



# Kinematics of ventrally mediated grasp-to-eat actions: right-hand advantage is dependent on dorsal stream input

Clarissa Beke<sup>1</sup> · Jason W. Flindall<sup>1,2</sup> · Claudia L. R. Gonzalez<sup>1</sup>

Received: 12 October 2017 / Accepted: 21 March 2018 / Published online: 27 March 2018  
© Springer-Verlag GmbH Germany, part of Springer Nature 2018

## Abstract

Studies have suggested a left-hemisphere specialization for visually guided grasp-to-eat actions by way of task-dependent kinematic asymmetries (i.e., smaller maximum grip apertures for right-handed grasp-to-eat movements than for right-handed grasp-to-place movements or left-handed movements of either type). It is unknown, however, whether this left-hemisphere/right-hand kinematic advantage is reliant on the dorsal “vision-for-action” visual stream. The present study investigates the kinematic differences between grasp-to-eat and grasp-to place actions performance during closed-loop (i.e., dorsally mediated) and open-loop delay (i.e., ventrally mediated) conditions. Twenty-one right-handed adult participants were asked to reach to grasp small food items to (1) eat them, or (2) place them in a container below the mouth. Grasps were performed in both closed-loop and open-loop delay conditions, in separate sessions. We show that participants displayed the right-hand grasp-to-eat kinematic advantage in the closed-loop condition, but not in the open-loop delay condition. As no task-dependent kinematic differences were found in ventrally mediated grasps, we posit that the left-hemisphere/right-hand advantage is dependent on dorsal stream processing.

**Keywords** Reach-to-grasp · Kinematics · Dorsal stream · Ventral stream · Asymmetries · Grasp-to-eat

## Introduction

The two visual stream hypothesis states that there are distinct visual pathways in the human brain; the vision-for-perception pathway and the vision-for-action pathway (Goodale and Milner 1992; Goodale et al. 2004; Milner and Goodale 2008). This theory posits that after information passes from the retina to the primary visual cortex in the occipital lobe, that information is concurrently processed in both the temporal cortex (ventral stream) and the parietal cortex (dorsal stream), and that these two streams use that information to

serve discrete functions. The vision-for-perception (ventral) stream processes visual input in terms of form, colour, and relative size. This processing represents conscious vision, and is the basis for long-term visual memory. In contrast, the vision-for-action (dorsal) stream processes visual information entirely for the purpose of informing motor action; it is unconscious and, because this system does not form memories, it is entirely online (Goodale et al. 1994; Hu et al. 1999). The online nature/real-time component of the dorsal visual stream is validated by kinematic studies showing that ventrally mediated grasps (i.e., those performed without visual feedback of the moving limb, a.k.a “open-loop” movements) are reliably distinguished from dorsally mediated movements (i.e., those performed with visual feedback, a.k.a “closed-loop” movements) through consistent kinematic differences, including longer overall movement times, lower peak velocities, wider maximum grip apertures (MGAs), and elongated deceleration phases (Flindall et al. 2014; Hesse and Franz 2010; Hu et al. 1999; Westwood and Goodale 2003). While the shift from dorsal to ventral control is instantaneous (and contingent upon the removal of vision), the influence of the dorsally mediated movement plan may still be measured for a brief period in the kinematics of the

✉ Jason W. Flindall  
jason.flindall@psych.ubc.ca

Clarissa Beke  
c.beke@uleth.ca

Claudia L. R. Gonzalez  
claudia.gonzalez@uleth.ca

<sup>1</sup> The Brain in Action Laboratory, Department of Kinesiology, University of Lethbridge, 4401 University Dr W, Lethbridge, AB T1K 6T5, Canada

<sup>2</sup> Department of Psychology, University of British Columbia, 2136 West Mall, Vancouver, BC V6T 1Z4, Canada

executed movement (Heath and Binsted 2007; Heath and Westwood 2003). The dorsally mediated plan decays exponentially, with full decay occurring after, at most, 2000 ms—these movements [i.e., “open-loop delay (2000 ms)” movements; Heath and Westwood 2003; Hesse and Franz 2010] have been shown to be kinematically indistinguishable from ventrally mediated movements produced after longer delays (anywhere from 5 to 30 s; Hu et al. 1999).

During movements mediated by the dorsal stream, kinematic asymmetries have been described in a number of pointing and aiming studies. That is to say, when we reach outward toward a target with an intent to point at or touch it, our kinematics differ depending on which hand we decide to use. In general, when right-handers are pointing with online visual feedback, the right hand is faster and more accurate while the left hand is quicker to initiate a movement (Boulinguez et al. 2001; Carson et al. 1990, 1993; Elliott et al. 1993), thus constituting a dominant-hand advantage for goal-directed aiming movements. There are a number of theories that put this advantage into context of a left-hemisphere/right-hand advantage for goal-directed actions, including the dynamic dominance hypothesis (Mutha et al. 2013) and the visual-feedback integration model (Roy et al. 1994). The dynamic dominance hypothesis posits that there are distinct neural mechanisms responsible for the optimization of dominant vs. non-dominant aiming movements (Mutha et al. 2013). Specifically, the dominant arm-hemisphere system optimizes dynamic control of movements, whereas the non-dominant arm-hemisphere system optimizes end-point equilibrium control. Pointing and aiming asymmetries supporting this hypothesis have been reported in multiple studies (Duff and Sainburg 2007; Schaefer et al. 2009; Shabbott and Sainburg 2008; Tomlinson and Sainburg 2012; Wang and Sainburg 2007). The visual feedback integration model states that during movements, regardless of whether or not visual feedback is available, the left-hemisphere is more efficient at processing feedback in general, resulting in greater accuracy when using the right hand. This model posits that the left-hemisphere/right-hand system requires either less time to detect and correct errors, and/or less information on which to base corrections (Roy et al. 1994). It is important to clarify that this model was proposed in light of reach-to-point asymmetries, however, and therefore, may not apply to grasping movements; the asymmetries predicted by this model have not been identified in simple grasp-to-lift or grasp-to-place actions (Tretriluxana et al. 2008). That is, despite the well-described dominant-hand preference for grasping, reach-to-grasp actions show comparatively few asymmetries (Annett et al. 1979). When reaching movements are coupled with grasping actions, left- and right-handed movements show only minor (if any) kinematic asymmetries. Grosskopf and Kuhtz-Buschbeck (2006) found no significant difference between left- and

right-handed movements when participants were asked to grasp-to-place a small cylinder onto a nearby target. Similarly, when Tretriluxana et al. (2008) asked participants to grasp-to-lift cylinders of varying sizes while occluding vision of their moving hands and limbs, they observed only minor asymmetries in the scaling of early grip aperture velocity to target size for the left hand, but not the right hand, during the first 150 ms of the movement. No such difference existed at time of maximum grip aperture (MGA). In another study, when participants were asked to grasp illuminated wooden dowels, the results showed no differences between the hands in terms of MT, PV, MGA, or the timing of any of these variables (Carnahan 1998). Critically, none of these studies reported kinematic asymmetries in MT or RT that would be expected from the reach-to-point literature; however, these studies also used grasping tasks with simple non-functional (or semi-functional) goals (e.g., grasp-to-hold, -lift, or -place), when studies have shown that the purpose of a movement may significantly affect the manner in which it is performed.

