

Contents lists available at ScienceDirect

Journal of Experimental Child Psychology

journal homepage: www.elsevier.com/locate/jecp

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



Jason W. Flindall*, Claudia L.R. Gonzalez

The Brain in Action Laboratory, Department of Kinesiology, University of Lethbridge, Lethbridge, Alberta T1K 3M4, Canada

ARTICLE INFO

Article history: Received 8 October 2014 Revised 23 January 2015

Keywords: Kinematics Development Bimanual Left-hand Hand-to-mouth Grip aperture

ABSTRACT

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

© 2015 Elsevier Inc. All rights reserved.

* Corresponding author. E-mail address: jason.flindall@uleth.ca (J.W. Flindall).

http://dx.doi.org/10.1016/j.jecp.2015.01.011 0022-0965/© 2015 Elsevier Inc. All rights reserved.

Introduction

The hand-to-mouth movement is among the earliest developing goal-directed movements (Piaget & Cook, 1953). Fetuses demonstrate a right-hand preference for hand-to-mouth movements before birth (Hepper, McCartney, & Shannon, 1998), and infants as young as 1 year demonstrate a right-hand preference for self-feeding actions (Sacrey, Arnold, Whishaw, & Gonzalez, 2013). Although some have argued that degree of handedness is not fully stable until later years (Coren, Porac, & Duncan, 1981; McManus et al., 1988; Michel, Babik, Sheu, & Campbell, 2014; Rönngvist & Domellöf, 2006), these observations regarding hand-to-mouth movements have led some researchers to posit that the direction of handedness is established during the pre- and perinatal periods (Levy, 1976). In fact, multiple studies have documented a lateralized hand preference for grasping in infants as young as 6 months (Claxton, Keen, & McCarty, 2003; Ferre, Babik, & Michel, 2010; Hopkins & Rönnqvist, 2002; Michel et al., 2014; Morange-Majoux, Peze, & Bloch, 2000; Nelson, Campbell, & Michel, 2013; Rönnqvist & Domellöf, 2006). They have shown that, when presented with a solitary object (most often a small plush toy), infants will more often prefer their right hands for unimanual grasps. Although this early development of right-hand preference for simple object acquisition has been reported by some researchers (Nelson et al., 2013; Rönnqvist & Domellöf, 2006), others have reported that hand preference for reach-to-grasp actions is not present (or at least not consistent) until much later in development (Fagard & Marks, 2000; Nelson et al., 2013; Sacrey et al., 2013). For instance, a right-hand preference for grasping rings to remove them from a column is not apparent until a child is 21 months old (Fagard & Marks, 2000), and a robust hand preference for other grasp-to-manipulate tasks does not appear until up to several months later (McManus et al., 1988; Sacrey et al., 2013; Vauclair & Imbault, 2009). Because the initial mechanical requirements of grasping actions are virtually identical (Karl & Whishaw, 2013), it must be the end goal (or action intent, i.e., what the child is going to do with the object after acquiring it) that dictates the difference in the two sets of findings.

Action intent has been shown to modulate kinematics of the reach-to-grasp actions in adults (Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Ansuini, Santello, Massaccesi, & Castiello, 2006; Armbrüster & Spijkers, 2006; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987; Sartori, Straulino, & Castiello, 2011) and in young children (Chen, Keen, Rosander, & Von Hofsten, 2010; Claxton et al., 2003). These studies have focused primarily on the kinematics of the reach rather than those of the grasp, however, and have not investigated whether asymmetries exist between the hands. Given the preference for right-hand use during grasping actions, one might speculate that kinematic asymmetries favoring the right hand would be clearly observable. However, studies in adults have demonstrated that left-handed movements are carried out with the same precision, timing, and preparation as their (more common) right-handed equivalents (Grosskopf & Kuhtz-Buschbeck, 2006; Tretriluxana, Gordon, & Winstein, 2008). Perhaps a way to investigate kinematic differences in reach-to-grasp actions is to use an ecologically relevant task. The previous studies have used grasp-to-lift or grasp-to-place actions, which one might argue have little ecological relevance. Because the hand-to-mouth movement has been presented as a potential archetype for all grasps (Iwaniuk & Whishaw, 2000; Whishaw, Sarna, & Pellis, 1998), investigation into this movement may prove to be effective in revealing manual asymmetries.

Kinematic investigations on the hand-to-mouth movement are seldom performed (Castiello, 1997; Desmurget et al., 2014; Ferri, Campione, Dalla Volta, Gianelli, & Gentilucci, 2011; Flindall & Gonzalez, 2014). The few studies that have investigated the kinematics of hand-to-mouth/grasp-to-eat movements showed that adults produce smaller maximum grip apertures (MGAs) when grasping an item with intent to eat than when grasping the same item with intent to place (Ferri, Campione, Dalla Volta, Gianelli, & Gentilucci, 2010; Flindall & Gonzalez, 2013). This task-dependent behavior is limited to movements performed with the right hand; left-handed movements show no kinematic difference between grasp-to-eat and grasp-to-place actions (Flindall & Gonzalez, 2013, 2014; Flindall, Stone, & Gonzalez, 2015). Smaller MGAs for the grasp-to-eat task may be considered as a kinematic advantage for two reasons. First, larger MGAs have been described as a mechanism used to compensate for uncertainty regarding the size, location, or stability of a target (Berthier, Clifton, Gullapalli, McCall, & Robin, 1996; Flindall, 2012; Gentilucci, Toni, Chieffi, & Pavesi, 1994; Harvey et al., 2001; Jakobson

59

& Goodale, 1991; Schettino, Adamovich, & Poizner, 2003; Wing, Turton, & Fraser, 1986); given this interpretation, it naturally follows that smaller MGAs may signify increased certainty about the target's intrinsic and/or extrinsic characteristics. Second, smaller MGAs are considered as more energetically efficient because peak grip-closing velocity, grip-closing time, and other energetic requirements are reduced when the MGA more closely approximates the absolute size of the target (Bootsma, Marteniuk, MacKenzie, & Zaal, 1994).

