



Hear speech, change your reach: changes in the left-hand grasp-to-eat action during speech processing

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Abstract

Research has shown that the kinematic characteristics of right-hand movements change when executed during both speech production and processing. Despite the variety of prehension and manual actions used to examine this relationship, the literature has yet to examine potential movement effects using an action with a distinct kinematic signature: the hand-to-mouth (grasp-to-eat) action. In this study, participants performed grasp-to-eat and grasp-to-place actions in (a) a quiet environment and (b) while processing speech. Results during the quiet condition replicated the previous findings; consistently smaller grasp-to-eat (compared to grasp-to-place), maximum grip apertures appeared only when using the right hand. Interestingly, in the listen condition, smaller maximum grip apertures in the grasp-to-eat movement appeared in both the right and left hands, despite the fact that participants were right-handed. This paper addresses these results in relation with similar behaviour observed in children, and discusses implications for functional lateralization and neural organization.

Keywords Kinematics · Speech processing · Dual task · Laterality · Grasp-to-eat

Introduction

The sophistication of both our vocal and gestural repertoire is inarguably a feature which distinguishes humans from other mammals. How we achieved such unparalleled complexity, particularly in reference to speech, is not well understood. One debated theory (Gentilucci and Corballis 2006; Levinson and Holler 2014) is that manual actions like prehension played a vital role in the advancement of communication and, eventually, speech. The Gestural Theory of Language frames the development of communication in an evolutionary context, taking into account both manual and vocal movement (Rizzolatti and Arbib 1998; Waters and Fouts 2002; Arbib 2005). Details of the theory have changed over time, but the central concept remains that spoken language (i.e., a system of verbal gestures) is built upon a foundation of manual gestures; early hominids first developed manual gestures for communicative purposes, and gradually paired these movements with vocalizations (Corballis 2003).

The result is a repertoire of standardized symbolic sounds (i.e., language) replacing a set of manual signals (De Condillac 1947; Hewes 1973, 1976; Rizzolatti and Arbib 1998; Waters and Fouts 2002; Rizzolatti and Craighero 2004). This theory is important to consider when investigating interactions between speech and grasping, particularly as it underscores the depth and nature of the relationship, and emphasizes functional context (Hewes 1973).

Evidence of a consistent interaction between speech and manual movements is observable in many studies. One example includes research using transcranial magnetic stimulation (TMS) to measure increases in hand motor-evoked potential (MEP) amplitudes when stimulation is paired with either speech production or speech perception (Floel et al. 2003). When compared to baseline MEPs, researchers found a significant increase in MEP amplitude (measured from the first dorsal interosseous muscle of both left and right hands) when participants were asked to either read-aloud or quietly listen to fairy tales. The authors concluded that speech, even passively perceived speech, causes bilateral sub-threshold activation within hand regions of primary motor cortex (M1), regardless of handedness or language lateralization.

This change in activation may be responsible for changes in prehension kinematics, as evidenced by numerous behavioural studies investigating manual tasks performed during

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speech production. While participants are speaking they generally: initiate their grasping movements more quickly (i.e., have shorter reaction times) (Vainio et al. 2013, 2014, 2015; Tiainen et al. 2016); move faster (higher peak velocities) (Fargier et al. 2012); produce stronger grip forces (Frak et al. 2010); and change the peak distance between the thumb and index finger (maximum grip aperture) while reaching (Glover et al. 2004). For example, when pronouncing the name of a large, graspable object (e.g., “apple”) while reaching-to-grasp an unrelated object, participants produced larger maximum grip apertures (MGAs) compared to when pronouncing the noun for a smaller object (e.g., “grape”), despite grasping objects of identical size (Glover et al. 2004). These studies describe how speech production may influence grasp-to-transport, grasp-to-lift, or simple grasp-to-hold movements. One specific type of action absent from the described body of literature is the grasp-to-eat movement.

The grasp-to-eat movement is an action which features regularly in our daily lives and plays a vital role in our survival. Nearly, half of all primate (human and non-human) prehension involves hand-to-mouth transport (Graziano 2008), indicating that grasp-to-eat and other hand-to-mouth movements hold special significance not only with respect to our movement repertoire (Graziano et al. 2005), but with respect to their neural underpinnings (Bonini et al. 2012). When a macaque performs a grasp-to-mouth/body movement, specific neurons are activated in the inferior arcuate sulcus (area F5; in the premotor region), along with other sections vital to motor control (Rizzolatti et al. 1988; Bonini et al. 2012). That these neurons demonstrate unique activation for certain goal-directed action suggests that such movements, specifically the grasp-to-eat movements, hold particular evolutionary value (Rizzolatti et al. 1988; Grafton et al. 1996; Graziano 2008; Bonini et al. 2010, 2012). What is most relevant for the overall purpose of this study is that within the same F5 area in macaques, neurons are also active during observation of a grasping action (Caggiano et al. 2016). These mirror neurons may play a role in the development of communication (including speech) by facilitating the transition from gestural to verbal language (Rizzolatti and Fadiga 1998; Corballis 2003; Gentilucci and Corballis 2006). By processing the purpose behind an action, it is easier to understand actor intent, and create symbolic meaning from such movement. While these studies focused on non-human primates, research conducted in humans generates support for the existence of mirror neurons in humans (Corballis 2003, 2010). If so, relatively “simple” actions, such as grasping-to-eat, could have played a role in the development of language.

