer to use their right hands for these types of actions (M. Annett, 1967, 1970)? Second, if the reach-to-grasp action is a sum of reaching kinematics coupled with the hand pre-shaping components of the grasp (Jeannerod, 1984; Karl & Whishaw, 2013), what happens to the robust manual asymmetries described in reaching studies when a grasp is incorporated into the reaching movement? An answer to both questions may lie in the type of action investigated in the above studies. That is to say, the purpose of the actions we instruct our participants to make seems to have a significant effect on the way in which they ultimately produce these movements.

Effects of Actor Intent on Reach-to-grasp Kinematics

In addition to intrinsic and extrinsic target parameters described by Jeannerod (Jeannerod, 1984, 1986a, 1986b), many studies show that reach-to-grasp kinematics are also affected by secondary movements embedded within a functional chain. That is, kinematics of an outward reach-to-grasp movement are at least partially determined by what we plan to do with that target after we grasp it. This finding has been reported numerous times for a large range of movements, including grasp-to-lift vs. grasp-to-pour (Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Ansuini, Grigis, Massaccesi, & Castiello, 2009; Crajé, Lukos, Ansuini, Gordon, & Santello, 2011), grasp-to-raise (Armbrüster & Spijkers, 2006), open (e.g., with a jar; Friedman and Flash (2007)), and throw, place, or pass to a confederate (Ansuini et al., 2008; Armbrüster & Spijkers, 2006; Becchio, Sartori, Bulgheroni, & Castiello, 2008). We adjust the speed and timing of the outward reach dependent on whether we are grasping-to-move or grasping-to-use an item (Friedman & Flash, 2007; Valyear, Chapman, Gallivan, Mark, & Culham, 2011) or bring it near the mouth (Cavallo, Koul, Ansuini, Capozzi, & Becchio, 2016; Naish, Reader, Houston-Price, Bremner, & Holmes, 2013). In general, these studies all report similar findings; namely that the initial outward grasping action, when serving a secondary task or embedded in a functional chain, will be adjusted to fit the mechanical requirements of that secondary or subsequent action. When we intend quick, ballistic secondary actions with the to-be-grasped object (e.g., throwing or tossing movements), those initial grasps are completed with faster peak velocities and shorter movement times than grasps whose secondary actions require a higher degree of precision or control (e.g., -place or –pass movements; Ansuini et al., 2008; Armbrüster & Spijkers, 2006). Interestingly, none of these studies reported any lateralized effects of task (though only Armbrüster & Spijkers (2006) tested left-handed movements). These studies show that we adjust our hand position and contact points according to the purpose of the movement, but not necessarily that those positions or contact points vary based on the hand used to complete the movement. In other words, if we are grasping a kitchen spoon to move it into a drawer, we will of course grasp it differently (with different reach kinematics, arm and wrist postures, and grasp contact points) than when grasping the spoon to stir soup within a pot (Valyear et al., 2011).

None of this is surprising; it is intuitive that we will adapt our postures when grasping to serve the mechanical requirements of the secondary action we wish to perform. But what if those secondary actions are identical in terms of biomechanical requirements? In a series of recent studies, Flindall, Gonzalez, and colleagues contrasted kinematics of grasping actions, differing in terms of end-goal, directed toward small cereal items (11-15 mm diameters). These actions required the participant to begin the movement in the same start position, assume the same starting posture, reach-to-grasp the same objects from the same distal location, and bring those targets back toward the body. The only difference between grasps concerned the ultimate goal of those actions; the participant was instructed to grasp the target with intent to either a) place it in a container located just beneath the chin, or b) eat it (Flindall & Gonzalez, 2013, 2014, 2015, 2016, 2017; Flindall, Stone, & Gonzalez, 2015). While the kinematics of the reach (i.e., MT, PV, PVt) were found to be identical between the two tasks (save for a few un-reproducible differences - see Flindall & Gonzalez, 2015, 2016, 2017), the authors reported a consistent effect on MGA linked with right-handed grasp-to-eat movements. Specifically, when using their right hands, participants generate significantly smaller MGAs when grasping with intent to eat the target compared to when grasping with intent to place the target into the near-mouth container. When grasping with their left hands, they use the same kinematics for both grasp-to-place and grasp-to-eat actions. Right-handed grasp-to-eat MGAs are not only significantly smaller than right-handed grasp-to-place MGAs, they are significantly smaller (by the same magnitude) than left-handed grasp-to-place and grasp-to-eat MGAs. This right-hand lateralized task-dependent signature, first described in right-handers (Flindall & Gonzalez, 2013), was similarly described in left-handers (who also showed a right-hand lateralization, implying that practice with the dominant hand is not responsible for the signature's appearance; see Flindall et al., 2015) and in children over the age of 10 (Flindall & Gonzalez, 2015)8. Further studies into this effect show that actually chewing and consuming the target was unnecessary; simply intending to bring a food item into the mouth was enough to elicit smaller maximum grip apertures during the grasp (Flindall & Gonzalez, 2014). Nor is it necessary that the target even be edible; inedible nylon hex nuts, when grasped with intent to bring to the mouth, also elicit the same lateralized kinematic signature (Flindall & Gonzalez, 2016). To test whether the kinematic signature was simply the left-hemisphere/right hand system's way of reacting to the added precision requirements of placing an item into the mouth versus the container, the authors replaced the wide-aperture bib with a narrow-aperture shot glass; the kinematic signature, again, was unaffected (Flindall & Gonzalez, 2017). Finally, to ensure that simple mouth movement was not responsible for right-hand task differences, participants were asked to "eat" and "place" as before while either keeping their mouths closed throughout the action (touching the item to their lips before discarding it in the "eat" condition), or opening their mouths as if to accept the item (bringing it directly to the container in the "place" condition). Once more, only the real grasp-to-eat actions elicited smaller MGAs; both "place" conditions, regardless of mouth movement, as well as the closed-mouth "eat" condition, elicited significantly larger MGAs (Flindall & Gonzalez, 2016). Importantly, this kinematic signature that identifies and distinguishes the grasp-to-eat (or, more rightly,

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[8] Though in children younger than 10 and approximately 25% of left-handers the signature manifests bimanually, the consistent rightward lateralization of the kinematic signature suggests a left-hemisphere origin for the grasp-to-eat motor plan.

hand-to-mouth) action from the grasp-to-place action manifests during the outward movement towards the target, during a period when (with respect to biomechanics) there should be no differentiation between the two movements. The signature cannot be attributed to precision, direction, distance, or speed requirements of the secondary movement, nor can it be explained solely as a by-product of practice with the dominant or preferred hand (Flindall et al., 2015). In the end, these studies suggest a unique motor plan for bringing a to-be-grasped item into the mouth, one that is either lateralized to the left-hemisphere, or at least accessible only during right-handed movements.

Meta-Analysis Methods and Results

To illustrate this signature, we performed a meta-analysis on data collected by Flindall, Gonzalez, and colleagues, as parts of studies previously published (Flindall & Gonzalez, 2013, 2014, 2015, 2016, 2017) and in preparation (van Rootselaar, Flindall, and Gonzalez, 2017; Beke, Flindall, and Gonzalez, 2017). While the collected experiments varied with respect to research question, experimental conditions, and total number of trials, they all shared control conditions (i.e., grasp-to-eat and grasp-to-place tasks) allowing for a simple within-subject analysis of kinematics of the reach and grasp using a participant pool far larger than anything reported to-date in the kinematic literature.

All kinematic variables were taken directly from datasets used in manuscripts by Flindall, Gonzalez, and colleagues, listed in Table 1. Our analysis was limited to those experiments including data from both left and right hands, and using the same small cereal items (Cheerios™ and FrootLoops™, 11 and 15mm average diameter, respectively). A total of 119 participants [97 right-handers (67 females, 30 males) and 22 left-handers (11 females, 11 males)] were included in analysis. Because the above studies were primarily focused on investigating the limits of the grasp-to-eat effect on maximum grip aperture, additional kinematics of the reach and grasp were not always reported. Any kinematic variables not included in original publications were calculated from the raw data files, revisited at the time of this manuscript's preparation. Methods for variable calculation, participant demographics, and criterion for individual exclusion may be found in the original manuscripts. Only those data associated with control trials were included in statistical analyses; conditions unique to each experiment (e.g., "grasp-to-spit" trials, Flindall & Gonzalez, 2014) were excluded from the current data set. For full descriptions of these control tasks, see Flindall and Gonzalez (2013). Participant handedness was not included as a between-subjects factor or covariate in our analyses for two reasons. First, results from Flindall et al. (2015) suggest that left-handers, as a group, are not significantly different from right-handers in terms of their grasp-to-eat behaviour. Second, differences in group size between the two populations preclude any meaningful conclusions being drawn from differences found.

Results 1: 3-way ANOVA

In Table 2, we report means ± standard errors for the following kinematic variables: maximum grip aperture (MGA), reported in mm; movement time (MT), reported in milliseconds; peak resultant velocity of the wrist (PV), reported in meters/second; relative time of peak velocity (PVt), reported as a percentage of MT; relative time of MGA (MGAt), also reported as a percentage of MT; and variability of MGA (vMGA), representing the standard deviation of within-condition MGAs, reported in millimeters. We ran a within-subject three-way analysis of variance, with factors size (small, large), hand (left, right), and task (eat, place), on these means. Significant main effects and interactions from that ANOVA are reported below.

Table 1 – Sources and brief demographics of participants included in meta-analysis.

Paper	Participants
Flindall, J. W., & Gonzalez, C. (2013). On the Evolution of Handedness: Evidence for Feeding Biases. *PLoS ONE, 8* (11), e78967. [See Appendix 1.]	n=11; 9 females, 0 left handed
Flindall, J. W., Stone, K., & Gonzalez, C. (2015). Evidence for right-hand feeding biases in a left-handed population. *Laterality: Asymmetries of Body, Brain and Cognition, 20* (3), 287-305 [See Appendix 2.]	n=21; 11 females, 21 left handed
Flindall, J. W., & Gonzalez, C. (2014). Eating interrupted: the effect of intent on hand-to-mouth actions. *Journal of Neurophysiology, 112* (8), 2019-2025. [See Appendix 3.]	n=12; 7 females, 1 left handed
Flindall, J. W., & Gonzalez, C. (2017). The inimitable mouth: task-dependent kinematic differences are independent of terminal precision. *Experimental Brain Research*, 1-8. [See Appendix 6.]	n=25; 15 females, 0 left handed
van Rootselaar, N., Flindall, J. W., & Gonzalez, C. (submitted). Hear speech, change your reach: Changes in left-hand grasp-to-eat kinematics during simultaneous speech processing.	n=29; 22 females, 0 left handed
Beke, C., Flindall, J. W., & Gonzalez, C. (submitted). Grasping from memory: left hemisphere grasp-to-eat advantage is dependent on vision.	n=21; 14 females, 0 left handed

Table 2 – Between-participant means and standard errors for reach and grasp kinematics, averaged by condition. Variables reported are MT (movement time), PV (peak velocity), PVt (time of peak velocity), MGA (maximum grip aperture), vMGA (mean inter-trial variability of maximum grip aperture), MGAt (time of MGA), and vMGA (variability of maximum grip aperture). Significant within-subject 3-way ANOVA results [factors hand (left, right), task (eat, place), and size (small, large)] by main effect (H: hand; T: task; S: size) and interaction (e.g., HxT: Hand x Task) are listed below columns for each kinematic measure.

Size	Hand	Task	MT (ms)	PV (m/s)	PVt (%MT)	MGA (mm)	MGAt (%MT)	vMGA (mm)
Small	Left	Eat	952 ± 21	.769 ± .02	30.2 ± 0.4	22.7 ± 0.5	54.7 ± 0.9	2.73 ± .12
		Place	937 ± 20	.759 ± .02	30.7 ± 0.5	22.9 ± 0.4	55.3 ± 0.9	2.72 ± .12
	Right	Eat	949 ± 20	.769 ± .02	29.7 ± 0.3	20.4 ± 0.4	55.8 ± 1.0	2.52 ± .10
		Place	932 ± 20	.761 ± .02	30.3 ± 0.4	22.4 ± 0.5	55.3 ± 1.0	2.71 ± .12
Large	Left	Eat	891 ± 17	.773 ± .02	32.0 ± 0.5	27.2 ± 0.5	59.3 ± 1.0	3.00 ± .16
		Place	878 ± 17	.760 ± .02	32.4 ± 0.5	27.9 ± 0.5	59.7 ± 0.9	2.88 ± .15
	Right	Eat	877 ± 17	.764 ± .02	32.1 ± 0.4	25.0 ± 0.5	61.5 ± 0.9	2.53 ± .16
		Place	873 ± 18	.756 ± .02	32.1 ± 0.4	27.0 ± 0.5	60.7 ± 0.9	3.01 ± .20
		ANOVA Results:	S	T, SxH	S	S, H, T, HxT	S	S, HxT

Target size was found to affect all kinematic variables save peak velocity (Table 2). Strong main effects of target size were identified for MT, F (1, 118)=135.20, p<.001, η2=.534, PVt, F (1, 118)=124.27, p<.001, η2=.513, MGA, F (1, 118)=853.01, p<.001, η2=.878, and MGAt, F (1, 118)=163.79, p<.001, η2=.581. In addition, a weak main effect of size was found in vMGA, F (1, 118)=4.76, p=.031, η2=.039. These effects, identical to those reported elsewhere (Bootsma, Marteniuk, MacKenzie, & Zaal, 1994), show that reach-to-grasp actions directed toward smaller targets have an elongated post-peak velocity phase of the movement; this lengthening of the deceleration phase results in longer MTs, and earlier relative PVts and MGAts. MGA is also smaller and slightly more consistent when grasping smaller targets. A Size x Hand interaction was found on PV, F (1, 118)=8.39, p=.004, η2=.066. Paired-sample t-tests revealed that this effect was due to smaller items eliciting faster PVs in right handed movements (.765 ± .02 m/s) than large items (.760 ± .02 m/s), t (118)=3.001, p=.003. This effect of size was not present during left-handed movements, t (118)=-1.068, p>.2.

A main effect of hand was found on MGA, F (1, 118)=18.16, p<.001, η2=.133, wherein right-handed movements produced smaller MGAs (23.7 ± .43 mm) than did left-handed movements (25.2 ± .45 mm). No other kinematic variables differed as a function of hand used.

A main effect of task was found on PV, F (1, 118)=7.25, p=.008, η2=.058, wherein grasp-to-eat movements elicited marginally faster PVs (.769 ± .02 m/s) than did grasp-to-place movements (.759 ± .02 m/s). A strong main effect of task was found on MGA, F (1, 118)=37.73, p<.001, η2=.242, wherein grasp-to-eat movement elicited smaller MGAs (23.85 ± .42 mm) than did grasp-to-place movements (25.08 ± .41).

A strong Hand x Task interaction was found on MGA, F (1, 118)=17.41, p<.001, η2=.129, while a weak Hand x Task interaction was found on variability of MGA, F (1, 118)=5.22, p=.024, η2=.042. Follow-up paired-sample t-tests revealed that both of these effects stemmed from the same origin; grasp-to-eat movements completed with the right hand had smaller MGAs (22.7 ± .42mm) than did left-handed grasp-to-eat movements (25.42 ± .44mm), t (118)=-6.354, p<.001, and right-handed grasp-to-place movements (24.74 ± .48mm), t (118)=-7.187, p<.001 (Figure 1). These smaller MGAs were also more consistent, with less variability in right-handed grasp-to-eat movements (2.52 ± .11 mm) than in left-handed grasp-to-eat movements (2.87 ± .13 mm), t (118)=-2.925, p=.004, and right-handed grasp-to-place movements (2.86 ± .13 mm), t (118)=-2.204, p=.029. No other main effects or interactions reached statistical significance (p>.05).

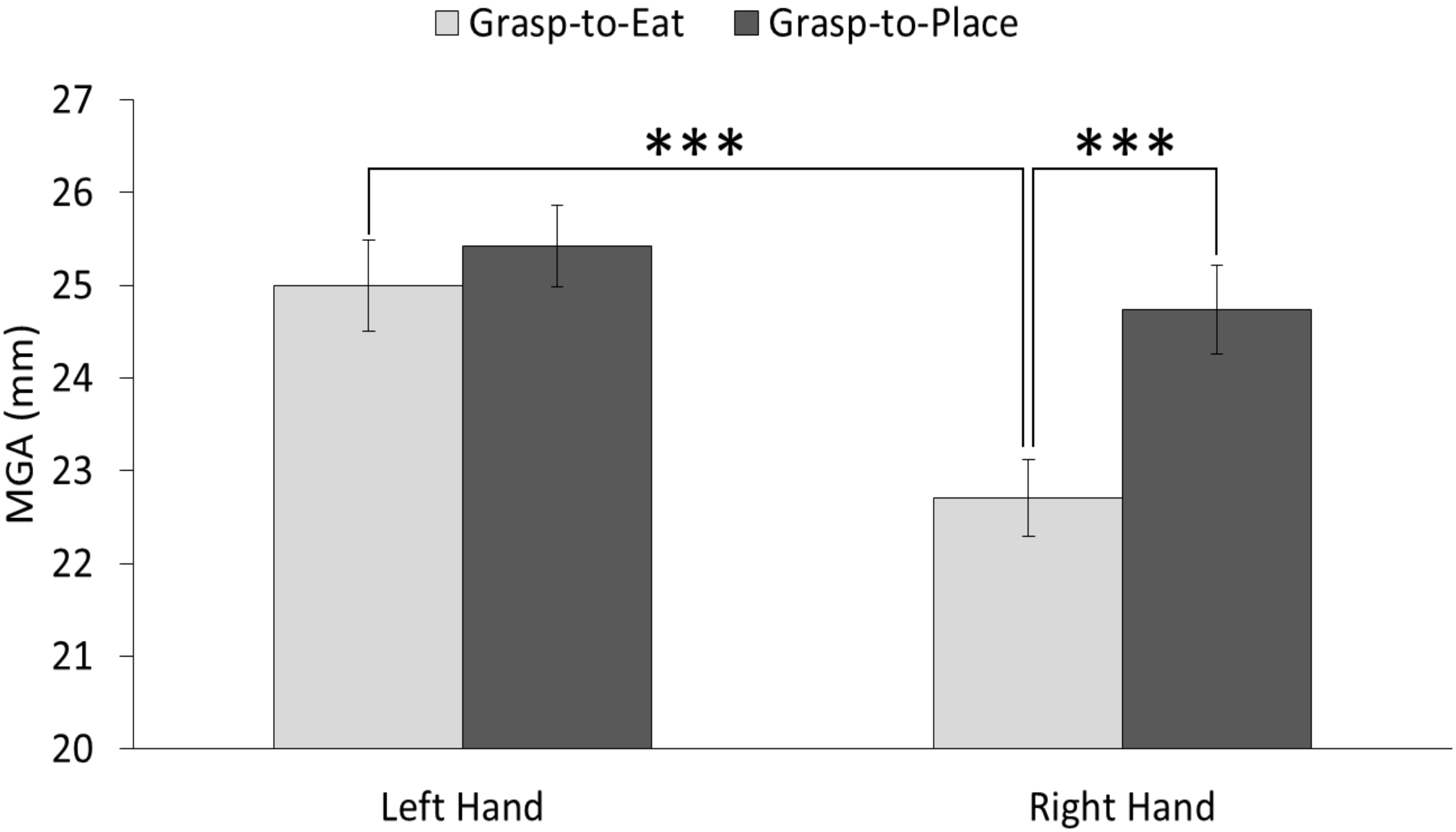

Figure 1 – Maximum grip apertures of left- and right-handed grasp-to-eat and grasp-to-place movements. Right-handed grasp-to-eat movements produce significantly smaller MGAs than do right-handed grasp-to-place movements or left-handed movements of either type (*** p< .00001).

Results 2: 2 x 2-way ANOVAs

To highlight the contrast between our results and those in the majority of reach-to-grasp kinematic studies (i.e., those employing a simple grasp-to-place task), we divided our data by task (eat vs. place) and ran two complimentary 2-way ANOVAs, with factors hand (left, right) and size (small, large). The results of these ANOVAs are reported below.

Table 3 – Between-participant means and standard errors for reach and grasp kinematics, split by task and averaged by hand (left, right) and size (small, large) conditions. Variables reported are MT (movement time), PV (peak velocity), PVt (time of peak velocity), MGA (maximum grip aperture), vMGA (mean inter-trial variability of maximum grip aperture), MGAt (time of MGA), and vMGA (variability of maximum grip aperture). Significant within-subject 2-way ANOVA results [factors hand (left, right), and size (small, large)] by main effect (H: hand; S: size) and interaction (e.g., HxS: Hand x Size) are listed below columns for each kinematic measure within each task group.

Task	Hand	Size	MT (ms)	PV (m/s)	PVt (%MT)	MGA (mm)	MGAt (%MT)	vMGA (mm)
Place	Left	Small	937 ± 20	.759 ± .02	30.7 ± 0.5	22.9 ± 0.4	55.3 ± 0.9	2.72 ± .12
		Large	878 ± 17	.760 ± .02	32.4 ± 0.5	27.9 ± 0.5	59.7 ± 0.9	2.88 ± .15
	Right	Small	932 ± 20	.761 ± .02	30.3 ± 0.4	22.4 ± 0.5	55.3 ± 1.0	2.71 ± .12
		Large	873 ± 18	.756 ± .02	32.1 ± 0.4	27.0 ± 0.5	60.7 ± 0.9	3.01 ± .20
		ANOVA Results:	S	HxS	S	S	S	
Eat	Left	Small	952 ± 21	.769 ± .02	30.2 ± 0.4	22.7 ± 0.5	54.7 ± 0.9	2.73 ± .12
		Large	891 ± 17	.773 ± .02	32.0 ± 0.5	27.2 ± 0.5	59.3 ± 1.0	3.00 ± .16
	Right	Small	949 ± 20	.769 ± .02	29.7 ± 0.3	20.4 ± 0.4	55.8 ± 1.0	2.52 ± .10
		Large	877 ± 17	.764 ± .02	32.1 ± 0.4	25.0 ± 0.5	61.5 ± 0.9	2.53 ± .16
		ANOVA Results:	S	HxS	S	H, S	H, S	H

Main effects of Size were observed in both Eat and Place ANOVAs on the following kinematic variables of the reach and grasp: MT, F (1, 118)>105.98, p<.001, η^2>.473; PVt, F (1, 118)>58.31, p<.001, η^2>.331; MGA, F (1, 118)>570.38, p<.001, η^2>.829; and MGAt, F (1, 118)>111.62, p<.001, η^2>.486. In both Eat and Place tasks, grasps toward small items had longer MTs with earlier relative PVts (indicating longer deceleration phases), as well as smaller MGAs which occurred relatively earlier in the movement (again, consistent with longer deceleration phases).

Main effects of Hand were found in the grasp-to-eat task, affecting all variables of the grasp: MGA, F (1, 118)=40.37, p<.001, η^2=.255; MGAt, F (1, 118)=4.79, p=.031, η^2=.039; and vMGA, F (1, 118)=8.56, p=.004, η^2=.068. When grasping items to eat with their right hands, participants produced smaller (22.7±.42mm), relatively later (58.6±.9%MT), and less variable (2.52±.11mm)maximum grip apertures than when grasping to eat with their left hands (MGA, 25.0±.49mm; MGAt, 57.0±.9%MT; vMGA, 2.87±.13mm). Notably, no main effects of hand were found within the grasp-to-place movement, on any kinematic variable (all p>.1).

Significant Hand x Size interactions were found in PV, again consistent in both grasp-to-eat, F (1, 118)=5.70, p=.019, η^2=.046, and grasp-to-place, F (1, 118)=4.03, p=.047, η^2=.033, tasks. Follow-up paired sample t-tests, conducted separately for each interaction, revealed that both interactions were due to faster peak velocities achieved when grasping small targets with the right hand (see Table 3 for means and standard errors). However, neither within-task comparison (Eat, t (118)=2.380, p=.019; Place, t (118)=1.936, p=.052) was significant following Bonferroni correction (p>.0125).

Discussion

In the current review, we analysed data collected in six separate experiments conducted from 2013-2017. These experiments shared control conditions in which participants were asked to reach-to-grasp small cereal items (small, Cheerios™ and large, Froot Loops™) in order to either a) bring those items to their mouths for consumption (grasp-to-eat), or b) bring those items to a container hanging just below their chins (grasp-to-place). Kinematic measures of the outward grasping movement (movement time, MT; peak velocity, PV; relative time of peak velocity, PVt; maximum grip aperture, MGA; relative time of MGA, MGAt; and between-trial variability of MGA, vMGA) were analysed for left- and right-handed movements. We analysed these data using a 3-way analysis of variance with factors Hand (left, right), Task (eat, place), and Size (small, large). No differences between the hands were found for any kinematic measure, save within MGA. Follow-up comparisons for a Hand x Task interaction on the same variable revealed that the main effect of hand (as well as the main effect of task) was driven by significantly smaller MGAs in the right-hand eat condition; no MGA difference was found between left-hand eat and place conditions, nor was there a significant difference between right- and left-hand place conditions (Fig. 1). To facilitate comparisons with the majority of the grasping kinematics literature, we also conducted two 2-way ANOVAs with factors Hand (left, right) and Size (small, large) for Place and Eat conditions, separately. These ANOVAs confirmed that all significant kinematic differences between left- and right-handed actions were limited to the grasp-to-eat task. Within the Place condition, no difference between the hands manifested within any kinematic measures.

This finding is consistent with the kinematic literature, which finds no difference (or inconsistent difference) between the left and right hands in terms of kinematics (Flindall et al., 2014; Grosskopf & Kuhtz-Buschbeck, 2006; Seegelke et al., 2011; Smeets & Brenner, 2001; Tretriluxana et al., 2008). Conversely, asymmetries in the Eat condition, for all kinematic measures of the grasp component (MGA, MGAt, and vMGA) were robust; right-handed maximum grip aperture is smaller, relatively later (i.e., with shorter closing time), and more precise (i.e., less variable) than were left-handed maximum grip apertures. This finding is important for two reasons: first, these effects, isolated as they are to grasp-to-eat movements, highlight the robust kinematic difference between two tasks that differ only in actor intent. The grasp-to-eat and grasp-to-place movements analyzed here share identical mechanical requirements, right down to distance and direction of the secondary (functional) movement. Thus, the difference between tasks cannot be explained as a functional adaptation to optimize execution of a secondary movement. Second, the fact that these kinematic differences favour the right hand suggest that whatever neural mechanism is responsible for their production is most likely lateralized to the left hemisphere. These findings are discussed below in terms of their relevance with respect to the dual visuomotor channel theory of grasping.

The dual visuomotor channel theory of grasping states that the neural circuits responsible for the shaping of the grasp component of prehensile movements reside in the dorsolateral grasp channel. This channel, beginning in visual cortex (V3A), includes structures in parietal cortex (AIP) and frontal cortex (PMv) before reaching M1. PMd may also be involved in the control of grasping (see Davare et al., 2011), however PMd is more often considered part of the dorsolateral reach channel (Karl & Whishaw, 2013). In macaques, the anterior intraparietal sulcus (aIPS; the analog of human AIP) has been shown through neuroimaging studies to contain populations of visuomotor neurons that respond selectively to the type of grasp being performed (i.e., whole-hand or precision grasp; Davare et al., 2011). More precisely, a variety of studies, be they neuroimaging (Astafiev et al., 2003; Begliomini, Nelini, Caria, Grodd, & Castiello, 2008; Gallivan, McLean, Valyear, Pettypiece, & Culham, 2011) or electrophysiological (Desmurget et al., 2009) imply that, in both humans and non-human primates, this region is more important for planning reach-to-grasp movements than for their execution. Conversely, areas PMv (and to a lesser extent, PMd) in the frontal cortex, while tightly linked with activity in AIP/aIPS (Davare et al., 2011; Grol et al., 2007), is comparatively more active during effective execution (Bonini et al., 2010) or direct observation (Ferri et al., 2015) of grasps.