Several studies have shown that differences in kinematics of reach-to-grasp movements with different end-goals may partially depend on the functional purpose of those movements. That is, two movements, both made with the dominant hand, and both with identical mechanical requirements, may show robust kinematic differences if those movements serve different functional purposes. These differences, such as changes in MGA and finger positioning, have been observed when comparing grasp-to-place and grasp-to-eat actions (Ferri et al. 2010; Flindall and Gonzalez 2013, 2014; Flindall et al. 2015; Naish et al. 2013), and grasp-to-place, grasp-to-lift, and grasp-to-throw actions (Ansuini et al. 2008; Armbrüster and Spijkers 2006; Marteniuk et al. 1987). If the after grasp movements have different end goals, the movement parameters (e.g., the deceleration phase prior to object contact; Armbrüster and Spijkers 2006), and the positioning of the fingers at target contact (Ansuini et al. 2008) of the reach and grasp movement change. For example, Ansuini et al. (2008) asked participants to complete five grasping actions toward a bottle of water, with each grasp having a different end-goal. Participants were asked to either lift and throw the bottle, pour out its contents, place it accurately on a target, pass it to the experimenter, or simply grasp and hold it. They found that the movement time for each of the grasp types was significantly affected by the purpose of the grasp; MTs were longest in the simple grasp-to-hold task and shortest in the grasp-to-throw task, consistent with the idea that the initial outward movements are facilitative towards the secondary (in this case, hold or throw) actions. Similarly, in a seminal study by Marteniuk et al. (1987), researchers found that when participants were asked to grasp a disk using their thumb and index finger and either place it or throw it into a box, the duration of the deceleration phase

was longer when grasping-to-place than when grasping-to-throw. Together, these studies show that the planning and execution of a sequence of actions is modified based on the intention that drives the movement (Ansuini et al. 2008; Armbrüster and Spijkers 2006; Ferri et al. 2010; Marteniuk et al. 1987).

One such movement with distinct kinematics is the grasp-to-eat action. Our lab has published numerous reports on a lateralized, task-dependent kinematic signature associated with this movement. Specifically, we show that participants produce smaller MGAs when grasping-to-eat (or even simply bringing to the mouth; Flindall and Gonzalez 2014, 2016) small targets, compared to when grasping-to-place those same targets in a near-mouth container (Flindall and Gonzalez 2013, 2014). Interestingly, this task-dependent effect on MGA manifests as a kinematic asymmetry in a reach-to-grasp movement; because it is limited to right-handed movements, the effect suggests a differentiation between the grasp-to-eat and grasp-to-place actions localized within the left-hemisphere. Note that this task-dependent effect of smaller MGAs in the right-handed grasp-to-eat action may be described as a kinematic advantage favoring the right hand, as grip closing time, peak grip closing velocity, and metabolic energy requirements are decreased when MGA more closely matches the absolute target size (Bootsma et al. 1994; Flindall and Gonzalez 2017). However, because larger MGAs may also constitute a kinematic advantage (e.g., in cases of reduced actor confidence, or reduced visual feedback availability, when larger MGAs allow for a larger margin of error while grasping), we refer to the effect as a kinematic signature in the absence of data respecting metabolic cost or actor confidence (Flindall and Gonzalez 2017). Still, even among the majority of left-handers, this signature is lateralized to right-handed movements; left-handed movements normally show no such task-dependent difference, except in children younger than age 10 (Flindall et al. 2015) and in a fraction of left-handed adults (Flindall et al. 2015). However, these studies have all featured visually guided actions, and as such it remains unknown if this kinematic signature relies on dorsal stream processing. The purpose of the present study is to address this question.

To this end, we asked participants to perform grasp-to-eat and grasp-to-place actions in two sessions; one session under closed-loop conditions, with full visual feedback, and another session under open-loop delay conditions (i.e., memory-guided; see Heath and Binsted 2007; Heath and Westwood 2003). Given the results of our previous investigations, we predicted that right handed grasp-to-eat movements performed with full visual feedback (i.e., under closed-loop conditions) would produce significantly smaller MGAs than right-handed grasp-to-place movements and left-handed movements in either task. A priori contrasts were planned

according to these predictions. If the kinematic signature for grasp-to-eat actions were dependent on dorsal stream processing, then we should find no difference between grasp-to-eat and grasp-to-place MGAs in the open-loop delay condition. If instead the kinematic signature is independent of visual feedback then grasp-to-eat actions will display significantly smaller MGAs than grasp-to-place movements in both closed-loop (CL) and open-loop delay (OL-D) conditions.