The unique processing of the grasp-to-eat action translates into distinctive behavioural outcomes. The previous studies found a kinematic distinction between grasp-to-eat

and grasp-to-place actions, lateralized to right-handed movements (Flindall and Gonzalez 2013, 2016). Specifically, when grasping-to-eat, the right hand produces consistently smaller maximum grip apertures (MGAs) than when grasping-to-place, despite moving an identical target towards a similar location (container located near the mouth). This finding should not be trivialized and counted in with the previous research which suggests a right-hand preference for performing precision grasps (Vainio et al. 2006; Gonzalez and Goodale 2009), as the previous studies struggle to identify significant kinematic differences during a complete grasp-to-place action (Smeets and Brenner 2001; Flindall et al. 2014). While it may appear logical to associate the effect with right-hand dominance, a follow-up study found that the effect was still predominantly right-hand lateralized among left-handed participants (Flindall et al. 2015). Instead, the authors framed the reduced grip aperture as an artifact of phylogeny, developing from postural changes in primate ancestors which enabled the sophistication of manual grasping and resulted in preferential hand use and population level handedness. This dominance could manifest as a tendency for primates (including humans) to use the right hand for object manipulation and the left hand for stability (MacNeilage et al. 1987; Flindall and Gonzalez 2013; Meguerditchian et al. 2013; Stone et al. 2013). As the grasp-to-eat action may have played a role in the evolutionary development of handedness and language, examining this action alongside speech in a dual-task paradigm could provide new insight into this interaction. To avoid the obvious interference of attempting simultaneous eating mouth movement (opening to accept, closing to chew, and subsequently swallowing a grasped object), while speaking, participants instead actively listened to speech while performing grasp-to-eat actions. According to several recent studies, speech processing activates similar neural areas as does speech production (Wilson et al. 2004; Agnew et al. 2013; Cheung et al. 2016). As they are, ultimately, distinct processes, it is important to note that there are differences in the strength and pattern of neural activation between listening and producing speech. Compared to production, speech processing creates higher levels of right-hemisphere activation (Wilson et al. 2004). However, as there is still a significant increase in left-hemisphere activity compared to the baseline, an increase that is comparable to that observed during speech production, we contend that speech processing creates a neural state functionally similar to that observed during speech production (Wilson et al. 2004; Specht 2014). Furthermore, fMRI and EEG measures indicate that areas responsible for processing speech demonstrate changes in activity during motor cortex activation [especially manual movement (Wikman et al. 2015; Tiainen et al. 2017)]. All told, the overall similar pattern of neural activation elicited during speech processing, combined with other findings from fMRI

research, qualifies it as an appropriate tool to investigate a possible interaction between speech and the lateralized kinematic signature of grasp-to-eat actions. Although limited in number, the previous behavioural studies indicate that concurrent speech processing can have similar effects on kinematics as speech production, in which kinematic measures such as reaction time or grip force demonstrate interference effects from concurrent speech processing (Frak et al. 2010; Vainio et al. 2014).

The purpose of this study was to examine how speech processing influences execution of a manual action using a well-documented lateralized kinematic signature—smaller MGAs unique to the right-handed grasp-to-eat movement. Right-handed participants completed blocks of grasp-to-eat and grasp-to-place actions directed towards small cereal items both when sitting silently (in a quiet environment) while listening to excerpts from an audiobook. If the interaction of speech and grasping is mediated through functional lateralization (similar left-hemisphere localization of right-hand motor control and speech production/processing), any significant kinematic interference during speech processing should be limited to right-handed movement, ultimately resulting in the disappearance of the lateralized grasp-to-eat effect when listening to an audiobook. Succinctly, processing speech should nullify significant differences between the grasp-to-eat and grasp-to-place conditions, resulting in statistically similar kinematics between left- and right hands for both types of movement. During the quiet trials (control), we expect to observe the same effect demonstrated by Flindall and Gonzalez (2013, 2014, 2016), namely, significantly smaller MGAs for grasp-to-eat actions when participants use the right hand compared to the left hand. Finally, the cognitive load increase caused by processing speech, while simultaneously performing a grasping task should affect other kinematic measures. The previous dual-task studies (not necessarily related to speech) report significant changes to metrics such as increased movement time (MT), increased variability in maximum grip aperture (vMGA), and decreases in peak velocity (PV) (Dromey and Benson 2003; Guillery et al. 2013). We predicted that participants will be less consistent in their grasping performance while focussing on speech processing, reflected by increases in MT and vMGA, and decreased PV in the right hand.

