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REGULAR ARTICLE

Earlier and more robust sensorimotor discrimination of ASL signs in deaf signers during imitation

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ABSTRACT

Prior research suggests that the amount of experience an individual has with an action influences the degree to which the sensorimotor systems of their brain are involved in the subsequent perception of those actions. Less is known about how action experience and semantic knowledge impact sensorimotor involvement during imitation. To address this question, we collected electroencephalograms (EEG) while deaf signers and hearing non-signers imitated one-handed and two-handed ASL signs. During observation, deaf signers showed early differentiation in alpha/beta power between the one- and two-handed sign conditions, whereas hearing non-signers showed this discrimination only later. During sign imitation, deaf signers showed increased power. Thus, in an imitative context, deaf signers engage anticipatory motor preparation in advance of action production, while hearing non-signers engage slower, more memory-related processes to help them complete the complex task.

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KEYWORDS

Alpha rhythm; beta rhythm; imitation; signed language; EEG; sensorimotor

1. Introduction

To the unlearnt eyes, the blur of signing hands is challenging to follow. Fluent deaf signed language users produce and understand layers of serial and simultaneous actions with their body, hands, and face, easily communicating complex linguistic content through the visual-manual modality. Recent research has shed light on how signers exhibit differences in visual perception and motion processing, in some cases in response to sign-related stimuli (Kubicek & Quandt, 2019), and in other cases in response to non-sign stimuli (Peressotti et al., 2018; Quandt & Kubicek, 2018; Williams et al., 2016). However, little is known about how people perceive signs in imitative contexts. In an imitative context, an observer watches with the intent to reproduce the action that they see. Many cognitive neuroscience studies of signed language processing engage participants in a unidirectional sign-perception task, such as lexical decision tasks, in which the participants are not intending to produce signed responses. While non-imitative tasks provide important information about how the brain processes signs, they do so in a context which is removed from signed language as a bi-directional, interactive, and communicative form of action. Learning a new language relies heavily upon imitation, as has been studied especially in the case of

signed language learning (Ortega et al., 2019; Ortega & Morgan, 2015). Here, we consider how deaf signers and hearing non-signers process signs when asked to imitate them – a task which presents a significant challenge to most hearing non-signers.

1.1. Neural correlates of sign perception and production

There are significant similarities in the neural organisation of the language production networks for spoken and signed languages (Emmorey et al., 2016; MacSweeney et al., 2008), and significant overlaps in how gesture, communicative action, speech, and sign intertwine with one another (Drijvers et al., 2018; Ortega et al., 2019; Schembri et al., 2005). Mental representations and processing of signs share many correlates with the representation and processing of speech (Blanco-Elorrieta et al., 2018; Corina et al., 1999; Evans et al., 2019; Petitto et al., 2016). For instance, deaf signers recruit the left superior temporal gyrus when seeing signed phrases, much like hearing speakers do when listening to speech (MacSweeney et al., 2002). While signed languages and spoken languages have fundamental similarities in their neural organisation due to the amodality of phonetic information (Emmorey et al., 2014;

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Petitto et al., 2016), there are also important differences in the neurobiology of how spoken and signed languages are represented in the brain (Emmorey et al., 2014; Evans et al., 2019).

Some differences in motion-related networks between signers and non-signers suggest that these regions adapt to the perception and production demands of the signed language modality, in ways that also vary with regard to physiological hearing status (Allen et al., 2013; Emmorey et al., 2016; Kanazawa et al., 2017). For instance, visual perceptual differences in signers are well-documented. Signed language users show differences in perception of sign-related body movements (Poizner, 1983) or sign-relevant body positioning (Almeida et al., 2016), and the spatial maps of where visual attention is allocated in the focal region and/or periphery of the visual field (Dye et al., 2007; Stoll & Dye, 2019). Signers may also show greater sensitivity to observed handshapes (Baker et al., 2005; Morford et al., 2008) although there are contradictory findings in this area (Gimeno-Martínez et al., 2019). Overall, accumulating evidence shows that people with extensive signed language expertise exhibit differences in perception of sign-related stimuli, but the full extent and nature of these differences is yet to be understood.