The current theory of grasp execution states that motor plans begin with object vision in the dorsal visuomotor stream (i.e., in AIP) as an intent to perform a given reach-to-grasp action based on visual information conveying object properties and affordances (Karl & Whishaw, 2013). That intent is passed along to PMv, where an appropriate motor plan is selected from a repertoire of known grasping movements, specifying aspects such as hand posture and appropriate points of contact for the fingers (Davare et al., 2006). This plan travels to PMd and M1, the latter of which in turn activates the proximal and distal musculature necessary to accomplish the goal first decided upon in parietal cortex (Begliomini et al., 2008; Castiello & Begliomini, 2008). During execution, somatosensory and visual feedback from the moving limb is compared to expectations from the original plan via reciprocal connections between AIP and PMv, with adjustments made to the final approach phase of the movement as required (Davare et al., 2011). Notably, any context of lateralization is conspicuously absent from this framework. The kinematic results reported in the current review suggest that when intent-based motor plans are selected in posterior parietal cortex, the left and right hands may not have equal access to those plans. Alternatively, intent may be equally accessible, but the translation of that intent into an appropriate motor act changes when moving with the left hand.

Kinematic studies of grasp-to-place movements (including those within the current review) show that, contrary to expectations, the left and right hands are identical in terms of movement execution. We show here, however, that robust kinematic differences exist between the hands when, instead of grasping-to-place, one intends to grasp an item to bring it to the mouth. Because these kinematic differences exist where no mechanistic differences in the outward movement or secondary requirements of the grasp would predict them, their origin must lie in hemispheric asymmetries within the neural circuits responsible for their production.

Given that the asymmetries observed were limited to the kinematics of the grasp, we propose that the dorsolateral grasping circuit is not equally represented in the left and right hemispheres. The left-hemisphere/right-hand system has access to a motor plan for grasp-to-eat actions that the left-hand does not; instead, the left-hand uses a plan that is kinematically indistinguishable from the grasp-to-place motor plan, which in turn is identical to that used by the right hand for grasp-to-place actions. Given that this kinematic signature for grasp-to-eat and other hand-to-mouth actions is evident in the pre-contact phase of the movement, it is likely that the hemispheric asymmetry resides in AIP, PMv, or both.

First, let us consider whether it is likely that AIP is asymmetrical in terms of functional ability. fMRI studies show bilateral activation of AIP during grasp planning and execution (Begliomini et al., 2008; Culham et al., 2006). Thus, it is possible that an intention to move (or a motor plan intention) is stored bilaterally, likely accessible by either hand. This is supported by the fact that bilateral disruption of AIP is required to disrupt a reach-to-grasp movement already in progress (Davare, Andres, Clerget, Thonnard, & Olivier, 2007). If the shape or size of the to-be-grasped target changes unexpectedly, however, then unilateral disruption is sufficient to change the ongoing kinematics of the grasp (Tunik, Frey, & Grafton, 2005). Similarly, unilateral disruption of AIP will disable grip formation if that disruption is delivered during the planning phase of the grasp (Glover, Miall, & Rushworth, 2005). This implies that while AIP may unilaterally influence grasp kinematics during the planning phase of a movement, this plan is shared between hemispheres by the time the grasp is executed, and M1 may access the plan from either hemisphere as long as the biomechanical requirements of the movement remain stable. While this and other evidence suggests that motor plans may originate in AIP, and that they may be lateralized at this level, the presence of bilateral AIP activation during grasp planning makes it unlikely that this region is responsible for asymmetries in kinematics. If both hands have access to both ipsilateral and contralateral parietal cortex, why then do we observe kinematic asymmetries? No, it is more likely that hemispheric asymmetries reside in frontal cortex, specifically in ventral premotor regions.

PMv is the human homologue for area F5 in the macaque grasping circuit; in macaques, this region holds both canonical and mirror neurons that are active during the execution and observation of functional grasping movements, respectively (Ferri et al., 2015). However, unlike macaque area F5, the human homologue for this region is not symmetrical; activation of PMv in humans during the observation of a simple grasping movement favours the right hemisphere (Ferri et al., 2015). While at first a right-hemisphere dominance for motor observation seems counter-intuitive, these results make perfect sense if we assume unequal representation of specific motor plans. Let us presume that the left-hemisphere/right-hand system has greater access to a more diverse repertoire of movements; when observing a *general* reach-to-grasp movement, without indication of functional relevance, it is natural that the right-hemisphere/left-hand system will respond more strongly given the generalized function of these right hemisphere regions. Activation within the left-hemisphere is likely to be far more precise, tied to *specific* goal-oriented movements than is activation in the right-hemisphere. Detection of these networks will no doubt rely on a wider variation of observed (and possibly performed) tasks within future neuroimaging studies.

Future Directions

Detection of a precise network (‘precise,’ in terms of both function and anatomy) may prove difficult if we rely solely on fMRI. The spatial resolution of the BOLD response may be insufficient to differentiate between distinct grasping motor plans, given their anatomic proximity and similar efficiencies (Graziano, 2006; Graziano et al., 2005). In comparison, direct electrical stimulation studies, as performed by Graziano et al. (2005) in macaques and by Desmurget et al. (2009) in humans, are conceptually perfect, but prohibitively invasive. Because direct electrical stimulation in humans is typically performed only secondarily (i.e., during surgeries intended to address a potentially unrelated neurological issue, as when excising a tumor or disconnecting seizure-prone cortex), it is unlikely that we will have opportunity to test the effectual differences between premotor stimulation in *both* left- and right-hemispheres in a single subject. Between-patient studies are of course an alternative, however a within-patient study may be necessary, especially if those patients are left-handed (Flindall et al., 2015).

Virtual lesions, administered via TMS, may prove more useful in identifying task-specific circuits in prefrontal cortex. Recognition of grip-functionality has been shown to be disrupted via magnetic stimulation of the inferior frontal cortex (Jacquet & Avenanti, 2015), though that study made no attempt to vary the goal of the grasping movement, therefore we cannot say for certain whether such disruption would similarly affect grasps based on their end-goals.

Other non-invasive electrophysiological techniques (e.g., electroencephalography; EEG) may also aid us in understanding the lateralization of task-dependent circuits. EEG has already been used to differentiate between the parietal and frontal contributions to the reach-to-grasp planning and execution phases, respectively (van Schie & Bekkering, 2007), although the potential asymmetry of these contributions has not yet been fully investigated. The mu signal is a repeating electrical rhythm measured via EEG over sensorimotor cortex; this wave, usually in the 7.5-12 Hz range, is supressed while performing motor actions, while observing another perform a motor action, and while imagining oneself performing a motor action (Pineda, 2005). Furthermore, the characteristics of this suppression differ depending on the type of action one imagines him or herself performing (Pfurtscheller, Brunner, Schlögl, & Da Silva, 2006). In an object-action recognition task for example, mu suppression is often greater for familiar, congruent, or functionally-relevant actions than it is for incongruent, unfamiliar, or irrelevant actions (Kumar, Riddoch, & Humphreys, 2013). By observing differences in mu suppression during a variety of functionally different but mechanically similar tasks, it may be possible not only to differentiate between grasp-to-eat and grasp-to-place actions, but to directly assess whether any such differences show signs of hemispheric lateralization.

Conclusion

In this brief review, we highlight the limitations of the dual visuomotor channel theory for grasping with respect to lateralized dissociations between simple reach-to-grasp actions. Through kinematic analyses we demonstrate that simple movements with identical mechanical requirements and similar secondary goals may differ significantly from one another, and that such differences cannot be explained by intrinsic or extrinsic target properties, nor by functional adaptations to secondary movements. This, in turn, implies a neural distinction based entirely upon the functional relevance (or end-goal) of the grasp. We further speculate on the neural circuits responsible for this distinction, and suggest a left-hemisphere lateralization of these circuits. Non-invasive research protocols are suggested to further investigate these hypotheses.

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Appendices

Appendix 1: On the Evolution of Handedness: Evidence for feeding biases

Title: On the Evolution of Handedness: Evidence for feeding biases

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Abstract

Many theories have been put forward to explain the origins of right-handedness in humans. Here we present evidence that this preference may stem in part from a right hand advantage in grasping for feeding. Thirteen participants were asked to reach-to-grasp food items of 3 different sizes: SMALL (Cheerios®), MEDIUM (Froot Loops®), and LARGE (Oatmeal Squares®). Participants used both their right- and left-hands in separate blocks (50 trials each, starting order counterbalanced) to grasp the items. After each grasp, participants either a) ate the food item, or b) placed it inside a bib worn beneath his/her chin (25 trials each, blocked design, counterbalanced). The conditions were designed such that the outward and inward movement trajectories were similar, differing only in the final step of placing it in the mouth or bib. Participants wore Plato liquid crystal goggles that blocked vision between trials. All trials were conducted in closed-loop with 5000ms of vision. Hand kinematics were recorded by an Optotrak Certus, which tracked the position of three infrared diodes attached separately to the index finger, thumb, and wrist. We found a task (EAT/PLACE) by hand (LEFT/RIGHT) interaction on maximum grip aperture (MGA; the maximum distance between the index finger and thumb achieved during grasp pre-shaping). MGAs were smaller during right-handed movements, but only when grasping with intent to eat. Follow-up tests show that the RIGHT-HAND/EAT MGA was significantly smaller than all other hand/task conditions. Because smaller grip apertures are typically associated with greater precision, our results demonstrate a right-hand advantage for the grasp-to-eat movement. From an evolutionary perspective, early humans may have preferred the hand that could grasp food with more precision, thereby maximizing the likelihood of retrieval, consumption, and consequently, survival.

Introduction

Previous research has indicated that the defining characteristic of handedness, that is, a lateralized manual hand preference, does not develop until 21 months of age in humans (Cochet, 2011; Fagard & Marks, 2000; Vauclair & Imbault, 2009). Many manipulative tasks do not show lateralization until much later in development (Cornwell, Harris, & Fitzgerald, 1991; B. Hopkins & Rönnqvist, 1998; Lewkowicz & Turkewitz, 1982; Peters, 1983). With few exceptions, children younger than 4 years of age do not demonstrate a hand preference for manipulative reach-to-grasp actions on non-food objects; instead, they use whichever hand is ipsilateral to the target object (Cox & Smitsman, 2006; Leconte & Fagard, 2006). Recently, however, it has been shown that when the target is a food-object, children as young as one will demonstrate a robust right-hand preference for the reach-to-grasp action (Sacrey, Arnold, Whishaw, & Gonzalez, 2012). In the Sacrey et al. study, 3- to 5-year-old children were presented with food items (Froot Loops®) and non-food items of comparable size and colour (LEGO® construction blocks) and their hand preference for reaching-to-grasp the items was recorded. A right-hand preference for grasping the blocks was found in the 4- and 5-year old cohorts, but not in the 3-year old group; this finding was consistent with previous research (Cox & Smitsman, 2006; Leconte & Fagard, 2006). When the target was a food-object, however, 3-year-olds showed a greater than 80% right hand preference for grasping. In fact, when younger groups were tested, this preference was observed in children as young as one year of age (Sacrey, Arnold, et al., 2012). This finding suggests that a right hand preference for reach-to-grasp for food (henceforth referred to as grasp-to-eat) develops earlier, and perhaps is altogether separate from hand preference for reach-to-grasp for objects to manipulate (i.e., grasp-to-place). This suggestion is further supported by studies which show that infants are able to produce accurate hand-to-mouth movements earlier than accurate reach-to-grasp movements (Lew & Butterworth, 1997). If hand preference is susceptible to the end goal of an action, it is reasonable to speculate that kinematics may also vary according to the actor's intent.

Several studies describing the kinematics of prehension have shown that the end goal of an action significantly influences the kinematics of the reach and grasp (Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Ansuini, Santello, Massaccesi, & Castiello, 2006; Armbrüster & Spijkers, 2006; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987; Sartori, Straulino, & Castiello, 2011). In movements with a similar initial lifting phase, but different consecutive movements (i.e. with differing intent; for example, grasp-to-place versus grasp-to-throw), peak velocity, peak deceleration, and peak grip aperture of the approach phase of the grasp movement have been shown to vary according to the purpose of the grasp (Armbrüster & Spijkers, 2006). While food has been used as a target in kinematic analyses (Castiello, 1997, 1998; Castiello, Bonfiglioli, & Bennett, 1998; Parma, Ghirardello, Tirindelli, & Castiello, 2011; Parma, Roverato, et al., 2011) and imaging studies (Castiello et al., 2000), few have investigated whether action intention influences movement kinematics when grasping a food item. In the only such study (of which we are aware), participants were asked to reach and grasp a sugar cube in order to put it in their own mouths (presumably to eat), in the mouth of another person (i.e. a conspecific), or in a fake mouth placed over their own mouths. The results showed greater automaticity for movements directed to the self than either the conspecific or the fake mouth (Ferri, Campione, Dalla Volta, Gianelli, & Gentilucci, 2010). These studies indicate that the final objective or purpose for which a reach-to-grasp action is executed significantly influences the kinematics of the movement. They also demonstrate the sensitivity of kinematic parameters when detecting differences in seemingly similar actions.

Investigations into the kinematics of left- versus right-handed movements have shown, at most, only minor differences between the hands in reach-to-grasp actions (Begliomini, Nelini, Caria, Grodd, & Castiello, 2008; Flindall, 2012; Grosskopf & Kuhtz-Buschbeck, 2006; Tretriluxana, Gordon, & Winstein, 2008). For example, (Grosskopf & Kuhtz-Buschbeck, 2006) used a reach-to-grasp task in which a cylindrical object was grasped and placed into a target slot to compare kinematic data between the left and right hands of participants. Other than a minor difference in insertion time (in which the dominant hand was faster than the non-dominant hand), the researchers found no significant differences in movement kinematics between the hands. This is quite puzzling given that, if the right hand is used preferentially for the grasp-to-place action, and this preference is to be driven by a kinematic advantage, one would expect to find kinematic differences between the hands. The studies cited above, however, have used grasp-to-place tasks in their search for manual asymmetries. Where hand differences are absent in the grasp-to-place movement, perhaps they may be found in the grasp-to-eat movement. This speculation would be supported by research suggesting, first, that prehension originally evolved as a grasp-to-eat action (Goodale, 1990; Whishaw, 2003) and second, that the right hand preference for grasp-to-eat movements develops years earlier than does the preference for the grasp-to-manipulate (aka grasp-to-place) movement (Sacrey, Arnold, et al., 2012).

In the present study, we investigate if the grasp-to-eat action is different from the grasp-to-place action for both right- and left-handed movements. To this end, we measured reach and grasp kinematics of 13 participants who were instructed to reach-for and grasp food items of various sizes to either a) bring the food item to the mouth and eat it (grasp-to-eat), or b) place the food item in a bib located just beneath their chin (grasp-to-place). Both tasks used the same types of food items, required the same types of grasping movement, and differed only in the end-point goal of the movement.

Methods

Participants

Thirteen right-handed University students (11 female; average age 20.3 years) participated in the experiment and received course credit for their participation. Handedness was determined through a modified Edinburgh handedness questionnaire (Oldfield, 1971). All participants gave informed written consent prior to the onset of 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 #2011-022). Participants were able to withdraw from the study at any time without consequence.

Materials

Three infra-red 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 anatomical snuff box). Two Optotrak Certus camera bars [Northern Digital, Waterloo, ON, Canada] recorded IRED position during each trial at 200 Hz for 5 seconds. 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 Corporation, San Pedro, CA, USA] and NDI First Principles [Northern Digital, Waterloo, ON, Canada].

Participants were seated before a self-standing height-adjustable triangular pedestal (Fig. 1). The pedestal held individual cereal food items (presented one at a time) of 3 different sizes: SMALL (Cheerios®, mean diameter 11 mm), MEDIUM (Froot Loops®, mean diameter 15 mm), and LARGE (Oatmeal Squares®, mean length 21 mm). These targets were chosen based on their distinct sizes and familiarity. 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 (Whishaw et al., 2002).

Procedure

Participants sat behind the pedestal, with their hand placed comfortably on their lap (fingertips of thumb and index finger together) between trials. Targets were presented in a pseudo-random order, such that the participant was naïve to the size of the food item until the beginning of the trial, when the goggles transitioned to their transparent state. After 1000ms of transparency during which the participant had full view of their hand and target, an audible go-signal ('beep') was presented, informing the participant that they should begin the reach-to-grasp movement "at a comfortable pace." After grasping the target between the thumb and index finger in a precision grip, participants would either a) ingest the item completely (EAT condition), or b) place the item in a bib hanging below their chin (PLACE condition) (Fig. 1). Investigators replaced food items between trials, while the liquid crystal goggles were in a closed (opaque) state. EAT and PLACE task conditions were presented in blocks of 25 trials (8 SMALL, 8 MEDIUM, 9 LARGE, randomized), with start order counterbalanced between participants. Participants were informed of task requirements at the beginning of each block. After both blocks were completed, IREDs were transferred to the participant’s other hand, and the process was repeated. Hand start order was counterbalanced between participants.

Figure A1.1 – Experimental set-up. Left: Participant reaches-to-grasp presented target (item shown: Froot Loop®). Center: PLACE task requires participant to grasp the target and place it in the bib hung below their chin. Right: EAT task requires participant to eat the target after grasping. Note that participants wear the bib throughout all blocks, regardless of start order or current task, and that all grasps are completed using only the index finger and thumb. The subject of this figure has given written informed consent, as outlined in the PLoS consent form, to publication of these photographs.

Analyses

Kinematic comparisons were made between reach-to-grasp phases of each movement. Movement time (MT) was calculated as the difference between time of grasp contact[9] and 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 represents the span during which the participant reached outward toward the target. Peak velocity (PV) was defined as the maximum resultant velocity the participant achieved during their reach towards the target. Deceleration phase duration (DP) was calculated as the time during which the participant was decelerating while still reaching outwards toward the target (time of grasp contact minus time of PV); it is reported as a percentage of total movement time. Maximum grip aperture (MGA) was measured as the peak resultant distance achieved between the thumb and index finger prior to the time of grasp contact[10]. Variability of MGA (vMGA) is the standard deviation of the MGAs of each Hand/Task/Size grouping.

Data Processing

We determined kinematic parameters using finite differences in the two-step method[11]. Data were collected via NDI First Principles, all kinematic calculations were performed on unfiltered data using Microsoft Excel 2010, and statistical analyses were completed using PASW Statistics 18.0.0. Two participants were missing critical data on greater than 10% of trials due to camera line-of-sight failure, and as such were removed from analyses. The 11 remaining participants were missing critical data on an average of 2.9% (range: 2-7%) of trials. The offending trials were removed from further analysis. Trials were averaged by condition, with 3-way within-subject repeated measures analyses of variance [Hand (LEFT/RIGHT) x Task (EAT/PLACE) x Size (SMALL/MEDIUM/LARGE)] run on condition means. Alpha significance for initial ANOVA results was set at $p<.05$. Post-

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[9] The time of grasp contact was defined as the point at which: i) the subject's outward speed dropped below .02 m/s, and ii) their corrected grip aperture plateaued at the approximate diameter of the target.

[10] Between Hand comparisons required GA calculations to be corrected for IRED placement, as grip aperture calculations were based on distance between the IREDs, rather than actual distance between subject fingertips. We achieved this correction by averaging the resting grip apertures (after removing outliers) recorded per participant per hand, and subtracting that constant from all associated MGA values. This correction factor allows us to control for slight variations in IRED placement between the hands as well as variations in hand size within participants. In the interest of being complete, ANOVAs were also run on uncorrected data; the significant effects observed and reported below did not change.

[11] Using the two-step method, average speed at time *n* is calculated by determining displacement between times *n-1* and *n+1*, and dividing that displacement by the elapsed time between those two points. The method can be expressed by the formula $v_n = [P_{n+1} - P_{n-1}] / \Delta t$, where v is velocity, P is position, n is a single time point in the output data, and Δt is time elapsed between points *n-1* and *n+1*.

hoc comparisons were conducted via paired sample t-tests, with Bonferroni corrections applied where necessary. 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.

Table A1.1 – Means and standard errors of reach and grasp kinematics. Units are recorded in column headers.

			MT (ms)	PV (m/s)	DP (%MT)	MGA (mm)	vMGA (mm of SD)
Left	Place	Small	854 ± 29	.659 ± .040	67.4 ± 1.1	21.66 ± 1.34	2.95 ± .43
		Medium	839 ± 30	.656 ± .035	66.8 ± 0.9	24.79 ± 1.49	3.21 ± .31
		Large	827 ± 31	.679 ± .041	67.1 ± 1.1	30.71 ± 1.48	4.33 ± .57
	Eat	Small	858 ± 13	.681 ± .039	67.1 ± 1.2	21.07 ± 1.59	3.20 ± .38
		Medium	869 ± 20	.665 ± .039	68.1 ± 0.9	24.10 ± 1.60	3.63 ± .23
		Large	838 ± 16	.681 ± .038	66.6 ± 1.0	29.51 ± 1.47	3.94 ± .46
Right	Place	Small	865 ± 38	.678 ± .026	69.0 ± 0.8	19.40 ± 1.18	2.98 ± .33
		Medium	850 ± 38	.661 ± .025	68.0 ± 0.8	23.02 ± 1.38	3.50 ± .33
		Large	870 ± 51	.673 ± .028	67.6 ± 1.0	28.86 ± 2.03	3.38 ± .43
	Eat	Small	876 ± 31	.681 ± .029	68.8 ± 0.5	16.48 ± 1.08	2.64 ± .35
		Medium	852 ± 38	.674 ± .030	67.4 ± 1.0	19.57 ± 1.19	2.74 ± .36
		Large	827 ± 32	.680 ± .029	67.1 ± 0.6	25.71 ± 1.62	3.18 ± .37

Hand

A main effect of hand was observed for MGA [F (1, 10)=7.902, p=.018, η2=.441], with the RIGHT hand producing significantly smaller MGAs (22.17 ± 1.29 mm) than the LEFT hand (25.31 ± 1.38 mm). No other variables displayed a significant main effect of hand.

Task

A main effect of task was observed for MGA [F (1, 10)=19.317, p=.001, η2=.659], with smaller MGAs associated with the EAT task (22.74 ± 1.25 mm) than the PLACE task (24.74 ± 1.21 mm). No other variables displayed a significant main effect of task.

Size

Main effects of size were observed for MT [F (2, 20)=7.004, p=.005, η2=.412], PV [F (2, 20)=6.713, p=.006, η2=.402], DP [F (2, 20)=6.082, p=.009, η2=.378], MGA [F (2, 20)=71.485, p<.001, η2=.877], and vMGA [F (2, 20)=6.042, p=.009, η2=.377]. Larger targets were associated with shorter movement times (with shorter associated deceleration phases), and larger, more variable maximum grip apertures. Grasps directed towards the MEDIUM target achieved significantly higher peak velocities than did those compared to the LARGE target but not the SMALL target. The results of post-hoc analyses are reported in Table 2.

Table A1.2 – Means and standard errors of reach and grasp kinematics, collapsed across hand and task. Main effects of size were discovered for all variables; final column reports significant paired t-test results for comparisons between SMALL, MEDIUM, and LARGE food items. Significant alphas have been Bonferroni-adjusted for 3 tests. Bars join pairs which are significantly different (*p*<.0167).

	MT (ms)	PV (m/s)	DP (%MT)	MGA (mm)	vMGA (mm of SD)
SMALL	863 ± 23	.675 ± .032	68.1 ± 0.8	19.65 ± 1.17	2.94 ± .19
MEDIUM	852 ± 27	.664 ± .031	67.5 ± 0.8	22.87 ± 1.22	3.27 ± .17
LARGE	840 ± 27	.678 ± .032	67.1 ± 0.8	28.70 ± 1.46	3.71 ± .19

Hand X Task

A significant Hand X Task interaction was observed on MGA, F (1, 10)=6.887, p=.025, η2=.408 (Fig. 2). Follow-up paired-samples t-tests revealed that right-handed MGAs in the EAT condition (20.59 ± 1.18) were significantly smaller than those in the PLACE condition (23.76 ± 1.45), t (10)=5.134, p<.001. Left-handed EAT (24.89 ± 1.48) and PLACE (25.72 ± 1.34) conditions were not significantly different from each other, t (10)=1.272, p=.232. In fact, MGAs of the right hand for the PLACE condition did not differ from MGAs of the left hand in either condition (p>.15). That is, only right hand MGA for the EAT condition was significantly different from all other conditions (p≤.001). Post-hoc paired-sample t-tests showed that this effect was consistent across all size conditions (Fig. 3). No other Hand X Task interactions were observed.

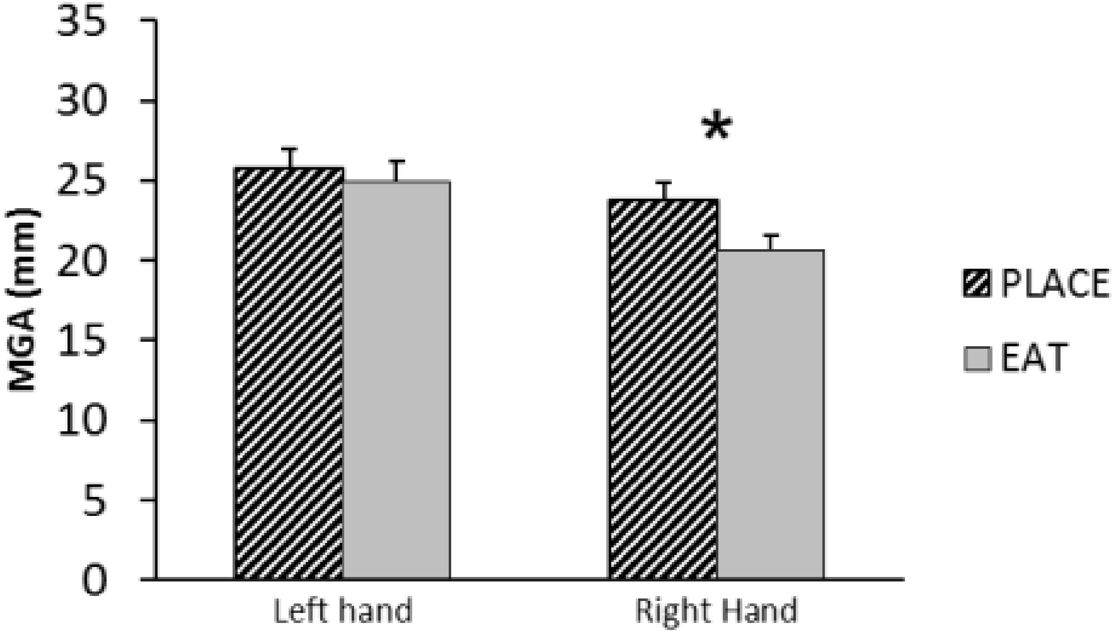

Figure A1.2 – Hand x Task interaction on MGA. Values shown are means + standard errors. PLACE and EAT conditions were significantly different from each other in right-handed movements only; left-handed movements were not significantly affected by task.

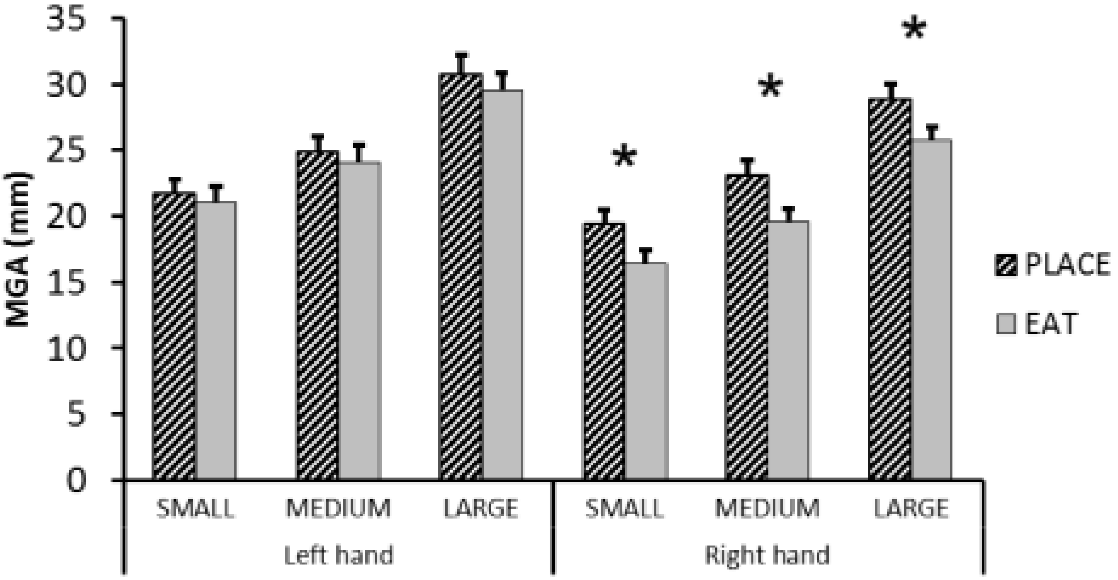

Figure A1.3 – MGA displayed by Hand X Task X Size. The observed Hand X Task interaction (Fig. 2) is consistent across all size conditions. Significance shown (*) has been Bonferroni-adjusted for 6 tests (*p*<.00833).