Methods

Participants

Thirty-three right-handed young adults (22 females, mean age of 22.1 ± 2.13 years) agreed to participate in the current study in exchange for course credit. Each completed a language questionnaire, where they confirmed English

as their first language, and reported any experience speaking or learning additional languages. Data collected from two bilingual participants were removed from analyses. Participants' hand dominance was determined through self-report, and confirmed via a modified Waterloo–Edinburgh handedness questionnaire (Oldfield 1971; Brown et al. 2006). All participants provided informed consent prior to starting the experiment and were aware of the option to withdraw at any time during the experiment. These procedures were approved by the University of Lethbridge Human Subject Research Committee (protocol #2016-002).

Materials

Materials and procedures were very similar to those used in the previous studies by Flindall and Gonzalez (2013). A Certus Optotrak Camera (Northern Digital, Waterloo, ON, Canada) tracked the movement of three infra-red light emitting diodes (IREDS) attached to the hand of the participant. We secured the markers with medical tape to the distal phalanges of the thumb and index finger, and the medial styloid process of the wrist. Placement of the diodes afforded a comfortable pincer/precision grasp for each participant, while simultaneously providing an unobstructed line of sight between the IREDS and the camera. IRED position information during each trial was collected at 100 Hz for 4 s.

After providing informed consent, the participant sat in a stationary chair, arms length away from an independent standing pedestal. We adjusted the pedestal to approximate sternum height to enable comfortable prehension of targets without interfering with the grasp (Whishaw et al. 2002). Next, we positioned the triangular platform of the pedestal (base 85 mm, height 80 mm) with the base towards the participant. Participants wore a solid plastic bib with an open pocket. We adjusted the pocket as near to the participant's mouth as possible (approximately 170 mm below the mouth). Individuals wore Plato Liquid Crystal Goggles (Translucent Technologies, Toronto, ON, Canada) to obstruct their view of the pedestal between trials, concealing the precise size of the grasping target until the beginning of each trial. We used Cheerios™ (average diameter 11 mm) and Froot Loops™ (average diameter 15 mm) as grasping targets. Experimental timing was coordinated through Superlab (Cerdus Corporation, San Pedro, CA, USA) and NDI First Principles (Northern Digital, Waterloo, ON, Canada). We used a single analog speaker (Harmon Kardon Rev A00 Computer Speakers) to play audio recordings from an Apple iPod Nano (6th gen). The audio stimuli consisted of four 3-min excerpts from an audiobook recording of “Percy Jackson and the Olympians: The Titan's curse” (Riordan 2007).

Procedure

Participants sat in front of the pedestal and familiarized themselves with the reaching environment before donning the bib and goggles. Before beginning data collection, we explained the procedure and guided each participant through several practice trials. Grasp-to-eat trials required participants to grasp the cereal (placed on the pedestal) and eat it, while grasp-to-place trials required participants to pick up the cereal and place it in the bib hanging beneath their chin (Fig. 1). We organized the blocks according to a 2 (Hand; left/right) \times 2 (Task; eat/place) \times 2 (Audio; quiet/listen) factorial design, resulting in 8 blocks of 16 trials each, for a total of 128 trials. Participants completed 4 blocks with each hand; 16 trials of either grasp-to-eat or grasp-to-place, completed in silence (quiet) or while listening to an audiobook (listen). We attached IREDS to the participant's specified starting hand and assigned them a condition to complete for the following 16 trials (i.e., grasp-to-eat and listening to the audiobook). After participants finished all four conditions with their starting hand, we removed the IREDS and attached them to the opposite hand, repeating each of the four conditions in the same order. We counterbalanced starting hand and condition order between participants. Seventy-five percent of target items were Cheerios™, with the remaining 25% Froot Loops™, presented in a pseudo-random order. We included different sized targets to ensure that participants scaled their grip appropriately to the size of each target. All participants correctly scaled their MGA to target size.

Only trials which used Cheerios as the target item were included in statistical analyses.

At the beginning of each trial, the participants rested their hand on their lap, index finger, and thumb resting together. Trials began with the transition of the goggles to a translucent state, enabling sight of the target item; participants then grasped the single cereal piece that had been placed on the pedestal at “their own comfortable, natural pace”. Depending on the required task for the block, they either ate the cereal piece or placed it in the bib. The goggles remained translucent for 3000 ms, allowing participants ample time to complete the full action with vision and return to the rest position. After the goggles returned to an opaque state, the investigator placed a new cereal item on the stand and triggered the next trial. During the listen condition, the participant was instructed to listen closely to the audiobook. The story segment played from the onset of the block to the conclusion of the story; the experimenter controlled the pacing of the block, such that the segment's end coincided with completion of all 16 grasps. After each listen block, participants were presented with six questions related to the content of the audiobook excerpt, and asked to give a summary of recalled events. This was done to determine if participants maintained attention to the story throughout the grasping trials.