1.2. Mirroring, experience, and sign

The human mirror neuron system (MNS) may play an important role in imitation and perception of human actions, and thus, has been the focus of a fair amount of inquiry regarding signed language (Corina & Knapp, 2006; Emmorey, 2014; Mole & Turner, 2017; Okada et al., 2016; Ostarek & Huettig, 2019). Typically, brain regions making up the MNS are recruited both during the perception and the production of actions, causing similar neural activity during observation and execution of the same action (Rizzolatti & Fabbri-Destro, 2009). The MNS appears to also be involved in response to aural input (Jenson et al., 2014; Saltuklaroglu et al., 2017; Thornton et al., 2017), perception of speech reading (Swaminathan et al., 2013), and perception of robotic voices (Di Cesare et al., 2017). Research supports the notion that the MNS is somehow involved in language processing, although there are significant disagreements over its role (Emmorey, 2014; Gallese et al., 2011; Mole & Turner 2017). Given that signed languages constitute a unique overlap of language, action production, and action comprehension, it is possible that unique insights may be gained from studying mirroring-related processes in groups of experienced signers.

Ample evidence suggests that mirroring-like activity, such as the vicarious involvement of the somatosensory

and motor cortices during action perception, may be sensitive to the observer's own past experiences. The relation between action experience and mirroring-like activity is complex, with some research suggesting that greater experience with an action leads to increased sensorimotor involvement during subsequent perception (Calvo-Merino et al., 2005, 2006, 2010; Cannon et al., 2014; Denis et al., 2017: Ouandt & Marshall, 2014). In contrast, some findings suggest the opposite effect: that with greater action experience, the sensorimotor systems of the brain become more efficient at processing observed actions (Babiloni et al., 2010; Vogt et al., 2007) and thus show less activity. In recent years it has become clear that there is likely a non-linear relationship between action experience and involvement of the sensorimotor system during observation (Gardner et al., 2015, 2017a, 2017b).

Viewing signers as "action experts" within the domain of a signed language has yielded complex and contradictory results. Some researchers have asked whether deaf signers, due to their extensive use of the hands and body for language, may show increases in mirroring activity when perceiving a signed language. One body of work suggests that these processes have little to no role in the higher-level neural and cognitive processing of signed languages (Corina & Knapp, 2006; Emmorey et al., 2010; Okada et al., 2016; Rogalsky et al., 2013). Several reports found no evidence to support the involvement of mirroring during sign perception (Rogalsky et al., 2013), and in fact generally suggested that signers recruit less of the sensorimotor system during sign perception, possibly because they are relying more on linguistic processing (Möttönen et al., 2016). Some findings suggest that deaf signers' neural representations of action processing differ from hearing nonsigners' (Corina et al., 2007; Emmorey et al., 2010, 2011; Mole & Turner, 2017). It is possible that deaf signers' communicative action processing is highly efficient, reducing sensorimotor system activity but not disengaging from it, due to their extensive expertise in extracting meaning from complex action (Gardner et al., 2015, 2017a, 2017b). As well, the consideration of mirroring-like processes in signers hinges upon the definition of mirroring (Mole & Turner, 2017). Here, we turn our interest toward the broader involvement of an observer's somatosensory and motor cortices during the perception of another's action, rather than a narrowly-defined human mirror neuron system analogous to that studied originally in macaques (Corina & Knapp, 2006).

The relationship between mirroring and experience with signed language may well be non-linear. Indeed, adult American Sign Language (ASL) learners seem to rely more on mirroring-related processes when their ASL vocabulary is weak, suggesting that at least for adult learners, reliance on mirroring-like processes may constitute a compensation in the face of weak linguistic knowledge of ASL (Williams et al., 2017). However, a recent study (Kubicek & Quandt, 2019), showed that while deaf signers show overall less involvement of the sensorimotor cortices during sign perception, the specific sensorimotor characteristics of observed signs were encoded in their sensorimotor cortices. Thus, while the overall pattern of signers showing less vicarious sensorimotor processing echoed the conclusions of prior functional neuroimaging work, both signers and non-signers were in fact drawing upon their own sensorimotor representations to parse the details of the signs they were observing.

Analysing the oscillatory activity of the cortex using electroencephalography (EEG) provides valuable information about what regions of the cortex are active in an action observer's brain, which can yield fine-grained information about the timing and sensitivity of cortical sensorimotor processing during action perception and production. Common EEG measurements of sensorimotor activity in the human brain are alpha (8–13 Hz) and beta (14-30 Hz) rhythms measured at centrally-located scalp electrodes, which index the electrophysiological oscillations emanating from the primary sensory and motor cortices (Arnstein et al., 2011; Bowman et al., 2017; Fox et al., 2016). The central alpha (also termed "mu") rhythm reflects activity in the pre-central gyrus, while the sensorimotor beta rhythm emanates from the pre-and post-central gyri (Tzagarakis et al., 2010). Sensorimotor alpha rhythms display lower power (event-related desynchronisation; ERD) during action processing, whether in perception, imagination, or production, and the beta rhythm tends to show similar patterns, although it may index slightly different aspects of action. The activity of these sensorimotor EEG rhythms is quite sensitive to the observer's own experiences, with much research revealing modulations of alpha and beta power depending on the observer's prior sensory and motor experiences with observed actions (Cannon et al., 2014; Denis et al., 2017; Quandt et al., 2012; Simonet et al., 2019). Recent work shows that sensorimotor alpha and beta rhythms can reflect mirroring-like processes during sign observation (Kubicek & Quandt, 2019) and also when deaf signers read English words (Quandt & Kubicek, 2018).

