TIME FOR ACTION: REACHING FOR A BETTER UNDERSTANDING OF THE DYNAMICS OF COGNITION

On the Neurocircuitry of Grasping: The influence of action intent on kinematic asymmetries in reach-to-grasp actions

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Abstract

Evidence from electrophysiology suggests that nonhuman 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 largely precludes analogous investigations in humans. In this review, we 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., grasp-to-eat and grasp-to-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. We contend that this asymmetry may be responsible, at least in part, for the preponderance of right-hand dominance among the global population.

Keywords Reach-to-grasp · Grasp-to-eat · Kinematics · Asymmetries · Dual visuomotor channel · Grip aperture · Handedness

The two visual streams theory posits that visual information projects to two distinct networks. Visual information for perception arises from early visual areas to project ventrally to temporal areas, where features like colour, shape, form, and relative size are processed. In contrast, visual information for the production of action projects dorsally to the parietal cortex, where relevant object parameters (e.g., motion, absolute size, egocentric location) are processed unconsciously (Goodale & Milner, 1992; Milner & Goodale, 2008). In the years since these streams were first described in humans, research has shown that the dorsal "vision-for-action" stream can be subdivided even further, into dorsomedial and dorsolateral visuomotor streams, each with its own unique inputs, projections, and function.

Originally it was thought that these streams each served one of the functional components of grasping, as labelled by Jeannerod (1984). Jeannerod theorized that prehension movements are composed of two distinct, temporally integrated components: a reach component, responsive to extrinsic target properties (e.g., location, both relative to the body and to other objects in the environment), and a grasp component, responsive to intrinsic target properties (e.g., size and shape; Jeannerod, 1986a, 1986b). Early reports assigned these "reach" and "grasp" roles to dorsomedial and dorsolateral channels, respectively (Karl & Whishaw, 2013; Rizzolatti & Matelli, 2003). Thus, this form of the dual visuomotor channel theory implies that grasp execution is based entirely on the requirements imposed by the environment.

However, recent kinematic evidence 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 toward targets with multiple potential affordances) differ based on the ultimate purpose of the grasp. The grasp-to-eat action 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 (Beke, Flindall, & Gonzalez, 2018; Flindall & Gonzalez, 2013, 2014, 2015, 2016, 2017; Flindall, Stone, & Gonzalez, 2015; van Rootselaar, Flindall, & Gonzalez, 2018).

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This review begins with an overview of the dual visuomotor channel theory for grasping, and presents supporting evidence 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 (thus far) also alone in terms of reliable kinematic asymmetries between left-handed and right-handed grasps. We suggest an addendum to the dual visuomotor channel theory of grasping—namely, that grasps are not produced 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 then adapted to current target parameters as needed. We finish with an overview of behavioural and archaeological evidence surrounding several theories on the evolutionary origins of right-hand dominance in humans. Based on our kinematic evidence, we posit that the motor plan supporting the hand-to-mouth movement is lateralized to the right-hand/left-hemisphere system, and that such a right-hand advantage for self-feeding may be partially responsible for right-hand dominance in humans (MacNeilage, Studdert-Kennedy, & Lindblom, 1987).

Vision-for-action in the parietal cortex

The parietal cortex's role in transforming vision into action is well established (Goodale, 2011; Goodale & Milner, 1992; Milner & Goodale, 2008). Visual information, beginning in primary visual centers in the 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 stream adapts visual information into our conscious perception of relative size, colour, shape, luminance, and identity, and supports the formation of memory. In contrast, dorsal stream processing is unconscious, short term, and functions solely to facilitate interaction with the world; an object's absolute size and egocentric location are processed by the dorsal stream to enable quick and efficient action toward that object.

The distinct functions of these visual centers have been defined with evidence from neuropsychology (Heider, 2000; Karnath, Rüter, Mandler, & Himmelbach, 2009; Milner et al., 1991), neuroimaging (Culham, Cavina-Pratesi, & Singhal, 2006; Gallivan & Culham, 2015; Pettypiece, Goodale, & Culham, 2010), and behavioural studies (Franz, Hesse, & Kollath, 2007; Hu, Eagleson, & Goodale, 1999; Whitwell, Striemer, Nicolle, & Goodale, 2011). These streams do not act in isolation but rather in concert to quickly generate functionally relevant actions (Hesse, Lane, Aimola, & Schenk, 2012; Schenk & McIntosh, 2010). Damage to dorsal stream regions in the parietal cortex, or to visual regions that feed the parietal cortex, often results in reaching and grasping deficits, including an inability to move the hand efficiently toward a target or to appropriately shape

the fingers to the size of a to-be-grasped item (Jakobson, Archibald, Carey, & Goodale, 1991; Perenin & Vighetto, 1988). Thus, both *reaching* (transport of the hand to a distal location), and *grasping* (appropriate shaping of the hand and fingers for target acquisition) can be traced back to the 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 dual visuomotor channel theory of reaching and grasping

The dual visuomotor channel theory of grasping posits that reach-to-grasp actions are composed of distinguishable "reach" and "grasp" components, themselves arising from distinct visuomotor circuits (Jeannerod, 1981). These components are distinguished based on their functions, mechanisms of control, and environmental influences. The reach component transports the hand to the target, whereas the grasp component shapes the hand for target acquisition and control. With respect to biomechanics, these components are distinguished by their effectors: 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 by the target properties to which they respond; reach kinematics are adjusted primarily based on a target's extrinsic properties, such as its location, whereas the mechanics of the grasp respond mainly to intrinsic target properties, like its size and shape.

Early support for this theory of reach and grasp distinction came almost entirely from observations of stable temporal coupling between the otherwise distinct reach and grasp kinematics (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), the result being that MGA was reliably achieved at approximately 75% of MT (Jeannerod, 1984). Support for this interpretation also came from neuroimaging (Culham et al., 2006; Grol et al., 2007), electrophysiology (Bonini et al., 2012; Graziano, Aflalo, & Cooke, 2005), and neurophysiological studies (Davare, Andres, Cosnard, Thonnard, & Olivier, 2006; Olivier, Davare, Andres, & Fadiga, 2007) that could differentiate between pure reaching and reaching-and-grasping. Neuroimaging studies assigned the reach and grasp components to distinct parieto-frontal networks, giving us labels for the dorsomedial "reach" pathway (connecting the superior parietal lobule, SPL, to the dorsal premotor cortex) and the dorsolateral "grasp" pathway (connecting the inferior parietal lobule to ventral premotor cortex; Rizzolatti & Matelli, 2003). While the

functionally assigned labels of the "reach" and "grasp" pathways have since been challenged (for example, area V6A in the dorsomedial pathway facilitates grasping actions as well as arm transport; see Binkofski & Buxbaum, 2013; Fattori, Breveglieri, Bosco, Gamberini, & Galletti, 2017), together, these pathways constitute the cortical grasping network (Grafton, 2010). The dorsomedial pathway connects area V3A (which receives input from primary visual cortex, V1) in the occipital cortex to the parietal reach region (PRR) in the posterior parietal cortex, on the superior section of the anterior bank of the parieto-occipital sulcus (Pitzalis et al., 2013). The parietal reach region, which includes the superior occipitoparietal complex (SPOC; also known as V6A) and medial intraparietal sulcus (mIPS), projects to the dorsal premotor cortex (PMd) before connecting to primary motor cortex (M1). The dorsolateral pathway also starts in V3A, which projects to area MT before connecting to the anterior intraparietal sulcus (aIPS; area AIP in macaques) on its way to ventral premotor cortex (PMv) and M1 (Davare et al., 2006). The dorsomedial and dorsolateral circuits integrate in M1 to produce the temporally consistent reach-to-grasp movements that we perform dozens if not hundreds of times per day.