Analysis

The primary kinematic variable of interest was maximum grip aperture (MGA), as this variable has consistently

Fig. 1 Procedure: participants initiated a reach upon the opening of the goggles, as pictured in the left panel. According to the block, participants completed the movement by bringing the item to their mouth to eat (center) or placing the food item in the bib (left). Both blocks were repeated with each hand during both a listen condition (paying close attention to presented audiobook sections) and a quiet (no background noise) condition



revealed a specific Hand by Task effect in the previous studies conducted with this paradigm (Flindall and Gonzalez 2013, 2014, 2016). To enable within participant between-hand comparisons, we calculated a corrected MGA value by subtracting the participant's average resting grip aperture (the distance between the IREDs on the participant's clasped thumb and index finger, while their hand rested on their leg at the beginning of each trial) from the maximum grip aperture of each trial. By correcting MGA independently for each participant, variance in the shape of an individual's hands and the placement of the IREDs cannot erroneously contribute to any effect of hand on our within-subject analysis of MGA (Flindall and Gonzalez 2013).

The following additional kinematic characteristics were calculated according to Euclidean displacement, or the smallest distance between the IREDs on the wrist, index finger, and thumb at any point during the outward movement towards the target (prior to grasp onset). Grasp onset was determined as the point at which (a) grip aperture plateaued, indicating prolonged target contact, and (b) wrist velocity reached a minimum, indicating that movement of the wrist stopped during the grasp. Other kinematic variables included variability of MGA ($vMGA$), calculated as the standard deviation of MGA within each Hand \times Task \times Listen block, peak resultant velocity (PV) of the wrist marker, reaction time (RT), defined as the first frame in which the wrist marker achieved a speed exceeding 5% of PV, movement time (MT), measured as the difference between RT and time of grasp onset, and deceleration phase duration (DP), measured as percent of MT that occurred between PV and grasp onset.

We calculated kinematic variables for each trial using unfiltered position values of each IRED in Microsoft Excel (16.0), and averaged these variables per condition block. Data was averaged to provide a better understanding of the typical grasp executed by a participant under the conditions dictated by the trial. If a participant incorrectly completed a trial (e.g., ate instead of placed, or vice versa, or knocked a target to the ground), if line-of-sight errors resulted in critical data loss, or if two or more variables within a trial were outliers (± 2 SDs from the block's mean) that trial was removed from analysis and not replaced. If more than 50% of trials in a single block, or 10% of trials overall were uninterpretable, that participant was excluded from the final analyses. Data from four of our original 33 participants were removed from the current study, leaving 29 (average of $6.18 \pm 3.0\%$ of trials removed) for inclusion in a 2 (Hand) \times 2 (Task) \times 2 (Audio) repeated measures analysis of variance (ANOVA). Statistical analyses were conducted using IBM SPSS Statistics (23) (IBM Corp 2013).

To test recollection of the four audiobook excerpts, average quiz scores used were calculated for each participant. These story scores were used in combination with calculated

change in MGA (averaged quiet MGA subtracted from averaged listen MGA) for each hand to assess the presence of any relationship between recall ability and grasp kinematics. Two Kendall-tau b correlations were conducted: one between story score and right-hand MGA change and one between story score and left-hand MGA change.

Results

Attention

Audiobook quiz results were assessed, but did not affect kinematic analysis. On average, participants answered 61 percent (± 0.54) of the questions correctly (scores ranged from 35 to 79%). Due to non-normal data, we ran Kendall-Tau b correlations comparing quiz scores to difference in MGA during the quiet versus listen conditions in both the left hand and right hand. No significant correlations were found between the quiz score and MGA difference in the right hand, $\tau = -0.046$, $p = 0.73$ (two-tailed), or the left hand $\tau = 0.030$, $p = 0.82$ (two-tailed). As each participant could produce a summary of the excerpt, the story scores were disregarded and all participants were included in the previous kinematic analyses.

Kinematics

Means and standard errors for all variables are reported in Table 1. All significant main effects and interactions are reported below. Post-hoc comparisons (and planned a-priori comparisons) were conducted via paired-sample t test, with Bonferroni correction applied where appropriate.

Hand

There was a main effect of hand on RT, $F(1,28) = 6.449$, $p = 0.019$, $\eta^2 = 0.21$. The right hand (389 ± 127 ms) reacted significantly slower than the left hand (371 ± 131 ms).