1.3. Sensorimotor processing during sign imitation

Action perception may occur in a context where the observer is simply watching someone else's movements, or it may occur in an imitative context, wherein the observer plans to reproduce the actions she sees. Seeing an action when one intends to copy it changes the neural profile of the observation (Decety et al., 2002). Both imitation and action observation recruit frontal premotor, parietal, and temporo-occipital cortices (Caspers et al., 2010). However, imitation particularly engages the inferior parietal cortex, primary somatosensory cortex, and the inferior frontal cortex, which is also involved in language processing (Caspers et al., 2010; Decety et al., 2002). Many experimental tasks used in prior sign perception studies involved passive sign observation (Corina et al., 2007; Kubicek & Quandt, 2019; MacSweeney et al., 2004; McCullough et al., 2012), wherein the perceiver was not overtly planning to reproduce the signs they saw. In the current study, we aimed to assess whether long-term expertise with ASL would result in enhanced or reduced involvement of the sensorimotor cortex in response to the sensorimotor characteristics of signs during imitation, in comparison to individuals unfamiliar with ASL.

We ask here how signers and non-signers perceive signs, not only looking at overall neural responses to observing a sign, but also the extent to which the sensorimotor systems of these observers are sensitive to the specific sensorimotor characteristics of the observed sign. This provides a more fine-grained view of how sensorimotor systems are involved in perception. We probed this question by asking participants to view, then imitate, signs produced either using only one hand, or signs produced using both hands. In prior work, comparing neural responses related to one- and two-handed signs has yielded robust differences in sensorimotor EEG (Kubicek & Quandt, 2019; Quandt & Kubicek, 2018) and in PET measures of cortical activity (Emmorey et al., 2016). Because producing two-handed signs recruits the right sensorimotor cortex more greatly due to the involvement of the left hand, seeing the same pattern during sign observation can reveal that the observer is drawing upon his or her own internal motor plans for how the sign should be carried out (e.g. recruiting more right sensorimotor cortex when seeing a two-handed sign, which involves the left hand).

Understanding the differences in the oscillatory profile of sensorimotor EEG activity during an imitation task could improve the current understanding of how signers see and make sense of others' signs. While imitation of a single sign is still far different from a natural signed conversation, the combination of sign observation with the sign production is a richer, more socially-relevant task (Krishnan-Barman et al., 2017). This study will examine if experience with ASL could lead to changes in sensorimotor processing of actions compared to individuals who do not know ASL. For signers, imitating signs is a word production task, whereas for non-signers, imitating signs is a pure action-imitation task. For non-signers, attempting to imitate a sign may invoke neural networks supporting gesture, meaningless action production, and/or mirroring. Although the task for hearing non-signers is vastly different from the task that deaf signers are executing, we sought to uncover whether, and how, these differences were instantiated in the neurodynamics during the task, with a particular focus on the sensorimotor network.

Based on the prior work regarding these questions, we pitted the following two possible hypotheses against each other: (1) Deaf Signers will show increased sensorimotor activity during sign imitation, and greater differentiation between sign types, due to greater prior experience and semantic knowledge of the signs; versus (2): Deaf Signers will show less sensorimotor system activity and less differentiation of sign types in the sensorimotor system, because for those individuals sign imitation involves language systems of the brain more robustly than sensorimotor systems.

Given that recent evidence supports the latter claim (Kubicek & Quandt, 2019), we predicted our analyses would generally support that hypothesis. However, the current study uniquely engaged participants in an imitative paradigm, and given that participants were required to copy the signs they saw, we predicted that while observing with the intent to imitate, both groups would show different sensorimotor EEG responses to one-handed compared to two-handed signs, but the effect would be stronger in the Hearing Non-Signers, due to their unfamiliarity with the stimuli and the resultant need to focus on the basic physical parameters of the observed communicative actions. We also anticipated that while producing signs, Hearing Non-Signers would show more robust differentiation between one- and two-handed signs, again due to the novelty of the communicative actions requiring complex motor plans for implementation.