## Methods

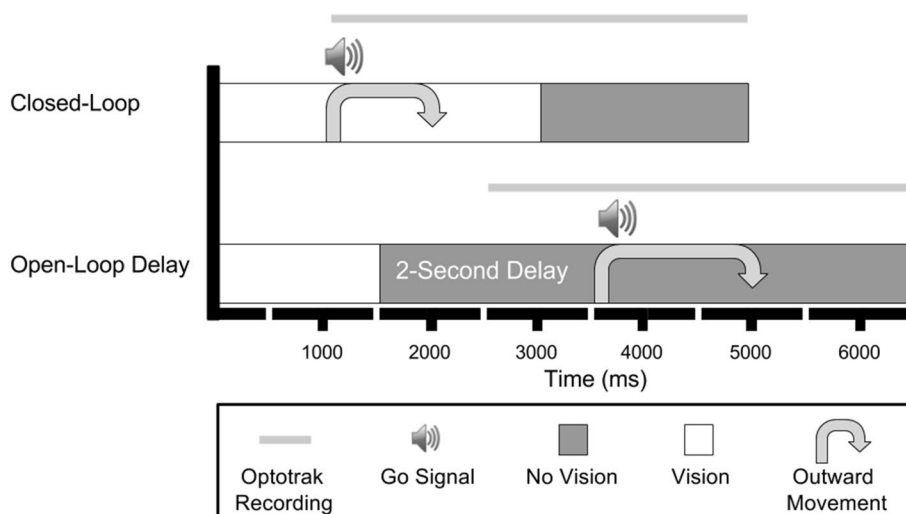
### Participants

Twenty-one right-handed undergraduate students (14 females; mean age of 20.9 years) participated in the experiment in exchange for course credit. All participants gave written informed consent before beginning the study. Participants were able to withdraw from the study at any time without consequence. Handedness of each individual was self-reported and confirmed via modified Waterloo/Edinburgh Handedness Questionnaire (Cavill and Bryden 2003; Oldfield 1971; Stone et al. 2013). The E-WHQ asks participants to report their hand preference for 22 common actions via a 5-point Likert scale, where  $-2/-1$  indicates always/usually left, and  $+1/+2$  indicates usually/always right. Thus, a score of  $-44$  would suggest a participant always uses her left hand, and a score of  $+44$  suggests she always uses her right hand. Participants reported an average handedness score of  $33.95 \pm 4.31$  (range 24–44), indicating a moderate to strong right-hand preference for all participants. Note that participants were not recruited or excluded based on handedness, as we have previously shown that left-handers behave similarly to right-handers with respect to grasp-to-eat kinematics (Flindall et al. 2015).

### Instrumentation

Materials and methods were similar to those used in previous studies by Flindall and Gonzalez (2013, 2014, 2016; Flindall et al. 2015). Three infrared light emitting diodes (IREDs) were placed on the participant's hand: one on the distal phalanx of the thumb, slightly lateral with respect to the nail; one on the distal phalanx of the index finger, slightly medial with respect to the nail; 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), positioned overhead, recorded IRED position during each trial at 200 Hz for 4000 ms. Throughout the experiment, the participants wore Plato Liquid-crystal glasses (Translucent Technologies, Toronto, ON, Canada) to control visual feedback availability. Participants wore a container (specifically, a child's bib) under their neck where they

**Fig. 1** The experimental design with a timeline of the two conditions: closed-loop and open-loop delay. Vision represents when the Plato goggles are in a transparent (open) state. No vision represents when the Plato goggles are in a translucent (closed) state. Movement represents the average amount of time participants are performing the outward reach-to-grasp action



were asked to place the targets during the grasp-to-place task. The bib was also worn during the grasp-to-eat task. All conditions were controlled using Superlab 4.5 (Cedrus Corporation, San Pedro, CA, USA) and NDI First Principles (Northern Digital, Waterloo, ON, Canada).

## Procedure

Participants were seated on a chair in front of a rectangular pedestal that was positioned at sternum height. Individual cereal food items (presented one at a time) of two different sizes, small (Cheerios<sup>®</sup>, mean diameter of 11 mm) and large (Froot Loops<sup>®</sup>, mean diameter of 15 mm), were placed on the pedestal in pseudorandom order. The distance between the participant and the pedestal was adjusted to each participant's maximum stationary reach-to-grasp distance (i.e., 100% of comfortable reach distance, with elbow at full extension, without leaning forward).

## Protocol

The study used a within-subject design in which the participants were instructed to complete a closed-loop condition and an open-loop delay condition in two sessions. To avoid the potential confounds of fatigue and inattention, sessions were completed at the same time on 2 days separated by 48 h (for a similar design, see Castiello et al. 1998). Session order and starting condition were counterbalanced between participants. During each session, the participants performed grasp-to-eat actions and grasp-to-place actions in blocks of 20 trials each (10 small targets, 10 large targets, pseudo-randomly presented) per hand, for a total of 40 trials per-hand per-session (160 trials total). Block-order was counterbalanced between participants, but was kept constant within-participants for each hand and visual-feedback condition.

Participants were seated directly behind a pedestal with their reaching hand placed comfortably on their lap with index and thumb fingertips touching, in a way that all three markers were visible to the overhead Optotrak Certus camera. Trials began with participants seated in a rest position with the glasses in a translucent (closed) state. The experimenter would place a target (Cheerio<sup>®</sup> or Froot Loop<sup>®</sup>) on the pedestal before the trial began. As may be seen in Fig. 1, closed-loop trials began with the glasses transitioning to a transparent (open) state, at which time the Optotrak would begin recording. 1000 ms later, an audible beep (go signal) would signal the participant to initiate the reach-to-grasp movement toward the target. The participant would then grasp the target to either eat it or place it in the bib, depending on the current block's instructions. After completing the movement, participants would return to the rest position, the glasses would transition back to a translucent (closed) state, and the experimenter would replace the food item for the next trial. In the open-loop delay sessions, participants would begin each trial in the rest position, just as they would in the closed-loop trials. As shown in Fig. 1, the open-loop delay trials began when the Plato goggles transitioned to a transparent state, allowing the participant to view the to-be-grasped target. This viewing period lasted 1500 ms,<sup>1</sup> after which point the goggles transitioned back

<sup>1</sup> During pilot testing, the open-loop delay condition viewing period was set at 1000 ms to match that of our closed-loop condition. However, participants expressed frustration at this seemingly short viewing period and blamed subsequent errors on its brevity; specifically, they would often knock the target off the pedestal, perform the movement with excessive slowness, and/or express that they were unable to even identify the target before the viewing period would end. We concluded that the viewing period was too brief, and added 500 ms. This elongated viewing period eliminated the majority of both trial errors and participant frustrations. While the difference in the viewing period length may have had a significant effect on reaction times, we consider this a necessary trade-off in exchange for consistently successful movements in the open-loop delay condition. In light of this

to their opaque state. After a 2000 ms delay, the go signal would again serve to instruct the participant to begin grasping the target. Optotrak recording would begin 1000 ms into the delay period (i.e., after the glasses had transitioned to their opaque state, but prior to the go signal for the start of the movement). After the participant completed the grasping movement, they would return to the rest position and await the start of the next trial. We chose a 2000 ms delay as this reflects the maximum interval necessary for dorsal stream information to fully decay (i.e., there is no significant difference with respect to kinematics between a 2000 and 5000 ms, or even a 30,000 ms delay; Heath and Binsted 2007; Heath and Westwood 2003; Hu et al. 1999).

## Data processing

Infrared light emitting diodes position 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 19.0. Trials were excluded from the analysis if the participant failed to grasp the target correctly; these “incorrect grasps” included those trials where the participants failed to react to the go signal, used an inappropriate grasp (e.g., with thumb and middle finger), or accidentally knocked the target from the pedestal. In such cases the participant was gently reminded of the instructions, and the offending trial was removed from analyses and not repeated. As a result of these errors, an average of 0.345% of trials were removed per participant (closed-loop average 0.45%, range 0–2 trials per participant; open-loop delay average 0.24%, range 0–1 trials per participant).