Task

A main effect of Task was found in MGA, $F(1,28) = 28.42$, $p < 0.001$, $\eta^2 = 0.50$; MGA was smaller when grasping-to-eat the target (20.21 ± 0.62 mm) compared to grasping-to-place (21.92 ± 0.63 mm). PV was also affected according to task $F(1,28) = 6.23$, $p = 0.019$, $\eta^2 = 0.18$; participants moved more quickly when grasping-to-eat (0.63 ± 0.19 m/s) than when grasping-to-place (0.62 ± 0.20 m/s). There was a main effect of Task on RT, $F(1,28) = 5.06$, $p = 0.032$, $\eta^2 = 0.15$, which indicated that participants initiated movement more quickly during grasp-to-place trials (371 ± 124 ms) than during grasp-to-eat trials (389 ± 133 ms). Finally, DP

Table 1 Grasp-to-eat and grasp-to-place kinematics

Hand	Task	Listen	MGA (mm)	vMGA (mm)	PV (m/s)	RT (ms)	MT (ms)	DP (%MT)
Left	Eat	Quiet	21.4 ± 3.8	2.73 ± 1.1	0.64 ± 0.19	355 ± 133	973 ± 173	72 ± 3.6
		Listen	20.3 ± 3.7	3.23 ± 1.6	0.63 ± 0.17	376 ± 137	971 ± 191	72 ± 3.4
	Place	Quiet	22.7 ± 4.2	2.89 ± 1.2	0.62 ± 0.19	337 ± 136	954 ± 165	70 ± 4.8
		Listen	22.8 ± 4.0	3.11 ± 1.8	0.62 ± 0.20	357 ± 116	952 ± 172	72 ± 3.5
Right	Eat	Quiet	19.8 ± 4.8	2.48 ± 1.2	0.62 ± 0.19	381 ± 137	956 ± 182	71 ± 2.7
		Listen	19.0 ± 4.6	2.87 ± 1.6	0.62 ± 0.19	376 ± 125	976 ± 179	72 ± 3.1
	Place	Quiet	22.0 ± 5.2	2.75 ± 1.2	0.61 ± 0.18	360 ± 131	939 ± 176	71 ± 2.9
		Listen	20.9 ± 4.9	2.66 ± 1.3	0.60 ± 0.22	374 ± 113	954 ± 157	71 ± 3.2

Listed values are means ± SE of: maximum grip aperture (MGA), variability (within-condition standard deviation) of MGA (vMGA), peak velocity (PV), deceleration phase (DP), movement time (MT), and reaction time (RT), divided according to hand, task, and listen condition

demonstrated changes according to task, $F(1,28) = 4.82$, $p = 0.037$, $\eta^2 = 0.15$. Participants spent slightly less time in DP when grasping-to-place ($71 \pm 1\%$ MT) compared to when grasping-to-eat ($72 \pm 1\%$ MT).

Audio

A main effect of auditory input was found in MGA, $F(1,28) = 4.40$, $p = 0.045$, $\eta^2 = 0.14$. MGA was smaller when listening to speech (20.70 ± 0.64 mm) compared to the quiet condition (21.43 ± 0.62 mm).

Hand × task × audio

No significant two-way or three-way interactions were observed between any kinematic variables. However, because we reported a significant hand × task interaction on MGA in the previous studies [smaller MGAs during right-handed grasp-to-eat movements, compared to right-handed grasp-to-place or left-handed movements of either

type; see Flindall and Gonzalez (2013, 2014, 2016)], we performed a-priori t tests comparing these conditions. We tasks between hands, and hands between tasks, in both listen conditions to determine if the previous interaction between hand and task MGAs was present. The analysis revealed a significant difference between right-handed eat and place MGAs in the quiet condition, with eat MGAs (19.67 ± 0.84 mm) being significantly smaller than place MGAs (21.80 ± 0.90 mm), $t(33) = 5.18$, $p < 0.001$ (see Fig. 2). Consistent with the results of the previous studies, the difference between eat and place MGAs in the quiet conditions within left-handed movements was not significant ($p = 0.22$). The same eat < place effect was observed in the right hand during the listen condition, with eat MGAs (18.96 ± 0.78 mm) once again significantly smaller than place MGAs (20.80 ± 0.85 mm), $t(33) = 4.29$, $p = 0.002$. Unexpectedly, this effect was also found in the left hand listen condition, where grasp-to-eat MGAs (20.17 ± 0.65) were significantly smaller than grasp-to-place MGAs (22.68 ± 0.68), $t(33) = 4.82$, $p < 0.001$. These results indicate that when listening to speech, the characteristic