The primary aim of the current study was to investigate the previously identified right-hand advantage for the grasp-to-eat movement in a group of typically developing children. To this end, we compared MGA during right- and left-handed grasp-to-place and grasp-to-eat movements made by children aged 7 to 12 years. Two groups-20 children aged 7 to 9 years and 20 children aged 10 to 12 years—were asked to grasp small food items to either eat them or place them in a receptacle located near the mouth with both their dominant and non-dominant hands in separate blocks. This analysis also afforded us the opportunity to describe other reach-and-grasp kinematics during these movements. Although the kinematics of dominant-hand grasp-to-place movements in children have been described in numerous studies (Duemmler, Franz, Jovanovic, & Schwarzer, 2008; Kuhtz-Buschbeck, Stolze, Jöhnk, Boczek-Funcke, & Illert, 1998; Olivier, Hay, Bard, & Fleury, 2007; Pryde, Roy, & Campbell, 1998; Rönngvist & Rösblad, 2007; Schneiberg, Sveistrup, McFadyen, McKinley, & Levin, 2002; Zoia et al., 2006), few studies have contrasted these actions with those performed with the non-dominant hand (cf. Rönnqvist & Rösblad, 2007), resulting in an absent frame of reference for manual asymmetries in typically developing children. The secondary aim of the current study, therefore, was to describe both reach and grasp kinematics of right- and left-handed grasp-to-eat/grasp-to-place movements, thereby addressing somewhat the dearth of information regarding kinematic asymmetries in children.

Method

Participants

A total of 40 children aged 7 to 12 years participated in the current study. This age range was chosen because it was the broadest range possible using our collection paradigm. Preliminary testing revealed that children younger than 7 years were unable to complete the testing session (approximately 45 min) without becoming bored, fidgety, or otherwise distracted; this negatively affected both the quantity and quality of kinematic data collected. Because the average age of onset for puberty is just under 13 years (Harris, Prior, & Koehoorn, 2008), children older than 12 years were preemptively excluded from the study. Handedness was determined by self-report and confirmed via a modified Waterloo/Edinburgh Handedness Questionnaire (Oldfield, 1971; Stone, Bryant, & Gonzalez, 2013), completed with the aid of a parent or guardian. Participants were not excluded based on reported hand preference because many previous investigations on grasping and prehension have shown comparable results between left- and right-handers (Boulinguez, Velay, & Nougier, 2001; Flindall et al., 2015; Gonzalez, Whitwell, Morrissey, Ganel, & Goodale, 2007; Stone et al., 2013). Participants gave oral consent prior to data collection. Written informed consent was provided on each participant's behalf by a parent or guardian on admission to the study in accordance with the principles expressed in the Declaration of Helsinki and with the approval of the University of Lethbridge Human Subjects Research Committee (Protocol 2013-065). Children received a small toy and a \$10 gift certificate to a local bookstore in appreciation for their participation. Participants were able to withdraw from the study at any time without consequence.

Materials

Three infrared light emitting diodes (IREDs) were placed on each participant's hand: two on the distal phalanges of the thumb and index finger, slightly proximal with respect to the nails, and one on the wrist at the medial aspect of the styloid process of the radius. An Optotrak Certus camera bar (Northern Digital, Waterloo, Ontario, Canada) recorded IRED position during each trial at 200 Hz

for 5 s. Motion capture and audio equipment were controlled using Superlab 4.5 (Cedrus, San Pedro, CA, USA) and NDI First Principles (Northern Digital).

Participants were seated in front of a self-standing height-adjustable triangular pedestal (Fig. 1). The pedestal held cereal food items of different sizes that were presented individually. Both small (Cheerios, mean diameter 11 mm) and large (Froot Loops, mean diameter 15 mm) targets were used. These targets were chosen based on their familiarity to participants and their distinct sizes (Flindall & Gonzalez, 2013, 2014). The distance to the pedestal was normalized to each participant's reach distance (100% of length from shoulder to index finger with elbow at full 180° extension). The heights of the pedestal and chair were adjusted for each participant such that the food was at a comfortable reach height (approximately level with the base of the sternum of the seated participant) but also such that the edge of the pedestal did not act as a direct obstacle during the reach-to-grasp movement (Flindall & Gonzalez, 2013, 2014; Whishaw et al., 2002).

Procedure

The participant was seated behind the pedestal with the reaching hand (thumb and index fingertips together) placed comfortably on his or her lap (Fig. 1A). Targets were placed on the pedestal in a pseudo-random order. An auditory tone ("beep") sounded at the beginning of each trial, indicating that the participant should begin the reach-to-grasp movement (Fig. 1B) and subsequently either *eat* the target (Fig. 1C) or *place* the target in a bib hung snugly under his or her chin (Fig. 1D). Participants were instructed to grasp the targets "as quickly and as accurately as possible" but with an emphasis on accuracy over speed. Each condition (eat or place) was carried out in a separate block of 20 grasps (10 small and 10 large, pseudo-randomized order), with initial task and hand start order counterbalanced between participants. After both tasks were completed with the starting hand, IREDs were shifted to the participant's opposite hand and the tasks were repeated in the same order.