The idea that the reach component of the reach-to-grasp action is supported by the same neural structures as those that produce pure reaches (e.g., reach-to-touch, reach-to-aim, or reach-to-point movements) has been examined through attempts to split these movements into their fundamental components. Researchers have typically separated 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., Cavina-Pratesi et al., 2010; Freud et al., 2018; Grol et al., 2007), ostensibly isolating the hand shaping of the grasp from the transport function of the reach. However, kinematic evidence from reach-to-point and reach-to-grasp studies implies that the reach-to-grasp movement is not simply the addition of a "grasp" component to a reach; instead, these mechanically similar movements may have entirely separate cortical and evolutionary foundations.

Hints of these distinctions can be found in landmark electrophysiological and neuroimaging studies; studies that have previously been 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 the reach, reach-to-grasp, hand-to-mouth, and other ecologically relevant movements may be elicited by electrically stimulating distinct anatomical regions (Cooke & Graziano, 2004a, 2004b; Graziano, 2006; Graziano et al., 2005; Graziano, Taylor, & Moore, 2002). Generally, stimulation of 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 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). Graziano and colleagues showed that not only were reach and grasp movements elicited by stimulation of distinct regions but also that that stimulation resulted in *reliable* movements toward consistent end-points, regardless of the muscle recruitment required for their execution. For example, when a hand-to-mouth movement was elicited, the animal's hand would move to its mouth regardless of its initial posture—whether that movement required an extension or flexion of the shoulder or elbow, or inward or outward wrist rotation, stimulation always brought the hand to the mouth. This shows that, contrary to popular belief and longstanding interpretation of early stimulation experiments (see Penfield & Boldrey, 1937), the macaque motor system 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 is that movements that appear similar in their mechanical execution may have entirely distinct neural origins; a distinction stemming from differences in their functional purpose.

Data from human neuroimaging studies implies a similar reach and grasp distinction. In one fMRI study, Cavina-Pratesi and colleagues investigated the posterior parietal cortex's contributions to the transport and grip components of reach-to-grasp actions (Cavina-Pratesi et al., 2010). Participants produced manual actions toward near (i.e., located immediately adjacent to the hand) or far targets (located at the maximum reachable distance from the hand). These actions were either *touch* movements (i.e., contact the target with the knuckles of the hand, without specific hand preshaping) or grasp-to-*lift* movements (with appropriate hand shaping and digit contact). These distance and action manipulations allowed Cavina-Pratesi and colleagues to isolate the transport ("reach") and grip ("grasp") components of prehension, respectively. They report increased neurovascular activity within dorsomedial areas (specifically, SPOC and the rostral SPL) associated with the reach (i.e., for far compared with near targets), and increased activation of dorsolateral areas (specifically, bilateral aIPS and left PMv) when grasping (i.e., for grasp movements relative to touch movements). Since then, however, more sensitive neuroimaging techniques have shown more functional overlap between "reach" and "grasp" areas, suggesting that information relevant for action is computed more broadly, and that the dorsomedial and dorsolateral streams might instead support prehension in a hierarchical fashion (for review, see Gallivan & Culham, 2015). For example, dorsomedial area SPOC shows activation consistent with adaptation to recurring hand and wrist postures in repeated reach-to-grasp actions, suggesting that this region plays a key role in programming these postures for grasping (Monaco et al., 2011). This conclusion is supported by similar findings from neurophysiological recording studies on macaques (Filippini et al., 2017). While the reach versus grasp distinction may not be absolute, the dorsomedial and dorsolateral streams appear at least somewhat specialized for these two aspects of prehension.

Neurophysiology experiments in humans also support this distinction. 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 or dorsal premotor cortex (PMv or PMd, respectively). Virtual PMv lesions impaired hand preshaping during a reach-to-grasp action, altering the fingertip contact points when grasping to lift a small object. Conversely, virtual PMd lesions altered the coupling between the grasp and lift components of that same action (Davare, Kraskov, Rothwell, & Lemon, 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). The authors interpret this distinction in terms of the type of grip used (i.e., whole-hand vs. precision); however, they overlook the implications of a movement's functional goal with respect to one's grip selection. One might grasp the same apple to either pass it to a companion or to take a bite, and (as we will show in the section titled Effects of Actor Intent on Reach-to-Grasp Kinematics) the type of grasp one adopts may depend more on the action's end-goal than on the intrinsic properties of the object.

In sum, there is convergent evidence from electrophysiology, neuroimaging, and psychophysical studies that the reach-to-point and reach-to-grasp actions, despite sharing a transport component, are produced from relatively specialized 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 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 assess not only the end-point accuracy of goal-directed movements but also their temporal and spatial parameters as well. Woodworth noticed that pointing movements were characterised by two phases; an initial, ballistic phase, quick and relatively uniform between movements, and a comparatively slower approach phase, characterized by fine adjustments toward the target (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 nondominant left, especially in conditions of speed imperatives and reduced visual feedback—a finding that has been echoed in numerous studies conducted since (Carnahan, 1998; Elliott et al., 2010; Mieschke, Elliott, Helsen, Carson, & Coull, 2001; Roy & Elliott, 1986, 1989). Modern motion-capture studies show that regardless of handedness, right-handed aiming movements have higher peak velocities (Roy, Kalbfleisch, & Elliott, 1994), shorter movement times (Barthélémy & Boulinguez, 2002; Roy et al., 1994; van Doorn, 2008), and more efficient approach phases (Lavrysen, Elliott, Buekers, Feys, & Helsen, 2007; Mieschke et al., 2001; Roy et al., 1994) than do left-handed movements (Boulinguez, Velay, & Nougier, 2001b; Lavrysen et al., 2007). Conversely, when participants are asked to move as quickly as possible, 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 (Boulinguez, Nougier, & Velay, 2001a), 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 hemispheric specialization (for a brief review, see Grouios, 2006). First, 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 reach, and therefore requires fewer adjustments during the approach/deceleration phase (J. Annett, Annett, Hudson, & Turner, 1979). In simplest terms, this theory states that the right-hand advantage stems from a left-hemisphere specialization in motor output accuracy. Second, the feedback processing theory posits that asymmetries in manual aiming stem not from motor-output asymmetries, but rather from a left-hemisphere advantage for the processing of visual feedback during the ongoing movement (Flowers, 1975). Because the left-hemisphere/right-hand system is less negatively affected by impoverished visual feedback conditions than is the right-hemisphere/left-hand system, the left hemisphere must be more efficient at translating vision into action. One advantage of the feedback processing 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 when responding to target perturbations (Boulinguez, Nougier, et al., 2001). Third on our list is the lateralized attention theory, which states that manual kinematic asymmetries are due to attentional biases favouring the dominant hand (Peters, 1981). That is, right-handers pay more attention to their right hands and are more effective at

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 hemispheric dominance, but in terms of hemispheric specialization for different aspects of movement. In contrast with theories discussed above, 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 than the "dominant" left hemisphere, the right hemisphere has its own advantages and contributions to motor control. In a series of complimentary experiments, Sainburg and colleagues measured how participants respond to unexpected torques or resistance perturbations during left and/or right-handed reaches. Sainburg established that the left hemisphere is optimized for the dynamic control of movement by demonstrating that right-handed participants are better able to correct directional/trajectory manipulations with their dominant hands (Mutha, Sainburg, & Haaland, 2011; Schaefer, Haaland, & Sainburg, 2009). Meanwhile, the same participants are more efficient at correcting force-related end-point manipulations when using their non-dominant left hands (Bagesteiro & Sainburg, 2003; Duff & Sainburg, 2007). In other words, 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 (Wang & Sainburg, 2007).