Hand X Task X Size

No significant Hand X Task X Size interactions were observed.

MGA Scaling Analysis

To further investigate the MGA results reported above, we analyzed the sensitivity of the MGA to changes in target size by plotting each subject's MGA versus average target size in each hand and task condition (Fig. 4) (R. L. Whitwell, C. L. Striemer, D. A. Nicolle, & M. A. Goodale, 2011b) . To test for differences in scaling, we subjected the regression slopes to a 2 (Hand) x 2 (Task) ANOVA (Borchers & Himmelbach, 2012; R. L. Whitwell, C. L. Striemer, D. A. Nicolle, & M. A. Goodale, 2011). The results of our ANOVA indicate that the slopes were not significantly different between hands (F (1, 10)=0.307, p=.592, η2=.03) or tasks (F (1, 10)=0.777, p=.399, η2=.072), nor was there a significant interaction (F (1, 10)=0.15, p=.707, η2=.015). This finding suggests that the Hand x Task interaction effect observed is not a result of a difference in scaling ability; rather, right hand pre-shaping is simply less wide when the end-goal of the movement is to eat.

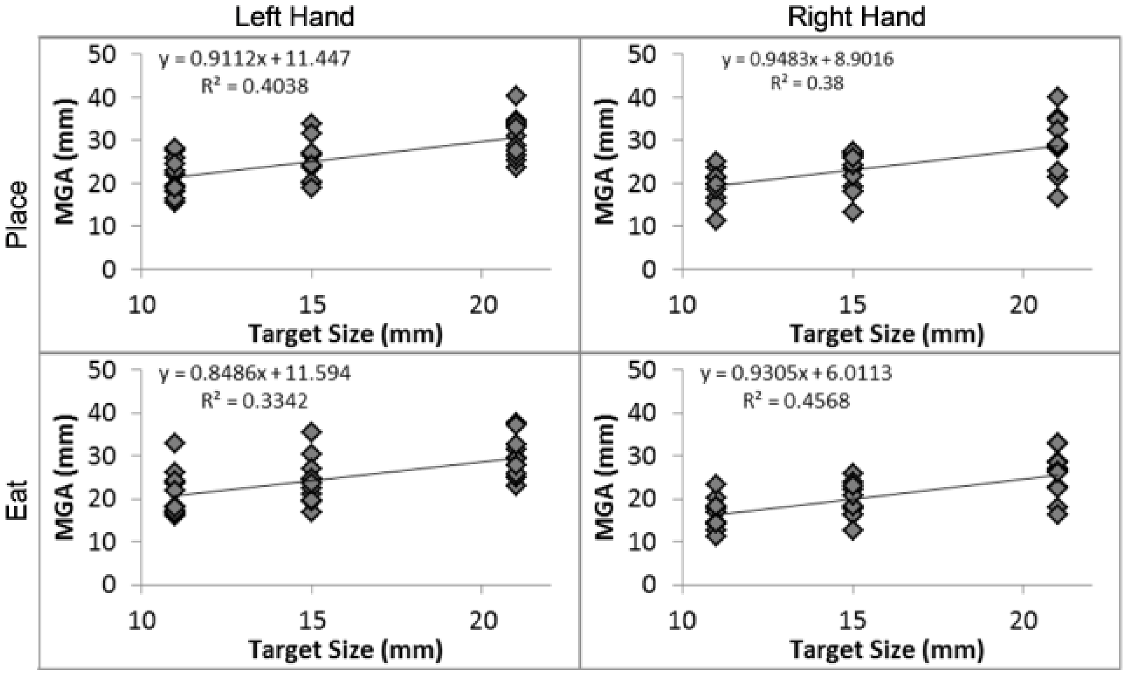

Figure A1.4 – MGA and slope for all Hand x Task conditions. Slopes between conditions were not significantly different.

Discussion

While many studies have documented the kinematics of reach-to-grasp actions, few have compared these between hands, and (to the best of our knowledge) none of these have used a grasp-to-eat task. In the current study, participants reached-to-grasp food items in order to either a) eat the item (grasp-to-eat) or b) place the item in a bib located just beneath their chin (grasp-to-place). The bib was chosen for the grasp-to-place task in order to maintain movement trajectory in both the initial approach and the majority of the post-grasp transport phase. Participants completed these tasks with both their left and right hands. Our main finding was that participants prepared a smaller maximum grip aperture when grasping with intent to eat, but only in right-handed movements. This effect was consistent across all three sizes of food items, and present in all participants. We offer three possible, non-competing interpretations of this finding. First, our results provide behavioural support for the evidence in humans and non-human primates that prehensile movements can differ in their neural correlates based on action intent. Specifically, we differentiate between grasp-to-eat and grasp-to-place actions. Second, the results may be interpreted as evidence that visually-guided grasping can be influenced by experience. And finally, because the grasp-to-eat movement almost certainly predates other types of manipulative actions, we speculate that the current findings may provide evidence for an evolutionary scenario in which handedness stems, at least in part, from a right hand advantage in the grasp-to-eat movement.

The results from the present study differentiated between grasp-to-eat and grasp-to-place actions at the kinematic level. Previous studies have shown that affordances and intentions have significant effects on the kinematics of a movement. Such studies have reported differences in the reach-to-grasp kinematics of throwing and placing actions (Marteniuk et al., 1987), grasp-to-lift and grasp-to-show actions (Ferri, Campione, Dalla Volta, Gianelli, & Gentilucci, 2011), and grasp-to-feed and grasp-to-manipulate actions (Ferri et al., 2010). In one previous study participants were asked to bring a cube of sugar to the mouth or to a mouth-like aperture (Ferri et al., 2010). Consistent with that study, we found an effect of task on grasp kinematics wherein MGAs were smaller when the object was to be placed in the mouth, rather than simply in a location near the mouth. Unlike Ferri et al., who reported differences in movement time and deceleration time duration, however, we did not observe an effect of task in any other measures. This suggests that the smaller MGA for the grasp-to-eat movement in the current study is not due to differences in other kinematic parameters. Although numerous studies have explored the effects of intentions on movement kinematics, few have yet investigated whether these effects are conserved in left-handed movements (cf. Armbruster & Spijkers, 2006). Ours is the first study to demonstrate that action intent affects grasping movements differently according to the hand used. Specifically, we show that the right-handed grasp-to-eat movement is more accurate (i.e., produces a smaller margin of error within hand pre-shaping) than both the right-handed grasp-to-place movement, and indeed left-handed movements of both types. It should be noted that this advantage was not due to more precise scaling of right-handed grasping (MGA slopes between the EAT and PLACE conditions revealed similar grip aperture scaling for both hands), but rather the right-hand grasps were produced with a smaller margin of error when the target was to be eaten. This could be considered as an advantage for two reasons. First, numerous reach-to-grasp studies have shown that MGA is remarkably sensitive to target uncertainty such that increases in uncertainty are linked with larger MGAs. For example, if vision of the target or reaching limb is removed at the beginning of a grasp (introducing target and movement uncertainty), MGA is larger than in movements directed to the same target with full visual feedback (Berthier, Clifton, Gullapalli, McCall, & Robin, 1996; Flindall, 2012; Gentilucci, Toni, Chieffi, & Pavesi, 1994; Harvey et al., 2001; Jakobson & Goodale, 1991; Schettino, Adamovich, & Poizner, 2003; Wing, Turton, & Fraser, 1986). This increase in MGA is even larger when a brief delay is introduced between vision restriction and movement onset such that the grasp is initiated and completed entirely from memory (Flindall, 2012; Hu, Eagleson, & Goodale, 1999; Hu & Goodale, 2000). Thus, target uncertainty can result in the production of larger MGAs, presumably as a means of compensation via wider margins of error (Jakobson & Goodale, 1991). Second, smaller MGAs could be considered more efficient because peak grip-closing velocity, grip-closing time and metabolic energy requirements are reduced when the MGA more closely approximates the absolute size of the target (Bootsma, Marteniuk, MacKenzie, & Zaal, 1994).

Kinematic differences between grasp-to-eat and grasp-to-place actions may stem from differences in their neural correlates. Electrophysiological studies on non-human primates have shown that different cortical regions are responsible for grasp-to-eat versus grasp-to-manipulate actions. In an influential account of motor cortex organization and function, Graziano (2006) described several experiments which demonstrate a motor cortex organized not around specific control of muscles, but rather around producing complex coordinated behaviours. When a macaque’s motor cortex was directly stimulated using long electrical pulses of 500-1000ms (the approximate duration of a typical prehensile movement), the macaque produced behaviourally-relevant actions. Long-train stimulation yielded reaching movements (Graziano, Aflalo, & Cooke, 2005), grasp-to-manipulate movements (Graziano, Cooke, Taylor, & Moore, 2004), and hand-to-mouth grasping movements (Graziano et al., 2005). These movements were context-relevant and goal-oriented. Notably, the grasp-to-manipulate movement and the hand-to-mouth grasping movement were produced by stimulating two distinct anatomical locations (Graziano, 2006). Single-neuron recording studies performed by Fogassi et al. (2005) and Bonini et al. (Bonini et al., 2010; Bonini et al., 2012) have identified task-specific neurons in both the inferior parietal area PFG and ventral premotor area F5 in macaques. The researchers have shown that individual neurons respond differentially to the purpose of the grasp (place vs. eat) rather than to the object being grasped (Fogassi et al., 2005), the pre- or post-contact kinematics of the action (Bonini et al., 2010; Fogassi et al., 2005), or the hand shape required for successful prehension (Bonini et al., 2012). These results, along with those of others (Kaas, Gharbawie, & Stepniewska, 2011; Kaas, Stepniewska, & Gharbawie, 2012), suggest that the grasp-to-manipulate and grasp-to-eat actions are supported by neural networks with discrete origins. Although unknown, it is probable that similar distinctions exist in the human brain. While the invasiveness of these studies make them infeasible to perform with human participants, and the limitations of fMRI make reach-to-eat tasks difficult, researchers have nevertheless been able to highlight circuits in the human parietal cortex that respond selectively based on action intent (Culham, Cavina-Pratesi, & Singhal, 2006; Grefkes & Fink, 2005; Olivier, Davare, Andres, & Fadiga, 2007). For example, using fMRI, researchers have identified discrete regions activated by movements that share similar kinematics but differ in their purpose. Selective activation of the superior parieto-occipital cortex (SPOC) during planning and execution of aiming movements (Gallivan, Cavina-Pratesi, & Culham, 2009), and anterior intraparietal sulcus (aIPS) activation during grasping (Binkofski et al., 1998; Frey, Vinton, Norlund, & Grafton, 2005; Gallivan, McLean, Valyear, Pettypiece, & Culham, 2011) have been shown. Most recently, Gallivan et al. (2011) found that when participants were given a choice to either grasp or touch one of several target cubes, both the chosen target and movement intention could be accurately predicted from activation of specific locations within the aIPS. These studies show that although movements may share similar kinematics, it is the actor’s intent that will determine the neural origin of the movement.

In terms of experience, it is possible that the right-hand advantage found in this study relates to the increased amount of practice executing the grasp-to-eat movement with this hand. As mentioned in the introduction, the right-hand preference for grasp-to-eat movements develops several years earlier than does the preference for grasp-to-place movements. In fact, the hand-to-mouth/ grasp-to-eat movement is one of the first movements to arise in human infants (Piaget & Cook, 1953). Fetuses have been observed to make this movement in the womb for the purpose of thumb-sucking and furthermore have demonstrated a right-hand preference for this and other hand-to-face movements (Hepper, Mccartney, & Shannon, 1998). Behaviourally, a right-hand preference for the grasp-to-eat movement has been demonstrated in young infants (Sacrey, Karl, & Whishaw, 2012) and has been contrasted with the grasp-to-place movement (Sacrey, Arnold, et al., 2012). These studies have shown that children as young as one year of age prefer to use their right hands for grasping, but only when performing the grasp-to-eat movement. When children are required to grasp other, non-edible objects (e.g. toys or blocks), a right hand preference is not visible until children reach 4 years of age (Cox & Smitsman, 2006; Leconte & Fagard, 2006; Sacrey, Arnold, et al., 2012). These findings demonstrate that right hand preference for the grasp-to-eat action develops considerably earlier than the right hand preference for other manipulative movements. These additional years of experience, which coincide with a critical period in the development of coordination and consistency in the reach-to-grasp movement (Forssberg, Eliasson, Kinoshita, Johansson, & Westling, 1991; Forssberg et al., 1992; Schneiberg, Sveistrup, McFadyen, McKinley, & Levin, 2002), might be responsible for the right hand kinematic advantage in the grasp-to-eat action. Furthermore, practice has also been shown to alter the kinematics of both reach (Wong, Kistemaker, Chin, & Gribble, 2012) and reach-to-grasp movements (Gonzalez, Ganel, Whitwell, Morrissey, & Goodale, 2008) in adulthood. For example, one study demonstrated that awkward grasps (grasps made using the thumb and ring finger) are initially sensitive to a visual illusion. However after one hour of practice with the awkward grasp for three consecutive days, the effect of the illusion on the awkward grasp was reduced to an extent where the awkward grasp pre-shaping resembled that of the more common pincer grasp (Gonzalez et al., 2008). Importantly, this reduction was only observed for right-handed movements; left-handed grasp scaling remained susceptible to the effects of the illusion regardless of practice. The authors speculated that the right hand control system is able to incorporate previous experience into hand pre-shaping for grasping purposes. This ability may be the source of smaller right-hand MGAs observed in the current study. In sum, if we have more experience with our right-hand for the grasp-to-eat movement during development, and this practice results in both increased coordination and increased target certainty, then it is reasonable to speculate that we would produce grip apertures with smaller margins of error in the grasp-to-eat movement.

While the current study investigated this effect exclusively in right-handed participants, we predict that left-handed individuals would also demonstrate smaller MGAs in the grasp-to-eat movement. However, as left-handers represent a more heterogeneous group with respect to hemispheric lateralization (Hecaen & Sauguet, 1971; Szaflarski et al., 2002), we would expect that the MGA effect described here would not be consistently confined to the dominant hand between participants. As has been demonstrated before, while some left-handers prefer the use of their dominant left hands for grasping, a subset of left-handers exhibit a preference for their non-dominant right hands for grasping (Begliomini et al., 2008; Gonzalez, Ganel, & Goodale, 2006;

Gonzalez & Goodale, 2009; Stone, Bryant, & Gonzalez, 2012). It is tempting to speculate that this subset would resemble right-handers in their grasp-to-eat behaviour, producing smaller MGAs when using their right hands for this task. Meanwhile, left-handers who prefer to grasp with their dominant hands would express the reverse behaviour; that is, they would produce smaller grasp-to-eat MGAs when using their left-hands. Future studies will investigate this possibility.

Finally, when considered from an evolutionary perspective, the results of this study may provide insight into why 90% of the global population is right-handed. It has long been speculated that animal prehension evolved from grasp-to-eat actions (Goodale, 1990; MacNeilage, Studdert-Kennedy, & Lindblom, 1987; Rogers, 2002; Whishaw, 2003). While handedness in humans is often measured by our lateralization of tool-use, some researchers argue that the development of skilled praxis in primates stems from early behaviour in food preparation or capture (Whishaw, 2003). One theory, known as the postural origins theory (MacNeilage, 2007; MacNeilage et al., 1987), posits that the evolution of right-handedness in humans and other great apes began from a right-hand specialization for postural maintenance, co-opted for foraging when prosimians evolved to utilize a more upright stance. The right-hand/left-hemisphere system, then specialized for the production of the precise grip-forces necessary to maintain arboreal positions, was perfectly suited for the fine manipulations necessary to husk nuts, peel fruit, and grasp other fragile food when bimanual foraging became possible (MacNeilage et al., 1987). This theory is consistent with observations of population level right-hand preference for grasp-to-eat actions in several species, including chimpanzees (Pan troglodytes) (W. D. Hopkins, Cantalupo, Wesley, Hostetter, & Pilcher, 2002; W. D. Hopkins, Russell, Hook, Braccini, & Schapiro, 2005; Pouydebat, Reghem, Borel, & Gorce, 2011), gorillas (Gorilla gorilla) (W. D. Hopkins et al., 2011), bonobos (*Pan paniscus*) (W. D. Hopkins et al., 2011), and humans (Homo sapiens) (Pouydebat et al., 2011; Sacrey, Arnold, et al., 2012). Additional support for this theory comes from the similarities between human and chimpanzee grasping behaviour. In humans, lateralization of prehension is predominantly rightward-biased, especially for precision grips (Gonzalez et al., 2006; Gonzalez & Goodale, 2009; Pouydebat et al., 2011) and grasp-to-eat actions (Pouydebat et al., 2011; Sacrey, Arnold, et al., 2012); chimpanzees show a similar pattern of right-hand preference for grasp-to-eat actions, with right-hand use increasing with the precision requirements of the grasp (Pouydebat et al., 2011). Furthermore, the development of the precision grip from juvenile to adulthood follows a similar trajectory in both humans and chimpanzees. When grasping small objects, members of both species tend to use the less precise whole-hand or power-grips as juveniles, gradually shifting to more controlled precision grips as adults (Pouydebat et al., 2011). This observation further strengthens the position that handedness is driven by the right hand's ability for precision grasping. All told, these studies suggest that left-hemisphere specialisation for precise visually-guided movements in humans has shared origins with the right hand preference for grasp-to-eat movements observed in chimpanzees and other great apes.

As numerous studies have explored the possible link between the lateralization of praxis and language (Corballis, 2003; Stout & Chaminade, 2009) (namely, that the left-hemisphere lateralization of gesture developed as a predecessor to language in Homo sapiens), it is tempting to speculate that the hand preference for the grasp-to-eat action is a good candidate for the neural basis upon which hand preference for praxis (i.e. tool use and gesturing) and eventually language evolved (for review, see Corballis (2003)). Recent work by Pulvermüller and colleagues (Boulenger, Hauk, & Pulvermüller, 2009; Pulvermüller, 2005) has demonstrated that language and motor regions are cortico-cortically linked; hearing or reading words coupled with specific body parts ("kick" and "lick," for example) differentially activates the motor cortex areas associated with those parts of the body (Pulvermüller, 2005), and that this 'semantic somatotopy' is critically related to higher level language comprehension (Boulenger et al., 2009). Regarding asymmetries, other investigations have shown that the degree of left-hemisphere lateralization for language is linearly related to the degree of right-hand preference for everyday activities (Knecht et al., 2000), particularly that for precision grasping (Gonzalez & Goodale, 2009). As has been argued before (Gonzalez et al., 2008; Gonzalez & Goodale, 2009), the lateralization of precision grasping may in fact predate the development of specific circuits for praxis and language, evidenced by the aforementioned left-hemisphere specialization for precision grip observed in chimpanzees (W. D. Hopkins et al., 2002; W. D. Hopkins et al., 2005).

Conclusion

In conclusion, the results of the current investigation show a kinematic dissociation between the grasp-to-eat and grasp-to-place actions. This dissociation, however, was only present within right-handed movements. More importantly, the results demonstrate a right-hand advantage for the grasp-to-eat action. We speculate that this advantage could have served as the basis for the well-known right hand dominance for manual functions. An examination of the neuroanatomical and neurophysiological correlates of this finding may provide fresh insight into the evolutionary origins of handedness in humans.

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Appendix 2: Eating Interrupted: The effect of intent on hand-to-mouth actions

Title: On the Evolution of Handedness: Evidence for feeding biases

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Abstract

Evidence from recent neurophysiological studies on non-human primates as well as from human behavioural studies suggest 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 behavioural evidence suggests certain networks are lateralized to the left hemisphere. Specifically, when participants used their right hands 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 either a) eat them, b) place them in a bib, or c) place them between their lips, then toss them into a nearby receptacle. Participants performed each task with large and small food items, using both their dominant and non-dominant 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.

Keywords:

kinematics, asymmetries, right hand, grasping, left hemisphere

Introduction

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 show few, if any, asymmetries between the hands (e.g., Grosskopf and Kuhtz-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 & Gonzalez, 2013). Smaller grip apertures may be considered advantageous as peak-grip closing velocity, grip closing time, and metabolic energy requirements are reduced when MGA more closely matches absolute target size (Bootsma et al., 1994). As 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 behavioural reports, is also supported by electrophysiological data. Studies on non-human 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 behaviourally-relevant movements, including reach-to-grasp, grasp-to-inspect, and hand-to-mouth actions (Graziano, 2006; Graziano et al., 2005; Graziano, Cooke, Taylor, & Moore, 2004; Graziano et al., 2002). 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., 2012; Bonini et al., 2011; 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 mouths, as well as to grasp non-food 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, as these regions have been implicated in the organization of goal-directed reach-to-grasp actions (Bonini et al., 2010; Bonini et al., 2011; Fogassi et al., 2005). They 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 behavioural studies. Specifically, it has been demonstrated that kinematics of reach and grasp actions vary not only between grasp-to-eat and grasp-to-place movements (F. Ferri, Campione, Dalla Volta, Gianelli, & Gentilucci, 2010; Naish et al., 2013), but also between grasp-to-lift, grasp-to-place, and grasp-to-throw actions (Ansuini et al., 2008; Armbrüster & 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 & Gonzalez, 2013). In that study, Flindall and Gonzalez argued that smaller peak grip apertures when 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 hands, 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 in Flindall and Gonzalez (2013), where each participant was asked to reach-to-grasp small food items to either a) eat them, or b) place them in a bib hanging below his/her chin. The 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 counter-balanced blocks with both the dominant (right) and non-dominant (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 behaviour 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 (seven right-handed females, average age 20.4 years; four right-handed males, average age 21.8 years; one left-handed male, age 19) 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, mechanical injury, or received specific training encouraging non-dominant hand use for 1 month or more. Participants were not excluded based on reported hand preference, as many previous investigations on grasping and prehension have shown comparable results between left- and right-handers (Boulinguez et al. 2001b; Flindall et al. 2014b; 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 #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 infra-red 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 anatomical snuff box). An Optotrak Certus camera bar [Northern Digital, Waterloo, ON, Canada] recorded IRED position during each trial at 200 Hz for 5 seconds. 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 Corporation, San Pedro, CA, USA] and NDI First Principles [Northern Digital, Waterloo, ON, Canada].

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 based on 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 pseudo-random order such that participants were naive to the target item's size prior to the beginning of each trial. Trials began with the Plato goggles transitioning to a transparent state ("opening"), at which point the participant became aware of the size of the target food item. An auditory tone ("beep") sounded 1000 ms following the opening of the goggles, indicating to the participant that he/she should begin the reach-to-grasp movement, and subsequently either *eat* the target (Fig. 1B), *place* the target in a bib hung snugly under his/her chin (Fig. 1C), or place the item between their lips, return their reaching hand to the start position, 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, pseudo-randomized 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.

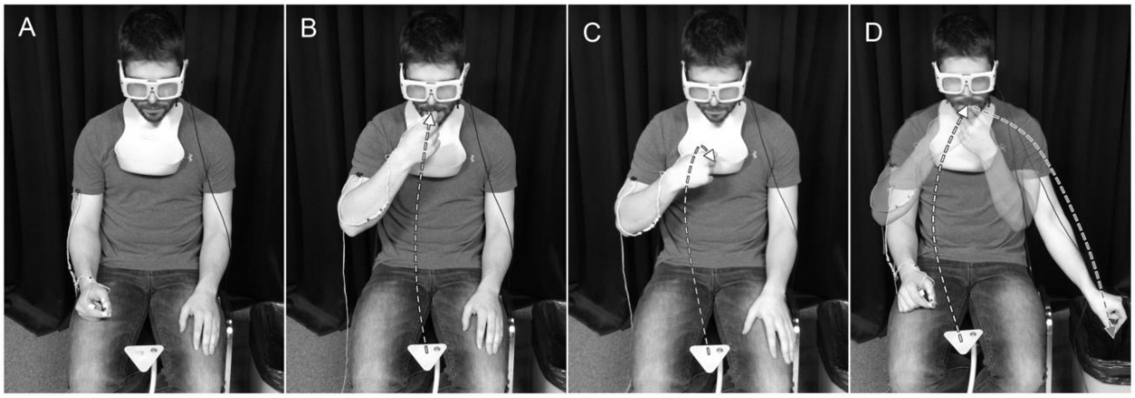

Figure A2.1 – Experimental procedure. (A) Participants began each trial in a rest position with their thumb and forefinger together. Subsequent actions varied by condition. (B) EAT condition required participants to pick up the target and eat it. (C) PLACE condition required participants to pick up the target and place it in a bib hanging below their chin. (D) SPIT condition required participants to pick up the food item, place it between their lips, remove it from their mouths 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.

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 i) the subject's outward speed dropped below .02 m/s, and ii) their 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 their outward movement towards 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 outwards toward the target (time of grasp contact minus time of PV); it is reported as a percentage of total movement time. Because it is reported as a percentage of total movement time, time of peak velocity and acceleration phase durations can be calculated by 1 – DP. As statistical analyses on these three variables (acceleration phase duration, time of PV, and deceleration phase duration) would return identical results, only DP means and analyses are reported here. Maximum grip aperture (MGA) was measured as the peak resultant distance between the thumb and index finger prior to the time of grasp contact. As 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 maximum grip aperture (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 with Microsoft Excel 2010. Statistical analyses were completed using PASW Statistics 18.0.0. If a participant moved to grasp the target prior to 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 3-way within-subject repeated measures analyses of variance [Hand (left/right) x Task (eat/place/spit) x Size (small/large)] run on condition means. Alpha significance for initial ANOVA results was set at p<.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.

Table A2.1 – Means and standard errors of reach and grasp kinematics. Units are recorded in column headers.

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

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*=.017, η^2=.420], DP [F (1, 11)=6.023, *p*=.032, η^2=.354], and MGA [F (1, 1)=85.393, *p*<.001, η^2=.886]. Movement times toward large food items (M=761 ms, SD=173 ms) were shorter than those toward small food items (M=786 ms, SD=168 ms), as participants spent a larger portion of the movement decelerating toward small food items (M=67.4%, SD=3.0%) than they did toward large food items (M=66.5%, SD=3.4%). As expected, participants also opened their hands wider when grasping large food items (M=29.8mm, SD=5.7mm) than they did when grasping small food items (M=25.3mm, SD=6.2mm).

Task

A main effect of task was observed for PV [F (2, 22)=7.202, *p*=.004, η^2=.396]. Follow-up t-tests revealed that participants achieved higher peak velocities when grasping to spit (M=1.56m/s, SD=.31m/s) than when grasping to place (M=1.44m/s, SD= 0.31m/s) [t (11)=-3.14, *p*=.009]. T-tests revealed that grasp-to-spit PVs were also higher than grasp-to-eat PVs (M=1.48m/s, SD=0.31m/s), however this effect was not significant following Bonferroni correction [t (11)=-2.75, *p*=.019]. The difference between eat and place PVs was not significant (*p* > .05).

Hand x Size

An interaction between Hand and Size was observed for PV [F (1, 11)=5.749, *p*=.035, η^2=.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*=.005]. Specifically, participants reached higher PVs with their left hands (M=1.50m/s, SD=0.33m/s) than they did with their right hands (M=1.47m/s, SD=0.30m/s). No other significant Hand x Size interactions were observed.