Analyses

Kinematic comparisons were made between reach-to-grasp phases of each trial. Reach kinematics were calculated from displacement of the wrist marker. These measurements included MT (movement time), PV (peak velocity), and PVt (time of peak velocity). MT represents the span during which the participant reached outward toward the target and was calculated as the difference between reaction time and time of grasp contact. Reaction time was calculated as the time following the go signal at which the participant achieved a resultant velocity equal to 5% of his or her peak velocity, and grasp contact was said to have occurred when the participant's wrist reached its lowest velocity



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

immediately preceding the return movement. PV was calculated as the maximum resultant velocity the participant achieved during his or her outward movement toward the target, again measured from the wrist marker. PVt was calculated as the absolute time at which PV occurred minus reaction time and divided by overall MT. PVt is reported as a percentage of MT. Grasp kinematics include MGA and MGAt (time of MGA). MGA was measured as the peak resultant distance between the thumb and index finger prior to grasp contact. MGAt, like PVt, is reported as a percentage of MT and was calculated in the same way. To allow comparisons between left- and right-handed movements, participants grasped a 31.25-mm-wide block at the beginning and end of data collection. A correction factor was then calculated from IRED separation distance during this grasp. This correction factor was applied to all MGA measurements to compensate for IRED placement variability between participants (Tang, Whitwell, & Goodale, 2014). Because variability has been used in the past to measure the point in time at which a movement becomes learned (Schneiberg et al., 2002), variability of reach and grasp kinematics are also reported: vMT (variability of movement time), vPV (variability of peak velocity), vPVt (variability of time of peak velocity), vMGA (variability of maximum grip aperture), and vMGAt (variability of time of maximum grip aperture). These were calculated as the standard deviations of the variables within each hand/task/size grouping for each participant.

Data processing

Data were collected via NDI First Principles, with kinematic calculations performed on unfiltered data with Microsoft Excel 2010. Statistical analyses were completed using IBM SPSS Statistics Version 19. If a participant moved to grasp the target prior to the go signal, or if a participant failed to grasp the target correctly (e.g., accidentally knocking the target to the floor, using his or her middle finger to grasp the target), the offending trial was removed from analysis and not repeated. Data from 2 participants in the younger group were removed from analyses because of wrist marker failure over more than 30% of trials. Among the remaining participants, on average 2.19 trials per participant were removed as a result of these behavioral or mechanical errors. Remaining trials were averaged by condition with three-way within-participant repeated-measures analysis of variance (ANOVA) [Hand (left or right) \times Task (eat or place) \times Size (large or small)] run on condition means. Alpha significance for initial ANOVA results was set at p < .05. Post hoc comparisons were conducted via paired-samples *t*-tests. Estimate of effect size is reported using partial η^2 . Kinematic data were binned into two groups based on each participant's age at time of participation. Young children (7-9 years, n = 18, average)age = 8.22 \pm 0.878 years, 6 girls and 12 boys, 1 left-handed) and older children (10–12 years, n = 20, average age = 10.85 ± 0.813 years, 13 girls and 7 boys, 1 left-handed) were analyzed separately. Because previous investigations involving adults found that the lateralization and magnitude of MGA difference was unrelated to handedness as measured by questionnaire (Flindall et al., 2015), lefthanded children were not automatically excluded from analyses. To confirm that their inclusion did not change the outcome of the investigation, identical ANOVAs were run on data from right-handed participants only; all significant main effects and interactions (reported below) remained significant. Because the inclusion of left-handed participants did not affect the strength of the reported effects, only the results from the more inclusive analyses are reported.

Results

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

Reach kinematics

Movement time

A main effect of size was observed on MT in both younger children, F(1, 17) = 34.35, p < .001, $\eta^2 = .669$, and older children, F(1, 19) = 82.71, p < .001, $\eta^2 = .813$. In both groups, children took longer

 Table 1

 Between-participant means and standard errors for reach and grasp kinematics for younger children aged 7 to 9 years (n = 18).

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

Note. Values are reported for all hand, task, and target size conditions. Significant ANOVA results by main effect (H: hand; T: task; S: size) and interaction (e.g., H × T: Hand × Task) are listed in the bottom row. Variables reported are MT (movement time), PV (peak velocity), PVt (time of peak velocity, expressed as a percentage of MT), MGA (maximum grip aperture), and MGAt (time of maximum grip aperture, expressed as a percentage of MT). Mean inter-trial variability is also reported for all variables.

 Table 2

 Between-participant means and standard errors for reach and grasp kinematics for older children aged 10 to 12 years (n = 20).

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

Note. Values are reported for all hand, task, and target size conditions. Significant ANOVA results by main effect (H: hand; T: task; S: size) and interaction (e.g., H × T: Hand × Task) are listed in the bottom row. Variables reported are MT (movement time), PV (peak velocity), PVt (time of peak velocity, expressed as a percentage of MT), MGA (maximum grip aperture), and MGAt (time of maximum grip aperture, expressed as a percentage of MT). Mean inter-trial variability is also reported for all variables.

to complete movements toward small targets ($M_{young} = 988 \pm 36 \text{ ms}$; $M_{old} = 909 \pm 29 \text{ ms}$) than they did toward large targets ($M_{young} = 905 \pm 32 \text{ ms}$; $M_{old} = 836 \pm 27 \text{ ms}$). With respect to MT, no other main effects or interactions were observed.

Variability of movement time

Among younger children, a main effect of hand was observed on vMT, F(1, 17) = 15.33, p = .001, $\eta^2 = .474$. Younger children produced more consistent movements in terms of MT when using their right hand. This asymmetry was not observed in older children (p > .50). Main effects of size on vMT were observed in both the young group, F(1, 17) = 9.22, p = .007, $\eta^2 = .352$, and the older group, F(1, 19) = 16.33, p < .001, $\eta^2 = .462$, where movement times for small targets ($M_{young} = 171 \pm 12 \text{ mm}$; $M_{old} = 151 \pm 9 \text{ mm}$) were more variable than movement times for large targets ($M_{young} = 134 \pm 9 \text{ mm}$; $M_{old} = 112 \pm 7 \text{ mm}$). With respect to vMT, no other main effects or interactions were observed.

Peak velocity

No main effects or interactions were observed.

Variability of peak velocity

No main effects or interactions were observed.

