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The neural circuits recruited for the production of signs and fingerspelled words

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ABSTRACT

Signing differs from typical non-linguistic hand actions because movements are not visually guided, finger movements are complex (particularly for fingerspelling), and signs are not produced as holistic gestures. We used positron emission tomography to investigate the neural circuits involved in the production of American Sign Language (ASL). Different types of signs (one-handed (articulated in neutral space), two-handed (neutral space), and one-handed body-anchored signs) were elicited by asking deaf native signers to produce sign translations of English words. Participants also fingerspelled (one-handed) printed English words. For the baseline task, participants indicated whether a word contained a descending letter. Fingerspelling engaged ipsilateral motor cortex and cerebellar cortex in contrast to both one-handed signs and the descender baseline task, which may reflect greater timing demands and complexity of handshape sequences required for fingerspelling. Greater activation in the visual word form area was also observed for fingerspelled words compared to one-handed signs. Body-anchored signs engaged bilateral superior parietal cortex to a greater extent than the descender baseline task and neutral space signs, reflecting the motor control and proprioceptive monitoring required to direct the hand toward a specific location on the body. Less activation in parts of the motor circuit was observed for two-handed signs compared to one-handed signs, possibly because, for half of the signs, handshape and movement goals were spread across the two limbs. Finally, the conjunction analysis comparing each sign type with the descender baseline task revealed common activation in the supramarginal gyrus bilaterally, which we interpret as reflecting phonological retrieval and encoding processes.

1. Introduction

Although much is known about the neural systems involved in the production of speech sounds (e.g., Guenther, 2006), we know very little about the neural circuits that are recruited during the production of manual signs. Speech involves coordination of the larynx and vocal tract which are located along the midline of the body; in contrast, the primary linguistic articulators for sign language are the hands and arms which are independent, symmetrical articulators controlled by contralateral motor cortex and ipsilateral cerebellar cortex. Direct contrasts between sign and speech production in hearing bilinguals fluent in American Sign Language (ASL) and English have revealed greater activation for signing than speaking in the superior parietal lobule (SPL), as well as in the supramarginal gyrus (SMG) (Braun, Guillemin, Hosey, & Varga, 2001; Emmorey, McCullough, Mehta, & Grabowski, 2014; Zou et al., 2012; see also Emmorey, Mehta, & Grabowski, 2007, for evidence from deaf signers). A primary goal of the present study was to investigate the role of such sign-specific production regions by examining the neural substrates that support the articulation of different types of signs that vary in their phonological features: one-handed signs produced in "neutral space" (no body contact), "body-anchored" signs produced at specific locations on or very near the body, two-handed signs produced in neutral space, and one-handed fingerspelled words that involve the production of complex sequences of handshapes in neutral space. Examples of these types of signs are provided in Fig. 1. This is the first study to examine how several sign-specific phonological features (i.e., number of hands, body contact, and handshape complexity) affect the neural substrates involved in lexical production.

Previously, Corina, San Jose-Robertson, Guillemin, High, and Braun (2003) investigated the production of one-handed ASL signs in a positron emission tomography (PET) study in which right-handed deaf signers were asked to repeat one-handed signs