While our primary variable of interest was MGA, additional kinematics of both the reach and grasp are included in our primary analyses. Movement time (MT) is reported in milliseconds, and represents the span during which the participant reached outward toward the target. It is calculated as the difference between reaction time [the point at which resultant velocity at the wrist exceeds 5% of peak velocity (PV)] and time of grasp onset, determines as the point when (a) the participant’s grip aperture reached a stable state (GA remained within  $\pm 1$  mm of a given aperture for a minimum of 10 frames, determined on a per-trial basis), and (b) the participant’s wrist velocity reached a nadir prior to the return movement. PV was calculated as the maximum resultant velocity of the wrist marker during the outward movement;

its time of occurrence (PVt) is reported as a percentage of MT. Resultant velocities were computed from raw position information via the two-step method, 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 frame in the output data, and  $\Delta t$  is time elapsed between frames  $n-1$  and  $n+1$ . Maximum grip aperture (MGA) was calculated as the maximum resultant distance between thumb and index finger IREDs prior to grasp onset; its time of occurrence (MGAt) is reported as a percentage of MT. To enable within-participant comparisons between hands, a correction factor was subtracted from all MGA values. We calculated this correction factor by measuring closed-grip IRED separations at the beginning of each trial, removing outliers (those  $\pm 2.5$  SDs from the within-hand resting grip aperture mean), and averaging the remaining values by hand  $\times$  vision condition (Flindall and Gonzalez 2013; Flindall et al. 2015). Variability of MGA (vMGA) and variability of MT (vMT) are calculated as the standard deviation of MGA and MT respectively within each visual feedback  $\times$  hand  $\times$  task  $\times$  size condition.

Kinematic variables were averaged by size within each block condition, with a 4-way repeated-measures analysis of variance [vision (closed-loop/open-loop delay)  $\times$  hand (left/right)  $\times$  task (eat/place)  $\times$  size (small/large)] run on those means. Means  $\pm$  SE and ANOVA results are reported in Table 1. Respecting our main variable of interest (MGA), trials were considered outliers if the absolute value of the MGA’s within-hand  $z$ -score for that trial was  $> 2.5$ ; these trials were also removed from analyses (closed-loop, average 0.77%, range 0–1 trials per participant; open-loop delay average 0.54%, range 0–2 trials per participant). The same technique was used to screen for outlier trials with respect to MT (closed-loop, average 1.2%, range 0–3 trials per participant; open-loop delay 1.2%, range 0–5 trials per participant). A secondary analysis was performed whereby data was split by visual condition, collapsed across size, and submitted to two 2-way ANOVAs (factors hand  $\times$  task). Alpha significance for each ANOVA was set at  $p < 0.025$ . Post hoc and planned a priori comparisons were conducted via paired-sample  $t$  tests, with Bonferroni corrections applied for the former, as appropriate. Estimate of effect size is reported using partial  $\eta^2$ . To ensure that outlier removal did not have a significant effect on our results, we ran concurrent analyses on both cleaned and uncleaned datasets; all main effects and interactions were consistent, indicating that outlier removal had no effect on the overall shape of our data.

## Results

Between-subject means and standard errors of all measurements are reported in Table 1. Significant main effects and interactions of the initial 4-way ANOVA are reported below.

Footnote 1 (continued)

confound, and because our participants were specifically instructed to “move at a comfortable pace, with an emphasis on accuracy, not speed,” we do not include analyses on reaction time in the current report.



**Table 1** Between-participant means and average standard errors of reach (MT, PV, PVt, vMT) and grasp (MGA, MGAt, vMGA) kinematics by block conditions

				MT (ms)	PV (m/s)	PVt (%MT)	vMT (ms)	MGA (mm)	MGAt (%MT)	vMGA (mm)
Closed-loop	Left	Eat	Small	923 ± 45	1.58 ± 0.06	30.7 ± 0.9	102 ± 12	22.91 ± 1.1	54.8 ± 2.4	3.26 ± 0.3
			Large	835 ± 36	1.58 ± 0.06	33.4 ± 0.8	75 ± 6	28.51 ± 1.3	62.8 ± 2.1	3.40 ± 0.3
	Place	Small	Small	932 ± 50	1.59 ± 0.06	31.3 ± 1.4	106 ± 13	23.82 ± 1.0	52.9 ± 2.3	3.61 ± 0.4
			Large	833 ± 40	1.57 ± 0.06	34.8 ± 1.3	72 ± 7	29.32 ± 1.2	61.2 ± 2.1	3.69 ± 0.3
	Right	Eat	Small	937 ± 45	1.60 ± 0.06	29.9 ± 0.9	139 ± 19	20.79 ± 1.0	54.2 ± 2.2	3.18 ± 0.2
			Large	821 ± 35	1.60 ± 0.06	33.2 ± 0.9	75 ± 9	26.12 ± 1.0	62.5 ± 2.1	2.98 ± 0.2
	Place	Small	Small	894 ± 45	1.60 ± 0.06	30.0 ± 0.7	104 ± 14	22.32 ± 1.1	53.7 ± 2.3	3.57 ± 0.4
			Large	795 ± 37	1.59 ± 0.06	33.5 ± 1.0	65 ± 5	27.92 ± 1.1	61.2 ± 2.5	3.43 ± 0.3
Sig. CL 2-way ANOVA results								H, T		
Open-loop delay	Left	Eat	Small	1573 ± 70	1.40 ± 0.05	18.9 ± 0.7	316 ± 25	29.92 ± 2.1	40.1 ± 1.0	4.41 ± 0.4
			Large	1381 ± 62	1.39 ± 0.05	21.3 ± 0.7	216 ± 25	37.14 ± 2.1	44.7 ± 1.3	4.75 ± 0.4
	Place	Small	Small	1583 ± 78	1.41 ± 0.06	19.3 ± 1.0	324 ± 32	30.67 ± 2.0	40.3 ± 1.4	4.01 ± 0.4
			Large	1370 ± 59	1.38 ± 0.06	21.7 ± 0.7	240 ± 26	37.53 ± 2.0	45.0 ± 1.5	4.29 ± 0.3
	Right	Eat	Small	1628 ± 93	1.41 ± 0.06	18.8 ± 0.9	288 ± 24	29.31 ± 1.8	40.0 ± 1.7	3.83 ± 0.4
			Large	1466 ± 81	1.39 ± 0.06	20.5 ± 0.9	218 ± 15	36.83 ± 1.7	43.3 ± 1.8	4.03 ± 0.3
	Place	Small	Small	1640 ± 94	1.41 ± 0.06	18.9 ± 0.9	343 ± 26	28.96 ± 1.6	38.4 ± 1.8	4.25 ± 0.4
			Large	1430 ± 77	1.40 ± 0.06	22.0 ± 1.3	252 ± 27	36.53 ± 1.7	44.2 ± 1.7	4.41 ± 0.4
Sig. OL-D 2-way ANOVA results								T		
Sig. 4-way ANOVA results				V, S, V × S	V, S	V, S	V, S, V × T, V × S	V, S, V × S	V, S, V × S	V