Time of peak velocity

A main effect of size was observed on PVt in both younger children, F(1, 17) = 23.75, p < .001, $\eta^2 = .583$, and older children, F(1, 19) = 53.58, p < .001, $\eta^2 = .738$. In both groups, children achieved PV relatively later in the movement when reaching toward the large targets ($M_{young} = 30.7 \pm 0.7\%$; $M_{old} = 33.0 \pm 0.8\%$) than when reaching toward the small targets ($M_{young} = 28.3 \pm 0.9\%$; $M_{old} = 30.4 \pm 0.8\%$). This would indicate that all children spent relatively more time in the post-peak velocity (i.e., deceleration) phase of the movement when reaching toward small targets. A main effect of hand was observed in the young group, F(1, 17) = 8.66, p = .009, $\eta^2 = .337$, where younger children achieved peak velocity relatively earlier in the movement when reaching with their left hand ($M_{young} = 28.7 \pm 0.8\%$) than when reaching with their right hand ($M_{young} = 30.3 \pm 0.8\%$). A Hand × Size interaction was found among older children, F(1, 19) = 5.80, p = .026, $\eta^2 = .234$; follow-up *t*-tests indicated that in reaches directed toward large targets, left-handed reaches achieved peak velocity relatively earlier in the movement ($M_{old} = 32.1 \pm 0.8\%$) than did right-handed reaches ($M_{old} = 34.0 \pm 1.1\%$), t(19) = -2.076, p = .05. When directed toward small targets, right- and left-handed reaches showed no difference in PVt (p > .40). No other main effects or interactions were observed.

Variability of time of peak velocity

No main effects or interactions were observed.

Grasp kinematics

Maximum grip aperture

A main effect of size was observed on MGA in both younger children, F(1, 17) = 175.93, p < .001, $\eta^2 = .912$, and older children, F(1, 19) = 190.25, p < .001, $\eta^2 = .909$, where participants opened their hand wider when grasping large targets ($M_{young} = 27.2 \pm 1.0 \text{ mm}$; $M_{old} = 28.1 \pm 0.6 \text{ mm}$) than they did when grasping small targets ($M_{young} = 23.4 \pm 0.9 \text{ mm}$; $M_{old} = 23.9 \pm 0.5 \text{ mm}$). A main effect of hand on MGA was observed in the young group, F(1, 17) = 4.32, p = .05, $\eta^2 = .203$, where it was found that, while grasping items of all sizes, younger children opened their left hand wider ($M_{young} = 26.7 \pm 1.1 \text{ mm}$) than they did their right hand ($M_{young} = 23.9 \pm 1.2 \text{ mm}$) regardless of task. This effect was not present in the older group (p > .40). A main effect of task on MGA was observed in both groups, where both younger children, F(1, 17) = 8.35, p = .010, $\eta^2 = .329$, and older children, F(1, 19) = 5.85, p = .026, $\eta^2 = .235$, opened their hand less wide when grasping targets with intent to eat ($M_{young} = 24.5 \pm 0.9 \text{ mm}$; $M_{old} = 25.4 \pm 0.6 \text{ mm}$) than when grasping targets to place them in a bib ($M_{young} = 26.1 \pm 1.1 \text{ mm}$; $M_{old} = 26.6 \pm 0.6 \text{ mm}$). Because this behavior is in contrast to the Hand × Task interaction observed among adults in previous studies (Flindall & Gonzalez, 2013, 2014; Flindall et al., 2015), data were split



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

by hand and task, and paired-samples *t*-tests were used to facilitate an in-depth comparison between these groups (Fig. 2). These tests revealed that among the young group the difference between tasks was significant in both left- and right-handed movements, t(17) < 2.06, p < .05, but among the older group the effect was significant only during right-handed movements, t(19) = -3.34, p = .003. When older children reached with their left hand, the difference between tasks was not significant, t(19) = -0.839, p > .40. With respect to MGA, no other main effects or interactions were observed.

Variability of maximum grip aperture

Among older children, a main effect of task was observed on vMGA, F(1, 19) = 6.42, p = .020, η^2 = .252, where older children produced more consistent MGAs when grasping items with intent to eat $(M_{old} = 3.2 \pm 0.2 \text{ mm})$ than when grasping them to place them in a bib $(M_{old} = 3.6 \pm 0.2 \text{ mm})$. No such effect was found among younger children (p > .05). vMGA Hand \times Task interactions were observed in both the young group, F(1, 17) = 6.09, p = .024, $\eta^2 = .264$, and the older group, F(1, 17) = 6.09, p = .024, $\eta^2 = .264$, and the older group, F(1, 17) = 0.09, F(1, 17) = 0.0919) = 4.11, p = .05, η^2 = .178. Follow-up *t*-tests revealed that in the young group this effect was due to a significant difference in variability of MGA between the left hand $(M_{\text{young}} = 4.1 \pm 0.4 \text{ mm})$ and the right hand ($M_{young} = 3.3 \pm 0.2$ mm), limited to the place task. There was no difference between younger children's hands during the eat task (p > .60). In the older group, the effect was due to lefthanded eat MGAs being significantly less variable (M_{old} = 3.0 ± 0.2 mm) than left-handed place tasks $(M_{\text{old}} = 3.9 \pm 0.2 \text{ mm})$. The difference between tasks was not significant during right-handed movements (p > .10). In both groups, the greatest variability among all conditions was during left-handed place movements (Fig. 3). Finally, a Task × Size interaction was observed on vMGA in younger children, F(1, 17) = 4.84, p = .042, $\eta^2 = .222$. Follow-up *t*-tests revealed that MGA was significantly more variable when grasping large targets to eat (M_{young} = 4.0 ± 0.4 mm) than when grasping small targets to eat $(M_{\text{young}} = 3.2 \pm 0.3 \text{ mm})$, t(17) = 2.711, p = .15. The difference was not observed during the place task (p > .80). No other main effects or interactions were observed.