Clearly, there exist multiple hypotheses of cerebral organization that may explain kinematic asymmetries in reach-to-touch, reach-to-aim, or reach-to-point movements. One would expect that the reach-to-grasp movement would show the same kinematic asymmetries predicted by these hypotheses—that is, if reach-to-grasp and reach-to-touch movements share the same transport component. 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, the introduction of marker-based motion capture systems in the early 1990s resulted in a great many studies on reach-to-grasp kinematics. 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 now able to report and describe kinematics unique to the hand preshaping component of the grasping action—that is, maximum grip aperture, timing of maximum grip aperture, and variability of maximum grip aperture. As when pointing, the reach-

specific kinematics of grasping actions are affected by extrinsic factors of distance (Kudoh, Hattori, Numata, & Maruyama, 1997), location (Paulignan, Frak, Toni, & Jeannerod, 1997), and visual feedback availability (Chieffi & Gentilucci, 1993; Goodale, 1990; Holmes, Mulla, Binsted, & Heath, 2011), as well as intrinsic factors like size (Castiello, Bennett, & Stelmach, 1993) and perceived fragility (Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987). However, somewhat unexpectedly, very few studies on reach-to-grasp kinematics attempt to validate the left/right asymmetries described in the pointing/aiming literature. Those few studies that do compare left-handed and right-handed grasps do not find the robust manual asymmetries that are so prevalent in the reach-to-point literature.

The first study (of which we are aware) comparing left-hand and right-hand grasping 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 both (i.e., between the index fingers of both hands). 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 study, Grosskopf and Kuhtz-Buschbeck (2006) asked right-handed participants to grasp a peg to fit it snugly into a nearby hole, either with or without visual feedback of the ongoing movement. While minor kinematic asymmetries were present when feedback was restricted (specifically, smaller early grip apertures during left-handed movements), when full visual feedback was available participants performed equally well with both hands. Absolutely no asymmetries were observed in reaction time, movement time, peak velocity, average velocity, maximum grip aperture, or any of the other precontact kinematic measures. In yet another study, when Seegelke, Hughes, and Schack (2011) asked participants to grasp a cylinder to either transport it laterally to a nearby pedestal or flip it over, they observed no between-hand differences on any outgoing kinematic measures; again, left and right handed grasps were symmetrical. When Tretriluxana, Gordon, and Winstein (2008) asked participants to grasp and lift small cylinders of various sizes with and without vision of the moving limb, they found slightly higher peak velocities and shorter movement times in the right hand, but again, only when visual feedback was restricted. Finally, Flindall, Doan, and Gonzalez (2014) asked participants to grasp a small water glass that was either nearly full or almost empty; aside from more consistent MGAs during right-handed grasps, the only asymmetry between left-handed and right-handed movements (a tendency for longer movement times in left-handed grasps) was found only when vision was fully restricted, and the movement was completed entirely from memory.

A common thread throughout these studies is that when simple reach-to-grasp movements are performed within comfortable, everyday conditions, asymmetries between the

kinematics of left-handed and right-handed movements are all but absent. This raises two important questions: First, if right-handed 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 preshaping 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 an analysis of action intent. That is to say, the purpose of the movements 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 (Jeannerod, 1986a, 1986b), many studies show that reach-to-grasp kinematics are also affected by secondary movements embedded in the functional chain. That is, the outward kinematics of a reach-to-grasp movement are at least partially determined by what we plan to do with that target after we acquire it. These differences have been replicated for a large range of movements, contrasting simple grasp-to-lift versus grasp-to-pour (Crajé, Lukos, Ansuini, Gordon, & Santello, 2011),grasp-to-raise (Armbrüster & Spijkers, 2006), grasp-to-open (e.g., with a jar; Friedman & Flash, 2007), and grasp-to-throw, grasp-to-place, or grasp-to-pass to a confederate (Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Becchio, Sartori, Bulgheroni, & Castiello, 2008). The speed and timing of our outward reach depends on whether we are grasping-to-move or grasping-to-use an item (Valyear, Chapman, Gallivan, Mark, & Culham, 2011), or grasping-to-bring it near the mouth (Cavallo, Koul, Ansuini, Capozzi, & Becchio, 2016). In general, these studies report that the initial outward grasping action will be adjusted to suit the mechanical requirements of that secondary or subsequent purpose. When we intend quick, ballistic secondary actions (e.g., throwing or tossing movements), 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., grasp-to-place or grasp-to-pass movements). Interestingly, none of these studies reported any lateralized effects of task (though only Armbrüster and Spijkers, 2006, tested left-handed movements). In other words, these studies show that if we are grasping, say, a kitchen spoon to move it into a drawer, we will grasp it with different reach kinematics, arm and wrist postures, and grasp contact points than when grasping it to stir soup within a pot (Valyear et al., 2011); they do *not* show that these kinematic

differences will vary between left-handed and right-handed actions.

None of this is inherently 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? Will we still adopt different postures for mechanistically identical but functionally distinct actions? 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. These actions shared nearly identical spatial parameters: participants began the movement from the same position, assumed the same starting hand posture, and reached-to-grasp the same objects from the same distal location, to bring those targets back toward the body. The only difference between the two grasps concerned the ultimate goal of those actions; participants grasped the targets with intent to either (a) place them in a container located just beneath the chin, or (b) eat them (Flindall & Gonzalez, 2013, 2014, 2015, 2016, 2017; Flindall et al., 2015). While left-hand and right-hand kinematics of the reach (i.e., MT, PV, PVt) were found to be identical in the grasp-to-place task, the authors reported a consistent MGA asymmetry linked with grasp-to-eat movements. Specifically, participants generate significantly smaller MGAs when grasping with intent to eat the target, but only when using their right hands. When grasping with their left hands, they produce the same hand preshaping 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; Flindall et al., 2015) and in children over the age of 10 (Flindall & Gonzalez, 2015). Though the signature manifests bimanually in children younger than 10 years and in approximately 25% of left-handers, its consistent rightward lateralization suggests a left-hemisphere origin. Further investigation shows that actually chewing and consuming the target is 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; nylon hex nuts, when grasped with the right hand, also elicit smaller MGAs when they are to be brought to the mouth (Flindall & Gonzalez, 2016). To test whether the kinematic signature was simply the left-hemisphere/right hand system's reaction 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 glass; the kinematic signature, again, was unaffected (Flindall & Gonzalez, 2017). To ensure that mouth movement itself was not responsible for observed task differences, participants were asked to "eat" and "place" as before while either keeping their mouths closed (touching the item to their lips before discarding it in the "eat" condition), or opening their mouths "as if to eat" the item (while still bringing it directly to the container in the "place" condition). Once more, only the true grasp-to-eat action elicited smaller MGAs; the closed-mouth "eat" action, as well as both "place" actions, elicited significantly larger MGAs, regardless of mouth movement (Flindall & Gonzalez, 2016). All told, this consistent kinematic signature distinguishing the grasp-to-eat/hand-to-mouth action from the grasp-to-place action cannot be attributed to precision, direction, distance, complexity (see the section titled Right-Handedness and Complex Movements), speed requirements of the secondary movement, or as a by-product of practice with the dominant or preferred hand (Flindall et al., 2015). Nor can it be explained by efficiency asymmetries with respect to movement planning; in all trials, participants were given a full second to plan their movements before being given the go signal, and participants were instructed to move "with an emphasis on accuracy, rather than speed." Instead, the signature implies a distinct motor plan for bringing a to-be-grasped item into the mouth; a plan that is either lateralized to the left hemisphere, or at least accessible only during right-handed movements.

Meta-analysis methods and results

Methods

To better illustrate this signature, we performed a meta-analysis on previously published data collected by Flindall, Gonzalez, and colleagues (Beke et al., 2018; Flindall & Gonzalez, 2013, 2014, 2015, 2016, 2017; Flindall et al., 2015; van Rootselaar et al., 2018). While the experiments varied with respect to question, experimental conditions, and total number of trials, they shared common controls (i.e., grasp-to-eat and grasp-to-place tasks), allowing for a simple within-subjects analysis of kinematics of the reach-and-grasp action using a participant pool far larger than anything reported in the kinematic literature to date.