Significant main effects and interactions revealed by statistical analyses are reported below each variable’s respective column (*V* vision, *H* hand, *T* task, *S* size)

**4-way ANOVA**

**Vision**

A main effect of vision was observed on all variables, all  $F(1, 20) \geq 13.4$ ,  $p \leq 0.002$ ,  $\eta^2 \geq 0.401$ . Relative to open-loop delay (OL-D) movements, grasps completed within the closed-loop (CL) blocks had higher PVs [ $1.591 \pm 0.055$  m/s (CL) vs.  $1.399 \pm 0.56$  m/s (OL-D)], shorter [ $871 \pm 39$  ms (CL) vs.  $1509 \pm 70$  ms (OL-D)] and more consistent [ $92 \pm 6$  ms (CL) vs.  $275 \pm 15$  ms (OL-D)] MTs, later relative PVts [ $32.1 \pm 0.7\%$ MT (CL) vs.  $20 \pm 0.7\%$ MT (OL-D)], as well as smaller [ $25.21 \pm 0.97$  mm (CL) vs.  $33.36 \pm 1.61$  mm (OL-D)], less variable [ $3.39 \pm 0.16$  mm (CL) vs.  $4.25 \pm 0.23$  mm (OL-D)], and relatively later [ $57.9 \pm 1.8\%$ MT (CL) vs.  $42.0 \pm 1.2\%$ MT (OL-D)] MGAs.

**Hand**

No main effects of hand were found for any variable (all  $p > 0.05$ ).

**Task**

No main effects of task were found for any variable (all  $p > 0.05$ ).

**Size**

A main effect of size was observed on all variables (except vMGA), all  $F(1, 20) \geq 5.811$ ,  $p \leq 0.026$ ,  $\eta^2 \geq 0.225$ , wherein participants had higher PVs [ $1.501 \pm 0.052$  m/s (small) vs.  $1.489 \pm 0.052$  m/s (large)], longer [ $1264 \pm 59$  ms (small) vs.  $1116 \pm 48$  ms (large)] and less consistent [ $215 \pm 14$  ms (small) vs.  $152 \pm 9$  ms (large)] MTs, earlier relative PVts [ $24.7 \pm 7\%$ MT (small) vs.  $27.6 \pm 6\%$ MT (large)], as well as smaller [ $26.09 \pm 1.16$  mm (small) vs.  $32.49 \pm 1.23$  mm (large)] and relatively earlier [ $46.8 \pm 1.3\%$ MT (small) vs.  $53.1 \pm 1.2\%$ MT (large)] MGAs.

**Interactions**

A vision × task interaction was observed on vMT,  $F(1, 20) = 6.263$ ,  $p = 0.021$ ,  $\eta^2 = 0.238$ . Follow-up *t* tests revealed that this interaction is due to MTs being

significantly more variable in the OL-D condition when grasping to place the target ( $349 \pm 22$  ms) than when grasping to eat the target ( $310 \pm 89$  ms),  $t(20) = -2.962$ ,  $p = 0.008$ . The difference between tasks was not significant in the CL condition ( $p > 0.2$ ).

Vision  $\times$  size interactions were observed on MT,  $F(1, 20) = 22.234$ ,  $p < 0.001$ ,  $\eta^2 = 0.526$ , vMT,  $F(1, 20) = 6.186$ ,  $p = 0.022$ ,  $\eta^2 = 0.236$ , MGA,  $F(1, 20) = 9.273$ ,  $p = 0.006$ ,  $\eta^2 = 0.317$ , and MGAt,  $F(1, 20) = 25.424$ ,  $p < 0.001$ ,  $\eta^2 = 0.560$ . Follow-up  $t$  tests revealed that all differences, both between-vision/within-size and between-size/within-vision, are significant and consistent with main effects (all  $p < 0.001$ ). To investigate whether the interaction might be attributed to a magnitude effect, between size differences were calculated for all participants by subtracting MT, vMT, MGAt, and MGA values for small targets from their corresponding values for large targets. We compared these difference scores between visual feedback conditions via paired-sample  $t$  tests, the results of which indicate that a magnitude effect was responsible for the observed vision  $\times$  size interactions on MT, MGA, and MGAt. With respect to MT, the difference between small and large targets was larger in the OL-D condition ( $-194 \pm 25$  ms) than in the CL condition ( $-101 \pm 11$  ms),  $t(20) = 4.709$ ,  $p < 0.001$ . With respect to MGA, the difference between small and large targets was also larger in the OL-D condition ( $7.29 \pm 0.54$  mm) than in the CL condition ( $5.51 \pm 0.30$  mm),  $t(20) = -3.352$ ,  $p = 0.003$ . Finally, with respect to MGAt, the between-size difference was significantly larger in the CL condition ( $8.0 \pm 0.9\%$ MT) than it was in the OL-D condition ( $4.6 \pm 0.7\%$ MT),  $t(20) = 5.042$ ,  $p < 0.001$ . The vision  $\times$  size interaction on vMT could not be attributed to a magnitude effect, as the difference scores both between sizes and between-vision conditions were not significantly different from one another ( $p > 0.1$ ). No other main effects or interactions were observed.

As we found vision and size to produce such large effects, and because these effects were consistent with those reported extensively in the literature (Berthier et al. 1996; Castiello et al. 1993; Hu et al. 1999; Hu and Goodale 2000; Paulignan et al. 1997), we divided our data by visual feedback condition and collapsed all variables across size to run in-depth analyses more relevant to our hypothesis (see Grosskopf and Kuitz-Buschbeck 2006, for similar analyses). Two 2-way ANOVAs with conditions of hand (left, right) and task (eat, place) were run on the resultant data sets. To control for the added likelihood of type I errors, we employed a Bonferroni-corrected alpha of  $p < 0.025$ . Main effects and interactions of those ANOVAs are reported below.