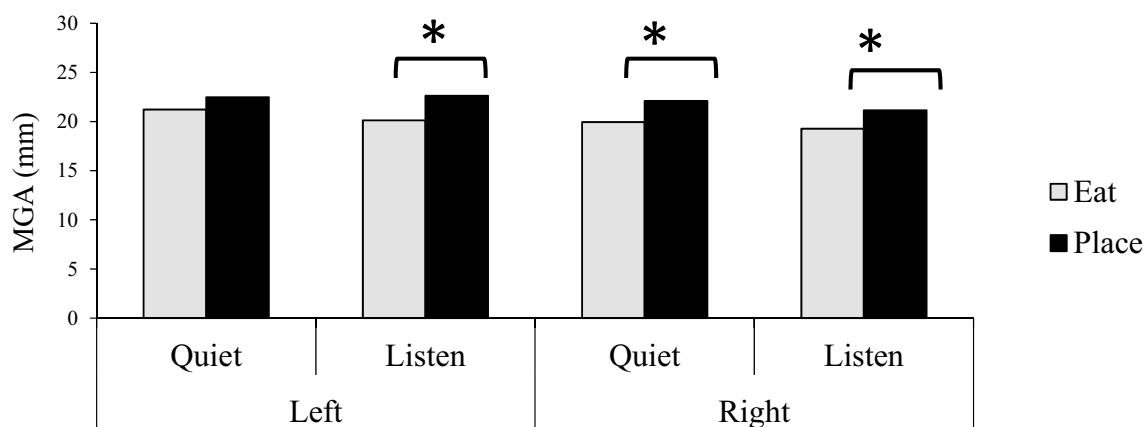


Fig. 2 A-priori investigation of Hand × Task × Audio in MGA. While listening to an audiobook, eat MGAs were significantly smaller than place MGAs in both hands. During the quiet condition, only the right

hand showed a significant difference according to task through a within-participant comparison

kinematic pattern typically observed in the right hand also appears in the left hand.

Discussion

The previous research suggests that a persistent relationship exists between speech and the performance of manual actions; that is, speech production and processing influences how we physically perform grasping actions (Gentilucci et al. 2004; Fargier et al. 2012; Rabahi et al. 2013; Vainio et al. 2013, 2015; Moseley and Pulvermuller 2014; Tiainen et al. 2016). In the current study, participants performed functionally distinct grasping actions both (a) while the actor and environment were quiet and (b) while actively listening to speech. We examined the effects of both auditory environments on various kinematics of grasp-to-eat and grasp-to-place actions. While there were several kinematic differences across a host of variables (reaction time, peak velocity, and deceleration phase duration), these were similar to the results from the previous studies (Flindall and Gonzalez 2014, 2016), and were not the focus of this study. Most importantly, these findings are not related to auditory experience, and they will not be discussed further. For the purposes of this study, the main kinematic measure of interest was maximum grip aperture (MGA). As expected, the results replicated findings previously reported by Flindall and Gonzalez (2013, 2014, 2016) and Flindall et al. (2015), namely, the grasp-to-eat action produced significantly smaller MGAs than the grasp-to-place action, limited to right-handed movements in the quiet condition. However, when listening to speech, the MGA signature was no longer lateralized; MGA was significantly smaller in the grasp-to-eat task than in the grasp-to-place task in both the right and left hands.

The finding that completing a speech comprehension task resulted in the grasp-to-eat kinematic characteristic manifesting in both hands is unexpected; because both examined functions are presumed to be left-hemisphere lateralized (i.e., speech processing and right-hand motor control), we predicted that any speech-related kinematic changes would be limited to the right hand. However, when listening to speech, the right hand did not demonstrate any significant deviation from the previously observed pattern of smaller MGAs during the grasp-to-eat action. Speech processing did not influence right-hand grasping kinematics. However, considering the discussed literature which demonstrates strong interactions between grasping and speech processes (Dromey and Benson 2003; Glover et al. 2004; Frak et al. 2010; Fargier et al. 2012; Vainio et al. 2013, 2014, 2015; Tiainen et al. 2016), such an explanation should be approached carefully. A perhaps more plausible explanation is that speech processing is not able to alter right-handed

grasp-to-eat actions in the same manner that it influences the kinematics of other reach-to-grasp movements. In other words, the persistence of the grasp-to-eat kinematic signature may be an indicator of the neural importance of the hand-to-mouth action. The previous studies have found evidence supporting the practical and evolutionary value of this action. It is one of the first manual movements infants that demonstrate (Hepper et al. 1998), and specialized neural properties have been observed in non-human primates for hand-to-mouth actions (Graziano et al. 2005). These examples highlight the important role of grasp-to-eat actions both in our daily lives and our evolutionary development. It may be so valuable that during secondary tasks (such as speech processing), the characteristic is preserved.