2. Materials and methods

2.1. Overall design

The current study and a previously published study from our lab (Kubicek & Quandt, 2019) represent separate aims of one larger data collection effort. All participants in the current study were also participants in that study, in which participants viewed ASL sign stimuli passively without imitating them. While the video stimuli were the same (from the ASL-Lex database; Caselli et al., 2016), in the current study they were presented in a newly randomised order and the task was different. Separate EEG recordings were collected consecutively during the data collection session – the passive-watching task was collected first, and the current imitation

Table 1. Formal education.

	Deaf	Hearing
High school	3 (16%)	0
Some college	2 (11%)	1 (5%)
Associates	0	1 (5%)
Bachelors	3 (16%)	6 (32%)
Some grad school	2 (11%)	2 (11%)
Masters	8 (44%)	8 (42%)
Doctorate	0	1 (5%)

Self-reported highest educational degree obtained for Deaf and Hearing participants. Percentages were rounded to the nearest whole number.

task followed. Participant, stimuli, and task descriptions regarding the current study are provided in more detail below.

2.2. Participants

Eighteen Deaf Signers and 19 Hearing Non-Signers were run through the experimental protocol. All participants were right handed. Participants spanned a wide range of educational backgrounds (Table 1). Deaf Signers self-identified as deaf and fluent in ASL (see Table 2 for language descriptors). The hearing nonsigners did not have any knowledge of any signed language, and they were all fluent in English. There were no other exclusions for this group based on language background, so the group included some multilingual people and was overall a heterogeneous group. All participants gave their informed consent prior to the experiment and were informed of their rights in accord with the Declaration of Helsinki. An ASL version of the informed consent was shown to all deaf participants. All deaf participants were run by a native or fluent ASL signer as the lead experimenter. The study was approved by the relevant IRB and participants were paid for their time.

2.3. Stimuli

The ASL stimuli were video clips retrieved from ASL-LEX (Caselli et al., 2016). Each video clip shows a woman producing one sign. Two types of videos were used, with 40 of each type, for a total of 80. One video type consisted

Table 2. De	mographics	and	ASL	use
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	Deaf	Hearing	t-test p value
Age (years)	31.4 (10.7)	27.4 (3.7)	.15
Current ASL use ^a	1.11 (.31)		
Current ASL understanding ^b	95.5 (5.1)		
Current ASL production ^b	92.4 (6.7)		
Age of ASL exposure	7.69 (8.73)		

Means and standard deviations listed.

^aSelf-reported rating on a 7-point scale ranging from 1 = "All the time" to 7 = "Only on special occasions (e.g. home for the holidays)".

^bSelf-rated proficiency on a sliding scale from 0 (poor) to 100 (fluent).

of signs that only use one hand ("one-handed", "1H"; i.e. GUILT). These signs were always produced with the dominant (right) hand. The other video type consisted of signs that use two hands ("two-handed", "2H"; i.e. FAMILY). Of the 40 two-handed signs, 24 were symmetrical. There were no significant differences between the signed 1-handed (1H) or 2-handed (2H) words or their English translations for any of the following measures: frequency, iconicity, flexion, phonological properties, imageability, sign onset time (ms), sign offset time (ms) and sign length (ms; for more information see Caselli et al., 2016). Action verbs and fingerspelled loan signs were not included in the stimulus set. See Table 3 for linguistic norms and timing data for all stimuli.

Each video started with a woman (a deaf native signer) sitting in a neutral position with her arms resting on her lap, and as the video continued, she raised her hands to produce an ASL sign, returning to neutral position after she finished. We conducted t-tests to assess whether the timing dynamics of one-handed and two-handed signs were similar. The onset of the sign from the start of the video clip did not differ between groups (1H: 523.0 ms, 2H: 550.6 ms, p = .57), nor did the offset of the signs in ms from start of video clip (1H: 1371.9 ms, 2H: 1187.9 ms, p = .53). The total length of the sign from onset to offset did not differ between groups (1H: 573.9 ms, 2H 637.3 ms, p = .22).

Using Adobe Premiere, we affixed a virtual audio trigger (a short beep) to the video clip at the onset of the sign, as defined by ASL-Lex norms (Caselli et al., 2016). The onset of the beep corresponded to the onset of the sign. The beep was never audible, but rather, was sent to a BrainProducts Trigger Box and converted into a TTL pulse. The TTL pulse was then recorded in parallel to the EEG signal in order to identify the time in the EEG signal corresponding to the time of the sign onset. Sign onset in the video was used as time 0 for all analyses.