## Closed-loop (CL) ANOVA

A main effect of hand was observed on MGA,  $F(1, 20) = 6.010$ ,  $p = 0.024$ ,  $\eta^2 = 0.231$ , wherein participants produced smaller MGAs when grasping with their right hands ( $24.27 \pm 0.97$  mm) than when grasping with their left hands ( $26.14 \pm 1.12$  mm). A main effect of task was also observed,  $F(1, 20) = 11.330$ ,  $p = 0.003$ ,  $\eta^2 = 0.362$ , wherein participants produced smaller MGAs when grasping to eat the target ( $24.58 \pm 1.00$  mm) than when grasping to place the target in a container below the mouth ( $25.83 \pm 0.99$  mm). No other main effects or interactions were observed ( $p > 0.025$ ).

To investigate whether our results were consistent with those we have previously reported (Flindall and Gonzalez 2013, 2014, 2016; Flindall et al. 2015) we conducted planned a priori  $t$ -tests comparing eat and place MGAs within each hand condition. (Note that because these comparisons were planned a priori, a per comparison alpha of 0.05 is appropriate; Veazie 2006). These tests revealed a significant difference between right-hand eat ( $23.44 \pm 0.97$  mm) and right-hand place ( $25.09 \pm 1.07$  mm) MGAs,  $t(20) = -2.524$ ,  $p = 0.020$ . Right-hand eat MGAs were also significantly smaller than left-hand eat MGAs ( $25.72 \pm 1.20$  mm) (Fig. 2). While the trend was similar during left-handed movements (i.e., eat MGAs smaller than place MGAs), the difference between tasks was not significant ( $p = 0.207$ ).

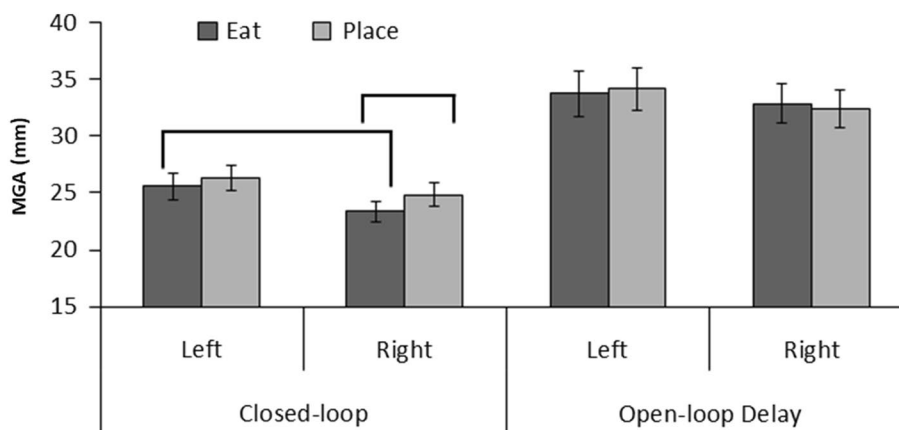
## Open-loop delay (OL-D) ANOVA

Consistent with the vision  $\times$  task interaction identified in our 4-way ANOVA, a main effect of task was observed on vMT,  $F(1, 20) = 11.762$ ,  $p = 0.003$ ,  $\eta^2 = 0.370$ . Again, this effect was due to MTs being significantly more variable when grasping to place ( $349 \pm 22$  ms) than when grasping to eat ( $310 \pm 89$  ms). No other main effects or interactions were observed.

Again, to investigate whether participant behaviour (now in the absence of visual feedback) was consistent with that which we have previously reported, we once more conducted planned a priori paired-sample  $t$  tests comparing MGAs between hands and tasks. These tests revealed no significant differences between eat and place conditions in either hand ( $p > 0.47$ ), nor did they show any MGA differences between left and right hands in either task ( $p > 0.36$ ) (Fig. 2). Thus, the expected task differences found both in previous investigations and here, in the CL condition, were entirely absent when visual feedback was unavailable.

## Discussion

Recent studies in our lab have identified a right hand grasp-to-eat signature when performing visually guided grasp-to-place and grasp-to-eat actions (Flindall and Gonzalez 2013,



**Fig. 2** MGA displayed by hand×task. Values shown are the mean and standard errors of MGA in each vision×hand×task condition, collapsed across size. In the closed-loop condition, place and eat tasks were significantly different from each other in right-handed movements only; movements made with the left-hand were not significantly affected by task. Right-handed place movements were not significantly different from left-handed movements of either type. In

the open-loop delay condition, there were no significant differences between place and eat tasks in either right- or left-handed movements. In sum: right handed grasp-to-eat actions generated smaller MGAs than right handed grasp-to-place actions, and left handed actions of either type, but only when visual feedback of the movement was available

2014, 2016; Flindall et al. 2015). Specifically, right-handed grasp-to-eat actions are performed with smaller MGAs than grasp-to-place actions despite those actions being performed toward identical targets. It is unknown whether this signature is reliant on dorsal stream processing; i.e., whether online visual feedback is necessary for smaller MGAs to manifest during grasp-to-eat movements. In the present study, we asked participants to perform the same grasp-to-eat and grasp-to-place actions used in previous studies, with and without online visual feedback. We found that visually guided grasp-to-eat actions showed both a main effect of Hand and a main effect of Task. While it is tempting to declare that these effects constitute evidence in support of a general asymmetry with respect to MGA production in grasping, our planned follow-up analyses revealed that the difference between left and right hands was only present when participants grasped the target with intent to eat. When grasping to place the same target no such asymmetry was observed, eliminating both the dynamic dominance hypothesis and the feedback integration model as relevant frameworks for our results. This is consistent with both the reach-to-grasp kinematic literature and results we have reported previously. Importantly, this task-dependent kinematic difference was absent during the memory-guided grasps. Based on these results, we conclude that the right-hand grasp-to-eat kinematic signature depends on processing of visual information from the dorsal visual stream.

When comparing the kinematics of visually guided grasps to those of memory-guided grasps, several differences emerge, including larger MGAs, higher PVs and longer MTs when movements are guided by memory (Flindall

et al. 2014; Heath and Binsted 2007; Heath and Westwood 2003; Hesse and Franz 2010; Hu et al. 1999; Westwood and Goodale 2003). Our study replicated these differences between visual feedback conditions, implying that our CL and OL-D conditions coincided with a shift from dorsal-stream to ventral-stream mediated grasps, respectively. With respect to the kinematic signature of interest, we found significant differences between the left- and right-handed MGAs in the closed-loop grasp-to-eat task, consistent with those we have previously described (Flindall and Gonzalez 2013, 2014, 2016; Flindall et al. 2015). This MGA effect was not found in the open-loop delay condition, suggesting that dorsal stream function is critical for neural distinction between mechanically identical but functionally distinct reach-to-grasp actions. This is the first investigation to describe a link between task-dependent kinematic differences and on-line dorsal stream processing.