In addition to the maintenance of the effect in the right hand, we found that the left hand adopted the right-handed movement pattern in the presence of a secondary task. While these results did not follow our predictions, it is not the first observation of smaller grasp-to-eat MGAs appearing in the left hand. In a 2015 report, Flindall and Gonzalez found that children younger than 10 years showed the same kinematic signature when performing grasp-to-eat actions with either hand (Flindall and Gonzalez 2015). The authors speculated that this bilateral task-dependent effect, which becomes right-hand lateralized in children older than 10 years (including adults), may disappear in the left hand as a result of natural synaptic pruning following consistent repeated use of the dominant hand for grasp-to-eat actions (Flindall and Gonzalez 2015). The results of the current study suggest the specialized grasp-to-eat MGA in the left hand may not be completely lost, merely suppressed. In developmental grasping studies, particularly those analyzing MGA, 10 years is repeatedly found as the approximate age when participants begin to exhibit adult-like grasping kinematics (Olivier et al. 2007; Stöckel and Hughes 2015; Alramis et al. 2016). Perhaps, the developmental process results in a natural inhibition of smaller grasp-to-eat MGAs in the left hand, but under specific circumstances (i.e., during simultaneous speech processing and grasping), this inhibition can be circumvented. This supposition does not completely account for the similarity in results with Flindall and Gonzalez (2015), as the younger children completed the grasping tasks in a silent environment and our participants exhibited the same bilateral effect only when processing speech. Research assessing the developing brain in children has found broader activation patterns during motor and cognitive tasks compared to adults (Thomas et al. 2004; Casey et al. 2005). In several studies, speech showed more right-hemisphere activation during language tasks in children compared to adults (Gaillard et al. 2000; Holland et al. 2001). As children develop, and synaptic pruning occurs, task-specific activation shifts from generalized to precise innervation, ultimately resulting in an adult-typical activation pattern. In other words,

while children are improving neural sophistication for various functions (including motor control), irregular activation patterns might prompt a bilateral reflection of the grasp-to-eat kinematic signature. In adults, activation of the left hemisphere via a lateralized task (speech processing) during left-hand grasping may allow the left hand to access the motor plan responsible for producing the kinematic signature, resulting in smaller MGAs for left-handed grasp-to-eat actions. If this explanation is correct, we would predict that other simultaneously executed left-hemisphere lateralized tasks (e.g., interpreting gestures) should also cause the manifestation of the smaller MGA signature in the left hand. Such activation may also occur during bimanual movements, or during transcranial stimulation, be it magnetic (TMS) or electrical (tCDS). Comparatively, we would predict that performing a right-hemisphere lateralised task (i.e., musical or visuospatial processing actions, or right-hemisphere TMS/tCDS) should not change the kinematics of the left hand, particularly in contrast to a control condition. There is yet, another simpler explanation. Speech processing is not a perfectly lateralized task, requiring activation of both left and right hemispheres (Floel et al. 2003; Wilson et al. 2004). If results do not follow the above predictions, it would indicate that the bilateral nature of speech may be the factor driving the observed results.

We previously hypothesized that MGA would be affected in the right hand, specifically via increased variability, as predicted by research examining dual-task effects between language and manual action. Past studies focussed on language production tasks and kinematic factors such as lip displacement, vocal and manual reaction time, movement time, and maximum grip aperture (Gentilucci et al. 2000; Dromey and Benson 2003; Glover et al. 2004; Singhal et al. 2005; Dromey and Shim 2008; Hesse et al. 2012). Across all studies, grasping actions performed concurrently with speech production results in a decrease in performance, as measured through increased lip displacement, slower RT for both vocal and manual movement, longer MTs, and increased MGAs. We did not replicate the findings of these studies, as RT did not increase and MT did not decrease (or significantly change) during the dual-task condition. We did observe a change in MGA in response to speech processing; however, with respect to the direction of this change, our results appear to be at odds with the previous research. Normally, dual-task interference results in a significant increase in MGA, ostensibly because such increases create greater allowances for the grip aperture margin of error (Singhal et al. 2005). In our study, we report a decrease in MGA in left-handed grasp-to-eat movements in response to speech processing as a secondary task. There are three alternative interpretations of this finding. First, it is possible that the decrease in MGA is not evidence of dual-task interference, but rather dual-task facilitation. In the previous grasp-to-eat

studies, authors posited that the observed smaller MGA in the right hand represented a kinematic advantage, based on decreased grip aperture closing time and a conservation of energy (Flindall and Gonzalez 2013, 2015). The additional neural activation resulting from speech processing may be facilitating the grasp-to-eat and grasp-to-place movements, evidenced by the overall significantly smaller MGAs during these actions.