All kinematic variables were taken directly from the data sets 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 Froot Loops™, 11 mm and 15 mm 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 this analysis. 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 criteria 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 a full description 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.[1] First, results from

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[1] To ensure that the inclusion of left-handed participants did not affect our overall conclusions with respect to the task-dependent asymmetries we discuss in this report, we performed separate supplementary analyses on our right-handed and left-handed participants (right-handers $n = 97$; left-handers $n = 22$). All main effects and interactions reported in this review were consistent between left-handed and right-handed participants, save for the following exceptions: [1] The main effect of *hand* on MGA (reported below) was limited to our right-handed participant sample, $F(1, 96) = 18.32, p < .001, \eta^2 = .160$; this effect was not significant among our left-handed participants ($p = .419$). Consistent with the main effect of *hand* on MGA reported in our main analysis, right-handers produced smaller MGAs when using their right hands than they do when using their left hands; the same trend was present in our left-handed group (right < left), though in this smaller sample the difference was not significant. [2] The main effect of *task* on PV, reported in our main analyses, was not significant in our right-handed group, $F(1, 96) = 2.21, p = .141, \eta^2 = .022$. While there was no significant difference between PVs in the *eat* ($.73 \pm .015$ m/s) and *place* ($.725 \pm .015$ m/s) tasks among our right-handed participants, the trend (eat > place) was consistent in both groups. This same effect was significant in our left-handed group, $F(1, 21) = 8.08, p = .010, \eta^2 = .278$. [3] A weak main effect of *hand* on MGAt was found in our right-handed sample, $F(1, 96) = 5.93, p = .017, \eta^2 = .058$; this effect was not significant in our left-handed participants ($p = .189$), nor was it found in our main analysis ($p = .130$). Right-handed participants reached their MGA relatively sooner when using their left hands (56.9% of MT) than when using their right hands (58.7% MT); this trend was reversed in left-handers, who had earlier MGAts when using their right hands (56.7% MT) than when using their left hands (59% MT), though, again, this difference was not significant. [4] The main effect of size on vMGA that we report in our main analysis was not significant in our left-handed sample. Left-handed participants showed the same trend observed in our right-handed participants, and our main analyses, namely that MGAs for smaller targets are more consistent (mean $SD = 2.617 \pm .21$ mm) than are MGAs for large targets (mean $SD = 2.688 \pm .21$ mm), though this difference was not significant, $F(1, 21) = 0.09, p = .772, \eta^2 = .004$. [5] The weak Hand × Task interaction on vMGA reported in our main analyses did not reach significance in our right-handed participants, $F(1, 96) = 3.88, p = .052, \eta^2 = .039$, nor did it reach significance in our left-handed participants, $F(1, 21) = 1.90, p = .182, \eta2 = .083$. Consistent with our main analysis, both right-handers and left-handers produced their most consistent MGAs when using their right hand. [6] A Task × Size interaction on vMGA, not present in our main analyses, was found in our left-handed participants, $F(1, 21) = 10.54, p = .004, \eta^2 = .334$. The source of this interaction is a significant difference in variability of MGAs when left-handers grasp large targets to eat (mean $SD = 2.35 \pm .18$ mm), versus when they grasp them to place (mean $SD = 3.02 \pm .24$ mm), $t(21) = -3.177, p = .005$. The eat/place comparison was not significant when grasping small targets ($p = 450$). Because (a) our main effect of interest that forms the foundation of this analysis (i.e., the Hand × Task interaction on MGA) was consistent between handedness groups; (b) the differences between analyses were limited to weak ($\eta^2 < .1$) or weakly significant ($.01 < p < .05$) effects; and (c) trends were consistent between samples (save for the main effect of *hand* on MGAt, which favoured the dominant hand in both groups), we limit our in-text reporting to analyses on our inclusive sample. The data used for all analyses have been made available at bit.ly/fg2019data (full link: https://osf.io/jdutc/?view_only=145d13ffc23b44ad9e76ae26d40a724b).

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

Source	Participants
Flindall, J. W., & Gonzalez, C. (2013). On the evolution of handedness: Evidence for feeding biases. *PLOS ONE, 8*(11), e78967.	*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.	*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.	*n* = 12; 7 females, 1 left-handed
Flindall and Gonzalez (2017). The inimitable mouth: Task-dependent kinematic differences are independent of terminal precision. *Experimental Brain Research, 235.6*, 1945–1952.	*n* = 25; 15 females, 0 left-handed
van Rootselaar, N., Flindall, J. W., & Gonzalez, C. (2018). Hear speech, change your reach: Changes in left-hand grasp-to-eat kinematics during simultaneous speech processing. *Experimental Brain Research,* 1–11.	*n* = 29; 22 females, 0 left-handed
Beke, C., Flindall, J. W., & Gonzalez, C. (2018). Kinematics of ventrally mediated grasp-to-eat actions: Right-hand advantage is dependent on dorsal stream input. *Experimental Brain Research, 236*, 1621–1630.	*n* = 21; 14 females, 0 left-handed

our investigation of left-handers suggest that they, as a group, are not significantly different from right-handers in terms of the grasp-to-eat Hand × Task interaction that forms the justification for these analyses (Flindall et al., 2015). Second, inconsistent main effects of hand, task, and/or size from individual studies (again, see Flindall & Gonzalez, 2015, 2016, 2017), combined with extreme differences in size between the two groups included here, preclude any meaningful conclusions being drawn from differences found; future projects in our lab aim to increase our sample of left-handed participants to enable such comparisons. Each of our participants provided written informed consent prior to testing, in accordance with the principles expressed in the Declaration of Helsinki and with the approval of the University of Lethbridge Human Subjects Research Committee.

Three-way ANOVA: Results

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-subjects 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.

Target size affected all kinematic variables save peak velocity (see Table 2). Strong main effects of target size were identified for MT, $F(1, 118) = 135.20$, $p < .001$, $\eta^2 = .534$; PVt, $F(1, 118) = 124.27$, $p < .001$, $\eta^2 = .513$; MGA, $F(1, 118) = 853.01$, $p < .001$, $\eta^2 = .878$; and MGAt, $F(1, 118) = 163.79$, $p < .001$, $\eta^2 = .581$. A weak main effect of size was found in vMGA, $F(1, 118) = 4.76$, $p = .031$, $\eta^2 = .039$. These effects,

identical to those reported elsewhere (Bootsma, Marteniuk, MacKenzie, & Zaal, 1994), confirm that reach-to-grasp actions directed toward smaller targets have an elongated postpeak velocity phase of the movement; this lengthening of the deceleration phase results in longer MTs, and earlier PVts and MGAts. MGA is also smaller and slightly more consistent when grasping smaller targets. A Size × Hand interaction was found on PV, $F(1, 118) = 8.39$, $p = .004$, $\eta^2 = .066$. Paired-samples *t* tests revealed that this effect was due to smaller items eliciting faster PVs (.765 ± .02 m/s) than large items (.760 ± .02 m/s), in right-handed movements only, $t(118) = 3.001$, $p = .003$. This effect of size was not significant during left-handed movements, $t(118) = -1.068$, $p > .2$.

A main effect of hand was found on MGA, $F(1, 118) = 18.16$, $p < .001$, $\eta^2 = .133$, 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 (cf. footnote 1).

A main effect of task was found on PV (cf. footnote 1), $F(1, 118) = 7.25$, $p = .008$, $\eta^2 = .058$, 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, $F(1, 118) = 37.73$, $p < .001$, $\eta^2 = .242$, wherein grasp-to-eat movement elicited smaller MGAs (23.85 ± .42 mm) than did grasp-to-place movements (25.08 ± .41).

A strong Hand × Task interaction was also found on MGA, $F(1, 118) = 17.41$, $p < .001$, $\eta^2 = .129$, while a weak Hand × Task interaction was found on variability of MGA, $F(1, 118) = 5.22$, $p = .024$, $\eta^2 = .042$. Follow-up paired-sample *t* tests revealed that both of these effects stemmed from task differences during right-handed movements; right-handed grasp-to-eat movements produced smaller MGAs (22.7 ± .42 mm) than did left-handed grasp-to-eat movements (25.42 ± .44 mm), $t(118) = -6.354$, $p < .001$, and right-handed grasp-to-place movements (24.74 ± .48 mm), $t(118) = -7.187$, $p < .001$ (see Fig. 1). These right-handed grasp-to-eat MGAs were also less variable (2.52 ± .11 mm) than those in left-handed grasp-

Table 2 Between-participant means and standard errors for reach and grasp kinematics, averaged by condition (N = 119).