Time of maximum grip aperture

A main effect of hand, F(1, 17) = 8.86, p = .008, $\eta^2 = .343$, was observed among younger children, where MGA was achieved earlier in the movement during right-handed grasps $(M_{young} = 52.8 \pm 2.1\%)$ than it was during left-handed grasps $(M_{young} = 57.2 \pm 1.5\%)$. A main effect of task was observed among younger children, F(1, 17) = 16.09, p < .001, $\eta^2 = .486$. MGA was reached relatively earlier in the movement when younger children grasped with intent to place $(M_{young} = 53.4 \pm 1.8\%)$ than when grasping the same item to eat $(M_{young} = 56.7 \pm 1.5\%)$. This effect was not present among older children (p > .05). A main effect of size was observed in both younger children, F(1, 17) = 23.30, p < .001, $\eta^2 = .578$, and older children, F(1, 19) = 22.45, p < .001, $\eta^2 = .542$, where MGA was reached relatively earlier in the movement while grasping the smaller targets $(M_{young} = 52.8 \pm 1.5\%)$; $M_{old} = 50.4 \pm 1.9\%)$ than when grasping larger targets $(M_{young} = 57.3 \pm 1.8\%)$; $M_{old} = 55.1 \pm 1.7\%)$. Finally, a Hand × Task × Size interaction was observed among older children, F(1, 19) = 4.94, p = .039, $\eta^2 = .206$. Follow-up *t*-tests revealed that although MGAt was always



Fig. 3. Hand \times Task interaction on vMGA in younger and older children. In both cases, significant differences appeared due to high variability in left-handed movements in the place task. An asterisk (*) indicates significant difference between conditions, p < .05.

relatively earlier in the movement when grasping small targets than when grasping large targets, t(19) > 3.33, p < .003, the difference between sizes was not significant when grasping to eat with the right hand (p > .05). With respect to MGAt, no other main effects or interactions were observed.

Variability of time of maximum grip aperture

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

Discussion

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

Actor intent has previously been shown to influence the kinematics of seemingly similar reach-tograsp actions. In adults, differences have been demonstrated not only between eat and place grasps

67

(Ferri et al., 2010; Flindall & Gonzalez, 2013, 2014; Flindall et al., 2015; Naish, Reader, Houston-Price, Bremner, & Holmes, 2013) but also between grasps for lifting, placing, and throwing actions (Ansuini et al., 2008; Armbrüster & Spijkers, 2006; Marteniuk et al., 1987). In the current study, actor intent was found to influence hand preshaping, with tighter, more consistent MGAs produced when grasping to eat rather than to place a small food item. Although kinematics of reach-to-grasp movements have been shown to vary with intent in children as young as 10.5 months (Chen et al., 2010; Claxton et al., 2003), this is (to our knowledge) the first study involving children in which such task-dependent differences have been shown to be asymmetric. Because previous studies measuring grasp kinematics (specifically those describing hand preshaping) in children have used either grasp-to-lift tasks (Pryde et al., 1998; Schneiberg et al., 2002; Smyth, Katamba, & Peacock, 2004; Zoia et al., 2006) or grasp-toplace tasks (Kuhtz-Buschbeck et al., 1998; Olivier et al., 2007; Rönnqvist & Rösblad, 2007), the current results represent a significant contribution to the developmental literature and a cautionary tale with respect to methodological considerations. Because we showed that the end goal of an action will affect grasp kinematics in children, we propose that researchers conducting developmental studies on reach-to-grasp actions should seek to address this influence in both experimental design and subsequent analysis.

The lateralized task effect observed in adults where MGA is smaller during right-handed grasp-toeat movements has been interpreted as a right-hand advantage for the grasp-to-eat movement. In turn, this has been put forward as a potential driver of population-level right-handedness in humans (Flindall & Gonzalez, 2013). However, another possibility is that this effect is a result of increased dominant hand practice with grasp-to-eat movements given that an early developing preference for grasp-to-eat actions would result in several more years of right-hand experience in those movements as compared with other grasping movements (Sacrey et al., 2013). In the current study, it was found that although the task-dependent difference in MGA production was present in both younger and older children, it was not lateralized until the children reached 10 to 12 years of age. If the rightward lateralization of grasp-to-eat actions were entirely a result of practice, one would expect both (a) a consistent leftward lateralization of the effect in the left-hand dominant population and (b) a lack of task-dependent kinematic differences in young children coupled with a gradual appearance of the grasp-to-eat advantage as children age and gain experience in using their dominant hand. When the effect was investigated in left-handers, the degree and direction of effect lateralization was found to be inconsistent among the tested population (Flindall et al., 2015). Furthermore, lateralization was found to be unrelated to degree of left-handedness as measured via questionnaire and also was found to be more significantly differentiated when presenting in the right hand (Flindall et al., 2015). In that study, the lack of consistent lateralization was interpreted as an indication that the effect was not a consequence of practice. In the current study, the kinematic advantage was present in both hands among younger children but was present only in the right hand among older children. In this age group, as in adults, the left-handed hand-to-mouth movement shares kinematic characteristics with grasp-to-place actions (Flindall & Gonzalez, 2014). Although only longitudinal data could speak to changes over time, it is possible that the eat and place tasks begin as separate and distinct movements in *both* hands but that the task specificity for hand-to-mouth actions may be lost in the left hand sometime during the peripubescent period. Following the results of these investigations, the hypothesis that unimanual advantage for feeding actions results from a dominant-hand practice effect must be rejected. The "retention" of this task-dependent effect in right-handed movements may be a result of Hebbian-type reinforcement, where neuronal adaptation is stabilized through persistent activation of synaptic networks (Hebb, 1949). Because the developing primate brain undergoes significant pruning of dendritic connections throughout childhood and into early adulthood (Elston, Oga, & Fujita, 2009; Huttenlocher & Dabholkar, 1997; Jacobs, Driscoll, & Schall, 1997; Petanjek et al., 2011; Woo, Pucak, Kye, Matus, & Lewis, 1997), it is possible to speculate that a bimanual advantage for hand-to-mouth movements, perhaps the result of a critical period during early childhood for the development of prehension (Forssberg, Eliasson, Kinoshita, Johansson, & Westling, 1991; Forssberg et al., 1992; Schneiberg et al., 2002), is only retained in one hand after a prolonged period of strong unimanual preference. However, as stated above, such a hypothesis would require longitudinal data to support and as such is beyond the domain of the current study. Regardless, the results of the current study do not provide direct support for the argument that handedness evolved as a result of feeding biases. Rather, the current evidence suggests that the handto-mouth kinematic advantage may be *retained* in the dominant hand rather than being an a priori foundation for development of hand dominance. Perhaps an investigation into the kinematics of grasp-to-eat actions in younger children (2–5 years) would yield different results. In addition, it is important to note that left-handed participants were included in our analysis based on data from adults showing limited kinematic differences between left- and right-handed populations. Because the current study demonstrates age-related kinematic differences, future investigations should include a larger sample of left-handed children to assess whether the pattern observed in left- and right-handed adults holds true among children. Finally, it would be interesting to see how the effect may present in seniors as well as whether and how it changes in neurological populations. Such data may afford insight into the true degree of lateralization between eat and place actions as well as provide a possible benchmark for detecting and monitoring the advancement of degenerative syndromes. Future research will be guided by these questions.