Size x Task

No interactions between Size and Task were observed for any variable.

Hand x Task

An interaction between Hand and Task was observed for MGA [F (2, 22)=6.236, *p*=.007, η^2=.362]. Follow-up t-tests revealed that this interaction was due to significantly larger MGAs [t (11)≥2.82, *p*≤.016] when grasping to place (M=28.12mm, SD=6.33mm) than when grasping to eat (M=25.75mm, SD=5.76mm) or spit (M=25.71, SD=5.06mm), but only during right-handed grasps. Right-handed Eat and Spit grasps were not significantly different from each other [t (11)=0.09, *p*=.929]. No significant differences were observed between tasks [t (11)≤1.01, *p*≥.203] during left-handed movements (Fig. 2). No significant Hand x Task interactions were observed for any other variable.

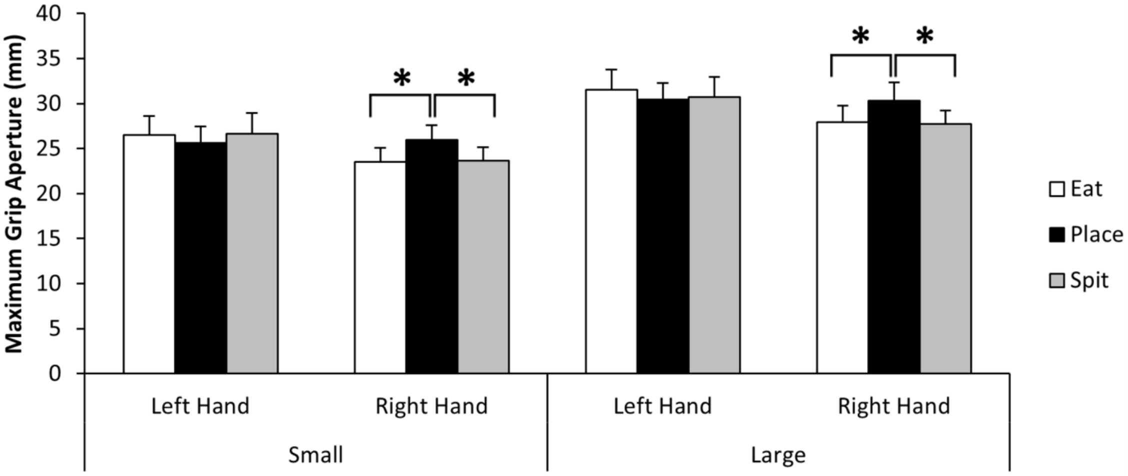

Figure A2.2 – Hand x Task interaction for MGA. MGAs produced in both the eat and spit tasks are significantly smaller than those produced in the place task (p ≤ .03) when using the right hand, for both small and large food sizes. No effect of task was observed during left-handed movements (p ≥ .203).

Hand x Size x Task

A significant Hand x Size x Task interaction was observed for DP [F (2, 22)=4.261, *p*=.027, η^2=.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*=.004]. Participants spent relatively more of the movement decelerating during left-handed actions (M=67.3%, SD=3.86%) than they did during right-handed actions (M=65.9%, SD=4.46%). No other comparisons were significant following Bonferroni correction [t (22)≤2.57, *p*≥.03].

Discussion

Previous research has shown 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 maximum grip apertures (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 two-fold: 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 a) eat them, b) place them in a bib located just beneath their chins, or c) place them briefly in their mouths 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 movement time (MT), deceleration phase duration (DP), peak velocity (PV), maximum grip aperture (MGA), and variability of maximum grip aperture (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 maximum grip apertures and longer movement times with longer relative deceleration phases. 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 x Task interaction observed on maximum grip aperture.

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 hands 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 not only share 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. As the grasping limb is no longer involved in the acts which 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 of 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 labelled the hand-to-mouth movement does not depreciate the evolutionary significance of their findings, as the primary purpose (that is to say, original, or even primal purpose) of the hand-to-mouth movement was almost certainly to facilitate consumption. While 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. As 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; b; Graziano et al. 2002). While 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 2000; 1997; Culham and Kanwisher 2001; Johnson-Frey et al. 2003), researchers have suggested that the human homologue of this region lies within the primary motor cortex, in BA 4 (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 which 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; Desmurget et al. 2014; Desmurget et al. 2013). 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), BA 4 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). As 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 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 favouring the dominant hand in reach-to-point actions are well documented (Boulinguez et al. 2001a; Carson et al. 1990; Carson et al. 1993; Elliott and Chua 1996; Elliott et al. 1993; Fisk and Goodale 1985; Roy and Elliott 1989; 1986; Velay et al. 2001), while 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. 2014a; 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, as participants produced smaller MGAs to eat while using their right hands 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-labelled 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, as participants were asked to grasp food items for all three tasks. Future studies will address these possibilities by including non-food 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, as 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.

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Appendix 3: Evidence for Right-hand Feeding Biases in a Left-handed Population

Title: Evidence for right-hand feeding biases in a left-handed population

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Abstract

We have recently shown that actions with similar kinematic requirements but different end-state goals may be supported by distinct neural networks. Specifically, we demonstrated that when right-handed individuals reach-to-grasp food items with intent to eat, they produce smaller maximum grip apertures (MGAs) than when they grasp the same item with intent to place it in a location near the mouth. This effect was restricted to right-handed movements; left-handed movements showed no difference between tasks. The current study investigates whether (and to which side) the effect may be lateralized in left-handed individuals. Twenty-one self-identified left-handed participants grasped food items of three different sizes while grasp kinematics were captured via an Optotrak Certus motion capture array. A main effect of task was identified wherein the grasp-to-eat action generated significantly smaller MGAs than did the grasp-to-place action. Further analysis revealed that similar to the findings in right-handed individuals, this effect was significant only during right-handed movements. Upon further inspection however, we found individual differences in the magnitude and direction of the observed lateralization. These results underscore the evolutionary significance of the grasp-to-eat movement in producing population-level right-handedness in humans as well as highlighting the heterogeneity of the left-handed population.

Keywords

grasp, left-hand, kinematics, prehension, asymmetries

Introduction

Many studies investigating kinematics of grasp-to-place or grasp-to-manipulate tasks have shown only minor differences between left and right-handed movements. That is, despite a marked preference to use the right hand for grasping (Gonzalez, Ganel, & Goodale, 2006; Gonzalez & Goodale, 2009; Stone & Gonzalez, 2013), participants perform right- and left-handed movements with near identical kinematics (Flindall, Doan, & Gonzalez, 2014; Grosskopf & Kuhtz-Buschbeck, 2006; Tretriluxana, Gordon, & Winstein, 2008). Recent research from our lab has shown that kinematic differences between left- and right-handed reach-to-grasp actions are not only identifiable, but are robust and ubiquitous among right-handed individuals (Flindall & Gonzalez, 2013). These differences are intrinsically linked with task, however, which may explain why it has proven difficult to isolate them in previous kinematic analyses. Specifically, we established that when right handed participants used their right (dominant) hands to grasp a small food item with the intention to eat it, they produced smaller maximum grip apertures during the pre-contact phase of the movement than if they used their non-dominant left hands. If participants grasped the same food items to instead place them into a receptacle near the mouth, then left- and right-handed movements shared similar kinematics. In other words, left-handed movements showed no differences between grasp-to-place or grasp-to-eat kinematics, and the kinematics of these tasks were identical to those seen in right-handed grasp-to-place actions. Right-handed grasp-to-eat actions, in contrast, displayed significantly smaller maximum grip apertures than grasps made in all other hand/task conditions.

The discovery of these task-dependent asymmetries favouring the right hand is supported by other studies highlighting differences in the grasp-to-place and grasp-to-eat movements, be they kinematic (Ferri, Campione, Dalla Volta, Gianelli, & Gentilucci, 2010, 2011), developmental (Sacrey, 2012; Sacrey, Arnold, Whishaw, & Gonzalez, 2012), or neural (Graziano, Aflalo, & Cooke, 2005; Graziano, Cooke, Taylor, & Moore, 2004). In terms of kinematics, Ferri et al. (2010) demonstrated that grasp-to-eat movements show greater automaticity than do grasp-to-place or grasp-to-feed movements. Regarding development, Sacrey et al. (2012) showed that a right-hand preference for grasp-to-eat movements develops in infants and toddlers several years earlier than the hand preference for grasp-to-place or grasp-to-manipulate movements. In electrophysiological studies involving macaques, Graziano and colleagues have shown that long-train stimulation of the primary motor cortex produced functional, multi-joint movements, including grasp-to-inspect and hand-to-mouth movements (Graziano et al., 2005; Graziano et al., 2004). Taken together, these studies support a theory of primate motor cortex organized not around control of individual muscles, but rather around the production of goal-oriented actions.

Because the asymmetries in the grasp-to-eat movement we previously identified favoured the right hand, we postulated that this advantage may have strongly influenced the development of the right-handedness found at the population level in humans. However, that study did not address the behavior of left-handed participants. Despite the fact that left-handers account for nearly 10% of the population (Annett, 1970; Briggs & Nebes, 1975), kinematic studies including left-handed participants are scarce. Multiple studies investigating behavior among left-handers have shown that many are not simply mirror-images of right-handers (Bryden, Mayer, & Roy, 2011; Shen & Franz, 2005). Instead, “left-handed” describes a remarkably heterogenic group, in which up to 50% of members are behaviourally indistinguishable from their right-handed counterparts in terms of hand choice for grasping (Bryden et al., 2011; Gonzalez et al., 2006; Gonzalez & Goodale, 2009; Stins, Kadar, & Costall, 2001; Stone, Bryant, & Gonzalez, 2013) and/or of grasping kinematics (Boulinguez, Velay, & Nougier, 2001; Stins et al., 2001). Based on these studies, it is reasonable to anticipate that a significant proportion of the left-handed population would behave in a manner similar to the right-handers in our previous investigation (Flindall & Gonzalez, 2013). In other words, while some left-handers may show both a preference for and a kinematic advantage with left-handed grasp-to-eat movements, many self-identified left-handers should exhibit smaller maximum grip apertures when grasping-to-eat with their right (in this case, non-dominant) hands. In the present study we investigated this possibility by looking at differences between grasp-to-eat versus grasp-to-place actions in the left and right hands of a left-handed population. A right-hand kinematic advantage would support a theory of left lateralized cortical structures producing grasp-to-eat actions, which in turn may have led to a species-wide preference for general right-hand use. In addition, it would rule out the simpler explanation that kinematic asymmetries arise from hand-use habits. Because we have previously argued that the earlier development of a right-hand preference for grasp-to-eat actions would translate into several additional years of experience in right-handed hand-to-mouth movements (Flindall & Gonzalez, 2013), we therefore (in the current study) assess kinematics among left handed participants – a group in which an experience-based advantage would presumably favour the left (i.e., opposite) hand. If, instead, the advantage is predominantly lateralized to the right, or to both hands, then this would suggest that the advantage cannot be explained by experience alone.

Twenty-one self-reported left-handed participants grasped food items of three different sizes, using both their dominant and non-dominant hands in order to either a) eat, or b) place the item into a bib located near the mouth. Based on the literature discussed above, we predicted two main outcomes from this research. First, we hypothesized that many left-handed participants would behave in a manner similar to the right-handed population, in that they would produce smaller maximum grip apertures when grasping with intent to eat, and that this behaviour would be lateralized to only one hand. Second, we predicted that the population would be heterogeneous with regards to which hand this behaviour is lateralized: that is, some participants would behave as mirror opposites to right-handers, producing smaller MGAs when grasping with their dominant hands (left-left handers). Other left-handers would behave as right-handers, producing smaller MGAs when eating with their non-dominant right hands (right-left handers). We predict this second group of right-left handers will constitute a significant portion of the left-handed population – perhaps as many as 50% (Derakhshan, 2006; Gonzalez & Goodale, 2009).

Methods

Participants

Twenty-one left-handed University students (average age 21.8 years, 11 females) participated in the experiment. Handedness was self-reported by the participant and confirmed through a modified Edinburgh/Waterloo handedness questionnaire (Oldfield, 1971; Stone et al., 2013). All participants gave informed written consent prior to the onset of 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 #2011-022). Participants were able to withdraw from the study at any time without consequence.

Materials

The materials and procedures mirrored those of Flindall and Gonzalez (2013). Briefly, three infra-red 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 anatomical snuff box). An Optotrak Certus camera bar [Northern Digital, Waterloo, ON, Canada] recorded IRED position during each trial at 200 Hz for 5 seconds. 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 Corporation, San Pedro, CA, USA] and NDI First Principles [Northern Digital, Waterloo, ON, Canada].

Participants were seated before a self-standing height-adjustable triangular pedestal. The pedestal held individual cereal food items (presented one at a time) of 3 different sizes: SMALL (Cheerios®, mean diameter 11 mm), MEDIUM (Froot Loops®, mean diameter 15 mm), and LARGE (Oatmeal Squares®, mean length 21 mm). These targets were chosen based on their distinct sizes and familiarity. 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 (Whishaw et al., 2002).

Procedure

Participants sat behind the pedestal, with their hand placed comfortably on their lap (fingertips of thumb and index finger together) between trials. Targets were presented in a pseudo-random order, such that the participant was naïve to the size of the food item until the beginning of the trial, when the goggles transitioned to their transparent state. After 1000ms of transparency during which the participant had full view of their hand and target, an audible go-signal ('beep') was presented, informing the participant that they should begin the reach-to-grasp movement "at a comfortable pace." After grasping the target between the thumb and index finger in a precision grip, participants would either a) ingest the item completely (EAT condition), or b) place the item in a bib hanging below their chin (PLACE condition) (Fig. 1). Investigators replaced food items between trials, while the liquid crystal goggles were in a closed (opaque) state. EAT and PLACE task conditions were presented in blocks of 25 trials (8 SMALL, 8 MEDIUM, 9 LARGE, randomized), with start order counterbalanced between participants. Participants were informed of task requirements at the beginning of each block. After both blocks were completed, IREDs were transferred to the participant's other hand, and the process was repeated. Hand start order was counterbalanced between participants.

Figure A3.1 – Experimental design. Left: Participants begin all reach-to-grasp actions in a "start position" with their hand resting on their lap, thumb and index finger together (item shown: Froot Loop®). Center: EAT task requires participant to eat the target after grasping. Right: PLACE task requires participant to grasp the target and place it in a bib hanging below his/her chin. Participants wore the bib throughout all blocks. PLATO™ liquid crystal glasses restricted participant vision between trials. Vision was unrestricted during grasps. All grasps were completed using only the index finger and thumb.

Analyses

As the primary focus of the current study was to replicate the methods of Flindall and Gonzalez (2013) in a group of left-handers, kinematic analyses were limited to maximum grip apertures. Maximum grip aperture (MGA) was measured as the peak resultant distance achieved between the thumb and index finger prior to the time of grasp contact. Between Hand comparisons required MGA calculations to be corrected for IRED placement, as grip aperture calculations were based on distance between the IREDs, rather than actual distance between subject fingertips. Grip aperture corrections were accomplished via the method described in Flindall and Gonzalez (2013), wherein we averaged the resting grip apertures recorded per participant per hand, and subtracted that constant from all associated MGA values. This correction factor allows us to control for slight variations in IRED placement between the hands as well as variations in hand size within participants (Flindall et al., 2014; Flindall & Gonzalez, 2013).

Data Processing

Data were collected via NDI First Principles, kinematic calculations were performed on unfiltered data using Microsoft Excel 2010, and statistical analyses were completed using IBM SPSS Statistics 19.0. Each participant's MGA measurements were inspected for normalcy within each Hand/Task/Size condition. Three participants required MGA winsorization within-condition, as their within-condition range of MGAs exceeded 20 mm (whereas the average within-condition MGA range for other participants was <9 mm). Outliers (MGA values more than 2 standard deviations outside the condition mean) were removed from analysis. An average of 3.2% of trials per participant (range 0-13%) were removed, with a further 3.0% of trials per participant (range 0-13%) lost due to either camera line-of-sight failure or participant error. In total, an average of 6.2% of trials were removed from each participant (range 0-15%). Remaining trials were averaged by condition, and further analyses were conducted on these averages. To assure that cleaning of the data did not bias the results, statistical analyses were conducted on both raw data (e.g., all trials included) and homogenized data. No differences were found between these two types of analyses. Significant results from homogenized data are reported below.

For our primary analysis, a three-way within-subject repeated measures analyses of variance [Hand (LEFT/RIGHT) x Task (EAT/PLACE) x Size (SMALL/MEDIUM/LARGE)] was run on condition means. To enable comparisons of the current results with those of Flindall and Gonzalez (2013), a secondary analysis was conducted wherein the data were split by Hand used (LEFT/RIGHT), and separate two-way ANOVAs [Task (EAT/PLACE) x Size (SMALL/MEDIUM/LARGE)] were run on the resulting sets. This secondary analysis also allowed us to consider between competing hypotheses of whether a predicted effect of task appeared as a result of practice, or of a lateralization of brain structures responsible for producing grasp-to-eat actions. Alpha significance for all ANOVA results was set at $p<.05$, and estimate of effect size is reported using partial η^2.

Results

Handedness Questionnaire

All participants self-reported as left-handers. The average score was -22.1 (± 2.8 SE; range -41 to +12) out of the possible range of -44 (strongly left-handed) to +44 (strongly right-handed). The results of the questionnaire suggest that four participants were of mixed handedness (scores from -12 to +12), despite self-identifying as left-handed. These participants were not excluded from analyses.

Primary Analyses (Within-subjects)

Significant within-subject main effects and interactions are reported below. Between subject means and standard errors of MGAs are reported in Table 1.

A main effect of size was observed, F (2, 40)=531.832, $p<.001$, $\eta^2=.964$, wherein participants scaled their MGA according to food size. Follow-up paired-sample t-tests indicated that all sizes were significantly different from one another (t (20)<-14.5, $p<.001$). A main effect of task was observed, F (1, 20)=7.115, $p=.015$, $\eta^2=.262$, wherein participants opened their hands less wide when grasping items in the EAT condition (M=28.481 mm, SE=1.084 mm) than they did in the PLACE condition (M=29.858 mm, SE=1.155 mm) (Fig.2). No other main effects or interactions were observed.

Table A3.1 – MGA means and standard errors by hand, size, and task. MGA values are reported in millimeters.

		Eat	**Place**
Left Hand	Small	22.7 ± 1.3	23.0 ± 0.9
	Medium	27.2 ± 1.1	27.9 ± 1.1
	Large	37.0 ± 1.3	37.6 ± 1.2
Right Hand	Small	23.9 ± 1.8	22.7 ± 1.3
	Medium	29.0 ± 1.5	27.2 ± 1.1
	Large	37.6 ± 1.5	37.0 ± 1.3

Secondary Analyses (Within-subjects, divided by hand)

In the original study (Flindall & Gonzalez, 2013), we found a significant Hand x Task interaction wherein the effect of task on MGA was lateralized to the dominant hand. In that study, we could not rule out the possibility that the MGA difference between the left and right hand was simply a result of increased practice with the dominant hand. If that were the case, then the left-handed participants tested in the current study should demonstrate the effect of task predominantly in their dominant (i.e., left) hands. To investigate this possibility, data from all subjects were split by Hand condition (LEFT/RIGHT), and secondary two-way ANOVAs [Task (EAT/PLACE) x Size (SMALL/MEDIUM/LARGE)] were run on the resulting data sets. If the task effect were due to practice, then left-handed participants should show the effect predominantly in their left hands. If instead the task effect were due to a lateralized brain network responsible for producing grasp-to-eat movements, then (depending on the direction of lateralization) the task effect should be observed either in the right, or both, hands. Significant within-subject main effects and interactions are reported.

Significant main effects of size were found for both left- (F (2, 40)=284.178, p<.001, η2=.934) and right-handed (F (2, 40)=312.944, p<.001, η2=.940) MGAs. Follow-up t-tests revealed that MGAs for all food sizes were significantly different from one another in both left-handed (t (20)<-11.5, p<.001) and right-handed (t (20)<-11.5, p<.001) grasps. When participants used their right hands, a main effect of task was again observed, F (1, 20)=5.332, p=.032, η2=.210, with the EAT condition (M=27.98, SE=1.06) producing smaller MGAs than the PLACE condition (M=30.20, SE=1.54). This effect was not significant during the participant's dominant left-handed movements, F (1, 20)=0.728, p=.404, η2=.035. It should be noted that although this analysis suggest a left hemisphere (right hand) lateralization for grasp-to-eat actions, the initial omnibus ANOVA failed to demonstrate a Hand x Task interaction, thus the data should be interpreted with caution. It is possible that the heterogeneity within the participant population was great enough to mask an interaction. The heterogeneity of the participant pool is investigated in our tertiary analysis.

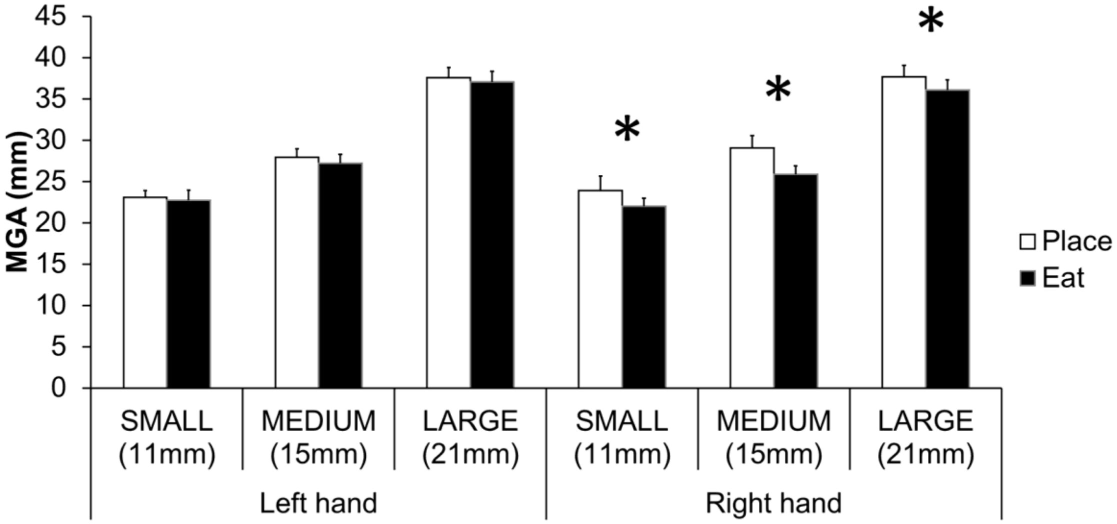

Figure A3.2 – Average MGA during left- and right-handed movements toward small, medium, and large food items during place and eat tasks. Tasks were significantly different from each other during right-handed movements only (p<.05).

Tertiary Analysis (Individual analyses)

In the previous study involving right-handed participants, the observed Hand x Task interaction was found in all participants. However, as shown by numerous studies, left-handers represent a less homogenous group with respect to lateralization as compared to right-handers. For this reason we investigated each participant included in the primary and secondary analyses on an individual basis. After averaging participant data across each condition, we did a case-by-case search for the expected pattern: that is, a smaller average MGA for EAT versus PLACE, consistent across all three food sizes, lateralized to one hand. As expected, this pattern was not found in all left-handers; instead, eight participants did not demonstrate the effect consistently (either the task effect was not consistent across all food sizes (n=5), or was in the direction opposite to that expected (i.e., PLACE<EAT) (n=3)). Of the remaining thirteen participants, seven demonstrated the effect only in their right hands ("right-left handers"), consistent with the results of our secondary analyses. Four more participants demonstrated the expected effect, but restricted to their *left* hands ("left-left handers"). The remaining two participants demonstrated the expected effect in both hands ("ambidextrous"), though the effect was stronger during right-handed movements in both cases.

Handedness Correlation Results

To determine whether our results (and the effective grouping of left-left handers, right-left handers, and ambidextrous) was linked with degree of left-hand preference as measured by the modified Edinburg/Waterloo handedness questionnaire, we determined the average difference between Eat and Place MGAs for the right and left hands of each participant. This analysis non-categorically measured the size of the effect for each participant. For example, If a participant displayed the task effect in their left hand only, this difference would be a positive value for their left hand (larger MGA in Place condition – smaller MGA in Eat condition), and a near-zero value for their right hand (representative of an insignificant difference between Eat and Place MGAs). Larger values are associated with larger differences between tasks. A Pearson correlation analysis was conducted to determine the degree of association between left- and right-handed task difference values and the scores on the modified Edinburg/Waterloo handedness questionnaire. No significant correlation was found, for either hand ($r^2<.025$, $p>.54$), indicating that degree of handedness as measured by the modified Edinburg questionnaire is unrelated to degree of lateralization measured from the size of our within-hand difference between tasks.

Monte Carlo Analysis

Monte Carlo analysis is a mathematical tool wherein random samples are generated to simulate the behaviour of a complex system (Hammersley & Handscomb, 1964). These samples may then be observed in order to infer the processes governing that system (Kalos & Whitlock, 2008). Monte Carlo analysis may also be used to test whether an observed sample distribution differs from one predicted by a random null-model (Roth, Kang, Batty, & Barthélemy, 2011; Trakhtenbrot & Kadmon, 2006). To test whether our effective groupings of left-left handers, right-left handers, and ambidextrous could be attributed to random chance or experimenter bias, we generated sample MGA data for each participant, and analyzed the results according to the methods described in our tertiary analysis. Random MGAs were generated using Microsoft Excel 2010, using the means and standard deviations of a participant's experimental MGAs, collapsed across hand and task. We did not collapse across size, as we observed a robust effect of size, persistent in all participants. The resulting random MGAs were again averaged across each condition, and analyzed according to the same methods as described in our tertiary (subject by subject) analysis. The data were randomized 10 000 times, and the numbers of left-left handers, right-left handers, and ambidextrous "participants" were tallied during each randomization. The results of these tallies are reported in Table 2, along with the expected and actual proportion for each lateralization. Figure 3 shows the probability of observing group membership of n out of 21 for each of the 3 groups, along with the probability of observing group membership of n for any of the 3 groups.

A one-group chi-square test was conducted to evaluate whether the group distribution as observed in our participant sample (n = 21; 19.0% left-left handers, 33.3% right-left handers, 9.5% ambidextrous, 38.1% none) differed significantly from the randomly-generated population (n = 210 000; 5.93% left-left handers, 5.94% right-left handers, 0.39% ambidextrous, 87.73% none). The participant sample group-membership proportion was found to be significantly different from the randomized population, $\chi^2(3, N=21) = 83.433, p < 5.63e^{-18}$.

Table A3.2 – Number of occurrences of n randomly-generated participants belonging to one of our assigned groups in 10 000 sample randomizations. Expected proportions are calculated by summing all group membership occurrences over 10 000 randomizations and dividing by generated population size (210 000).