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, H×S	S	S, H, T, H×T	S	S, H×T

Note. Variables reported are MT (movement time), PV (peak velocity), PVt (time of peak velocity), MGA (maximum grip aperture), vMGA (mean intertrial variability of maximum grip aperture), MGAt (time of MGA), and vMGA (variability of maximum grip aperture). Significant within-subject three-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 × Task) are listed below columns for each kinematic measure

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 were significant ($p > .05$).

Two two-way ANOVAs: Results

To highlight the contrast between our two tasks, and facilitate comparison between these 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 two-way ANOVAs, with factors hand (left, right) and size (small, large), the results of which are reported below.

Main effects of size were observed in both eat and place ANOVAs on the following variables: MT, $F(1, 118) > 105.98$, $p < .001$, $\eta^2 > .473$; PVt, $F(1, 118) > 58.31$, $p < .001$, $\eta^2 > .331$; MGA, $F(1, 118) > 570.38$, $p < .001$, $\eta^2 > .829$; and MGAt, $F(1, 118) > 111.62$, $p < .001$, $\eta^2 > .486$. In both tasks,
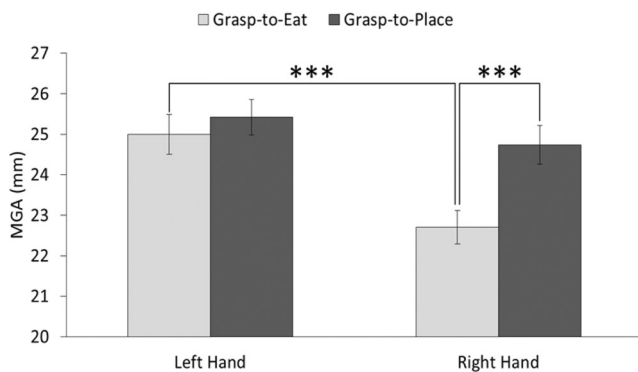

Fig. 1 Maximum grip apertures (between-participant means and standard errors) of left-handed and right-handed grasp-to-eat and grasp-to-place movements (N = 119). Right-handed grasp-to-eat movements produce significantly smaller MGAs than do right-handed grasp-to-place movements or left-handed movements of either type. ***$p < .00001$

grasps toward small items had smaller MGAs and longer MTs, with earlier relative PVts and MGAts (implying elongated deceleration/approach phases).

Main effects of hand were found in the grasp-to-eat task, affecting all grasp kinematics: MGA, $F(1, 118) = 40.37$, $p < .001$, $\eta^2 = .255$; MGAt, $F(1, 118) = 4.79$, $p = .031$, $\eta^2 = .039$; and vMGA, $F(1, 118) = 8.56$, $p = .004$, $\eta^2 = .068$. When grasping-to-eat with their right hands, participants produced smaller (22.7 ± .42 mm), relatively later (58.6 ± .9% MT), and less variable (2.52 ± .11 mm) maximum grip apertures than when grasping to eat with their left hands (MGA, 25.0 ± .49 mm; MGAt, 57.0 ± .9% MT; vMGA, 2.87 ± .13 mm). Notably, no main effects of hand were found within the grasp-to-place movement, on any kinematic variable (all ps > .10).

Significant Hand × Size interactions were found in PV, in both tasks; grasp-to-eat, $F(1, 118) = 5.70$, $p = .019$, $\eta^2 = .046$, and grasp-to-place, $F(1, 118) = 4.03$, $p = .047$, $\eta^2 = .033$. Follow-up paired-samples t tests revealed that both interactions were due to faster peak velocities achieved when grasping small (rather than large) targets, limited to the right hand (see Table 3 for means and standard errors). While these effects were consistent with results of our three-way ANOVA, neither within-task comparison, eat, $t(118) = 2.380$, $p = .019$; place, $t(118) = 1.936$, $p = .052$, was significant following Bonferroni correction (> .0125).

Discussion

General discussion

In the current review, we provide an analysis of data collected in separate experiments conducted from 2013–2017. These experiments shared control conditions in which participants were asked to reach to grasp small cereal items—small

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 ($N = 119$)

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	H×S	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	H×S	S	H, S	H, S	H

Note. 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 two-way ANOVA results [factors hand (left, right), and size (small, large)] by main effect (H: hand; S: size) and interaction (e.g., H×S: Hand × Size) are listed below columns for each kinematic measure within each task group

(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), for left-handed and right-handed movements, were analysed via a three-way ANOVA, with factors hand (left, right), task (eat, place), and target size (small, large). We found no differences between the hands for any kinematic measure, save within MGA. Follow-up comparisons revealed that the main effects of hand and task were 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-hand and left-hand place conditions (see Fig. 1). To facilitate comparisons with the grasping kinematics literature, we split our data by task (eat, place) and conducted two two-way ANOVAs, with factors hand (left, right) and size (small, large). These ANOVAs confirmed that all significant kinematic differences between left-handed and right-handed actions were limited to the grasp-to-eat task. Within the place task, no difference between the hands manifested within any kinematic measures. In contrast, asymmetries in the eat condition, for all kinematic measures of the grasp component (MGA, MGAt, and vMGA) were robust; right-handed MGAs are smaller, relatively later, and more precise (i.e., less variable) than are left-handed MGAs. This finding is important for two reasons: first, these effects, isolated as they are to grasp-to-eat movements, highlight the practical difference between two tasks that differ only with respect to 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 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 reaching and grasping: Neuroanatomy and lateralization

The dual visuomotor channel theory of grasping states that the neural circuits responsible for producing the *reach* and *grasp* components of reach-to-grasp movements are located in distinct channels within the dorsal vision-for-action stream. Recall that in nonhuman primates the vision-for-action stream's dorsolateral "grasp" pathway begins in area MT, which receives visual information from primary visual cortex (V1). MT projects to the inferior parietal lobule (IPL), in the fundus of the intraparietal sulcus (IPS), to areas AIP (area aIPS in humans) and VIP.[2]. AIP and VIP have reciprocal connections with ventral premotor cortex (PMv) areas F4 and F5, respectively. The dorsomedial "reach" pathway begins in occipital cortex, in visual areas V2, V3, and V3A in area PO; these regions in turn project to area V6 and V6A in the superior parietal lobule (SPL), which sends information to

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[2] Though the IPL also receives somatosensory input, the majority of its afferents arise in occipital regions of the dorsal stream (Rizzolatti & Matelli, 2003).

dorsal premotor cortex (PMd). PMd, like PMv, projects to M1.

PMd may also be involved in the control of grasping (Davare et al., 2011), even though PMd is considered part of the dorsomedial channel (Karl & Whishaw, 2013). Similarly, in macaques, the anterior intraparietal sulcus (AIP) in the dorsomedial channel has been shown to contain populations of visuomotor neurons that respond to the type of *grasp* being performed (i.e., whole-hand or precision grasp; Davare et al., 2011). In fact, 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; Filippini et al., 2017; Verhagen, Dijkerman, Medendorp, & Toni, 2013) imply that, in both humans and NHPs, 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 more active during effective execution (Bonini et al., 2010) or direct observation (Ferri et al., 2015) of grasps.

Instead of a functional dichotomy based on the "reach" and "grasp" components of prehension, converging evidence suggests that the dorsomedial and dorsolateral streams both support functional grasping, albeit hierarchically (Filippini et al., 2017; Gallivan & Culham, 2015; Verhagen et al., 2013). That is, instead of independently programming hand preshaping and limb transport, the dorsolateral and dorsomedial streams instead respectively support the *planning* and *execution* of grasping actions. Virtual lesion studies show that TMS applied to aIPS (in the dorsolateral stream) diminish alpha suppression associated with grasping movements early in the grasp (i.e., during planning and early execution); in contrast, TMS applied to sPOC (in the dorsomedial stream) only affects alpha suppression some 300 to 500ms after movement onset (Grol et al., 2007). Recent neuroimaging data reveal that dorsolateral areas, including aIPS, discriminate between real objects and 2-D images of those objects when planning a grasping movement as compared to a reaching one (Freud et al., 2018), again demonstrating this stream's involvement in planning movements.