With regard to the asymmetrical development of reach-to-grasp movements, younger children in our study were observed to produce larger MGAs, spend more time decelerating, and have less consistent MGAs and MTs when reaching with their left hand. These asymmetries were not present when older children grasped the same targets, suggesting that left-hand kinematics had matured to a level similar to that of the right hand by the end of the first decade of life. In other words, older childrenlike adults-showed no significant kinematic differences between the left and right hands. These results are similar to those from previous research on the development of dominant-hand grasping kinematics that found similar age-related decreases in MGA (Duemmler et al., 2008; Kuhtz-Buschbeck et al., 1998; Olivier et al., 2007; Zoia et al., 2006; cf. Smyth et al., 2004) and reach-to-grasp kinematic variability (Kuhtz-Buschbeck et al., 1998; Olivier et al., 2007; Schneiberg et al., 2002). In addition, the age-related reduction of these differences is in line with studies describing reach-tograsp asymmetries in the adult population that found only minor and subtle differences between leftand right-handed grasping actions (Flindall, Doan, & Gonzalez, 2014; Grosskopf & Kuhtz-Buschbeck, 2006; Tretriluxana et al., 2008). Because variable performance of an action is an essential characteristic of that action's development (Schneiberg et al., 2002), this unequal kinematic performance may be viewed as evidence that left- and right-hand grasp preshaping kinematics reach mature levels at different times, with right-hand kinematics maturing (i.e., attaining adult-like consistency between grasps) earlier than left-hand kinematics. The observed asymmetries among the youngest children may be an effect related to transient experience-related differences in ability between the dominant and non-dominant hands (Fagard & Marks, 2000; Sacrey et al., 2013; Vauclair & Imbault, 2009), immature development of the corpus callosum (Keshavan et al., 2002; Luders, Thompson, & Toga, 2010), intrinsic left-hemisphere advantages for prehension (Gonzalez & Goodale, 2009; Gonzalez et al., 2007; Goodale, 1988, 1990), or a combination of the above factors. Although it is beyond the scope of this study to further speculate on the underlying causes of these differences, the description of behavioral asymmetries is a critical first step in establishing a catalogue of reach-to-grasp kinematics in typically developing children. Such a catalogue will not only allow us to evaluate deficiencies in children affected by movement disorders but also allow us to judge the effectiveness of therapeutic programs on bimanual motor performance (Schneiberg et al., 2002).

Conclusion

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

Acknowledgments

This research was conducted with support from the Canadian Foundation for Innovation, Natural Sciences and Engineering Research Council of Canada (NSERC), Alberta Innovates - Health Solutions, and University of Lethbridge.