Group	0	1	2	3	4	5	6	7	8	9	10 - 21	Expected Proportion	Actual Proportion
Left-left Handers	2817	3577	2319	960	256	65	6	0	0	0	0	5.93%	19.04%
Right-left Handers	2725	3766	2280	877	267	72	11	2	0	0	0	5.94%	33.33%
Ambidextrous	9196	782	22	0	0	0	0	0	0	0	0	0.39%	9.52%
Any	618	1878	2647	2348	1461	700	252	75	15	6	0	12.27%	61.91%

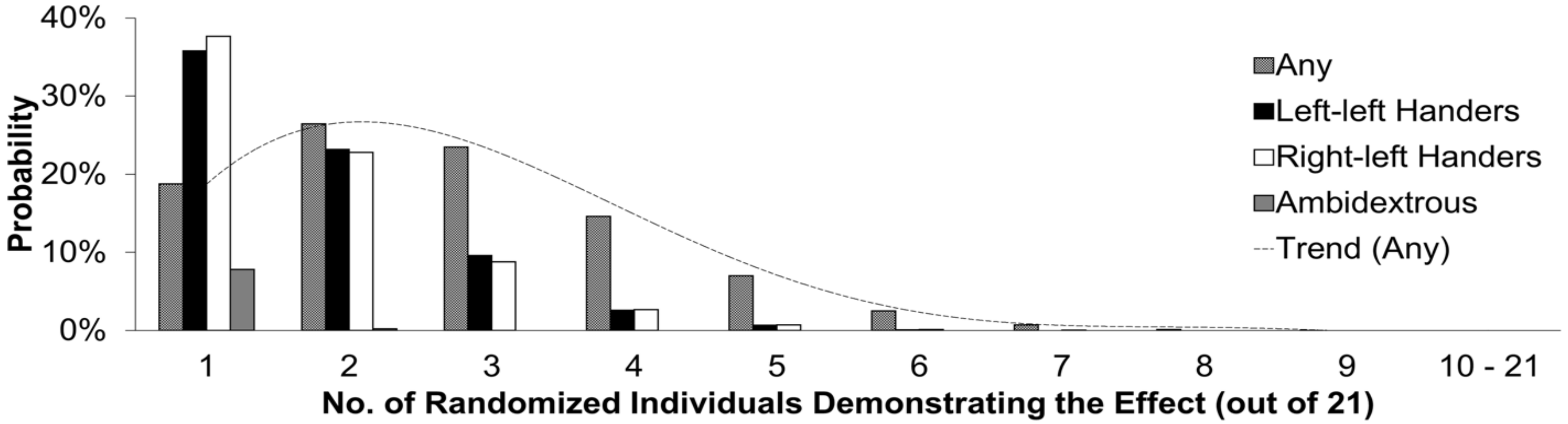

Figure A3.3 – Probability of observing group membership of x (1-21) in a randomly-generated sample (n = 21), for 3 groups (left-left handers, right-left handers, and ambidextrous). Membership in our participant sample was 7, 4, and 2, respectively, for a total membership of 13 of 21 (61.91%). The dotted line represents the total expected membership in any of these three groups (y = 1E-05x6 - 0.0003x5 + 0.0024x4 + 0.0038x3 - 0.1151x2 + 0.371x - 0.0743, R2 = 0.9996).

Discussion

We have recently shown that right-handed participants produce smaller maximum grip apertures (MGAs) when reaching to grasp food items with their dominant right hands, but only when they intend to eat those food items (Flindall & Gonzalez, 2013). If instead participants grasped the items to place them in a receptacle near the mouth, both dominant and non-dominant hands produced equally large MGAs. In the current study, this effect was investigated in a group of left-hand dominant participants. Twenty-one adults used their dominant and non-dominant hands to grasp small, medium, and large food items to either eat them or place them in a receptacle near the mouth. A main effect of task was found wherein grasp-to-eat actions produced significantly smaller MGAs than did grasp-to-place actions. This is the first study (of which we are aware) to show that the end goal of a reach-to-grasp action will affect the kinematics of that action in a population of left-handed individuals. This task-specific distinction also supports the theory of a goal-oriented organization of the human motor cortex, again for the first time in a left-handed population. To facilitate comparisons between our current results and those of our previous study (Flindall & Gonzalez, 2013), we performed two additional (i.e., secondary and tertiary) analyses on our data. In our secondary analysis, when we inspected dominant (left) and non-dominant (right) handed movements separately, the effect of task was found to be significant only during right-handed movements. This result supports the theory of a lateralized advantage for grasp-to-eat movements as discussed in our previous study (Flindall & Gonzalez, 2013), one that is unlikely to be a result of experience alone. While it should be noted that no Hand x Task interaction was observed in the initial omnibus ANOVA, this effect is also in agreement with the results of multiple behavioural and kinematic analyses of left-handers which show that many adult left-handed persons behave in a manner similar to that of the general right-handed population with regards to grasping (Begliomini, Nelini, Caria, Grodd, & Castiello, 2008; Bryden et al., 2011; Gonzalez et al., 2006; Gonzalez & Goodale, 2009; Stins et al., 2001; Stone et al., 2013). In our tertiary analysis, when we inspected participants on an individual basis, we found that the direction of lateralization of the main effect of task was not consistent throughout the group. The lateralized effect of task (i.e., smaller MGAs to eat, rather than place) was found in the right hand in seven participants, the left hand in four participants, both hands in two participants, and not consistently present (in either hand) in the remaining eight participants. This is in direct contrast to our previous study, where we found that the task effect was lateralized to the right hand in every one of our twelve adult participants (Flindall & Gonzalez, 2013). The non-homogenous nature of the tested population may also be responsible for the lack of Hand x Task interaction in the initial omnibus ANOVA.

Furthermore, the hand and degree to which the grasp-to-eat advantage manifested did not correlate with degree of left-hand preference as measured by a handedness questionnaire. Taken together, these results support the postulation that left-handed individuals are not always mirror images of right-handers, nor are they always identical to right-handers in terms of kinematic behaviour; rather, they represent a heterogeneous population in terms of degree and direction of functional lateralization (Bryden et al., 2011; Curt, Maccario, & Dellatolas, 1992; Gonzalez et al., 2006; Gonzalez & Goodale, 2009; Steenhuis & Bryden, 1999; Steenhuis, Bryden, Schwartz, & Lawson, 1990; Stins et al., 2001; Stone et al., 2013; Triggs, Calvanio, Levine, Heaton, & Heilman, 2000). These results are discussed in detail below.

Previous studies have shown that actor intent may have significant influence on the kinematic execution of a movement. Studies have reported differences in the reach-to-grasp phases of throwing and placing actions (Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987), lift and show actions (Ferri et al., 2011), and feed and place actions (Ferri et al., 2010; Flindall & Gonzalez, 2013). As has been previously demonstrated, participants in the current investigation produced smaller MGAs when the target object was to be placed in the mouth, rather than simply in a location near the mouth. Unlike previous investigations however, the current study investigated task-related behavioural differences in left-handed individuals. We show that the right-hand grasp-to-eat accuracy advantage previously identified in right-handers may be lateralized to either hand in left-handed persons. This accuracy advantage may be evolutionarily significant, as numerous reach-to-grasp studies have shown that MGA is sensitive to target uncertainty, and that increases in uncertainty are linked with larger MGAs (Berthier, Clifton, Gullapalli, McCall, & Robin, 1996; Flindall, 2012; Gentilucci, Toni, Chieffi, & Pavesi, 1994; Harvey et al., 2001; Jakobson & Goodale, 1991; Schettino, Adamovich, & Poizner, 2003; Wing, Turton, & Fraser, 1986). It has been proposed that larger MGA production may be a strategy to increase confidence in uncertain grasps by increasing the margin for error (Jakobson & Goodale, 1991). The fact that this kinematic advantage is inconsistently lateralized in left-handers suggests that, despite the probable link between grasp-to-eat lateralization and the evolution of handedness (Goodale, 1990; MacNeilage, Studdert-Kennedy, & Lindblom, 1987; Rogers, 2002; Whishaw, 2003), the neural basis for the grasp-to-eat advantage may be distinct from that for overall hand preference. Future research into the grasp-to-eat movement will be directed by this possibility.

Research has shown that a significant proportion of the population (9-14%) identify as left-handed (Annett, 1967). As left-handed individuals represent a group whose members are less consistently lateralized in terms of language processing (Gonzalez &

Goodale, 2009; Jörgens, Kleiser, Indefrey, & Seitz, 2007; Matsuo et al., 2001; Sommer, Ramsey, Mandl, & Kahn, 2002; Szaflarski et al., 2002), facial recognition areas (Badzakova-Trajkov, Häberling, Roberts, & Corballis, 2010; Willems, Peelen, & Hagoort, 2010), motor and premotor cortex activation patterns during simple movements (Cabinio et al., 2010; Matsuo et al., 2001; Verstynen, Diedrichsen, Albert, Aparicio, & Ivry, 2005), and hand preference for grasping (Bryden et al., 2011; Gonzalez et al., 2006; Gonzalez & Goodale, 2009; Stins et al., 2001; Stone et al., 2013), they are often excluded from study cohorts to reduce variance and increase statistical sensitivity (for review, see Willems, Van der Haegen, Fisher, and Francks (2014)). This presents a problem, as any conclusions drawn from studies which exclude left-handed participants can only be generalized to 86-91% of the population. In addition, such studies cannot reliably discuss evolutionary processes leading to right-hand dominance if they explicitly exclude the main source of variability in populations. Thus, a comprehensive analysis of prehension in the human population remains to be defined. In a previous study on right-handers, we found evidence that supports a theory of distinct neural networks regulating grasping tasks which are similar in their mechanics but differ in terms of end-goal (Flindall & Gonzalez, 2013). When right-handed people used their dominant hands, grasp-to-place movements directed toward food items presented with larger MGAs than did grasp-to-eat movements directed toward the same items. The goal of the present study was to investigate the existence of this effect in left-handed individuals. We confirmed the presence of this effect in a left-handed population but, in contrast with our previous study, the effect was not consistently lateralized to the dominant hand. That is to say, the left-handed participants in the current study do not represent as homogenous a group as did the right-handers investigated previously. Grasp-to-eat actions still often presented with smaller MGAs than did grasp-to-place actions directed toward the same targets, however whether this presented in the left or right hand varied between participants. This finding is significant as it expands the theory of a functionally organized human motor cortex to include all people, where it could previously only be applied to right-handers. In addition, by including left-handed participants we not only gathered data from a more representative sample, but we also provide evidence that the behaviours by which we should define handedness are not consistently lateralized. This study adds to the growing body of literature that describes left-handed persons in terms of mixed-lateralization of multiple behaviours. With regard to kinematic advantages in grasp-to-eat behaviour, we show here that left-handed people who, as a group are inconsistent in terms of direction and degree of lateralization, may contain a majority who are lateralized in the same manner as are right-handed people. This supports the hypothesis that population level right-handedness may have evolved as a result of this lateralized right-hand advantage of the grasp-to-eat action (Flindall &

Gonzalez, 2013; see also Goodale, 1990; MacNeilage, Studdert-Kennedy, & Lindblom, 1987; Rogers, 2002; Whishaw, 2003), and argues for the inclusion of left-handers in future kinematic and behavioural analyses. However, it also calls into question whether the current parameters by which we define handedness may be trusted to accurately predict an individual's behavioural lateralization.

In comparison to right-handed individuals, left-handed individuals are less consistently lateralized in terms of both behaviour and cortical organization (Willems et al., 2014). For example, some left-handers may prefer to use their right hands for certain fine motor skills, while others may display a rightward bias for power movements, such as those required in competitive sports (Peters, 1990). The current study found inconsistent lateralization of an advantage for grasping an object to eat, adding to this pattern of heterogeneity among left-handers. Handedness is most often determined based on hand use for a single task (e.g. writing) or a small number of skilled and unskilled tasks assessed via questionnaire; these methods of classification overlook the significance of variability for behaviour within an individual. Handedness questionnaires, for example, focus mainly on a small number of skilled tasks, while ignoring bimanual tasks or tasks part of a functional chain (e.g. making a cup of tea) (Scharoun & Bryden, 2014). Furthermore, questionnaires often do not address the confines imposed by context (Mamolo, Roy, Bryden, & Rohr, 2005; Mamolo, Roy, Rohr, & Bryden, 2006; Scharoun & Bryden, 2014). For example, one might prefer to open a door with her dominant hand while travelling through a familiar pathway in one direction, while consistently preferring her non-dominant hand while travelling in the other. In the current study, we found that lateralization of the grasp-to-eat advantage did not correlate with participant responses on a modified Edinburgh/Waterloo handedness questionnaire. While initially surprising, this finding is in accordance with several previous studies which have shown no correlation between hand preference/performance as measured by a behavioural task and that measured via questionnaire (Gonzalez et al., 2006; Gonzalez, Whitwell, Morrissey, Ganel, & Goodale, 2007; Peters, 1990; Porac & Coren, 1981; Steenhuis & Bryden, 1999). Because right-handers are more likely to be consistently lateralized in terms of multiple behaviours (Steenhuis & Bryden, 1999), handedness questionnaires may still demonstrate reliability in confirming the label of 'right-handed.' However, in light of the unpredictable lateralization of specific behaviours in self-identified left-handers, we propose that handedness questionnaires for left-handers should be interpreted with a certain degree of skepticism. If left-handed participants are unpredictably lateralized, then behavioural and kinematic investigations should not exclude them simply as a matter of course. Future behavioural studies should include left-handed participants not only to search for additional similarities between left- and right-handed people, but also to broaden the body of literature that describes this significant proportion of our global population.

To summarize, the current study investigated the lateralization of kinematic advantages in the grasp-to-eat task in left-handed people. While the kinematic advantage in question was present in 62% of left-handers, unlike right-handers the direction and degree of lateralization was inconsistent and unpredictable among those tested, demonstrating both the heterogeneity of the left-handed population, and the fact that the observed lateralized advantage is unlikely to be resultant from preference-related experience. These findings also reinforce the theory that population-level right-handedness has its origins at least partially in the grasp-to-eat movement. Finally, these results highlight the often unpredictable lateralization of specialized behaviours in left-handed people.

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Appendix 4: Children's Bilateral Advantage for Grasp-to-eat Actions becomes Unimanual by Age 10 Years

Title: Children's bilateral advantage for grasp-to-eat actions becomes unimanual by age 10 years

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Abstract

Studies have shown that infants tend to develop a lateralized hand preference for hand-to-mouth actions earlier than they do a preference for many other grasp-to-place or grasp-to-manipulate tasks, years even before direction of hand preference can be reliably determined. This observation has led to a series of studies contrasting the kinematics of grasp-to-eat and grasp-to-place actions in adults. These studies describe a robust kinematic asymmetry between left- and right-handed grasp-to-eat maximum grip apertures (MGAs), which has been interpreted as a right-hand advantage for feeding that may have led to right-handedness as observed on a global scale. The current study examines grasp-to-eat and grasp-to-place kinematics in two groups of typically developing children aged 7-12. It was found that the previously-described task difference is present in both hands among younger children, and that the effect does not become lateralized until the end of the first decade of life. Additional kinematics of both the dominant and non-dominant hands are described in detail, to augment a growing catalogue of reach-to-grasp action descriptions for typically developing children. The maturation of the right-hand advantage for grasp-to-eat actions is discussed in terms of an inherent right-hand/left-hemisphere bias for such actions, which may have influenced the development of population level right-handedness in humans.

Highlights:

- We contrast grasp-to-eat grasp-to-place kinematics in children aged 7-9 and 10-12
- Kinematic grasp-to-eat advantage identified in both groups (smaller MGAs produced)
- Bilateral advantage among young children; lateralized to right hand in older group
- Lateralization resembles adult behaviour; interpreted as advantage for self-feeding
- Grasp movement is described, adding to catalogue of normal developmental kinematics

Introduction

The hand-to-mouth movement is among the earliest developing goal-directed movements (Piaget & Cook, 1953). Fetuses demonstrate a right-hand preference for hand-to-mouth movements before birth (Hepper, Mccartney, & Shannon, 1998), and infants as young as one-year-old demonstrate a right-hand preference for self-feeding actions (Sacrey, Arnold, Whishaw, & Gonzalez, 2012). While some have argued that degree of handedness is not fully stable until later years (Coren, Porac, & Duncan, 1981;

McManus et al., 1988; Michel, Babik, Sheu, & Campbell, 2014; Rönnqvist & Domellöf, 2006), these observations regarding hand-to-mouth movements have led some researchers to posit that the direction of handedness is established in the pre- and perinatal period (Levy, 1976). In fact, multiple studies have documented a lateralized hand preference for grasping in infants as young as 6 months of age (Claxton, Keen, & McCarty, 2003; Ferre, Babik, & Michel, 2010; Hopkins & Rönnqvist, 2002; Michel et al., 2014; Morange-Majoux, Peze, & Bloch, 2000; Nelson, Campbell, & Michel, 2013; Rönnqvist & Domellöf, 2006). They have shown that, when presented with a solitary object (most often a small plush toy), infants will more often prefer their right hands for unimanual grasps. While this early development of right-hand preference for simple object acquisition has been reported by some researchers (Nelson et al., 2013; Rönnqvist & Domellöf, 2006), others have reported that hand preference for reach-to-grasp actions is not present (or at least not consistent) until much later in development (Fagard & Marks, 2000; Nelson et al., 2013; Sacrey, Arnold, Whishaw, & Gonzalez, 2013). For instance, a right-hand preference for grasping rings to remove them from a column is not apparent until a child is 21 months of age (Fagard & Marks, 2000), and a robust hand preference for other grasp-to-manipulate tasks does not appear until up to several months later (McManus et al., 1988; Sacrey et al., 2013; Vauclair & Imbault, 2009). Because the initial mechanical requirements of grasping actions are virtually identical (Karl & Whishaw, 2013), it must be the end-goal (or action intent: what the child is going to do with the object after acquiring it) that dictates the difference in the two sets of findings.

Action intent has been shown to modulate kinematics of the reach-to-grasp actions in adults (Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Ansuini, Santello, Massaccesi, & Castiello, 2006; Armbrüster & Spijkers, 2006; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987; Sartori, Straulino, & Castiello, 2011) and in young children (Chen, Keen, Rosander, & Von Hofsten, 2010; Claxton et al., 2003). These studies have focused primarily on the kinematics of the reach rather than those of the grasp, however, and have not investigated whether asymmetries exist between the hands. Given the preference for right-hand use during grasping actions, one might speculate that kinematic asymmetries favouring the right hand would be clearly observable. However, studies in adults have demonstrated that left-handed movements are carried out with the same precision, timing, and preparation as their (more common) right-hand equivalents (Grosskopf & Kuhtz-Buschbeck, 2006; Tretriluxana, Gordon, & Winstein, 2008). Perhaps a way to investigate kinematic differences in reach-to-grasp actions is to utilize an ecologically relevant task. The previous studies have utilized grasp-to-lift or grasp-to-place actions, which one might argue have little ecological relevance. As the hand-to-mouth movement has been presented as a potential archetype for all grasps

(Iwaniuk & Whishaw, 2000; Whishaw, Sarna, & Pellis, 1998), investigation into this movement may prove effective in revealing manual asymmetries.

Kinematic investigations on the hand-to-mouth movement are seldom performed (Castiello, 1997; Desmurget et al., 2014; Ferri, Campione, Dalla Volta, Gianelli, & Gentilucci, 2011; Flindall & Gonzalez, 2014). The few studies which have investigated the kinematics of hand-to-mouth/grasp-to-eat movements have shown that adults produce smaller maximum grip apertures (MGAs) when grasping an item with intent to eat than when grasping the same item with intent to place (Ferri, Campione, Dalla Volta, Gianelli, & Gentilucci, 2010; Flindall & Gonzalez, 2013). This task-dependant behaviour is limited to movements performed with the right hand; left-handed movements show no kinematic difference between grasp-to-eat and grasp-to-place actions (Flindall & Gonzalez, 2013, 2014; Flindall, Stone, & Gonzalez, 2014). Smaller MGAs for the grasp-to-eat task may be considered a kinematic advantage for two reasons. First, larger MGAs have been described as a mechanism used to compensate for uncertainty regarding the size, location, or stability of a target (Berthier, Clifton, Gullapalli, McCall, & Robin, 1996; Flindall, 2012; Gentilucci, Toni, Chieffi, & Pavesi, 1994; Harvey et al., 2001; Jakobson & Goodale, 1991; Schettino, Adamovich, & Poizner, 2003; Wing, Turton, & Fraser, 1986); given this interpretation, it naturally follows that smaller MGAs may signify increased certainty about the target's intrinsic and/or extrinsic characteristics. Second, smaller MGAs are considered more energetically efficient, as peak grip-closing velocity, grip closing time, and other energetic requirements are reduced when the MGA more closely approximates the absolute size of the target (Bootsma, Marteniuk, MacKenzie, & Zaal, 1994).

The primary aim of the current study was to investigate the previously-identified right-hand advantage for the grasp-to-eat movement in a group of typically developing children. To this end, we compared MGA during right- and left-handed grasp-to-place and grasp-to-eat movements made by children aged 7-12. Twenty children aged 7-9 and twenty children aged 10-12 were asked to grasp small food items to either eat them, or place them in a receptacle located near the mouth with both their dominant and non-dominant hands in separate blocks. This analysis also afforded us the opportunity to describe other reach-and-grasp kinematics during these movements. While the kinematics of dominant-hand grasp-to-place movements in children have been described in numerous studies (Duemmler, Franz, Jovanovic, & Schwarzer, 2008; Kuhtz-Buschbeck, Stolze, Jöhnk, Boczek-Funcke, & Illert, 1998; Olivier, Hay, Bard, & Fleury, 2007; Pryde, Roy, & Campbell, 1998; Rönnqvist & Rösblad, 2007; Schneiberg, Sveistrup, McFadyen, McKinley, & Levin, 2002; Zoia et al., 2006), few studies have contrasted these actions with those performed with the non-dominant hand (c.f. Rönnqvist & Rösblad, 2007), resulting in an absent frame of reference for manual asymmetries in typically developing children. The secondary aim of the current study was therefore to describe both reach and grasp kinematics of right- and left-handed grasp-to-eat/grasp-to-place movements, thereby addressing somewhat the dearth of information regarding kinematic asymmetries in children.

Materials and Methods

Participants

Forty children between the ages of 7 and 12 participated in the current study. This age range was chosen as it was the broadest range possible using our collection paradigm. Preliminary testing revealed that children younger than 7 were unable to complete the testing session (approx. 45 min) without becoming bored, fidgety, or otherwise distracted; this negatively impacted both the quantity and quality of kinematic data collected. As the average age of onset for puberty is just under 13 years old (Harris, Prior, & Koehoorn, 2008), children older than age 12 were pre-emptively excluded from the study. Handedness was determined by self-report and confirmed via a modified Waterloo/Edinburgh Handedness Questionnaire (Oldfield, 1971; Stone, Bryant, & Gonzalez, 2013), completed with the aid of the parent or guardian. Participants were not excluded based on reported hand preference, as many previous investigations on grasping and prehension have shown comparable results between left- and right-handers (Boulinguez, Velay, & Nougier, 2001; Flindall, Stone, et al., 2014; Gonzalez, Whitwell, Morrissey, Ganel, & Goodale, 2007; Stone et al., 2013). Participants gave oral consent prior to data collection. Written informed consent was provided on each participant's behalf by a parent or guardian 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 #2013-065). Each child received a small toy and a $10 gift certificate to a local book store in appreciation for their participation. Participants were able to withdraw from the study at any time without consequence.

Materials

Three infra-red 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. An Optotrak Certus camera bar [Northern Digital, Waterloo, ON, Canada] recorded IRED position during each trial at 200 Hz for 5 seconds. Motion capture and audio equipment were controlled using Superlab 4.5 [Cedrus Corporation, San Pedro, CA, USA] and NDI First Principles [Northern Digital, Waterloo, ON, Canada].

Participants were seated in front of a self-standing height-adjustable triangular pedestal (Figure 1). 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 based on their familiarity to the participants and their distinct sizes (Flindall & Gonzalez, 2013, 2014). 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 and chair were 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 & Gonzalez, 2013, 2014; 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 (Figure 1A). Targets were placed on the pedestal in a pseudo-random order. An auditory tone ("beep") sounded at the beginning of each trial, indicating to the participant that he/she should begin the reach-to-grasp movement (Figure 1B), and subsequently either eat the target (Figure 1C), or place the target in a bib hung snugly under his/her chin (Figure 1D). Participants were instructed to grasp the targets "as quickly and as accurately as possible," but with an emphasis of accuracy over speed. Each condition (eat or place) was carried out in a separate block of 20 grasps (10 small, 10 large, pseudo-randomized order), with initial task and hand start order counterbalanced between participants. After both tasks were completed with the starting hand, IREDs were shifted to the participants opposite hand, and the tasks were repeated in the same order.

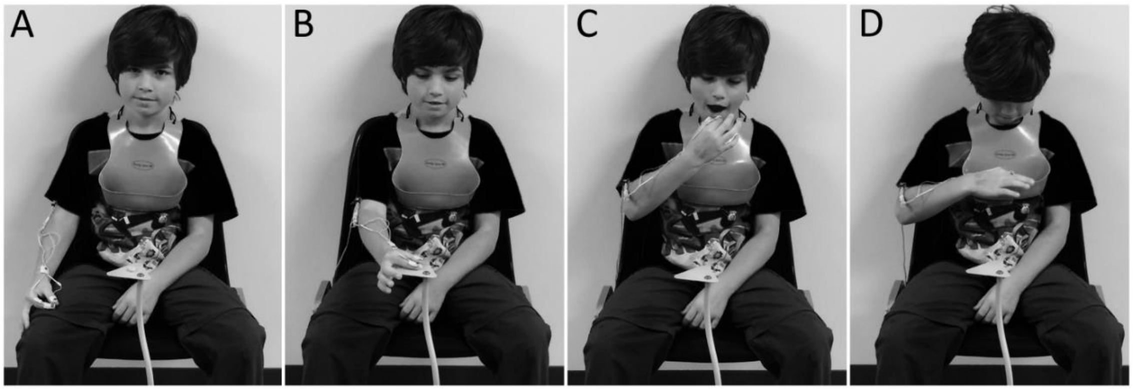

Figure A4.1 – Experimental procedure. A) The participant began each trial with his grasping hand resting on his lap, thumb and forefinger together. B) Following an auditory cue, participants grasped the target between thumb and forefinger. C) During half the trials, participants brought the item to the mouth to eat. D) During half the trials, participants placed the item in a bib. Tasks were completed in right- (shown) and left-handed blocks.

Analyses

Kinematic comparisons were made between reach-to-grasp phases of each trial. Reach kinematics were calculated from displacement of the wrist marker. These measurements included movement time (MT), peak velocity (PV), and time of peak velocity (PVt). MT represents the span during which the participant reached outward toward the target, and was calculated as the difference between reaction time and time of grasp contact. Reaction time was calculated as the time following the go signal at which a participant achieved a resultant equal to 5% of their peak velocity, and grasp contact was said to have occurred when the participant's wrist reached its lowest velocity immediately preceding the return movement. PV was calculated as the maximum resultant velocity the participant achieved during their outward movement towards the target, again measured from the wrist marker. PVt was calculated as the absolute time at which PV occurred, minus reaction time, and divided by overall MT. PVt is reported as a percentage of MT. Grasp kinematics include maximum grip aperture (MGA) and time of maximum grip aperture (MGAt). MGA was measured as the peak resultant distance between the thumb and index finger prior to grasp contact. MGAt, like PVt, is reported as a percentage of MT and was calculated the same way. To allow comparisons between left and right-handed movements, participants grasped a 31.25 mm-wide block along at the beginning and end of data collection. A correction factor was then calculated from IRED separation distance during this grasp. This correction factor was applied to all MGA measurements to compensate for IRED placement variability between participants participants (Tang, Whitwell, & Goodale, 2014). Because variability has been used in the past to measure the point at which a movement becomes learned (Schneiberg et al., 2002), variability of reach and grasp kinematics are also reported (vMT, vPV, vPVt, vMGA, and vMGAt). These were calculated as the standard deviations of each variable within each Hand/Task/Size grouping for each participant.

Data Processing

Data were collected via NDI First Principles, with kinematic calculations performed on unfiltered data with Microsoft Excel 2010. Statistical analyses were completed using IBM SPSS Statistics Version 19. If a participant moved to grasp the target prior to the go signal, or if he/she failed to grasp the target correctly (e.g., either accidentally knocking the target to the floor, or used his/her middle finger to grasp the target), the offending trial was removed from analysis and not repeated. Data from two participants in the younger group were removed from analyses because of wrist marker failure over >30% of trials. Among the remaining participants, an average of 2.19 trials per participant were removed as a result of these behavioural or mechanical errors. Remaining trials were averaged by condition, with 3-way within-subject repeated measures ANOVA

[Hand (left/right) x Task (eat/place) x Size (small/large)] run on condition means. Alpha significance for initial ANOVA results was set at p<.05. Post-hoc comparisons were conducted via paired-sample t-tests. Estimate of effect size is reported using partial η2. Kinematic data were binned into two groups based on each participant's age at time of participation. Young children (7-9 years old; n=18, average age 8.22 ± .878; 6 females; 1 left handed) and older children (10-12 years old; n=20, average age 10.85 ± .813; 13 females; 1 left handed) were analyzed separately. Because previous investigations involving adults found that the lateralization and magnitude of MGA difference was unrelated to handedness as measured by questionnaire (Flindall, Stone, et al., 2014), left-handed children were not automatically excluded from analyses. To confirm that their inclusion did not change the outcome of the investigation, identical ANOVAs were run on data from right-handed participants only; all significant main effects and interactions (reported below) remained significant. As the inclusion of left-handed participants did not affect the strength of the reported effects, only the results from the more inclusive analyses are reported.