Many studies have demonstrated kinematic differences between grasps with different end-goals (e.g., grasp-to-place and grasp-to-throw actions; see Marteniuk et al. 1987). It may be argued, however, that the specific kinematic differences described in those studies serve to facilitate the secondary<sup>2</sup> movement associated with the task. For example, grasp-to-pass and -lift movements are performed with lower peak velocities and shorter movement times

<sup>2</sup> “Secondary” referring here to the portion of the grasping movement occurring after target acquisition; we would argue that the grasp-to-throw movement, from initiation of the grasp, to grasp onset and target acquisition, to follow-through and target release, is a single unified movement, at least with respect to neural control.



than grasp-to-throw movements; it may be argued that the secondary act of throwing is itself a ballistic movement, and would, therefore, be facilitated by a more aggressive outward reach-to-grasp movement. If these kinematic differences are indeed facilitatory, then they are susceptible to interference by opposing environmental conditions; conditions which may normally result in contradictory changes to kinematics. As an example, the increase in speed observed in closed-loop grasp-to-throw movements may be countered by the decrease in speed necessitated by the uncertainty created by an open-loop delay condition. While no such study has been conducted, altered kinematics in this hypothetical study could not safely be attributed to either task-dependent changes or to natural changes after visual-stream control shifts. Luckily, the kinematic difference we observe between the grasp-to-eat and grasp-to-place task is arguably not facilitatory (though it may have been in our evolutionary past; see Flindall and Gonzalez 2013), and is unique to right-handed movements. Because the shift from dorsal to ventral control not only eliminated the difference between tasks but also negated the lateralized kinematic signature within the grasp-to-eat task, we may conclude that the task-dependent difference is entirely reliant on dorsal stream function. We provide a novel contribution to the literature, in that we show task-dependent differences (and, by extension, the distinct neurocircuitry from which they must arise) are contingent upon contribution from the dorsal visual stream.

The right-hand lateralization of this kinematic signature suggests that the neural circuits responsible for the grasp-to-eat/hand-to-mouth action are located within the left hemisphere (Flindall and Gonzalez 2013). The current results suggest that in addition to being left-hemisphere lateralized, the motor program responsible for the grasp-to-eat action is also likely localized in areas inaccessible to the ventral stream. Essentially, this finding ties the grasp-to-eat kinematic signature (and any advantage which it may bestow on right-handed movements) with online visual processing; this may be relevant with respect to the evolution of right-hand dominance in humans. Consider that all visual systems ultimately serve to guide behavior—and, that primates are visual (i.e., perceptual) animals that make discriminative decisions based on relevant visual stimuli to produce their motor actions (Milner and Goodale 2006). Additionally, many primates show right-hand preferences for grasping-to-eat (Hopkins et al. 2011, 2005), especially when they adopt a bipedal posture (Hopkins et al. 1993; Hopkins and de Waal 1995). If this right-hand preference for grasp-to-eat movements is related to the kinematic signature we have identified, then it stands to reason that the reliance on visual feedback and advantage for right-hand movements may work in tandem to encourage use of the right hand for grasp-to-eat and other evolutionarily significant movements. This may

explain why such a large proportion of the global human population is right-handed.

In the present study, we show that the grasp-to-eat motor plan is reliant on dorsal stream function. What is still unclear is whether the grasp-to-eat motor plan may be considered multi-phasic (i.e., consisting of an outward transport and grasp phase inextricably coupled with an inward transport to the open mouth) or if the grasp-to-eat action effectively ends after target acquisition, with the transport to the mouth representing a secondary action with its own motor plan. Ansuini et al. (2009) conducted a study wherein they separated phases of a grasp-to-pour movement with a 0, 1000, or 1800 ms delay at time of target contact. They found that in conditions where the grasp-to-pour action was interrupted after target contact, the kinematics of the outward movement changed; delayed secondary phases caused longer MTs within the initial grasp, and an increase in the size of the participants' grip aperture. We hypothesize that if a similar delay was inserted into the grasp-to-eat movement at the time of target contact, then it would similarly increase MGA. Such a finding would indicate that the grasp-to-eat motor program ends at contact/acquisition; alternatively, if grasp-to-eat MGA is unaffected by delay, then we may conclude that the outward grasp and subsequent transport to the mouth are conjoined and inseparable aspects of the grasp-to-eat action. Ongoing experiments in our lab aim to address this question.

## Conclusions

To summarize, the current study found that there are no kinematic differences between grasp-to-eat and grasp-to-place actions during memory-guided movements. The kinematic signature associated with right-handed grasp-to-eat actions was no longer present when that action was performed after a 2000 ms delay. This finding suggests that the grasp-to-eat kinematic signature is ultimately dependent upon dorsal stream processing, which in turn suggests that task-specific motor programs may be localized to dorsal stream regions. This link may be responsible for the preponderance of right-hand dominance among the human population.

## References

- Annett J, Annett M, Hudson P, Turner A (1979) The control of movement in the preferred and non-preferred hands. *Q J Exp Psychol* 31(4):641–652
- Ansuini C, Giosa L, Turella L, Altoè G, Castiello U (2008) An object for an action, the same object for other actions: effects on hand shaping. *Exp Brain Res* 185(1):111–119
- Ansuini C, Grigis K, Massaccesi S, Castiello U (2009) Breaking the flow of an action. *Exp Brain Res* 192(2):287–292