Current theories of grasp execution state that motor plans begin with information arising from primary visual areas in the occipital lobe. This information is passed to the dorsal visuomotor stream where it is translated into motor-relevant coordinates; a given reach-to-grasp action is based on visual information that conveys object properties and affordances (Karl & Whishaw, 2013). Recall, however, that information processed by the dorsal stream is ephemeral, and does not contribute to the formation of long-term memories (Hu & Goodale, 2000; Milner & Goodale, 2008); it therefore seems obvious that for object affordances to contribute to the grasp, some lasting knowledge regarding the properties and purpose of the to-be-grasped object must somehow reach the dorsal

stream from ventral "vision-for-perception" areas. The necessary connections certainly exist; in nonhuman primates, area V4 (in the ventral stream) shares connections with areas MT and LIP, and the anterior inferotemporal cortex (another ventral stream region) has reciprocal connections with AIP (for review, see Binkofski & Buxbaum, 2013). So while neither the dorsomedial nor the dorsolateral circuits *produce* memories, the dorsolateral circuit has the connections with ventral stream areas necessary to *use* memory when producing action. It is now believed that aIPS in the dorsolateral stream may produce movement plans based on target affordances and conscious decisions, a plan which is then adjusted by dorsomedial areas to fit current environmental context (Grol et al., 2007). During execution, somatosensory and visual feedback from the moving limb is compared to expectations from the original plan via reciprocal connections between aIPS 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 model. 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 analyses of grasp-to-place movements show that the left and right hands are identical in terms of movement execution. Here, however, we show that robust kinematic differences between the hands can be found 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 differences in the primary (acquisition) or secondary (functional) movement phases exist to predict them, their origin must lie in asymmetries within the neural circuits responsible for their production.

It is natural to speculate that these asymmetries lie somewhere within the visuomotor circuits responsible for producing grasp kinematics; however, in the absence of supporting neuroimaging data, such speculation is beyond the scope of this review. Instead, we pivot to discuss whether a lateralized advantage for grasp-to-eat actions is consistent with other well-established left hemisphere specializations (i.e., language, praxis, and complex movements). Concurrently, we briefly review several prominent theories on the evolutionary origins of dextrality, relating our grasp-to-eat performance asymmetry to each.

Origins and development of right-handedness in humans

Across all cultures, humans share a species-wide inclination towards right-hand dominance (Coren & Porac, 1977; Faurie, Schiefenhvel, leBomin, Billiard, & Raymond, 2005). While

individual animals are commonly observed to prefer one hand over the other, the species-wide consistency of hand preference in humans is unique (Cashmore, Uomini, & Chapelain, 2008; Corballis, 1989, 1997; Fitch & Braccini, 2013). In contrast, functional cerebral lateralization itself is hardly exceptional; lateralized advantages in auditory and visual perception are so common that many researchers believe that cerebral lateralization should be considered a rule of vertebrate development, rather than the exception (Fitch & Braccini, 2013). Still, the tendency toward right-hand preference, when considered in terms of degree and prevalence, sets humans apart from other vertebrates in general, and other primates in particular.

Despite decades of research, the precise origin of right-hand dominance is still being debated. As the proportion of the population exhibiting right-hand preference is consistent across cultures, and the fact that left-handed parents are more likely to have left-handed children than are right-handed parents (M. Annett, 1985), a genetic component is likely. Hypotheses proposed by Annett (M. Annett, 1985, 2013) and McManus (1985) have been used to generate plausible models for the spread of a "left-hemisphere dominance" gene through a population, arriving at the stable proportions we see today in the global population.

Annett and McManus conceived of similar mechanisms for the spread of left-hemisphere dominance for the control of manual behaviour and language. Annett's right-shift theory (M. Annett, 1985, 2013) proposes a single gene that biases one toward left-hemisphere cerebral dominance. That is, even those with only one copy of the right-shift gene[3] (i.e., RS^{+-}) are biased toward right-handedness. Annett's model is additive, such that those with two copies of the right-shift gene (RS^{++}) are more strongly biased toward left-hemisphere dominance, perhaps even to the detriment of right-hemisphere function (Corballis, 1997). Those without the gene (RS$^-$) have no bias, and handedness is essentially determined by chance. In a similar model, McManus proposes the existence of a gene which codes for lateralized cerebral dominance in general, without specifying a direction (McManus, 1985). McManus predicts a "dominance" gene (D) that pushes one toward cerebral asymmetry, and strongly lateralized function; another gene, the "chance" gene (C), pushes one toward hemispheric symmetry. In contrast with Annett's passive RS$^-$ allele, McManus's C gene might confer its own benefits (Corballis, 1997). The D gene, promoting cerebral dominance, may improve one's language, fine motor skills, and other left-hemisphere functions at the expense of other abilities typically lateralized to the right hemisphere (e.g., spatial skills like

navigation, or social skills like the ability to interpret emotional affect in others). In contrast, the C gene might decrease hemispheric dominance at the expense of language and praxis, but to the benefit of social and spatial skills. Because the specializations of both hemispheres are important for reproductive success, the model predicts greater fitness for heterozygotes (DC) than for homozygotes (either DD or CC), which is necessary to account for the real-life stability of the dextral:sinistral ratio (9:1). For the sake of simplicity, and because McManus's DD and DC phenotypes are analogous to Annett's homozygotes (RS++) and heterozygotes (RS+−), respectively, we will treat the two models as equivalent.

Both models predict hand preference proportions roughly equal to that observed in the real world. A strictly Mendelian interpretation predicts that roughly half of one-quarter of the population should be left-handed, which nearly equals the estimated 11%–13% prevalence of left-handedness reported by most researchers (Brackenridge, 1981; Levy, 1974; Porac & Coren, 1981). Of course, the simple genetic model for handedness is not perfect, having (at least) three obvious flaws. First, it does not account for hand preferences in twins who, even when genetically identical are often discordant with respect to handedness (Sicotte, Woods, & Mazziotta, 1999). Second, it does not account for similarities in language lateralization between left-handers and right-handers. If language and handedness are influenced by the same genes, and left-handedness arises by chance, then half of left-handers should have language lateralised to the right hemisphere; instead, 76% of left-handers have normal (left) lateralization for language (Fitch & Braccini, 2013). Third, while the genes in both models have been extensively modelled, they have yet to be actually identified.[4] Nevertheless, if the gene determining left-cerebral dominance improves evolutionary fitness, mathematical models provide a shockingly brief timeline for its spread through a population. Even conservative estimates are incredibly short; if DD provided even a 1% increase in evolutionary fitness compared to CC, right-handedness could have reached asymptotic levels in as few as 1,300 generations, or roughly 30,000 years (Corballis, 1997). This proposed celerity does not require that handedness be observed in NHPs, or even other hominids. Regardless, a significant amount of research has been conducted to assess whether our closest relatives show similar patterns of hand dominance.

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[3] Originally named for the side of handedness, the right-shift model was amended early on to more accurately reflect a leftward shift in cerebral dominance. For the sake of consistency in subsequent publications, Annett continues to refer to her model using the original "right-shift" moniker.

[4] On the basis of gender-based differences in the incidence of abnormal cerebral-lateralization disorders, some have proposed that the laterality gene may be on the X chromosome (Crow, 1995; Fisher et al., 1990). Others have proposed a connection with the gene responsible for *situs inversus,* a disorder in which the major visceral organs are reversed from their normal positions (Brown & Wolpert, 1990; Corballis & Morgan, 1978; Layton, 1976; though cf. McManus, Martin, Stubbings, Chung, & Mitchison, 2004). Again, however, the *situs inversus* gene has not been identified in humans, though researchers have localised it in mice to somewhere on chromosome 12 (Hanzlik et al., 1990).