Results

Significant main effects and interactions are reported below. Between-subject means and standard errors of all measurements are reported in Tables 1 (young group) and 2 (older group). Results are grouped by independent variable.

Table A4.1 – Between-subject means and standard errors for reach and grasp kinematics for younger children aged 7-9 (n = 18). Values are reported for all hand, task, and target size conditions. Significant ANOVA results by main effect (H = hand, T = task, S = Size) and interaction (e.g., HxT = hand by task) are listed in bottom row. Variables reported are: MT (movement time); PV (peak velocity); PVt (time of peak velocity, expressed as a percentage of MT); MGA (maximum grip aperture); MGAt (time of maximum grip aperture, expressed as a percentage of MT). Mean inter-trial variability is also reported for all variables.

			MT (ms)	PV (m/s)	PVt (%MT)	MGA (mm)	MGAt (%MT)	vMT (ms)	vPV (m/s)	vPVt (%MT)	vMGA (mm)	vMGAt (%MT)
Left	Eat	Big	896 ± 26	1.44 ± .06	29.7 ± .85	28.03 ± 1.3	57.1 ± 2.40	128 ± 14	.165 ± .01	5.5 ± .45	3.96 ± 0.3	11.4 ± .83
		Small	993 ± 36	1.43 ± .05	27.7 ± 1.14	23.38 ± 1.0	52.9 ± 1.90	208 ± 18	.171 ± .02	6.1 ± .59	2.81 ± 0.3	13.3 ± .96
	Place	Big	919 ± 40	1.45 ± .06	29.9 ± 1.01	29.66 ± 1.4	53.7 ± 2.68	160 ± 16	.180 ± .02	6.2 ± .72	4.04 ± 0.4	11.9 ± 1.06
		Small	997 ± 44	1.43 ± .05	27.5 ± 1.07	25.76 ± 1.3	47.7 ± 2.41	185 ± 23	.176 ± .01	5.6 ± .45	4.24 ± 0.4	14.1 ± .91
Right	Eat	Big	902 ± 38	1.32 ± .06	32.2 ± .93	25.10 ± 1.2	60.8 ± 1.64	128 ± 12	.154 ± .02	8.1 ± 1.4	3.97 ± 0.5	11.9 ± .85
		Small	970 ± 47	1.35 ± .06	29.4 ± .97	21.38 ± 1.2	56.0 ± 1.67	145 ± 14	.157 ± .01	6.4 ± .52	3.61 ± 0.5	11.3 ± .86
	Place	Big	899 ± 38	1.37 ± .07	31.1 ± .90	26.10 ± 1.3	57.5 ± 1.96	133 ± 15	.146 ± .01	5.8 ± .43	3.26 ± 0.2	12.5 ± .83
		Small	990 ± 38	1.38 ± .07	28.6 ± .86	22.90 ± 1.4	54.7 ± 1.92	158 ± 16	.144 ± .01	6.0 ± .54	3.27 ± 0.3	13.1 ± 1.02
ANOVA Results:			S		H; S	H; T; S	H; T; S;	S; H			HxT; TxS	HxS

Table A4.2 – Between-subject means and standard errors for reach and grasp kinematics for older children aged 10-12 (n = 20). Values are reported for all hand, task, and target size conditions. Significant ANOVA results by main effect (H = hand, T = task, S = Size) and interaction (e.g., HxT = hand by task) are listed in bottom row. Variables reported are: MT (movement time); PV (peak velocity); PVt (time of peak velocity, expressed as a percentage of MT); MGA (maximum grip aperture); MGAt (time of maximum grip aperture, expressed as a percentage of MT). Mean inter-trial variability is also reported for all variables.

			MT (ms)	PV (m/s)	PVt (%MT)	MGA (mm)	MGAt (%MT)	vMT (ms)	vPV (m/s)	vPVt (%MT)	vMGA (mm)	vMGAt (%MT)
Left	Eat	Big	834 ± 25	1.56 ± .04	32.6 ± .83	28.07 ± 1.0	55.6 ± 2.21	108 ± 9	.140 ± .01	5.4 ± 0.57	3.03 ± 0.2	12.1 ± .92
		Small	895 ± 29	1.58 ± .05	30.2 ± .70	24.51 ± 1.0	49.8 ± 2.43	134 ± 10	.162 ± .01	5.0 ± 0.33	3.00 ± 0.3	12.9 ± .56
	Place	Big	856 ± 34	1.51 ± .04	31.5 ± .83	29.29 ± 0.9	52.5 ± 2.35	125 ± 17	.156 ± .02	5.7 ± 0.36	4.01 ± 0.3	12.2 ± 1.02
		Small	930 ± 38	1.50 ± .04	29.9 ± 1.14	24.61 ± 1.0	49.2 ± 2.19	145 ± 19	.162 ± .02	5.2 ± 0.51	3.74 ± 0.3	12.7 ± .85
Right	Eat	Big	838 ± 28	1.45 ± .06	33.7 ± 1.14	26.71 ± 0.7	55.6 ± 1.83	117 ± 15	.143 ± .01	5.8 ± 0.44	3.39 ± 0.4	12.9 ± .84
		Small	898 ± 32	1.48 ± .06	30.9 ± .84	22.12 ± 0.6	52.0 ± 2.00	153 ± 13	.149 ± .01	5.8 ± 0.40	3.23 ± 0.3	12.6 ± .89
	Place	Big	815 ± 35	1.44 ± .05	34.2 ± 1.37	28.28 ± 0.9	56.6 ± 2.02	100 ± 7	.148 ± .01	6.5 ± 1.26	3.28 ± 0.3	10.7 ± .80
		Small	912 ± 38	1.46 ± .05	30.6 ± 1.09	24.32 ± 0.7	50.7 ± 2.44	171 ± 19	.147 ± .01	6.1 ± 0.37	3.45 ± 0.4	12.7 ± .81
ANOVA Results:			S		S; HxS	T; S	S; HxTxS	S			T; HxT	

Reach Kinematics

Movement Time

A main effect of size was observed on MT in both the younger, F (1, 17) = 34.35, $p<.001$, $\eta^2=.669$, and older children, F (1, 19)=82.71, $p<.001$, $\eta^2=.813$. In both groups, children took longer to complete movements toward small targets [M_{YOUNG}=988±36ms; M_{OLD}=909±29ms] than they did toward large targets [M_{YOUNG}=905±32; M_{OLD}=836±27ms]. With respect to MT, no other main effects or interactions were observed.

Variability of Movement Time

Among the younger children, a main effect of hand was observed on vMT, F (1, 17)=15.33, $p=.001$, $\eta^2=.474$. Young children produced more consistent movements in terms of MT when using their right hands. This asymmetry was not observed in the older group ($p>.5$). Main effects of size on vMT were observed in both young, F (1, 17)=9.22, $p=.007$, $\eta^2=.352$, and old, F (1, 19)=16.33, $p<.001$, $\eta^2=.462$, groups, wherein movement times for small targets [M_{YOUNG}=171±12mm; M_{OLD}=151±9mm] were more variable than movement times for large targets [M_{YOUNG}=134±9mm; M_{OLD}=112±7mm]. With respect to vMT, no other main effects or interactions were observed.

Peak Velocity

No main effects or interactions were observed.

Variability of Time of Peak Velocity

No main effects or interactions were observed.

Time of Peak Velocity

A main effect of size was observed on PVt in both the younger, F (1, 17)=23.75, $p<.001$, $\eta^2 = .583$, and older, F (1, 19)=53.58, $p<.001$, $\eta^2=.738$, children. In both groups, children achieved PV relatively later in the movement when reaching toward the large targets [M_{YOUNG}=30.7±0.7%; M_{OLD}=33.0±0.8%] than when reaching toward small targets [M_{YOUNG}=28.3±0.9%; M_{OLD}=30.4±0.8%]. This would indicate that all children spent relatively more time in the post-peak velocity (i.e. deceleration) phase of the movement when reaching toward small targets. A main effect of hand was observed in the younger group, F (1, 17)=8.66, $p=.009$, $\eta^2=.337$, where younger children achieved peak velocity relatively earlier in the movement when reaching with their left hands [M_{YOUNG}=28.7±0.8%] than when reaching with their right hands [M_{YOUNG}=30.3±0.8%]. A Hand x Size interaction, F (1, 19)=5.80, $p=.026$, $\eta^2=.234$, was found among the older children; follow-up t tests indicated that in reaches directed toward large targets, left-handed reaches achieved peak velocity relatively earlier in the movement [M_{OLD}=32.1±0.8%] than did right-handed reaches [M_{OLD}=34.0±1.1%], t (19)=-2.076, *p*=.05. When directed toward small targets, right- and left-handed reaches showed no difference in PVt (*p*>.4). No other main effects or interactions were observed.

Variability of Time of Peak Velocity

No main effects or interactions were observed.

Grasp Kinematics

Maximum Grip Aperture

A main effect of size was observed on MGA in both younger, F (1, 17)=175.93, *p*<.001, η^2=.912, and older, F (1, 19)=190.25, p<.001, η^2=.909, children, where participants opened their hands wider when grasping large targets [M_{YOUNG}=27.2 ± 1.0mm; M_{OLD}=28.1 ± 0.6mm] than they did when grasping small targets [M_{YOUNG}=23.4 ± 0.9mm; M_{OLD}=23.9 ± 0.5mm]. A main effect of hand on MGA was observed in the younger group, F (1, 17)=4.32, p=.05, η^2=.203, where it was found that, while grasping items of all sizes, younger children opened their left hands [M_{YOUNG}=26.7 ± 1.1mm] wider than they did their right hands [M_{YOUNG}=23.9 ± 1.2mm] regardless of task. This effect was not present in the older children group (p>.4). A main effect of task on MGA was observed in both groups, wherein both younger, F (1, 17)=8.35, *p*=.010, η^2=.329, and older, F (1, 19)=5.85, *p*=.026, η^2=.235, children opened their hands less wide when grasping targets with intent to eat [M_{YOUNG}=24.5±0.9mm; M_{OLD}=25.4±0.6mm] than when grasping targets to place them in a bib [M_{YOUNG}=26.1±1.1mm; M_{OLD}=26.6±0.6mm]. As this behaviour is in contrast with the Hand x Task interaction observed among adults in previous studies (Flindall & Gonzalez, 2013, 2014; Flindall, Stone, et al., 2014), data were split by hand and task and paired-sample t-tests were used to facilitate an in-depth comparison between these groups (Figure 2). These tests revealed that among the younger group, the difference between tasks was significant in both left- and right-handed movements, t (17)<2.06, *p*<.05, but among the older children the effect was only significant during right-handed movements, t (19)=-3.34, *p*=.003. When older children reached with their left-hands, the difference between was not significant, t (19)=-.839, *p*>.4. With respect to MGA, no other main effects or interactions were observed.

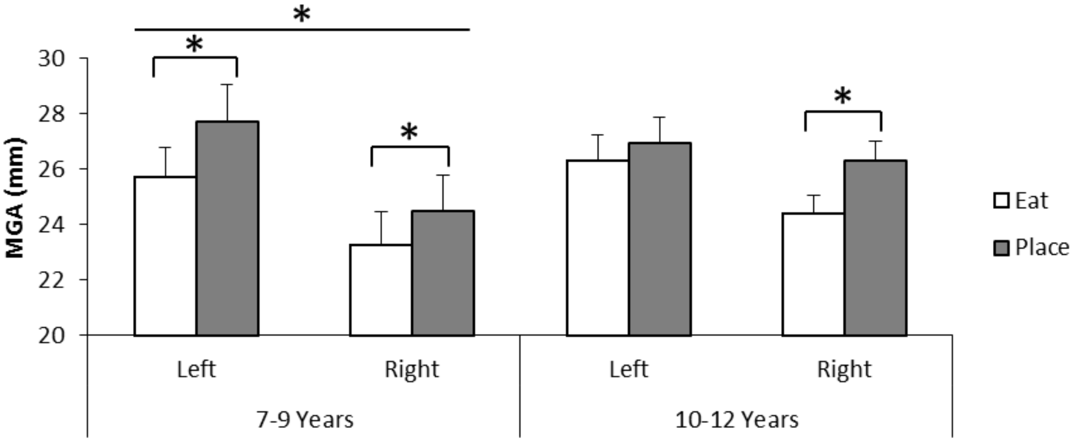

Figure A4.2 – MGA for right- and left-handed reaches in both eat and place tasks. Left-handed MGAs were significantly wider than right-handed MGAs in children aged 7-9. Significant differences between tasks were observed in right-handed movements for both age groups. Difference between tasks in left-handed movement was only significant among children aged 7-9. * indicates significant difference between conditions, p<.05.

Variability of Maximum Grip Aperture

Among older children, a main effect of task was observed on vMGA, F (1, 19)=6.42, p=.020, η^2=.252, wherein older children grasped food items more consistently when intent was to eat [M_{OLD}=3.2±0.2mm] rather than place [M_{OLD}=3.6±0.2mm]. No such effect was found among younger children (p>.05). vMGA Hand x Task interactions were observed in both the younger, F (1, 17)=6.09, p=.024, η^2=.264, and older, F (1, 19)=4.11, p=.05, η^2=.178, groups. Follow-up t-tests revealed that in the younger group, this effect was due to a significant difference in variability of MGA between the left [M_{YOUNG}=4.1±0.4mm] and right [M_{YOUNG}=3.3±0.2mm] hand, limited to the place task. There was no difference between younger children's hands during the eat task (p>.6). In the older group, the effect was due to left-handed eat MGAs being significantly less variable [M_{OLD}=3.0±0.2mm] than left-handed place [M_{OLD}=3.9±0.2mm] tasks. The difference between tasks was not significant during right-handed movements (p>.1). In both groups, the greatest variability among all conditions was during left-handed place movements (Figure 3). Finally, a Task x Size interaction was observed on vMGA in the younger children, F (1, 17)=4.84, p=.042, η^2=.222. Follow-up t-tests revealed that MGA was significantly more variable when grasping large targets to eat [M_{YOUNG}=4.0±0.4mm] than while grasping small targets to eat [M_{YOUNG}=3.2±0.3mm], t (17)=2.711, p=0.15. The difference was not observed during the place task (p>.8). No other main effects or interactions were observed.

Time of Maximum Grip Aperture

A main effect of hand, F (1, 17)=8.86, p=.008, η^2=.343, was observed among younger children, where MGA was achieved earlier in the movement during right-handed grasps [M_{YOUNG}=52.8±2.1%] than it was during left-handed grasps [M_{YOUNG}=57.2±1.5%]. A main effect of task was observed among younger children, F (1, 17)=16.09, p<.001, η^2=.486. MGA was reached relatively earlier in the movement when younger children grasped with intent to place [M_{YOUNG}=53.4±1.8%] than when grasping the same items to eat [M_{YOUNG}=56.7±1.5%]. This effect was not present among older children (p>.05). A main effect of size was observed in both younger, F (1, 17)=23.30, p<.001, η^2=.578, and older, F (1, 19)=22.45, p<.001, η^2=.542, children, wherein MGA was reached relatively earlier in the movement while grasping the smaller targets [M_{YOUNG}=52.8±1.5%; M_{OLD}=50.4±1.9%] than when grasping larger targets [M_{YOUNG}=57.3±1.8%; M_{OLD}=55.1±1.7%]. Finally, a Hand x Task x Size interaction was observed among older children, F (1, 19)=4.94, p=.039, η^2=.206. Follow-up t-tests revealed that while MGAt was always relatively earlier in the movement when grasping small targets than large targets, t (19)>3.33, p<.003, the difference between sizes was not significant when grasping to eat with the right hand (p>.05). With respect to MGAt, no other main effects or interactions were observed.

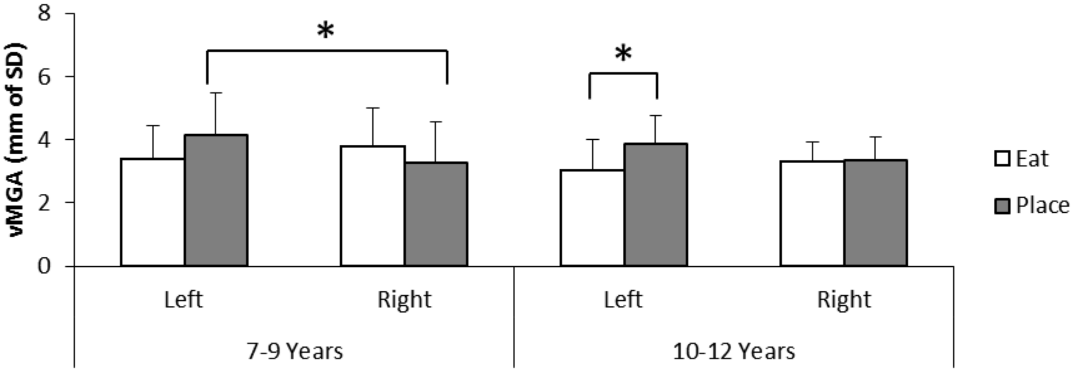

Figure A4.3 – Hand x Task interaction on vMGA in young and old children. In both cases, significant differences appeared due to a high variability in left-handed movements in the place task. * indicates significant difference between conditions, p<.05.

Variability of Time of Maximum Grip Aperture

A Hand x Size interaction on vMGAt was observed among younger children, F (1, 17)=6.43, *p*=.021, η^2=.274, where follow-up t-tests revealed that left-handed movements toward small targets [MYOUNG=13.7±0.7%] had significantly less consistent timing of MGA than did left-handed reaches toward large targets [M_{YOUNG}=11.6±0.9%], t (17)=-3.842, *p*<.001, and right-handed movements toward small targets [M_{YOUNG}=12.2±0.8%], t (17)=2.287, *p*=.035. No other main effects or interactions were observed.

Discussion

The primary purpose of the current study was to investigate the development of manual asymmetries in the kinematics of grasp-to-eat actions. This asymmetry has previously been described in adults, who produce right-handed grasp-to-eat movements with smaller MGAs than left-handed grasp-to-eat movements or grasp-to-place movements of either hand. As a secondary objective, right- and left-handed reach and grasp kinematics are described in typically developing children aged 7-12. Kinematics were measured (via Optotrak Certus motion-tracking system) while children were asked to grasp small food items to either eat, or place in a receptacle near the mouth. Participants performed these tasks in both right- and left- handed blocks. Hand and task start order was counter-balanced between participants. Children were separated into equal groups based on age (young, age 7-9, and old, age 10-12) with independent statistical analyses performed on each group. A main effect of hand wherein right-handed MGAs were significantly smaller than left-handed MGAs was present in the younger group, whereas older children showed less asymmetry in MGA production. Main effects of task were observed in both groups, as MGAs in the eat condition were less wide than those in the place condition. However, when separated by hand, planned comparisons between tasks revealed that while younger children demonstrated this effect in movements with either hand, among older children this effect was driven solely by a difference between eat and place movements performed with the right hand. In this older group, the difference between left-handed eat and place movements was not significant. With regards to the secondary objective of the study (i.e. the analysis of kinematic asymmetries in typically developing children), the younger group displayed main effects of hand on PVt, MGA, vMGA, and vMT, where left-handed grasps spent more time decelerating, had larger margins of error for grasping, and were more variable than were grasps performed with the right hand. These manual asymmetries were not present among children in the older group. The results regarding our primary and secondary objectives are discussed below in terms of relevant literature.

Actor intent has previously been shown to influence the kinematics of seemingly similar reach-to-grasp actions. In adults, differences have been demonstrated between not only eat and place grasps (Ferri et al., 2010; Flindall & Gonzalez, 2013, 2014; Flindall, Stone, et al., 2014; Naish, Reader, Houston-Price, Bremner, & Holmes, 2013), but also between grasps for lifting, placing, and throwing actions (Ansuini et al., 2008; Armbrüster & Spijkers, 2006; Marteniuk et al., 1987). In the current study, actor intent was found to influence hand pre-shaping, with tighter, more consistent MGAs produced when grasping to eat rather than place a small food item. While kinematics of reach-to-grasp movements have been shown to vary with intent in children as young as 10.5 months (Chen et al., 2010; Claxton et al., 2003), this is the first study involving children (of which we are aware) in which such task-dependant differences have been shown to be asymmetric. As previous studies measuring grasp kinematics (specifically, those describing hand pre-shaping) in children have used either grasp-to-lift (Pryde et al., 1998; Schneiberg et al., 2002; Smyth, Katamba, & Peacock, 2004; Zoia et al., 2006), or grasp-to-place tasks (Kuhtz-Buschbeck et al., 1998; Olivier et al., 2007; Rönnqvist & Rösblad, 2007), the current results represent a significant contribution to the developmental literature and a cautionary tale with respect to methodological considerations. As we show that the end-goal of an action will affect grasp kinematics in children, we propose that researchers conducting developmental studies on reach-to-grasp actions should seek to address this influence in both experimental design and subsequent analysis.

The lateralised task effect observed in adults wherein MGA is smaller during right-handed grasp-to-eat movements has been interpreted as a right hand advantage for the grasp to eat movement. In turn, this has been put forward as a potential driver of population level right-handedness in humans (Flindall & Gonzalez, 2013). However, another possibility is that this effect is a result of increased dominant hand practice with grasp-to-eat movements, as an early developing preference for grasp-to-eat actions would result in several more years of right-hand experience in those movements as compared to other grasping movements (Sacrey et al., 2012). Within the current study, it was found that while the task-dependent difference in MGA production was present in both the young and old children, it was not lateralized until the children reached 10-12 years of age. If the rightward lateralization of grasp-to-eat actions were entirely a result of practice, one would expect both i) a consistent leftward lateralization of the effect in the left-hand dominant population, and ii) a lack of task-dependant kinematic differences in young children, coupled with a gradual appearance of the grasp-to-eat advantage as children age and gain experience using their dominant hand. When the effect was investigated in left-handers, the degree and direction of effect lateralization was found to be inconsistent among the tested population (Flindall, Stone, et al., 2014).

Furthermore, lateralization was found to be unrelated to degree of left-handedness as measured via questionnaire, and also more significantly differentiated when presenting in the right-hand (Flindall, Stone, et al., 2014). In that study, the lack of consistent lateralization was interpreted as an indication that the effect was not a consequence of practice. In the current study, the kinematic advantage is present in both hands among younger children, but present only in the right hand among older children. In this age group, as in adults, the left-handed hand-to-mouth movement shares kinematic characteristics with grasp-to-place actions (Flindall & Gonzalez, 2014). While only longitudinal data could speak to changes over time, it is possible that the eat and place tasks begin as separate and distinct movements in both hands, but the task-specificity for hand-to-mouth actions may be lost in the left hand sometime in the peripubescent period. Following the results of these investigations, the hypothesis that unimanual advantage for feeding actions results from a dominant-hand practice effect must be rejected. The “retention” of this task-dependent effect in right-handed movements may be a result of Hebbian-type reinforcement, where neuronal adaptation is stabilised through persistent activation of synaptic networks (Hebb, 1949). As the developing primate brain undergoes significant pruning of dendritic connections throughout childhood and into early adulthood (Elston, Oga, & Fujita, 2009; Huttenlocher & Dabholkar, 1997; Jacobs, Driscoll, & Schall, 1997; Petanjek et al., 2011; Woo, Pucak, Kye, Matus, & Lewis, 1997), it is possible to speculate that a bimanual advantage for hand-to-mouth movements, perhaps the result of a critical period in early childhood for the development of prehension (Forssberg, Eliasson, Kinoshita, Johansson, & Westling, 1991; Forssberg et al., 1992; Schneiberg et al., 2002), is only retained in one hand after a prolonged period of strong unimanual preference. However, as stated above such a hypothesis would require longitudinal data to support, and as such is beyond the domain of the current study. Regardless, the results of the current study do not provide direct support for the argument that handedness evolved as a result of feeding biases. Rather, the current evidence suggests that hand-to-mouth kinematic advantage may be retained in the dominant hand, rather than being an a priori foundation for development of hand dominance. Perhaps an investigation into the kinematics of grasp-to-eat actions in younger children (2-5 years old) would yield different results. Also, it is important to note that left-handed participants were included in our analysis based on data from adults showing limited kinematic differences between left- and right-handed populations. As the current study demonstrates age-related kinematic differences, future investigations should include a larger sample of left-handed children to assess whether the pattern observed in left- and right-handed adults holds true among children. Finally, it would be interesting to see how the effect may present in seniors, as well as if and how it changes in neurological populations. Such data may afford insight into the true degree of lateralization between eat and place actions as well as provide a possible benchmark for detecting and monitoring the advancement of degenerative syndromes. Future research will be guided by these questions.

With regard to the asymmetrical development reach-to-grasp movements, younger children in our study were observed to produce larger MGAs, spend more time decelerating, and have less consistent MGAs and MTs when reaching with their left hands. These asymmetries were not present when older children grasped the same targets, suggesting that left-hand kinematics had matured to a level similar to those of the right hand by the end of the first decade of life. In other words, older children – like adults – showed no significant kinematic differences between the left and right hands. These results are similar to those from previous research on the development of dominant-hand grasping kinematics, which have found similar age-related decreases in MGA (Duemmler et al., 2008; Kuhtz-Buschbeck et al., 1998; Olivier et al., 2007; Zoia et al., 2006; c.f. Smyth et al., 2004) and reach-to-grasp kinematic variability (Kuhtz-Buschbeck et al., 1998; Olivier et al., 2007; Schneiberg et al., 2002). In addition, the age-related reduction of these differences is in line with studies describing reach-to-grasp asymmetries in the adult population which find only minor and subtle differences between left- and right-handed grasping actions (Flindall, Doan, & Gonzalez, 2014; Grosskopf & Kuhtz-Buschbeck, 2006; Tretriluxana et al., 2008). Because variable performance of an action is an essential characteristic of that action's development (Schneiberg et al., 2002), this unequal kinematic performance may be viewed as evidence that left- and right-hand grasp pre-shaping kinematics reach mature levels at different times, with right-hand kinematics maturing (i.e., attaining adult-like consistency between grasps) earlier than left-handed kinematics. The observed asymmetries among the youngest children may be an effect related to transient, experience-related differences in ability between the dominant and non-dominant hands (Fagard & Marks, 2000; Sacrey et al., 2012; Vauclair & Imbault, 2009), immature development of the corpus callosum (Keshavan et al., 2002; Luders, Thompson, & Toga, 2010), intrinsic left-hemisphere advantages for prehension (Gonzalez & Goodale, 2009; Gonzalez et al., 2007; Goodale, 1988, 1990), or a combination of the above factors. Although it is beyond the scope of this study to further speculate on the underlying causes of these differences, the description of behavioural asymmetries is a critical first step in establishing a catalogue of reach-to-grasp kinematics in typically developing children. Such a catalogue will allow us not only to evaluate deficiencies in children affected by movement disorders, but also allow us to judge the effectiveness of therapeutic programs on bimanual motor performance (Schneiberg et al., 2002).

Conclusion

The current study found that children aged 7-9 produce smaller MGAs when grasping to eat than when grasping the same item to place regardless of hand used, but that this difference is lateralized to right-handed movements in children aged 10-12. The study adds to existing literature by describing not only manual asymmetries in the development of grasp kinematics, but also the influence of actor intent on those actions. The kinematic difference between grasp-to-eat and grasp-to-place actions – which is independent of both intrinsic and extrinsic constraints related to the target – suggests a fundamental distinction between the production of these movements, one that is likely of neural origin. The potential difference in developmental trajectories of these grasps, from birth to pubescence and on to adulthood, should be reflected in the methodologies of future investigations.