- Armbrüster C, Spijkers W (2006) Movement planning in prehension: do intended actions influence the initial reach and grasp movement? *Mot Control* 10(4):311–329
- Berthier NE, Clifton RK, Gullapalli V, McCall DD, Robin D (1996) Visual information and object size in the control of reaching. *J Mot Behav* 28:187–197
- Bootsma RJ, Marteniuk RG, MacKenzie CL, Zaal FT (1994) The speed-accuracy trade-off in manual prehension: effects of movement amplitude, object size and object width on kinematic characteristics. *Exp Brain Res* 98(3):535–541
- Boulinguez P, Nougier V, Velay J-L (2001) Manual asymmetries in reaching movement control. I: study of right-handers. *Cortex* 37(1):101–122
- Carnahan H (1998) Manual asymmetries in response to rapid target movement. *Brain Cogn* 37(2):237–253
- Carson RG, Chua R, Elliott D, Goodman D (1990) The contribution of vision to asymmetries in manual aiming. *Neuropsychologia* 28(11):1215–1220
- Carson RG, Goodman D, Chua R, Elliott D (1993) Asymmetries in the regulation of visually guided aiming. *J Mot Behav* 25(1):21–32
- Castiello U, Bennett K, Stelmach G (1993) Reach to grasp: the natural response to perturbation of object size. *Exp Brain Res* 94:163–178
- Castiello U, Bennett K, Chambers H (1998) Reach to grasp: the response to a simultaneous perturbation of object position and size. *Exp Brain Res* 120(1):31–40
- Cavill S, Bryden P (2003) Development of handedness: comparison of questionnaire and performance-based measures of preference. *Brain Cogn* 53(2):149–151
- Duff SV, Sainburg RL (2007) Lateralization of motor adaptation reveals independence in control of trajectory and steady-state position. *Exp Brain Res* 179(4):551–561
- Elliott D, Roy EA, Goodman D, Carson RG, Chua R, Maraj BK (1993) Asymmetries in the preparation and control of manual aiming movements. *Can J Exp Psychol Revue canadienne de psychologie expérimentale* 47(3):570
- Ferri F, Campione GC, Dalla Volta R, Gianelli C, Gentilucci M (2010) To me or to you? When the self is advantaged. *Exp Brain Res* 203(4):637–646
- Flindall JW, Gonzalez CL (2013) On the evolution of handedness: evidence for feeding biases. *PLoS One* 8(11):e78967
- Flindall JW, Gonzalez CL (2014) Eating interrupted: the effect of intent on hand-to-mouth actions. *J Neurophysiol* 112(8):2019–2025
- Flindall JW, Gonzalez CL (2016) The destination defines the journey: an examination of the kinematics of hand-to-mouth movements. *J Neurophysiol* 116(5):2105–2113
- Flindall JW, Gonzalez CL (2017) The inimitable mouth: task-dependent kinematic differences are independent of terminal precision. *Exp Brain Res* 235(6):1945–1952
- Flindall JW, Doan JB, Gonzalez CL (2014) Manual asymmetries in the kinematics of a reach-to-grasp action. *Laterality Asymmetries Body Brain Cogn* 19(4):489–507
- Flindall JW, Stone KD, Gonzalez CL (2015) Evidence for right-hand feeding biases in a left-handed population. *Laterality Asymmetries Body Brain Cogn* 20(3):287–305
- Goodale M, Milner AD (1992) Separate visual pathways for perception and action. *Trends Neurosci* 15(1):20–25
- Goodale M, Jakobson L, Keillor J (1994) Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia* 32(10):1159–1178
- Goodale M, Westwood DA, Milner AD (2004) Two distinct modes of control for object-directed action. *Prog Brain Res* 144:131–144
- Grosskopf A, Kuhtz-Buschbeck JP (2006) Grasping with the left and right hand: a kinematic study. *Exp Brain Res* 168(1–2):230–240
- Heath M, Binsted G (2007) Visuomotor memory for target location in near and far reaching spaces. *J Mot Behav* 39(3):169–177
- Heath M, Westwood DA (2003) Can a visual representation support the online control of memory-dependent reaching? Evidence from a variable spatial mapping paradigm. *Mot Control* 7(4):349–365
- Hesse C, Franz VH (2010) Grasping remembered objects: exponential decay of the visual memory. *Vis Res* 50(24):2642–2650
- Hopkins WD, de Waal FB (1995) Behavioral laterality in captive bonobos (*Pan paniscus*): replication and extension. *Int J Primatol* 16(3):261–276
- Hopkins WD, Bennett AJ, Bales SL, Lee J, Ward JP (1993) Behavioral laterality in captive bonobos (*Pan paniscus*). *J Comp Psychol* 107(4):403
- Hopkins WD, Russell JL, Hook M, Braccini S, Schapiro SJ (2005) Simple reaching is not so simple: association between hand use and grip preferences in captive chimpanzees. *Int J Primatol* 26(2):259–277
- Hopkins WD, Phillips KA, Bania A, Calcutt SE, Gardner M, Russell J, Schapiro SJ et al (2011) Hand preferences for coordinated bimanual actions in 777 great apes: implications for the evolution of handedness in hominins. *J Hum Evol* 60(5):605–611
- Hu Y, Goodale M (2000) Grasping after a delay shifts size-scaling from absolute to relative metrics. *J Cogn Neurosci* 12(5):856–868
- Hu Y, Eagleson R, Goodale M (1999) The effects of delay on the kinematics of grasping. *Exp Brain Res* 126(1):109–116
- Marteniuk R, MacKenzie C, Jeannerod M, Athenes S, Dugas C (1987) Constraints on human arm movement trajectories. *Can J Psychol Revue canadienne de psychologie* 41(3):365
- Milner AD, Goodale M (2006) *The visual brain in action*. Oxford University Press, Oxford
- Milner AD, Goodale M (2008) Two visual systems re-viewed. *Neuropsychologia* 46(3):774–785
- Mutha PK, Haaland KY, Sainburg RL (2013) Rethinking motor lateralization: specialized but complementary mechanisms for motor control of each arm. *PLoS One* 8(3):e58582
- Naish KR, Reader AT, Houston-Price C, Bremner AJ, Holmes NP (2013) To eat or not to eat? Kinematics and muscle activity of reach-to-grasp movements are influenced by the action goal, but observers do not detect these differences. *Exp Brain Res* 225(2):261–275
- Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9(1):97–113
- Paulignan Y, Frak VG, Toni I, Jeannerod M (1997) Influence of object position and size on human prehension movements. *Exp Brain Res* 114:226–234
- Roy EA, Kalbfleisch L, Elliott D (1994) Kinematic analyses of manual asymmetries in visual aiming movements. *Brain Cogn* 24(2):289–295
- Schaefer SY, Haaland KY, Sainburg RL (2009) Hemispheric specialization and functional impact of ipsilesional deficits in movement coordination and accuracy. *Neuropsychologia* 47(13):2953–2966
- Shabbott BA, Sainburg RL (2008) Differentiating between two models of motor lateralization. *J Neurophysiol* 100(2):565–575
- Stone KD, Bryant DC, Gonzalez CLR (2013) Hand use for grasping in a bimanual task: evidence for different roles? *Exp Brain Res* 224(3):455–467
- Tomlinson T, Sainburg R (2012) Dynamic dominance persists during unsupported reaching. *J Mot Behav* 44(1):13–25
- Trethiluxana J, Gordon J, Winstein CJ (2008) Manual asymmetries in grasp pre-shaping and transport-grasp coordination. *Exp Brain Res* 188(2):305–315
- Veazie PJ (2006) When to combine hypotheses and adjust for multiple tests. *Health Serv Res* 41(3p1):804–818
- Wang J, Sainburg RL (2007) The dominant and nondominant arms are specialized for stabilizing different features of task performance. *Exp Brain Res* 178(4):565–570
- Westwood DA, Goodale M (2003) Perceptual illusion and the real-time control of action. *Spat Vis* 16(3):243–254