References

- 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. *Experimental Brain Research*, 185, 111–119.
- Ansuini, C., Santello, M., Massaccesi, S., & Castiello, U. (2006). Effects of end-goal on hand shaping. *Journal of Neurophysiology*, 95, 2456–2465.
- Armbrüster, C., & Spijkers, W. (2006). Movement planning in prehension: Do intended actions influence the initial reach and grasp movement? *Motor Control*, 10, 311–329.
- Berthier, N. E., Clifton, R. K., Gullapalli, V., McCall, D. D., & Robin, D. (1996). Visual information and object size in the control of reaching. Journal of Motor Behavior, 28, 187–197.
- Bootsma, R. J., Marteniuk, R. G., MacKenzie, C. L., & Zaal, F. (1994). The speed-accuracy trade-off in manual prehension: Effects of movement amplitude, object size, and object width on kinematic characteristics. *Experimental Brain Research*, 98, 535–541.
- Boulinguez, P., Velay, J.-L., & Nougier, V. (2001). Manual asymmetries in reaching movement control: II. Study of left-handers. Cortex, 37, 123–138.
- Castiello, U. (1997). Arm and mouth coordination during the eating action in humans: A kinematic analysis. *Experimental Brain Research*, 115, 552–556.
- Chen, Y. P., Keen, R., Rosander, K., & Von Hofsten, C. (2010). Movement planning reflects skill level and age changes in toddlers. Child Development, 81, 1846–1858.
- Claxton, L. J., Keen, R., & McCarty, M. E. (2003). Evidence of motor planning in infant reaching behavior. *Psychological Science*, 14, 354–356.
- Coren, S., Porac, C., & Duncan, P. (1981). Lateral preference behaviors in preschool children and young adults. *Child Development*, 52, 443–450.
- Desmurget, M., Richard, N., Harquel, S., Baraduc, P., Szathmari, A., Mottolese, C., et al (2014). Neural representations of ethologically relevant hand/mouth synergies in the human precentral gyrus. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 5718–5722.
- Duemmler, T., Franz, V. H., Jovanovic, B., & Schwarzer, G. (2008). Effects of the Ebbinghaus illusion on children's perception and grasping. *Experimental Brain Research*, 186, 249–260.
- Elston, G. N., Oga, T., & Fujita, I. (2009). Spinogenesis and pruning scales across functional hierarchies. Journal of Neuroscience, 29, 3271–3275.
- Fagard, J., & Marks, A. (2000). Unimanual and bimanual tasks and the assessment of handedness in toddlers. Developmental Science, 3, 137–147.
- Ferre, C. L., Babik, I., & Michel, G. F. (2010). Development of infant prehension handedness: A longitudinal analysis during the 6to 14-month age period. *Infant Behavior and Development*, 33, 492–502.
- Ferri, F., Campione, G. C., Dalla Volta, R., Gianelli, C., & Gentilucci, M. (2010). To me or to you? When the self is advantaged. *Experimental Brain Research*, 203, 637–646.
- Ferri, F., Campione, G. C., Dalla Volta, R., Gianelli, C., & Gentilucci, M. (2011). Social requests and social affordances: How they affect the kinematics of motor sequences during interactions between conspecifics. PLoS One, 6(1), e15855.
- Flindall, J. W. (2012). Manual asymmetries in the kinematics of reach-to-grasp actions (Master's thesis). University of Lethbridge.
- Flindall, J. W., Doan, J. B., & Gonzalez, C. (2014). Manual asymmetries in the kinematics of a reach-to-grasp action. *Laterality*, 19, 489–507.
- Flindall, J. W., & Gonzalez, C. (2013). On the evolution of handedness: Evidence for feeding biases. PLoS One, 8(11), e78967.
- Flindall, J. W., & Gonzalez, C. (2014). Eating interrupted: The effect of intent on hand-to-mouth actions. Journal of Neurophysiology, 112, 2019–2025.
- Flindall, J. W., Stone, K., & Gonzalez, C. (2015). Evidence for right-hand feeding biases in a left-handed population. *Laterality*, 20, 287–305.
- Forssberg, H., Eliasson, A., Kinoshita, H., Johansson, R., & Westling, G. (1991). Development of human precision grip I: Basic coordination of force. *Experimental Brain Research*, 85, 451–457.
- Forssberg, H., Kinoshita, H., Eliasson, A., Johansson, R., Westling, G., & Gordon, A. (1992). Development of human precision grip II: Anticipatory control of isometric forces targeted for object's weight. *Experimental Brain Research*, 90, 393–398.
- Gentilucci, M., Toni, I., Chieffi, S., & Pavesi, G. (1994). The role of proprioception in the control of prehension movements: A kinematic study in a peripherally deafferented patient and in normal subjects. *Experimental Brain Research*, 99, 483–500.
- Gonzalez, C., & Goodale, M. A. (2009). Hand preference for precision grasping predicts language lateralization. *Neuropsychologia*, 47, 3182–3189.
- Gonzalez, C., Whitwell, R. L., Morrissey, B., Ganel, T., & Goodale, M. A. (2007). Left handedness does not extend to visually guided precision grasping. *Experimental Brain Research*, 182, 275–279.
- Goodale, M. A. (1988). Hemispheric differences in motor control. Behavioural Brain Research, 30, 203-214.
- Goodale, M. A. (1990). Vision and action: The control of grasping. Norwood, NJ: Ablex.
- Grosskopf, A., & Kuhtz-Buschbeck, J. P. (2006). Grasping with the left and right hand: A kinematic study. *Experimental Brain Research*, 168, 230–240.
- Harris, M. A., Prior, J. C., & Koehoorn, M. (2008). Age at menarche in the Canadian population: Secular trends and relationship to adulthood BMI. *Journal of Adolescent Health*, 43, 548–554.

Harvey, M., Jackson, S. R., Newport, R., Krämer, T., Morris, D. L., & Dow, L. (2001). Is grasping impaired in hemispatial neglect? Behavioural Neurology, 13, 17–28.

Hebb, D. O. (1949). The organization of behavior: A neuropsychological theory. New York: John Wiley.