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Appendix 5: The Destination Defines the Journey: An examination of the kinematics of hand-to-mouth movements

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

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Abstract

Long-train electrical stimulation of the motor and premotor cortices of non-human 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 simply attributable to concurrent opening of the mouth while grasping. In Experiment 1, we use 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 use 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, independent of grasp-to-eat behavior.

New & Noteworthy:

Two experiments are 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) non-specific with respect to a target's edibility, and 2) dependent upon the concurrent opening of the mouth to accept the transported target.

Keywords:

grip aperture, grasp, hand, mouth, edible

Introduction

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 (500-1000 ms) electrical stimulation of the motor and pre-motor cortices yields context-relevant reaching (Graziano, Aflalo, & Cooke, 2005), grasp-to-manipulate (Graziano, Cooke, Taylor, & Moore, 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 when grasping to place a target object, while 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; c.f. Bruni, Giorgetti, Fogassi, & Bonini, 2015), induced reach-to-grasp kinematics (Bonini et al., 2010), or forced hand pre-shaping 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, Gharbawie, and Stepniewska (2011)]. It is yet unclear whether these actions are produced via a comparable framework in humans, though fMRI evidence shows that different neural networks are responsible for the planning of grasp versus touch movements [for review, see Grefkes and Fink (2005) and Gallivan and Culham (2015)]. The superior parieto-occipital cortex (SPOC) has been shown to be uniquely activated during touch and pointing movements (De Jong, Van der Graaf, & Paans, 2001; Kertzman, Schwarz, Zeffiro, & Hallett, 1997), while the anterior intraparietal sulcus (aIPS) has been linked to the planning of grasping actions (Cavina-Pratesi, Goodale, & Culham, 2007; Culham, Cavina-Pratesi, & Singhal, 2006; Gallivan & 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 behavioural evidence in humans supporting the neural division of “grasp-to-eat” and “grasp-to-place” movements (Ferri, Campione, Dalla Volta, Gianelli, & Gentilucci, 2010; Flindall & 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 pre-contact phase of the grasp is exclusive to right-handed actions (Flindall & 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 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 & 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 & 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 either a) eat them, b) place them in a small container near the mouth, or c) 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 & Gonzalez, 2014). Perhaps the grasp-to-eat movement identified may be part of a larger class of hand-to-mouth actions, exemplars 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 which 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 & Gonzalez, 2013, 2015; Flindall, Stone, & Gonzalez, 2015), or temporary placement in the mouth (e.g. "grasp-to-spit"; Flindall & 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, non-food 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 grasping food items, then such a plan would be inhibited when grasping unmistakably inedible non-food items. If this is the case, then MGAs should only differ between task conditions when grasping those items that are edible; MGAs when grasping non-food items should not differ between mouth and container conditions, as 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 either bring them 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 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 seconds. 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 Corporation, San Pedro, CA, USA*] and NDI First Principles [*Northern Digital, Waterloo, ON, Canada*].

Targets to be grasped consisted of both inedible (Experiment 1) and edible (Experiments 1 and 2) objects. Inedible targets were nylon hex nuts in both small (3/8” Nylon 10-32, diameter 9.53 mm) [*B&F Fastener Supply, Ramsey, MN, USA*] and large (Nylon 6/6 Hex Nut, diameter 14.29 mm) [*McMaster-Carr Supply Company, Elmhurst, IL, USA*] varieties. Nylon hex nuts are non-toxic, 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, non-food objects. Edible targets were small (Cheerios™, average diameter 11 mm) and large (Froot Loops™, average diameter 15 mm) cereal items, chosen both for their familiarity to participants and for their hypoallergenic nature (Flindall & 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 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 #2011-022). Handedness was determined via self-report and confirmed using a modified Edinburgh/Waterloo Handedness questionnaire (Cavill & Bryden, 2003; Oldfield, 1971; Stone, Bryant, & Gonzalez, 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 non-dominant hand use for one month 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 seventeen (mean age 20.1, 11 females) and eighteen participants (mean age 24.1, 13 females) 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 & Gonzalez, 2013; Whishaw et al., 2002).

Procedure (Experiment 1)

Participants were presented with target items individually in four blocks of twenty trials each. Blocks were defined by a 2 (item type; edible, inedible) x 2 (end-goal; mouth, container) factorial design. Large and small targets (ten of each) were pseudo-randomly presented in each block. Block order was counterbalanced between participants.

Each trial began with the participant seated behind the pedestal with her right hand (thumb and index finger together) placed comfortably on her lap (rest position). The liquid-crystal occlusion goggles worn by the participant remained in an opaque state between trials, meaning the participant was naïve 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 pseudo-random order in an effort to prevent the participant from pre-planning her 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 1000 ms later; this indicated to the participant that she was to reach out and grasp the target, and either place it in the container, or place it in her mouth, depending on block condition. If edible, the participant was instructed to eat the target after placing it in her mouth. In the case of inedible targets, the participant returned her right-hand to the rest position before removing the target from her 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 based on 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.

Procedure (Experiment 2)

Participants were presented with target items individually in four blocks of sixteen trials each. Blocks were defined by a 2 (Goal; mouth, container) x 2 (Mouth State; open, closed) factorial design. Eight food items of two sizes (small, large) were pseudo-randomly 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 to either their mouths, or to a container hanging beneath their chins. 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 et al. during previous experiments (Flindall & 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. 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.

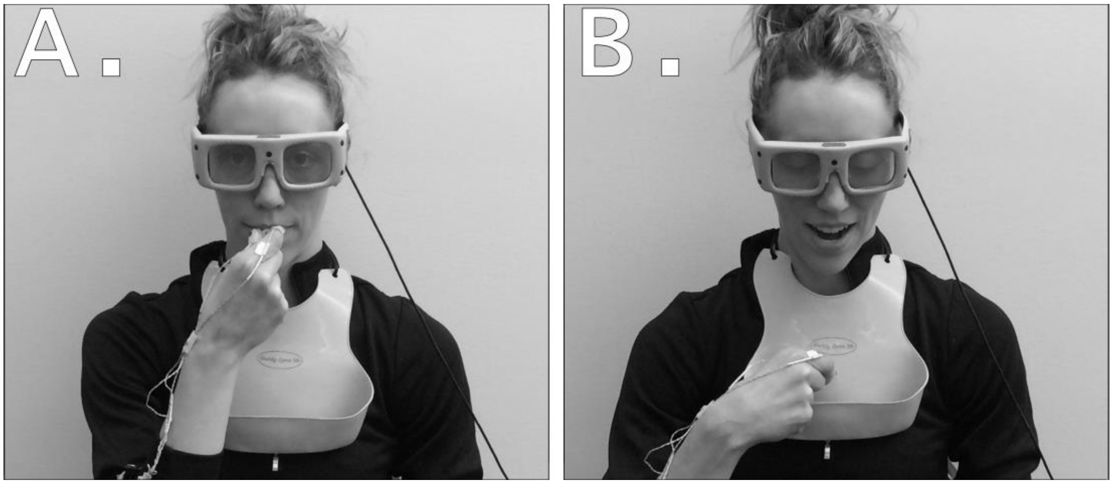

Figure A5.1 – Closed-Mouth (A) and Open-Container (B) conditions used in Experiment 2.

Data Analysis

Data were collected via NDI First Principles, 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 prior to 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 & 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 (reported here 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 (the time at which instantaneous wrist velocity reaches a minimum prior to the beginning of the return/transport phase of the action). Relative time of MGA (MGAt) typically occurs after PV (within the deceleration phase of the approach), and is reported here 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, as 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) x Goal (mouth, container) x Type (edible, inedible). Experiment 2 variables were also subjected to a three-way repeated measures ANOVA [Size (small, large) x State (open, closed) x Goal (mouth, container)]. Alpha significance for the ANOVAs was set at $p < .05$, with Bonferroni correction applied to post-hoc comparisons as necessary. Estimates of effect size are reported using partial eta-squared (η_p^2).

Results – Experiment 1

Table A5.1 – Between-participant means and standard errors for reach and grasp kinematics in Experiment 1, averaged by condition. Variables reported are MGA (maximum grip aperture), MT (movement time), peak resultant velocity (PV), and MGAt (time of MGA, expressed as a percentage of MT). Significant within-subject ANOVA results by main effect (S: size; G: goal) and interaction (SxG; Size x Goal) are listed below kinematic values for the edible and inedible targets.

Type	Goal	Size	MGA (mm)	MT (ms)	PV (m/s)	MGAt (%MT)
Edible	Mouth	Small	20.42 ± 0.9	928 ± 43	1.30 ± 0.1	57.8 ± 2.2
		Large	24.13 ± 1.0	872 ± 39	1.29 ± 0.1	61.1 ± 2.3
	Container	Small	22.42 ± 1.2	926 ± 44	1.28 ± 0.1	56.7 ± 2.6
		Large	26.20 ± 1.4	882 ± 41	1.28 ± 0.1	61.6 ± 2.3
2-way ANOVA Results:			G, S	S		S
Inedible	Mouth	Small	18.52 ± 1.1	1097 ± 56	1.36 ± 0.1	48.0 ± 2.6
		Large	28.16 ± 1.4	856 ± 36	1.34 ± 0.1	65.3 ± 1.7
	Container	Small	20.51 ± 1.2	1153 ± 59	1.28 ± 0.1	44.7 ± 2.6
		Large	30.31 ± 1.5	871 ± 40	1.28 ± 0.1	61.4 ± 1.7
2-way ANOVA Results:			G, S	S	G	S
3-way ANOVA Results:			T, S, G, T x S	T, S, T x S	G, T x G	T, S, T x S

3-way ANOVA

Results of the three-way ANOVA revealed a main effect of target type on MGA, F (1, 16) = 5.315, p = .035, η_p^2 = .249, where edible targets elicited smaller MGAs (23.4 ± 1.11mm) than did inedible targets (24.4 ± 1.27mm). A main effect of size was observed, F (1, 16) = 160.274, p<.001, η_p^2 = .909, wherein small targets elicited smaller MGAs (20.47 ± 1.08mm) than did large targets (27.20 ± 1.31mm). A main effect of goal on MGA was also observed, F (1, 16) = 14.147, p = .002, η_p^2 = .469, with smaller MGAs being produced for mouth directed movements (22.81 ± 1.09mm) than for movements directed toward the container (24.86 ± 1.30mm). Finally, a size x type interaction was also observed, F (1, 16) = 87.300, p<.001, η_p^2 = .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 ± 1.07mm) than did inedible targets (19.52 ± 1.17mm), t (16) = 3.283, p = .005, while the reverse was true for large targets, with inedible targets eliciting significantly larger MGAs (29.23 ± 1.48mm) than edible targets (25.22 ± 1.19mm), t (16) = -6.921, p <.001. However, this interaction is unsurprising given the discrepancies between edible and inedible targets within each size category[12].

A significant main effect of Goal was found for PV, F (1, 16) = 9.946, p = .006, η_p^2 = .383, where movements reached a higher PV when the grasped item was to be placed in the mouth (1.32 ± .1m/s) than when the item was to be placed in the container (1.28 ± 0.1m/s). A Type x Goal interaction was also observed on PV, F (1, 16) = 6.339, p = .023, η_p^2 = .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 ± 0.1m/s) than when the target was to be brought to the container (1.28 ± 0.1m/s), t (16) = 3.828, p = .001.

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[12] While size differences between small items in each category (~11mm and 9.53mm 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 (~15mm and 14.29mm, 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*<.001, η_p^2 = .750, with Froot Loops™ (25.2 ± 1.19mm) generating smaller MGAs than comparably-sized nylon hex nuts (29.2 ± 1.48mm). 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 will be explored in future studies within our lab, but is beyond the scope of the current report.

Significant main effects of item type, F (1, 16)>12.231, p<.003, η_p^2>.433, size, F (1,16)>89.631, p<.001, η_p^2>.849, and Type x Size interactions, F (1, 16)>39.093, p<.001, η_p^2> .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) x Goal (mouth, container)] in order to provide a clearer representation of our findings. The results of these ANOVAs are reported below.

2-way ANOVAs

MGA

A main effect of size was observed for both edible, F (1,16) = 101.531, p < .001, η_p^2 = .864, and inedible targets, F (1,16) = 149.557, p < .001, η_p^2 = .903. MGAs scaled for target size during grasps directed toward both edible (small 21.4 ± 1.07mm; large 25.2 ± 1.19mm) and inedible (small 19.5 ± 1.17mm; large 29.2 ± 1.48mm) targets. A main effect of goal was observed on MGAs for both edible, F (1,16) = 9.390, p = .007, η_p^2 = .370, and inedible targets, F (1,16) = 8.716, p = .009, η_p^2 = .353. In both cases, mean MGAs were smaller when an item was to be placed in the mouth (edible 22.3 ± 0.99mm; inedible 23.3 ± 1.28mm) than when an item was to be placed in the container (edible 24.3 ± 1.31mm; inedible 25.4 ± 1.36mm) (Fig. 2). No Goal x Size interactions were observed for either target type (p > .7).

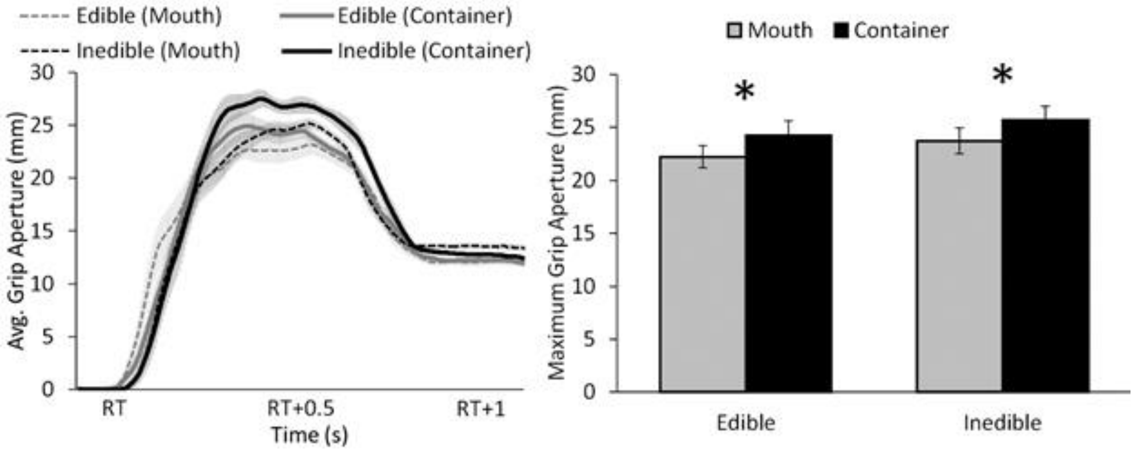

Figure A5.2 – Grip aperture differences between conditions in Experiment 1. LEFT: Average grip aperture over time for grasps directed toward large targets for an exemplary participant (participant TFO). Trials have been RT-aligned to best show differences in MGA between conditions. RIGHT: Means and standard errors of maximum grip apertures (MGAs), 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<.01).

MT

A significant main effect of size was found for both edible, F (1,16) = 33.7, $p < .001$, $\eta_p^2 = .678$, and inedible targets, F (1,16) = 76.7, $p < .001$, $\eta_p^2 = .827$. MT was significantly longer for smaller items (edible 927± 44ms; inedible 1125 ± 55ms) than it was for larger items (edible 878 ± 40ms; inedible 863 ± 37ms). 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, $p = .002$, $\eta_p^2 = .459$, where grasps achieved larger PVs when a hex nut was to be placed in the mouth (1.351 ± .07m/s) than when it was to be placed in the container (1.275 ± .06m/s). No other main effects or interactions were observed.

MGAt

A significant main effect of size was found for both edible, F (1,16) = 17.6, $p < .001$, $\eta_p^2 = .606$, and inedible targets, F (1,16) = 105, $p < .001$, $\eta_p^2 = .868$. MGAt occurred significantly earlier relative to total movement time during grasps toward smaller items (edible 57.3 ± 2.3%; inedible 46.4 ± 2.5%) than during grasps toward larger items (edible 61.4 ± 2.2%; inedible 63.3 ± 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.

Results – Experiment 2

Table A5.2 – Between-participant means and standard errors for reach and grasp kinematics in Experiment 2. Variables reported are MGA (maximum grip aperture), MT (movement time), peak resultant velocity (PV), and MGAt (time of MGA, expressed as a percentage of MT). Significant within-subject ANOVA results by main effect (S: size; St: mouth state; G: goal) and interaction (e.g. StxG; State x Goal) are listed in the bottom row.

State	Goal	Size	MGA (mm)	MT (ms)	PV (m/s)	MGAt (%MT)
Open	Mouth	Small	19.39 ± 0.7	848 ± 33	1.44 ± .08	53.7 ± 2.8
		Large	22.98 ± 0.6	836 ± 42	1.40 ± .08	56.3 ± 2.1
	Container	Small	21.00 ± 0.7	929 ± 49	1.43 ± .08	54.5 ± 2.2
		Large	24.22 ± 0.7	883 ± 38	1.41 ± .08	57.9 ± 2.0
Closed	Mouth	Small	22.49 ± 0.9	893 ± 40	1.45 ± .09	53.2 ± 2.3
		Large	25.51 ± 0.7	830 ± 36	1.44 ± .09	56.5 ± 2.3
	Container	Small	21.88 ± 1.0	979 ± 55	1.40 ± .09	50.1 ± 2.7
		Large	25.15 ± 0.9	878 ± 47	1.40 ± .09	56.0 ± 2.8
	ANOVA Results:		S, St, St x G	S, G, S x St	S	S

MGA

A main effect of size was observed, F (1,17) = 59.5, p < .001, η_p^2 = .778, where participants produced smaller MGAs for smaller targets (21.2 ± .753mm) than for larger ones (24.5 ± .629mm). A main effect of state was observed, F (1,17) = 10.2, p = .005, η_p^2 = .375, where smaller MGAs were produced when participants grasped items and then opened their mouths (21.9 ± .625mm) than when their mouths remained closed throughout the movement (23.8 ± .807mm). No main effect of goal was found, however a significant state x goal interaction was observed, F (1,17) = 7.42, p = .014, η_p^2 = .304. Post-hoc paired-sample t-tests revealed that this effect was due to a significant difference between open (21.2 ± .665mm) and closed (24.0 ± .806mm) states when the end-goal of the movement was the mouth, t (17) = 5.595, p < .001 (Fig. 3). When the end-goal of the movement was the container, there was no difference between open (22.6 ± .675mm) and closed (23.5 ± .906mm) conditions, t (17) = 1.161, p = .262. The difference between open-mouth and closed-container conditions was also significant, t (17) = 3.017, p = .008, replicating our results from Experiment 1. Finally, the difference between open-mouth and open-container conditions was suggestive, t (17) = 2.942, p = .011, however this difference was not significant following Bonferroni correction (α = .0083).

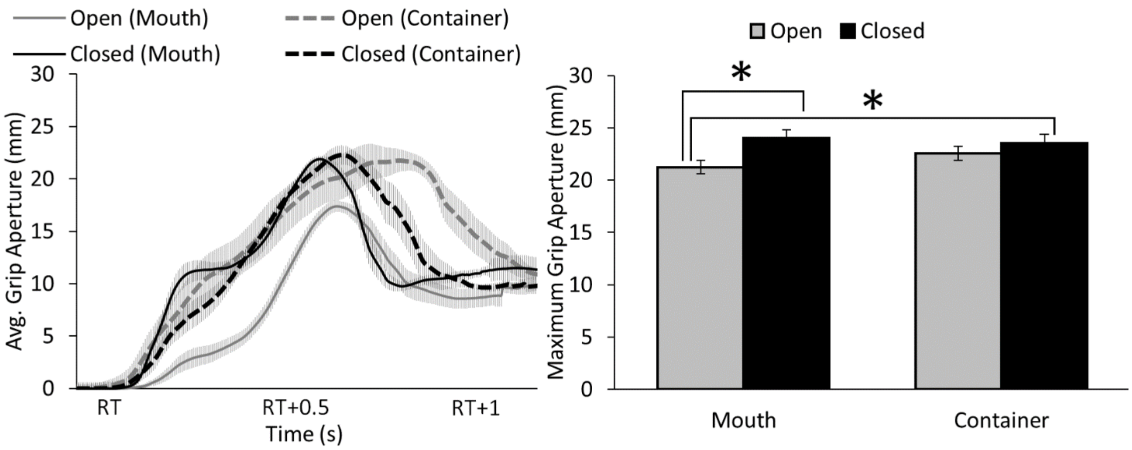

Figure A5.3 – Grip aperture differences between conditions in Experiment 2. LEFT: Average grip aperture over time during grasps directed toward large targets for a single exemplary participant (participant MMS). Trials have been RT-aligned to best show MGA differences between conditions. RIGHT: Means and standard errors of maximum grip apertures (MGAs), 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<.001) and closed-container conditions (p<.008). No other conditions were significantly different from one another following Bonferroni correction (p>.0083).

MT

A main effect of size was observed, F (1,17) = 29.768, $p < .001$, $\eta_p^2 = .637$, where grasps directed toward small targets (912 ± 42ms) took significantly more time to complete than grasps directed toward large targets (857 ± 38ms). A main effect of Goal was observed, F (1,17) = 9.647, p = .006, $\eta_p^2 = .362$, where grasps whose ultimate end-goal was the container (917 ± 45ms) took significantly longer to complete than did grasps whose ultimate end-goal was the mouth (852 ± 37ms). Finally, a size x state interaction was observed, F (1,17) = 17.320, p = .001, $\eta_p^2 = .505$. Post-hoc paired-sample t-tests revealed this effect was due to a significant difference between MTs when small (935 ± 47ms) and large (854 ± 41ms) targets were grasped when the mouth was to remain closed, t (17) = 7.11, $p<.001$. The difference between MTs for small (888 ± 41ms) and large (859 ± 39ms) targets in the open state conditions was non-significant following Bonferroni correction, t (17) = 2.392, p = .029.

PV

A significant main effect of size was found, F (1,17) = 7.339, p = .015, $\eta_p^2 = .302$, where grasps directed toward small targets achieved larger PVs (1.428 ± .09m/s) than did grasps directed toward large targets (1.413 ± .08m/s). No other main effects or interactions were observed.

MGAt

A significant main effect of size was found, F (1,17) = 14.2, p = .002, $\eta_p^2 = .454$. MGAt occurred significantly earlier relative to total movement time during grasps toward smaller items (52.9 ± 2.2%) than during grasps toward larger items (56.7 ± 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 (save PV for edible items, though a consistent non-significant trend was observed, p = .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 of 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 their mouths 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 their mouths firmly closed (teeth together, lips touching) whether they were to bring the item to their 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 their mouths to accept the grasped item (open-mouth condition). When bringing 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 & Campione, 2011). This may be explained by differences between the experiments; Gentilucci et al. instructed their participants to assume an open-mouth posture prior to initiating a grasp, while in the current experiment participants only opened their mouths 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 & 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 here 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 [c.f. Flindall and Gonzalez (2014)].

With respect to other kinematics of the reach and grasp (namely MT, PV, and MGAt), 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, Marteniuk, MacKenzie, & Zaal, 1994; Chieffi & 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 lab aimed at investigating these identity-dependent differences will follow the example set by Bruni et al. (2015), and match target size, shape, and colour 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 have observed that such movements were always paired with a simultaneous opening of the mouth (Graziano et al., 2005; Graziano, Taylor, & Moore, 2002). In the current study, we showed 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 here 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 behavioural (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Ferri, Campione, Dalla Volta, Gianelli, & Gentilucci, 2011) studies, support 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 & Whishaw, 2000; MacNeilage, Studdert-Kennedy, & Lindblom, 1987; Whishaw, 2003). While some have conversely proposed that the ancestral form of grasping in primates was primarily for arboreal locomotion (Szalay & Dagosto, 1988), it is nevertheless significant that all modern animals that display grasping behaviour do so for purposes of self-feeding (Iwaniuk & 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, Visser, & Prechtl, 1982; Hepper, Mccartney, & Shannon, 1998; Piaget & Cook, 1953; Rochat, Blass, & Hoffmeyer, 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 to 6 months of life (Pediatrics, Obstetricians, & Gynecologists, 2013). The prehension reflex in infants emerges at around the same time, at age 4-10 months (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). While 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, Arnold, Whishaw, & Gonzalez, 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 (Rönnqvist & Domellöf, 2006). Instead of measuring laterality through preference, some researchers suggest that kinematic proficiency may be a better predictor of lateralization into adulthood (Rönnqvist & 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, Konidaris, & Berthier, 2014). A task-dependent kinematic difference (as described in the current study), lateralized to a 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 is 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 here 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 she will eventually bring that toy to her mouth: but if she 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. While the results of our three-way ANOVA (and the two-way ANOVA with Goal and Target Identity as factors, see footnote 1) 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, while of comparable size to the cereal items, are not precisely the same; large hex nuts were 1mm smaller along the small axis (and 2mm wider along the long axis) than the average Froot Loop™, and small hex nuts were at least 2mm narrower than the average Cheerio™. Additionally, edible targets were not perfectly consistent in size or shape, even after sorting to remove outliers in each size category; Froot Loops especially have significant variability in shape and depth, with one side of a Froot Loop 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 which 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 lab aimed at investigating these potential differences dependent on target identity will follow the example set by Bruni et al. (2015), and match target size, shape, and colour as precisely as possible between target types.

In conclusion, the current study found 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.

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Appendix 6: The Inimitable Mouth: Task-dependent kinematic differences are independent of terminal precision

Title: The inimitable mouth: task-dependent kinematic differences are independent of terminal precision

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Abstract

Previous studies in our lab have described kinematic difference between grasp-to-eat and grasp-to-place movements, whereby participants produce smaller maximum grip apertures (MGAs) when grasping to bring the item to the mouth than when grasping to bring the item to a container near the mouth. This task difference is limited to right-handed movements, regardless of handedness; it has therefore been interpreted as evidence of left-hemisphere lateralization of the grasp-to-eat and other hand-to-mouth grasping movements. However, the difference in end-goal aperture may have accounted for both the kinematic signature (smaller MGAs) and their lateralized expression. Specifically, if the right hand is more sensitive to the precision requirements of secondary movements, it may have produced more precise MGAs for actions whose ultimate goal is the small-aperture mouth rather than a comparatively large aperture container. The current study addresses this question by replacing the previously-used bib with a small drinking glass whose aperture more closely resembles that of the mouth. 25 adult participants reached-to-grasp small cereal items to either a) eat them, or b) place them into a small-aperture glass hanging beneath their chin. Results once more showed a lateralised kinematic signature in the form of smaller MGAs for the eat action, demonstrating that the signature is not a result of lateralized sensitivity to a movement's secondary precision requirements. We discuss these results in terms of their impact on predominant theories regarding visual guidance of grasping movements.

Keywords:

Kinematics; grasp-to-eat; hand-to-mouth; precision; laterality.

Introduction

Approximately 90% of the global population identifies as right-handed – that is, 9 out of every 10 people worldwide prefer to use their right hand for simple day-to-day actions (Annett, 1967). Many of these people will not only believe they are better, more skilled, and more dexterous when using their (dominant) right hand, but may imagine that they are clumsy or maladept in comparison when using their (non-dominant) left hand (Maruff et al., 1999). In contrast, many studies investigating the kinematics of reach-to-grasp actions find only minor, if any, kinematic differences between left- and right-handed movements (Begliomini, Nelini, Caria, Grodd, & Castiello, 2008; Flindall, Doan, & Gonzalez, 2014; Grosskopf & Kuhtz-Buschbeck, 2006; Tretriluxana, Gordon, & Winstein, 2008). Why then do we feel that our dominant hands are more suited to dexterous tasks, like the reach-to-grasp movement? Why then is right-hand dominance so prevalent?