A second possible interpretation is that smaller MGAs in the left-hand reflect a disadvantaged kinematic movement. This may appear counter-intuitive, as we previously proposed that decreases in right-hand MGA are a mark of increased precision. However, it is conceivable that performing a precise grasping action with the non-dominant hand and attempting to carefully listen to the story resulted in increased tension (Guillery et al. 2013), and accordingly decreasing apertures. There are the previous cases, where MGA decreased in the right hand during a reaching task; for example, when participants reached past non-target objects to grasp a target, their MGAs decreased compared to a condition, where no obstacle was present. The decrease occurred, even though non-target objects were positioned in such a way that they would not interfere with the normal reaching route of the hand (Mon-Williams et al. 2001). An important note is that in addition to a decrease in MGA, Mon-Williams et al. (2001) noted significant changes in movement time and peak velocity. The previous studies examining instances of distracted/complex grasping have reported changes in one or both kinematic characteristics (Castiello et al. 1993; Jackson et al. 1995; Tipper et al. 1997; Gonzalez et al. 2008; Guillery et al. 2013). While these studies did not use speech processing or grasp-to-eat actions, the lack of significant changes in MT or PV in the present data suggests a different interpretation is required.

Another, more conservative interpretation is that smaller MGAs may not represent a kinematic advantage per se, but instead merely reflect a non-qualitative difference in the production of two movements. After all, while smaller MGAs may present an energy-based (or economic) advantage, they do not necessarily increase success while grasping. In addition, consider that under conditions of target uncertainty and/or reduced visual feedback, larger MGAs represent an advantageous kinematic adaptation (Jakobson and Goodale 1991). In the current case, we may say that the grasp-to-eat and grasp-to-place movements are kinematically distinct; we need not associate a value judgement with those differences to discuss the relevance of the difference itself, i.e., that the difference arises from distinct neural circuits associated with a movement's function (or end-goal) rather than its mechanics. The manifestation of the kinematic signature in the left hand reflects a change in the accessibility of the grasp-to-eat neural circuit by the left-hand/right-hemisphere system; whether the left-hand/right-hemisphere system can

access a consistently present left-hemisphere grasp-to-eat circuit in the presence of speech, or whether the processing of speech activates a dormant grasp-to-eat circuit in the right-hemisphere, remains to be seen.

Perhaps, the next intuitive step to advance our understanding of the role of functional lateralization in the observed interaction is to examine a left-handed population. However, this is not as simple as testing any participants who identify as left handed through a questionnaire. Completely aside from concerns of conflict between self-reported hand use and actual behaviour (Flindall and Gonzalez 2018), research also demonstrates that left handers are not a homogeneous group. That is, despite reporting more frequent left-hand use for daily tasks (Gonzalez and Goodale 2009), the majority of left handers still show smaller MGAs in the right hand during a grasp-to-eat action (Flindall et al. 2015), and smoother, more direct right arm movements during a reach-to-grasp task (Nelson et al. 2018). These participants, known as “right–left handers”, essentially mimic the behaviour of right handers, save for a few actions (e.g., writing and signing). In fact, only a small subset of left handers are “left–left handers”; left-handed people who typically demonstrate bilateral or right-lateralized language (Knecht et al. 2000; Gonzalez and Goodale 2009), dominant use of their left hand across grasping tasks (Stone et al. 2013), and smaller grasp-to-eat MGAs in their left hand (Flindall et al. 2015). Given the evidence provided from both left- and right–left handers, it is clear that attempting to study ‘left handers’ is not (strictly speaking) a sure method to gain insight into right-hander’s behaviour or neural organization, as left handers are not mirror images of right handers (Woytowicz et al. 2018). Therefore, before venturing forward and applying methods used in this study to a left-handed population, a more fruitful avenue would be to further examine lateralization of function (whether for grasping or language) in right handers.

A limitation of the current study is that despite listening to a similar length of audio book, the timing of individual trials during those excerpts was not controlled, meaning that each grasp could have been completed while listening to a broad variety of words. The previous studies have found that the meanings of the words we pronounce and process (“large” versus “small”) can result in different patterns of neural processing, and in turn, individually alter grasping kinematics (Fargier et al. 2012; Rabahi et al. 2013; Moseley and Pulvermuller 2014). We attempted to minimize potential interactions by deliberately choosing audiobook sections rich in description, without including sections that detailed verbs or descriptors involving action or specifically, manual movement. We counterbalanced audiobook excerpts to diminish the likelihood of specific trials being consistently performed with a specific word or general topic. With these controls in place, we believe it unlikely that the observed

effects were driven by the semantic qualities of individual words.

In conclusion, a novel left-hand manifestation of the grasp-to-eat kinematic signature was observed in adults for the first time. While listening to and processing speech, smaller maximum grip apertures for grasp-to-eat actions (relative to grasp-to-place actions) were maintained in the right hand, and were manifested in the left hand. The observed change represents the facilitation of a distinct grasping effect during a speech-processing task. Another important finding is the conservation of smaller MGAs in the right hand, despite completing a secondary speech-processing task. The resiliency of the characteristic kinematic effect may be indicative of the evolutionary importance of the action. The results contribute to our understanding of the grasp-to-eat kinematic signature, the development of language, as well as provide direction for future research investigating speech and grasping within an ecologically relevant paradigm.

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Compliance with ethical standards

Conflict of interest The authors have no conflicts of interest to declare.

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