Handedness in primates and early hominids

In their review on the topic, Fitch and Braccini (2013) concluded that, at the level of species, nonhuman primates (NHPs) show weak (if any) species-wide patterns of manual lateralization. Chimpanzees occasionally have a right-side bias for prehension, but it is limited and task specific. Baboons and chimpanzees may have a right-side bias for facial and manual gestures, but again, the bias is much weaker than that observed in humans. Interestingly, some primates (including marmosets, red-capped mangabeys, rhesus macaques, and chimpanzees) have consistent eye preferences when peering at *food* through a tube, but no preference when viewing nonfood items (Braccini, Lambeth, Schapiro, & Fitch, 2012; Hook-Costigan & Rogers, 1995). While these perception biases implicate task-specificity as an important factor when investigating lateralized behaviour, in this case they do not correlate with hand preference (Fagot & Vauclair, 1991). One should keep in mind that most observations come from animals in captive populations, where right-side biases for gestures and self-feeding may be influenced by their human caretakers (Cochet & Byrne, 2013; Fitch & Braccini, 2013). When wild populations are observed, hand preferences tend to be weaker, and even less likely to be group wide (Cochet & Byrne, 2013).

Even our closest NHP relatives, chimpanzees, represent an evolutionary lineage from which we diverged some four to 6 million years ago (Chen & Li, 2001). What about handedness in species more closely related to modern humans? Evolutionary biologists have analysed early hominid bones for size and wear asymmetries, and have identified exemplars of "likely right-handed" individuals from several of our closest relatives (Cochet & Byrne, 2013; Frayer et al., 2016; Steele, 2000), including *Homo erectus* (Walker & Leakey, 1993) and *H. Sapiens neanderthalensis* (Frayer, Fiore, Lalueza-Fox, Radovcic, & Bondioli, 2010; Trinkaus, Churchill, & Ruff, 1994). Unfortunately, it is difficult to infer population-level handedness from the fossil record, due to a paucity of fossilized samples in general, and bilaterally matched upper-limb bones in particular. Some researchers have looked to teeth for evidence of right-hand preference, arguing that the angle and orientation of striations found on the majority of Neanderthal teeth are consistent with scrapes from a crude knife held in the right-hand. While this method has been criticized (see Bax & Ungar, 1999), it is the best fossil evidence we have for population-level right-hand dominance in a nonhuman hominid.

Greater support for right-handedness in early hominids comes from archaeological studies of ancient technology and art. In a famous report, Toth (1985) determined that the majority (56%) of knapping flakes produced during the manufacture of stone tools had a shape and orientation consistent with right-handedness in the manufacturer. Follow-up studies suggest that more than 70% of stone flakes from the lower and middle Pleistocene (~1.5 million years ago) were made by right-handed knappers, and that the tools themselves had a chirality favouring right-handed use (Cornford, 1986; White, 1998).

Early hominid art has also been used to infer handedness, though the direction of laterality implied by cave drawings is mixed. The overwhelming majority of hand-print negatives suggest a right-handed artist, while the proportion of right-facing animals suggest that 50%–60% of prehistoric artists were probably *left*-handed (Cashmore et al., 2008).

Action intent and left-hemisphere dominance

Taken together, the combined observational, fossil, and archaeological evidence for right-handedness in our evolutionary past is at best weak, and at worst, problematic and/or conflicting (Cashmore et al., 2008; Cochet & Byrne, 2013; Corballis, 1989; Fitch & Braccini, 2013). Given that the necessary timeline for evolution of a right-handed gene is so brief, there is no reason to assume that nonhuman species need have been right-handed to explain modern incidence of right-hand preference. All we need to assume is that a shift to left-hemisphere dominance somehow lead to improved evolutionary fitness. There is considerable debate, however, as to whether right-handedness produced such an advantage in and of itself, or whether advantage from another left-hemisphere specialization provided the scaffold upon which right-handedness was built. The following section briefly reviews several hypotheses regarding the link between left-hemisphere specializations and right-hand dominance in general, relating our grasp-to-eat kinematic signature to each.

Right-handedness and language

Aside from handedness, the most well-known example of laterality is with respect to control of language. Given the consistent lateralization of speech and handedness, an association between these functions has long been suspected (Knecht et al., 2000a, b). However, while the vast majority of right-handers have language lateralized to the left hemisphere (Knecht et al., 2000a, b), the reverse is not true for left-handers; in fact, an overwhelming majority of left-handers (70%–80%) have normal lateralization for language (Cochet, 2016; Knecht et al., 2000a, b), leading some to postulate that genes driving handedness and lateralization of language act independently (Corballis, Badzakova-Trajkov, & Häberling, 2012). Of course, hand preference in left-handers is neither as consistent nor as strongly lateralized as it is in right-handers, confounding discussions about the possible link between handedness and language even further. Measures of hand preference vary significantly by task, with most left-handers producing patterns of behaviour that are identical to those of right-handers (Boulinguez et al., 2001a, b; Flindall et al., 2015; Stins, Kadar, & Costall, 2001). For

example, preferences for precision grasping and self-feeding seem to be lateralized to the left-hemisphere/right-hand system, even when the left-hand is dominant overall (Gonzalez, Flindall, & Stone, 2014; Sacrey, Arnold, Whishaw, & Gonzalez, 2013; Stone, Bryant, & Gonzalez, 2012). Nevertheless, there is evidence that handedness and language are somewhat related—at least, in humans, if not necessarily in our nearest relatives.

Aside from a small number of isolated examples, there is little evidence that NHPs have left-hemisphere bias for vocal communication (for review, see Corballis, 1989; Fitch & Braccini, 2013). This is not particularly surprising, given that complex language is uniquely human. The evidence for language in early hominids is similarly weak; cranial endocasts suggest there may have been left-hemisphere expansions in regions associated with language in modern humans (Begun & Walker, 1993; Holloway, 1981), though such evidence should probably be interpreted with skepticism (Holloway, 1978; cf. Falk, 1983).

Evidence for a causal link between language and handedness is buoyed by preference for meaningful or communicative gestures. Some NHPs gesture predominantly with their right hands when communicating with both humans and conspecifics (for review, see Fitch & Braccini, 2013). In addition, lateralized preferences for communicative gestures are more consistent than are preferences for manipulative actions, both within and between NHP individuals.

In adult humans, correlation between hand preference for gesturing and that for manipulative actions (e.g., grasping) is not always present; in some cases, the correlation may even be negative (Cochet, 2016). In contrast, children (even strongly left-handed children) have a distinct preference to use their right hands for declarative gestures—that is, when pointing at objects or people to whom they wish to refer (Jacquet, Esseily, Rider, & Fagard, 2012). This preference seems to be independent of overall hand preference for manipulative actions.[5]

With respect to manual kinematics, there is evidence that speech production may interfere with unimanual action performance. Lomas and Kimura (1976) investigated the influence of concurrent speech on the execution of several unimanual tasks. They found that while dominant-hand performance advantages were limited to right-handed participants, a concurrent speaking task interfered with this advantage. In contrast, our own investigation found a concurrent speech processing task to have no effect on the grasp-to-eat signature when participants used their right hands (van Rootselaar et al., 2018). Instead, listening to audiobook excerpts resulted in the effect manifesting in participants' *left* hands. This result may be related to the right hemisphere's role in interpreting pragmatics, analogy, and humour in

language (Abusamra, Côté, Joanette, & Ferreres, 2009; Shields, 1991), or to a temporary reduction in interhemispheric inhibition (Duque et al., 2007).

Of particular relevance to the handedness-language debate is our signature's inconsistent lateralization in left-handed participants (Flindall et al., 2015). It may be that the grasp-to-eat kinematic signature is predictive of language lateralization; unfortunately, we did not assess language lateralization in any of our studies. Future studies will investigate the kinematic signature in a large cohort of sinistrals, that we may infer the relationship between "abnormal" lateralization of the grasp-to-eat signature and abnormal lateralization of language.