- Hepper, P. G., McCartney, G. R., & Shannon, E. A. (1998). Lateralised behaviour in first trimester human foetuses. *Neuropsychologia*, 36, 531–534.
- Hopkins, B., & Rönnqvist, L. (2002). Facilitating postural control: Effects on the reaching behavior of 6-month-old infants. Developmental Psychobiology, 40, 168–182.
- Huttenlocher, P. R., & Dabholkar, A. S. (1997). Regional differences in synaptogenesis in human cerebral cortex. Journal of Comparative Neurology, 387, 167–178.
- Iwaniuk, A. N., & Whishaw, I. Q. (2000). On the origin of skilled forelimb movements. Trends in Neurosciences, 23, 372-376.
- Jacobs, B., Driscoll, L., & Schall, M. (1997). Life-span dendritic and spine changes in Areas 10 and 18 of human cortex: A quantitative Golgi study. *Journal of Comparative Neurology*, 386, 661–680.
- Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: A kinematic analysis of human prehension. *Experimental Brain Research*, 86, 199–208.
- Karl, J. M., & Whishaw, I. Q. (2013). Different evolutionary origins for the reach and the grasp: An explanation for dual visuomotor channels in primate parietofrontal cortex. Frontiers in Neurology, 4. http://dx.doi.org/10.3389/fneur.2013.00208.
- Keshavan, M. S., Diwadkar, V. A., DeBellis, M., Dick, E., Kotwal, R., Rosenberg, D. R., et al (2002). Development of the corpus callosum in childhood, adolescence, and early adulthood. *Life Sciences*, 70, 1909–1922.
- Kuhtz-Buschbeck, J., Stolze, H., Jöhnk, K., Boczek-Funcke, A., & Illert, M. (1998). Development of prehension movements in children: A kinematic study. *Experimental Brain Research*, 122, 424–432.
- Levy, J. (1976). A review of evidence for a genetic component in the determination of handedness. Behavior Genetics, 6, 429-453.
- Luders, E., Thompson, P. M., & Toga, A. W. (2010). The development of the corpus callosum in the healthy human brain. Journal of Neuroscience, 30, 10985–10990.
- Marteniuk, R., MacKenzie, C., Jeannerod, M., Athenes, S., & Dugas, C. (1987). Constraints on human arm movement trajectories. Canadian Journal of Psychology/Revue canadienne de psychologie, 41, 365–378.
- McManus, I., Sik, G., Cole, D., Mellon, A., Wong, J., & Kloss, J. (1988). The development of handedness in children. British Journal of Developmental Psychology, 6, 257–273.
- Michel, G. F., Babik, I., Sheu, C.-F., & Campbell, J. M. (2014). Latent classes in the developmental trajectories of infant handedness. Developmental Psychology, 50, 349–359.
- Morange-Majoux, F., Peze, A., & Bloch, H. (2000). Organisation of left and right hand movement in a prehension task: A longitudinal study from 20 to 32 weeks. *Laterality*, *5*, 351–362.
- Naish, K. R., Reader, A. T., Houston-Price, C., Bremner, A. J., & Holmes, N. P. (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. *Experimental Brain Research*, 225, 261–275.
- Nelson, E. L., Campbell, J. M., & Michel, G. F. (2013). Unimanual to bimanual: Tracking the development of handedness from 6 to 24 months. *Infant Behavior and Development*, 36, 181–188.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia, 9, 97–113.
- Olivier, I., Hay, L., Bard, C., & Fleury, M. (2007). Age-related differences in the reaching and grasping coordination in children: Unimanual and bimanual tasks. *Experimental Brain Research*, 179, 17–27.
- Petanjek, Z., Judaš, M., Šimić, G., Rašin, M. R., Uylings, H. B., Rakic, P., et al (2011). Extraordinary neoteny of synaptic spines in the human prefrontal cortex. Proceedings of the National Academy of Sciences of the United States of America, 108, 13281–13286. Piaget, J., & Cook, M. (1953). The origin of intelligence in the child. London: Routledge and Kegan Paul.
- Pryde, K. M., Roy, E. A., & Campbell, K. (1998). Prehension in children and adults: The effects of object size. Human Movement Science, 17, 743–752.
- Rönnqvist, L., & Domellöf, E. (2006). Quantitative assessment of right and left reaching movements in infants: A longitudinal study from 6 to 36 months. Developmental Psychobiology, 48, 444–459.
- Rönnqvist, L., & Rösblad, B. (2007). Kinematic analysis of unimanual reaching and grasping movements in children with hemiplegic cerebral palsy. *Clinical Biomechanics*, 22, 165–175.
- Sacrey, L. A. R., Arnold, B., Whishaw, I. Q., & Gonzalez, C. (2013). Precocious hand use preference in reach-to-eat behavior versus manual construction in 1- to 5-year-old children. *Developmental Psychobiology*, 55, 902–911.
- Sartori, L., Straulino, E., & Castiello, U. (2011). How objects are grasped: The interplay between affordances and end-goals. *PLoS One*, 6(9), e25203.
- Schettino, L., Adamovich, S., & Poizner, H. (2003). Effects of object shape and visual feedback on hand configuration during grasping. *Experimental Brain Research*, 151, 158–166.
- Schneiberg, S., Sveistrup, H., McFadyen, B., McKinley, P., & Levin, M. F. (2002). The development of coordination for reach-tograsp movements in children. *Experimental Brain Research*, 146, 142–154.
- Smyth, M. M., Katamba, J., & Peacock, K. A. (2004). Development of prehension between 5 and 10 years of age: Distance scaling, grip aperture, and sight of the hand. *Journal of Motor Behavior*, 36, 91–103.
- Stone, K., Bryant, D., & Gonzalez, C. (2013). Hand use for grasping in a bimanual task: Evidence for different roles? Experimental Brain Research, 224, 455–467.
- Tang, R., Whitwell, R. L., & Goodale, M. A. (2014). Explicit knowledge about the availability of visual feedback affects grasping with the left but not the right hand. *Experimental Brain Research*, 232, 293–302.
- Tretriluxana, J., Gordon, J., & Winstein, C. J. (2008). Manual asymmetries in grasp pre-shaping and transport-grasp coordination. *Experimental Brain Research*, 188, 305–315.
- Vauclair, J., & Imbault, J. (2009). Relationship between manual preferences for object manipulation and pointing gestures in infants and toddlers. *Developmental Science*, *12*, 1060–1069.
- Whishaw, I. Q., Sarna, J., & Pellis, S. (1998). Evidence for rodent-common and species-typical limb and digit use in eating, derived from a comparative analysis of ten rodent species. *Behavioural Brain Research*, *96*, 79–91.

- Whishaw, I. Q., Suchowersky, O., Davis, L., Sarna, J., Metz, G. A., & Pellis, S. M. (2002). Impairment of pronation, supination, and body co-ordination in reach-to-grasp tasks in human Parkinson's disease (PD) reveals homology to deficits in animal models. *Behavioural Brain Research*, 133, 165–176.
- Wing, A. M., Turton, A., & Fraser, C. (1986). Grasp size and accuracy of approach in reaching. Journal of Motor Behavior, 18, 245-260.
- Woo, T.-U., Pucak, M., Kye, C., Matus, C., & Lewis, D. (1997). Peripubertal refinement of the intrinsic and associational circuitry in monkey prefrontal cortex. *Neuroscience*, 80, 1149–1158.
- Zoia, S., Pezzetta, E., Blason, L., Scabar, A., Carrozzi, M., Bulgheroni, M., et al (2006). A comparison of the reach-to-grasp movement between children and adults: A kinematic study. *Developmental Neuropsychology*, 30, 719–738.