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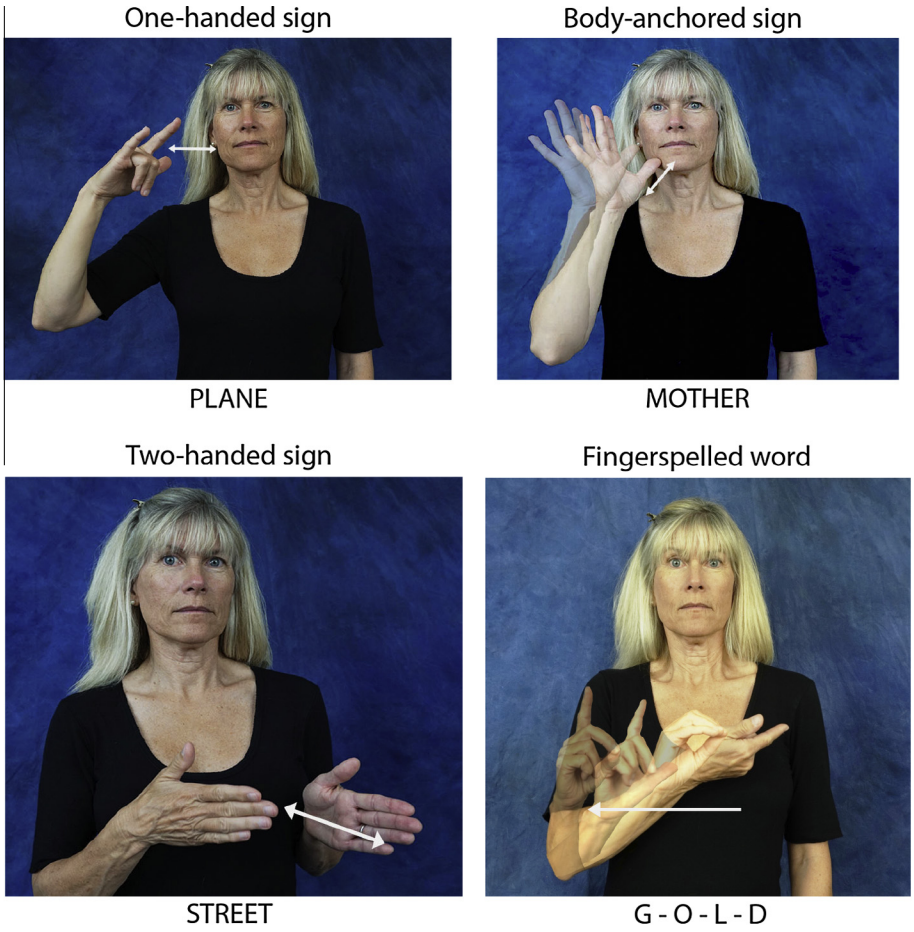

Fig. 1. Examples of the three different sign types and fingerspelling.

(all nouns) and to produce verbs associated with the nouns using only their right or left hand. Generating verbs with either hand (vs. noun repetition) produced very similar activation patterns in left lateral frontal regions associated with lexical-semantic processing (BA 44/45, 47) and with working memory and selection demands (BA 46). In addition, the conjunction analysis revealed that generating verbs with either hand produced activation in the right lateral cerebellum and along the cerebellar midline. Given that right-lateralized cerebellar activation was observed for left-handed sign production, Corina et al. (2003) suggested this cerebellar activation was associated with cognitive or linguistic processes involved in the verb generation task. The English-to-ASL translation task used in the present study (which is also a PET investigation) does not require the same cognitive or linguistic demands as verb generation, and thus we can investigate whether right lateral cerebellar activation is present under an easier task condition.

Further, Corina et al. (2003) reported that direct contrasts between left- and right-handed verb-generation versus their respective noun-repetition baselines revealed that right-handed signing was associated with greater activity in the precentral gyrus (BA 4/6) bilaterally, while left-handed signing was associated with greater activity in left parietal cortex (SPL and SMG). Corina et al. speculated that the surprising activation in right precentral gyrus for right-handed signing reflected active suppression of the left hand. The left hand is normally involved in sign production because many signs are two-handed with the non-dominant hand serving either as a mirror articulator or as a place of articulation (Sandler, 1993). When signers reverse dominance and sign with their left hand, they typically do not utilize the right hand because this hand may be occupied (thus forcing left-handed signing) and because bimanual co-ordination with reversed dominance is difficult. Here we investigate whether activation within the right precentral gyrus is observed when the left hand does not need to be suppressed because the targeted signs are all one-handed (some verbs produced in the Corina et al. study would normally have been articulated with both hands, thus requiring left-hand suppression). Corina et al. attributed the greater left parietal activation for left-handed than right-handed signing to the increased motor control demands when signing with the non-dominant hand. Here we investigate the specific role of left parietal regions in motor control during sign production by contrasting lexical signs and fingerspelled words, which differ in their motoric demands.

Specifically, ASL uses a one-handed fingerspelling system in which distinct handshapes represent letters of the English alphabet. This system is not universal - other signed languages use a two-handed system (e.g., British Sign Language; Sutton-Spence & Woll, 1999) or a different set of handshapes (and movements) to represent the orthography of the surrounding spoken language (see papers in Brentari, 2001). Fingerspelled words in ASL differ from ASL signs because lexical (monomorphemic) signs are limited to a sequence of at most two handshapes, with severe restrictions on the type of handshapes that can occur in the sequence (e.g., Brentari, 1998). In contrast, fingerspelled words are composed of strings of handshapes that are sequenced to spell out an English word. Signers fingerspell English words in a variety of contexts, such as expressing proper names, indicating specific English terms (e.g., technical jargon), or specifying concepts that do not have a