Right-handedness and praxis

The extent to which we rely on tools in our day to day lives is another factor that distinguishes humans from other animals. The link between right-handedness, language, and tool-use has been investigated for over a century, ever since researchers recognized that aphasia and apraxia were commonly comorbid (Liepmann, 1900, as cited in Goldenberg, 2003). Modern lesion studies confirm that victims of left hemisphere stroke are more likely to have difficulty pairing tools with an appropriate motor response than are right hemisphere stroke patients or age-matched controls (Kimura & Archibald, 1974; Laimgruber, Goldenberg, & Hermsdörfer, 2005; Rushworth, Nixon, Wade, Renowden, & Passingham, 1998). Colostomy patients also have difficulty matching tools with appropriate actions when using their left hands (Frey, Funnell, Gerry, & Gazzaniga, 2005), especially if the cue is impoverished (i.e., a line drawing of a hammer, rather than a photograph of one).

Of course, the left hemisphere's role in producing symbolic or pantomimed movements has also been investigated in healthy participants. Heath, Westwood, Roy, and Young (2002) showed that participants produced longer and straighter pantomimed sawing movements when using their right hands; movements were even more efficient if the participant was permitted to hold a real saw while pantomiming. Similarly, when healthy right-handed adults are asked to plan left-handed or right-handed tool-use actions, fMRI reveals that left-hemisphere regions (including networks in the posterior parietal cortex, posterior temporal cortex, inferior middle frontal cortex, and dorsolateral prefrontal cortex) are activated regardless of which hand participants plan to use (Johnson-Frey, Newman-Norlund, & Grafton, 2004). These studies imply that the left hemisphere is critical for both the selection of an appropriate movement, and the execution of that movement, regardless of one's overall hand preference.

The supposition that a distinct motor engram for hand-to-mouth movements appears to be lateralized to the left cerebral hemisphere is in line with the idea that left-hemisphere function is particularly important for selecting appropriate, learned motor actions in response to particular stimuli. It is difficult to

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[5] Though we remind the reader that hand preference for manipulative actions is not homogeneous; right-hand preference is more robust for hand-to-mouth movements than it is for other manipulative actions.

say, however, whether the grasp-to-eat kinematic signature is linked with the right-hand advantage for *tool use*, specifically; no tools were present in any of our experiments, and participants always grasped the targets with a precision grip and an empty hand. Nevertheless, it is not unreasonable to suggest that kinematic advantage for grasping for self-feeding might extend to tool-use for the same purpose. Ongoing studies within our group, involving a variety of culturally-diverse tools, aim to explore this possibility.

Consider that left-hemisphere damage results in motor impairments beyond those defined by apraxia; complex, sequential movements in general (e.g., speech, finger tapping) are negatively affected when the left-hemisphere is damaged (Harrington & Haaland, 1991). Even some aphasias (i.e., apraxia of speech) can be better described as motor disorders affecting purposeful complex movements of the mouth and vocal apparatus (Ziegler, 2008). Thus, it may be more accurate to say that the left hemisphere is specialized for the production of complex movements, rather than tool use specifically. How does right-hand preference relate to this specialization?

Right-handedness and complex movements

The left hemisphere's role in producing complex actions is again supported by lesion studies. Kimura and Archibald (1974) investigated whether symptoms of apraxia could be explained in terms of "complexity of movement" rather than in terms of "tool use" as such. They compared performance of simple and complex actions in stroke patients and age-matched controls and found that while left-hemisphere stroke patients were severely impaired on traditional tests of apraxia (as expected), they were no different from controls when performing or copying simple hand and finger movements. It was only during complex movements that left-hemisphere patients showed kinematic and temporal impairments. Harrington and Haaland (1991) tested left-hemisphere and right-hemisphere stroke patients on their ability to produce a series of hand postures in response to non-verbal cueing. They found that only left-hemisphere stroke patients were impaired in their ability to produce sequential postures; when the right hemisphere was damaged, impairments were absent.

Left-hemisphere dominance for producing complex movements extends beyond hand and arm movements; Goodale (1988) described asymmetries in the kinematics of complex mouth movements as well. Specifically, he showed that the right side of a person's mouth opens wider and faster when producing sound, both verbal and non-verbal alike. The asymmetry is even more pronounced for sounds embedded in a sequence; in fact, as a sequence grows longer and more complex, asymmetries become less and less subtle. Thus, the mouth, like the hands, shows evidence of predominantly left-hemisphere control during complex movements, even when those movements are bilateral (Goodale, 1988).

These studies all show that the left hemisphere is specialized for producing complex, sequential movements, and imply that speech and tool use are simply manifestations of this overarching specialization. In his review on the evolutionary history of laterality in humans, Corballis refers to this as a left-hemisphere advantage for *generativity* (Corballis, 1989). He proposes that specializations for speech, sequential movement control, and even perception may be related to an ability to construct novel "wholes" based on a repertoire of "constituent parts." In this respect, Corballis presents *speech* as a complex arrangement of phonemes, *perception* as recognition of euclidean shapes ("geons") arranged to form a given object, and complex *movements* (like grasping) as sequential arrangements of hand and limb postures (e.g., "release," "collection," "manipulation"; see Sacrey, Alaverdashvili, & Whishaw, 2009) to form new, functional ensembles. Much as one can learn to pronounce a novel word by "sounding it out" (i.e., distilling its constituent phonemes and re-creating the whole), one can learn a new action by "assembling" it from a repertoire of known postures. Corballis suggests that the left hemisphere is specialized for such generative processes.

The grasp-to-eat action differs from the grasp-to-place action in that it requires synchronized mouth movement in order to be successfully completed; it is, at its most basic level, more complex than the grasp-to-place movement to which we contrast it. It is of course possible that the lateralization of the grasp-to-eat signature may be a simple manifestation of the right hand advantage for complex movements, though we deem this unlikely for two reasons. First, when we tested this possibility directly, we found that requiring participants to open their mouths during the grasp-to-place action did not have a significant effect on MGA (Flindall & Gonzalez, 2017). That is, when participants opened their mouths "as if to eat the target" while bringing the target directly to the bib, MGA was not significantly different from the typical grasp-to-place task (produced without mouth movement). Second, in a similar study in which we asked right-handed participants to grasp-to-drink with their left and right hands, we found that participants produced identical MGAs regardless of which hand they used (Flindall et al., 2014). Even though the grasp-to-drink action shares the same trajectory and the same requirement to open the mouth as the grasp-to-eat action, MGA asymmetries were entirely absent. These studies seem to refute a general complexity argument for the origin of the grasp-to-eat kinematic signature; instead, the signature appears to be specific to movements in which an actor grasps a small object with intent to place it in their own mouth.

Right-handedness and the postural origins theory

The postural origins theory of right-hand dominance was first presented by MacNeilage et al. (1987). It posits that right-hand dominance arose out of structural and functional

adaptations for feeding. As our primate ancestors began to adopt a bipedal stance, they relied less and less on their upper limbs for postural support, freeing their hands for acquisition (and later, manipulation) of objects. The theory predicts an early left-hand advantage for reaching and acquiring targets, followed later (as postural support requirements are reduced even further) by a right-hand advantage for fine, manipulatory movements (MacNeilage, 2007). This theory lost much of its popular support when subsequent studies failed to find a reliable left-hand preference for reaching in nonhuman primates. However, given the evidence of right-hand advantage for grasp-to-eat actions presented here, and the critical importance of considering task specificity when investigating hand preference, perhaps it is time to revisit the postural origins theory and consider its merits in fresh light.

Conclusion

In this review, we highlight the limitations of the dual visuomotor channel theory for grasping with respect to lateralized dissociations between simple reach-to-grasp actions. Via 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 support secondary movements. This, in turn, implies a neural distinction based on the functional purpose of the grasp. The left-hemisphere/right-hand specialization for grasp-to-eat actions has particular relevance for existing theories on the origin of right-hand dominance in humans and shows that task-specificity should be carefully considered in any discussion about the merits of such theories.

Compliance with ethical standards

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