Recent studies in our lab have discovered kinematic asymmetries in a movement with ecological relevance that may shed some light on these questions. When participants grasp an object (in this case, a small cereal item) with the intent to place it into a container, they perform this movement with identical kinematics regardless of whether they use their right or left hand. However, if instead they grasp the object with the intent to eat the item (or even just place it in their mouth), their right-hand maximum grip aperture (MGA) more closely approximates the size of the target during the pre-contact phase of the movement than does their left hand (Flindall & Gonzalez, 2013, 2014). This right-hand kinematic signature[13] (smaller MGAs for hand-to-mouth grasps) is not dependent on handedness, as it presents in the non-dominant right hand among left-handers more often than it does in the dominant hand (Flindall, Stone, & Gonzalez, 2015). This suggests that hand-to-mouth actions, a subset of actions in which the evolutionarily significant grasp-to-eat action is included, are not only distinct from other grasp-to-place actions, but are left-hemisphere lateralized in the majority of humans. We have argued that this lateralization may have, over millennia, resulted in the pattern of right-hand dominance we see today among the global population.

Kinematic differences between mechanistically similar reach-to-grasp actions that differ in terms of end-goal have been well described in the literature. In addition to differences between grasp-to-place and grasp-to-eat actions discussed above [see also Ferri, Campione, Dalla Volta, Gianelli, and Gentilucci (2010)] , researchers have shown that participants spend more time decelerating toward a disc when they grasp-to-fit it into a slot than when they grasp-to-throw it away (Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987). In another study, researchers found that MGAs are larger, and deceleration phase is shorter when participants must throw a parallelipiped rather than place it or simply lift it (Armbrüster & Spijkers, 2006). When one grasps a bottle with intent to pour it, rather than place it, movement times are extended (Sartori, Straulino, & Castiello, 2011). In all of these examples, the kinematic differences suggest that reach-to-grasp movements are completed with greater care when those movements precede secondary actions that require a high degree of precision, even when the to-be-grasped object's size, shape, and location are unchanged. With respect to MGA, we observe smaller MGAs when the participant has full visual feedback of the limb and target

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[13] In previous manuscripts, we have referred to this task-dependent effect as a kinematic *advantage*, as peak grip closing velocity, grip closing time, and metabolic energy requirements are reduced when MGA more closely matches absolute target size (Bootsma et al., 1994). However, larger maximum grip apertures may also represent a kinematic advantage; for example, larger MGAs result in an increased margin for error, and may improve the odds for successful target capture in cases of target uncertainty (L. Jakobson & Goodale, 1991). In the absence of empirical data that would irrefutably support our use of the word *advantage*, we will instead use the broader expression of 'kinematic *signature*' to refer to the effect in question.

(Flindall et al., 2014; Hu, Eagleson, & Goodale, 1999; Hu & Goodale, 2000), and as grasp kinematics mature (Kuhtz-Buschbeck, Stolze, Jöhnk, Boczek-Funcke, & Illert, 1998; Olivier, Hay, Bard, & Fleury, 2007); conditions which, it could be argued, act to increase the participant's confidence in performing the reach-to-grasp action. These findings are in agreement with Fitts' Law, which predicts that movements will slow as precision requirements (or movement difficulty) increase (Fitts, 1954).

In a similar manner, requirements of precision embedded within the secondary phase of the grasp-to-eat movement may account for the kinematic signature we have described. In other words, task-dependent kinematic differences can be explained in terms of the visual system accounting for the greater precision requirements of the subsequent hand-to-mouth transport movement in a purely bottom-up fashion. In our previous studies, participants would either place the grasped food item into their mouths, or place it into a bib hanging beneath their chin. We originally conceived of these movements as functionally distinct (i.e., 'eat' vs. 'place'), however one may argue that the two movements may in fact be considered identical with respect to goal (i.e., placement), differing only in the aperture of that goal (the bib being several times larger than the mouth). If we accept this premise, then it is possible that the right-hand signature for hand-to-mouth movements may result not from a left-hemisphere lateralization of a "grasp-to-eat" engram as posited, but rather a right-hand sensitivity to the higher precision requirements of this hand-to-mouth placement. In other words, the hand-to-mouth movement may not be distinct due to any particular ecological relevance, but simply because the mouth represents a smaller aperture for placement relative to the bib, therefore representing a goal with greater precision requirements.

To test whether the size of the aperture into which the item was placed was responsible for task-dependent MGA asymmetries, we conducted an experiment wherein participants were asked to grasp small cereal items (Cheerios™, average diameter 11mm, and Froot Loops™, average diameter 15mm) to either eat them, or place them into a small-mouthed shot glass (diameter 28mm) hanging below their chin. Participants completed these grasp-to-eat and grasp-to-place tasks with both their left and right hands, in counter-balanced order. The kinematics of these movements were analyzed in a 2 (Hand; left and right) x2 (Task; eat and place) x2 (Target Size; small and large) ANOVA, the results of which are reported below.

Methods

Materials

The methods followed as closely as possible those of previous studies from our lab (Flindall & Gonzalez, 2013; Flindall et al., 2015). Briefly, three infra-red 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. An Optotrak Certus camera bar [Northern Digital, Waterloo, ON, Canada] recorded IRED position during each trial at 200 Hz for 5 seconds. Vision was restricted between trials using Plato Liquid-crystal glasses [Translucent Technologies, Toronto, ON, Canada] worn by the participant for the duration of the experiment. Motion capture and audio equipment were controlled using Superlab 4.5 [Cedrus Corporation, San Pedro, CA, USA] and NDI First Principles [Northern Digital, Waterloo, ON, Canada].

Participants

28 young adults (16 females, mean age 22.3 years) volunteered to participate in the experiment in exchange for course credit. 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 #2011-022). All participants identified as right-handed via self-report, which was confirmed through a modified Edinburgh/Waterloo Handedness questionnaire (Cavill & Bryden, 2003; Oldfield, 1971; Stone, Bryant, & Gonzalez, 2013), given to each participant following data collection. Participants were excluded from analysis if they had suffered neurological damage or recent mechanical injury affecting the dominant limb, if they had received specific training encouraging non-dominant hand use for one month or more, or if they failed to scale their grip aperture to target size with one or both hands. Left-handed participants were not explicitly excluded, however our blind recruitment yielded no left-handed volunteers. Data from three participants were removed because they failed to scale their grip aperture for differently-sized targets, leaving data from 25 young adults (15 females, mean age 22.3 years) available for statistical analysis. All participants were naïve to the purpose of the experiment prior to commencement.

Participants were seated 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), such that they could reach the target comfortably at maximum reach distance without leaning forward. The height of the pedestal was adjusted for each participant such that the target was 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 & Gonzalez, 2013; Whishaw et al., 2002).

Procedure

Each trial began with the participant seated behind the pedestal with her hand (thumb and index finger together) placed comfortably on her lap (“rest position”). The liquid-crystal occlusion goggles worn by the participant remained in an opaque state between trials, meaning the participant was naïve to the size and precise location of the target until the beginning of the trial. While the participant’s vision was thus occluded, the researcher placed large and small targets on the pedestal, one per trial, in a pseudo-random order in an effort to prevent the participant from pre-planning her 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 1000 ms later; this indicated to the participant that she was to reach out and grasp the target, and depending on block condition either a) eat it, or b) place it in a small glass hanging beneath her chin. The glass used was a cylindrical shot glass, with a mouth diameter of 28mm, attached either to a bib (the same one used in previous experiments, n=13; Figure 1A), or hanging freely (in case participants considered the bib a “safety net” during the precise placement task, n=12; Figure 1B). Participants were instructed to perform each grasp at a comfortable, natural pace, with an emphasis on accuracy over speed of movement.

Participants were presented with target items individually in four blocks of twenty trials each. Blocks were defined by a 2 (hand; left, right) x 2 (task; eat, place) factorial design. Large and small targets (ten of each) were pseudo-randomly presented in each block. Block order was counterbalanced between participants, however both eat and place tasks were always completed for the first hand before markers were shifted to the opposite hand; eat and place blocks were then completed in the same order for the second hand.

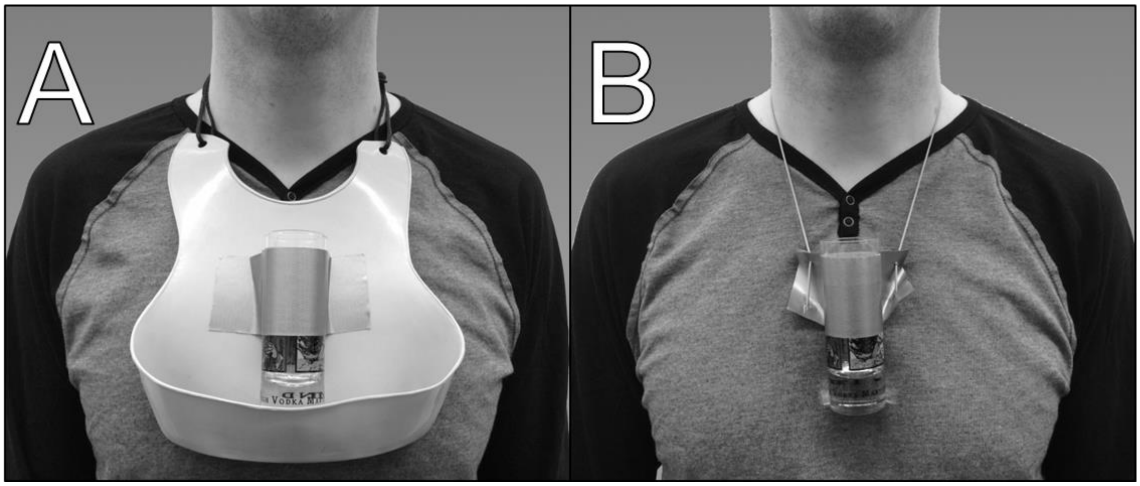

Figure A6.1 – Target for the Place condition. Participants in the first group (n=13) placed the target into a shot glass attached to the front of the bib used in previous experiments (Flindall and Gonzalez, 2013). The bib was removed for participants in the second group (n=12). The same shot glass was used as a target container for both groups.

Data Analysis

Data were collected via NDI First Principles, 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 prior to 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 & Gonzalez, 2013, 2014). Note that statistical tests were simultaneously run on uncorrected MGA values and that results of these tests were consistent between both data sets.

Variability of maximum grip aperture (vMGA; the standard deviation of MGAs within each condition, reported here in mm) has been used previously as a measure of consistency and surety, with increased variability associated with an increase in grasp difficulty and/or a decrease in actor confidence [e.g. via diminished visual feedback availability (Chieffi & Gentilucci, 1993; Flindall, 2012)]. Movement time (MT; reported here in ms) describes the speed at which a participant completes the required action. MT is measured as the time between reaction time and grasp onset. Reaction time is defined as the time at which the instantaneous velocity of the wrist marker exceeds 5% of the outgoing peak velocity (PV). Grasp onset was determined to have occurred when i) instantaneous wrist velocity reached a local minimum immediately prior to the beginning of the return-transport phase of the action, and ii) grip aperture approached a plateau, signifying the closing of the grip around the target. Time of peak velocity (PVt) is reported as a percentage of total MT. Time of MGA (MGAt) typically occurs after PVt, and is also reported as a percentage of total movement time. Earlier relative PVt (i.e., more relative time spent decelerating toward the target) and earlier MGAt have been associated with decreased actor confidence, and more online corrections in the grasping movement (Chieffi & Gentilucci, 1993; Flindall, 2012). Note that all 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, as Optotrak/IRED line-of-sight limitations within our data collection area prohibit the consistent collection of both outward and inward phases.

Results

A 3-way repeated-measures ANOVA with within-subjects factors of Hand (left, right), Task (eat, place), and Size (small, large) and the presence (n=13) or absence (n=12) of the bib as a between-subjects factor. The between-subjects factor was not found to be significant in any main effects or interactions, therefore data were collapsed across groups and a 3-way repeated measures ANOVA with factors Hand, Task, and Size was run on the resulting set. Means and standard errors for variables in each condition can be found in Table 1. Main effects and interactions may be found in Table 1, and are reported in detail.

Table A6.1 – Between-participant means and standard errors for reach and grasp kinematics, averaged by condition. Variables reported are MGA (maximum grip aperture), vMGA (mean inter-trial variability of maximum grip aperture), MT (movement time), PVt (time of peak velocity, expressed as a percentage of total movement time), and MGAt (time of MGA, expressed as a percentage of total movement time). Significant within-subject ANOVA results by main effect (H: hand; T: task; S: size) and interaction (e.g., HxT: Hand x Task) are listed below columns for each kinematic measure.

Hand	Task	Size	MGA (mm)	vMGA (mm)	MT (ms)	PV (m/s)	PVt (%MT)	MGAt (%MT)
Left	Eat	Small	22.79 ± 0.7	2.55 ± .22	955 ± 35	1.68 ± .06	27.9 ± 0.9	52.9 ± 2.2
		Large	27.46 ± 0.8	2.52 ± .27	881 ± 30	1.69 ± .05	29.6 ± 0.8	58.7 ± 1.8
	Place (Precise)	Small	22.71 ± 0.8	2.65 ± .25	957 ± 41	1.68 ± .06	28.2 ± 0.8	53.6 ± 1.8
		Large	27.28 ± 0.9	3.00 ± .28	908 ± 33	1.69 ± .06	29.4 ± 0.9	56.3 ± 2.4
Right	Eat	Small	22.77 ± 0.8	2.46 ± .16	931 ± 39	1.64 ± .05	28.9 ± 0.8	54.5 ± 2.2
		Large	27.16 ± 0.8	2.51 ± .19	871 ± 33	1.63 ± .05	30.8 ± 0.8	59.0 ± 1.9
	Place (Precise)	Small	20.25 ± 0.7	2.40 ± .17	945 ± 37	1.64 ± .05	27.7 ± 0.7	55.0 ± 1.9
		Large	25.15 ± 0.7	2.28 ± .19	869 ± 33	1.63 ± .05	29.5 ± 0.7	60.2 ± 2.0
	ANOVA Results:		T, S, HxT		S	HxS	S, HxT	S

MGA

A main effect of task was observed, F (1, 24)=8.766, p=.007, η_p^2=.268, wherein participants produced smaller MGAs when grasping to eat (23.82 ± 0.7mm) than when grasping to place (25.07 ± 0.7mm). A main effect of size was observed, F (1, 24)=295.277, p<.001, η_p^2=.925, where participants produced smaller MGAs for small targets (22.13 ± 0.6mm) than they did for large targets (26.76 ± 0.7mm). Finally, a Hand x Task interaction was observed, F (1, 24)=12.645, p=.002, η_p^2=.345. Post-hoc paired-sample t-tests revealed that this effect was due to significantly smaller MGAs being produced in the right-handed eat task (22.66 ± 0.7mm) than the left-handed eat task (24.98 ± 0.7mm; t (24)=3.431, p=.002) and the right-handed place task (24.98 ± 0.8mm; t (24)=4.580, p<.001). No other main effects or interactions were observed.

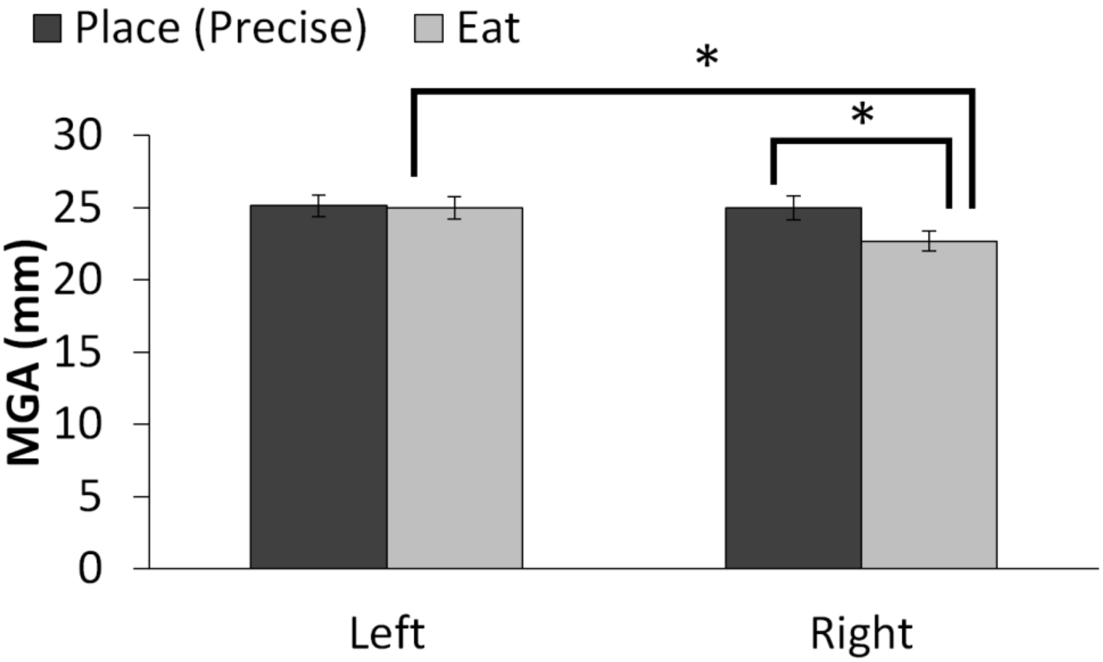

Figure A6.2 – Hand x Task interaction on MGA. Values shown are means + standard errors. Right-handed Eat movements produced significantly smaller MGAs when compared to right-handed place movements or left-handed eat movements. Left-handed movements were not significantly affected by task.

vMGA

No main effects or interactions were observed.

MT

A main effect of size was observed, F (1, 24)=47.241, $p<.001$, $\eta_p^2=.663$, wherein participants spent significantly more time moving toward small targets (947 ± 36ms) than they did toward large ones (882 ± 30ms). No other main effects or interactions were observed.

PV

An interaction between hand and size was observed, F (1, 24)=15.017, $p<.001$, $\eta_p^2=.385$. Post-hoc paired-sample t-tests revealed that this effect was due to the direction of difference between PVs for small and large items in either hand. During left-handed movements, slightly higher (though not significantly so, t (24)=1.833, p=.079) PVs were reached when grasping large items (1.69 ± .05m/s) than when grasping small items (1.68 ± .06m/s). The reverse was true during right-handed movements: slightly higher (again, not significantly so, t (24)=2.013, p=.055) PVs were reached when grasping small items (1.64 ± .05m/s) than when grasping large items (1.63 ± .05m/s). No other post-hoc tests were significant (all p>.07). No other main effects or interactions were observed.

PVt

A main effect of size was observed, F (1, 24)=62.624, $p<.001$, $\eta_p^2=.723$, wherein PVt occurred significantly earlier when grasping small items (28.2 ± 0.7%MT) than when grasping large items (29.8 ± 0.7). A Hand x Task interaction was also observed, F (1, 24)=6.288, p=.019, $\eta_p^2=.208$. Post-hoc paired sample t-tests revealed that this interaction was due to PVt occurring relatively later in the right-hand place condition (29.9 ± 0.8%MT) than in the right-hand eat condition (28.6 ± 0.6%MT), though this difference was not significant following Bonferroni correction (i.e., p>.0125), t (24)=2.6, p=.016. No other post-hoc tests were significant (all p>.06). No other main effects or interactions were observed.

MGAt

A main effect of size was observed, F (1, 24)=22.480, $p<.001$, $\eta_p^2=.484$, wherein MGAt occurred significantly earlier during grasps directed toward small items (54.0 ± 1.7%MT) than it did during grasps toward large items (58.6 ± 1.7%MT). No other main effects or interactions were observed.

Discussion

Recent studies in our lab have identified a right-hand kinematic signature for “grasp-to-eat” and other hand-to-mouth movements (Flindall & Gonzalez, 2013, 2014, 2015, 2016; Flindall et al., 2015). We have shown that hand-to-mouth actions employ smaller MGAs than grasp-to-place actions (in which the same object is placed into a container near the mouth), as long as these movements are performed with the right hand. However, a limitation of these studies has been that the hand-to-mouth and grasp-to-place tasks employed have differed in terms of the size of the aperture into which the target was ultimately placed. Thus, while the 'eat' and 'place' actions shared identical mechanical requirements for the outward movement, the transport component of the grasps differed in terms of end-goal precision requirements. To determine whether this difference in precision requirements within the secondary phase of each movement could account for the reported MGA asymmetries in the initial outward action, we asked participants to grasp small food items and either eat them (i.e., a hand-to-mouth action), or place them into a small-aperture shot glass near their mouth (i.e., a grasp-to-place task with comparatively high precision requirements). Results showed that the Hand x Task interaction observed in previous studies was not affected by using a small-aperture target for the grasp-to-place task; in other words, end-goal precision requirements are not responsible for the task-dependent kinematic asymmetries we have previously observed.

In the current study, we have endeavored to maintain the physical/mechanistic requirements as much as possible between our hand-to-mouth and grasp-to-place tasks. Both tasks maintained the same visual-feedback availability, the same hand start position, the same targets, the same direction of transport, and similar apertures of the end-goal for placement; the only way in which the two tasks differed was with respect to ultimate intent. In our grasp-to-place task, participants placed the food into a shot glass, whereas in the hand-to-mouth task, participants placed the food into their mouths. This difference in intent led to kinematic differences between the two movements, including an asymmetry in maximum grip apertures that appears to favour the right hand. While no left-handed participants took part in the current study, previous experiments within our lab lead us to believe that this right-hand signature is preserved in sinistrals (Flindall et al., 2015). The fact that kinematic differences exist between movements that differ only in terms of actor intent implies that there are high-level processes that influence the production of these simple movements. This is by no means revelatory; despite the unconscious nature of dorsal visual stream function, the vision-for-action system is not purported to be independent from the influence of conscious perception (Milner & Goodale, 2008). Similarly, the fact that actor intent is a conscious concept does not rule out the dorsal stream as the source of the kinematic signature for hand-to-mouth movements; the posterior parietal cortex is associated with high-level functions such as numeracy and working memory as much as it is with the skilled production of movement (Goodale, 2011). Instead, the significance of our results lies in the quantification of this influence; in other words, in addition to the effects of intrinsic target parameters and extrinsic environmental factors (location, presence of obstacles, etc.) on grasp kinematics that have been described to date, we may now gauge the small but significant influence of actor intent on the production of grasping kinematics. The effect's lateralization provides a simple and fortuitous control for these measurements; because the end-goal seems to only affect right-handed movements, the interaction of task (e.g., a high-level parameter) and obstacle avoidance (e.g., an environmental, low-level parameter) may be investigated using a within-participant design. Would the influence of high- and low-level constraints on reach-to-grasp kinematics overlap, or would they compound? The answer to this question may teach us about the organisation of output in the visuomotor system. Regardless, the possibility that any kinematic effects may be lateralized dictates that left-handed movements should no longer be ignored when designing behavioural or imaging studies of reach-to-grasp actions in humans.

We have postulated that the hand-to-mouth and grasp-to-place movements are generated from distinct engrams; that is, the hand-to-mouth and grasp-to-place grasping movements, which may be identical to each other in terms of mechanical requirements, are supported by distinct neural circuitry. This speculation is based on electrophysiological experiments in macaques showing that functionally-specific grasping actions can be elicited by precise differential stimulation of regions within the motor and premotor cortices (Graziano, 2006; Graziano, Aflalo, & Cooke, 2005; Graziano, Taylor, & Moore, 2002). However, it may be more parsimonious to suppose that conscious intent simply represents another layer of input upon which reach-to-grasp actions are produced. To determine whether this layer is dependent on visual input, we must assess whether task-dependent differences are present in memory-guided movements. If differences between the hand-to-mouth and grasp-to-place movement remain in during open-loop delay conditions (see Hu et al., 1999; Hu & Goodale, 2000), then we can say with some certainty that top-down processing is influencing the production of these movements. Alternatively, to test the contribution of the ventral stream to the grasp-to-eat action, one might introduce a delay of variable length between the outward grasp and inward transport of the hand-to-mouth movement. Multiple studies have shown that the dorsal stream retains visual information only for, at maximum, a few seconds (Hesse & Franz, 2010; Hu & Goodale, 2000). If a movement is planned, and vision of the scene is interrupted, the motor plan generated by the dorsal stream begins to degrade immediately; after as little as 2000ms, the kinematics of a movement planned with full vision will be indistinguishable from those of movements generated entirely from memory (Franz, Hesse, & Kollath, 2007; Hesse & Franz, 2010; Hu et al., 1999). Knowing this, it should be possible to test whether high-level decisions are influencing dorsal-stream mediated movements by inserting a pause at the time of target contact, prior to the transport phase of the grasp-to-eat and grasp-to-place tasks. If the grasp-to-eat signature discussed here is present even in a movement temporally separated from the transport phase, then higher-level factors (i.e., actor intent) must be influencing dorsal stream-mediated output. Ongoing investigations in our lab aim to address this question.

The results of the current study provide additional evidence for a right-hand kinematic signature applying to hand-to-mouth grasping movements. These asymmetries, tied as they are to the specific end-goal of the action (i.e., the mouth), appear to be independent of the difficulty/precision requirements pertaining to the size of that end-goal. In this regard, reach-to-grasp actions seem to violate Fitts' Law, which describes how changes in task difficulty will affect the speed at which we execute a reaching movement (Fitts, 1954). One early study on reach-to-grasp kinematics and their adherence to Fitts' Law found that kinematics during reaches that differ in terms of difficulty are identical up to peak deceleration, at which point time following peak deceleration increases with decreases in target size (Marteniuk, Leavitt, MacKenzie, & Athenes, 1990). Our results support these findings, as we found significant effects of size on MT; significant effects on PVt and MGAt can also be explained by a prolonged deceleration phase, as earlier relative timing of these variables will only occur if the deceleration phase of the movement is prolonged while length of the acceleration phase remains constant. With respect to MGA, however, the task difference we observe cannot be explained by Fitts' Law, for two reasons. First, the difference in end-goal aperture was consistent between tasks; therefore, we argue that the two tasks shared an equivalent level of difficulty, and yet kinematic differences remain. Second, and consistent with earlier studies, the task effect was limited to right-handed movements; while research on the applicability of Fitts Law on non-dominant reaching is limited, evidence suggests that it applies equally to pointing movements performed with either hand (Maruff et al., 1999). We conclude that the hand-to-mouth kinematic signature is not resultant from differences in task difficulty – in fact, there is increasing evidence that Fitts' Law may not apply to grasping movements at all. Although it has been shown that some grasping kinematics are weakly affected by task difficulty (e.g., grip aperture variability; see Flindall et al. (2014)), evidence suggests that reach-to-grasp kinematics are independent of even large manipulations to goal instability and overall difficulty (Cooper, Doan, Pellis, Whishaw, & Brown, 2005). If the reach-to-grasp movement does not adhere to Fitts' Law, this throws into question the notion of the reach-to-grasp movement as a composite of reaching and grasping actions (Jeannerod, 1984, 1986). It is possible that, rather than being a typical reach coupled with hand pre-shaping appropriate for the acquisition of a distal target, the reach-to-grasp movement is a product of entirely distinct motor planning circuits. That is, the reach-to-touch and reach-to-grasp movements, despite being similar in that they both require distal transport of the hand, may be the product of distinct and separate neural processes. After all, many animals are capable of reaching to touch or manipulate a distal target in simple fashion (e.g., a dog or cat may be able to reach for a ball with their paw or snout), but relatively few are capable of a true unimanual reach-to-grasp movement resulting in target acquisition and control. Additionally, the presence of robust asymmetries in reaching movements, and their relative absence in grasping movements, further suggests a neural separation between the two. This should be considered in functional imaging studies designed to investigate the neural origins of reaching and grasping movements.

Conclusion

The current study tested a previously described right-hand kinematic signature for hand-to-mouth actions (smaller MGAs versus grasp-to-place movements; Flindall & Gonzalez, 2013, 2014) using a grasp-to-place task with high precision requirements to determine whether differences in end-goal precision requirements could explain those task-dependent kinematic differences. Results suggest that the hand-to-mouth signature is not due to the precision requirements of the subsequent movement, as the right hand produces smaller MGAs even when precision requirements of the eat and place movement are closely matched. This finding demonstrates that high-level actor intent has the potential to subtly modify kinematics of a simple reach-to-grasp action, independent of changes relative to the environment in which the action is embedded.

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