2.4. Experimental procedure

All Deaf Signing participants were run by an experimenter fluent in ASL (most experimenters were deaf), with communication occurring in ASL. Deaf participants were shown an ASL version of the informed consent form prior to signing a paper copy. After providing informed consent, participants were brought into the experimental room. While the EEG cap was prepared, they filled out a language and educational background form. They viewed the experiment in E-Prime 2.0 (Psychology Software Tools, Sharpsburg, PA) on a computer monitor ~76 cm away. Prior to the task analysed for this project, participants had seen the same stimuli in a different context. Participants were instructed to view each individual ASL sign, and then when prompted, to produce their own imitation of what they just saw to the best of their ability. After a practice session of ten trials (showing video clips different from there experimental trials) to ensure that they understood the task, the experiment started.

A total of 80 trials were presented, divided into four blocks of twenty trials each. Each sign was seen one time throughout the course of the experiment. Each trial started with a fixation point (jittered ISI = 4–5 s); then the sign clip started, with an event marker triggered at the onset of the sign (see Figure 1). After the video clip ended, a screen stating "GO" was shown for three seconds, during which the participant produced the sign they just saw. Experimental scripts are available at https://osf.io/6rtqf/.

2.5. Electroencephalographic data

EEG was recorded from 64 active Ag/AgCl electrodes using an actiCAP setup (Brain Products GmbH, Germany), with SuperVisc electrode gel. EEG data was recorded and processed at a rate of 1000 Hz. Data was

		1H words: M (SD)	2H words: M (SD)	t-test p value
Word length Log frequency (SUBTLEX Log frequency (HAL) # phonemes Lexical Decision RT M Lexical Decision RT SD Naming RT M Naming RT SD Imageability	Word length	5.2 (1.7)	5.7 (2.2)	.25
	Log frequency (SUBTLEX)	5.6 (10.6)	14.3 (43.6)	.22
	Log frequency (HAL)	9.6 (1.7)	10.1 (1.5)	.24
	# phonemes	4.1 (1.1)	4.6 (1.3)	.10
	Lexical Decision RT M	605.6 (45.5)	616.2 (64.4)	.40
	Lexical Decision RT SD	202.1 (64)	215.4 (89)	.45
	Naming RT M	605.5 (42.6)	607.8 (42.5)	.81
	Naming RT SD	128 (58.1)	130.3 (53.1)	.85
	Imageability	509.5 (112.5)	543.6 (79.6)	.18
su	5 ,			
ASL norn	Frequency (ASL-Lex)	4.7 (.8)	4.6 (1.1)	.42
	lconicity	3.7 (1.7)	3.8 (1.4)	.90
ġ	Flexion	3.4 (2.2)	3.6 (2.2)	.69
ning	Sign onset from start of clip	523.02 (168.34)	550.55 (261.42)	.58
Sig	Sign duration	573.90 (227.08)	637.30 (230.78)	.22

Table 3. Linguistic norms and timing data for two categories of Stimuli.

1-handed (1H) words and 2-handed (2H) words, as in Quandt and Kubicek (2018) and Kubicek and Quandt (2019).



Figure 1. The trial structure. Participants saw one- or twohanded signs (Caselli et al., 2016) and then produced their own imitations of the signs when prompted by the word "GO".

recorded with a Cz reference and a grounded electrode at AFz. The EEG signals were amplified by each electrode's active amplifier, and then by a 24-bit actiCHAMP amplifier (Brain Vision LLC, Morrisville, NC). Hardware filter settings included a high-pass filter (.53 Hz) and a low-pass filter (120 Hz). The institutional approval for this study prohibits the public archiving of our participants' data, however, the data necessary for reproducing this work is available from the corresponding author upon request. A data-sharing agreement must be completed in advance of data sharing.

2.6. EEG data processing

The EEG data were preprocessed in EEGLAB (Delorme & Makeig, 2004). Each signal was re-referenced offline to the average signal of the mastoid electrodes. The rereferenced EEG data were filtered with .01 Hz highpass and 100 Hz lowpass filters and epochs of -1500-5000 ms were extracted from the continuous EEG signal around the onset of the sign (time 0). Each epoch was labelled as 1H or 2H depending on condition (one-handed or two-handed sign). The time period of -1500 ms to -1000 was used as a baseline for all analyses. The mean signal during this time period was removed from the epochs of interest. During the baseline period there was a fixation cross visible. Due to variability in the sign video clips, for 4 out of the 80 trials, the baseline also included a short view of the signing model appearing on screen (mean duration across those 4 trials = 255 ms), due to these clips having a later sign onset relative to the beginning of the video clip. A study file was formed with two conditions (1H signs; 2H signs) and two groups, Deaf Signers and Hearing Non-Signers. The event-related spectral perturbation was calculated from 8 to 25 Hz, using a 4-cycle wavelet with a Hanning-tapered window applied (number of frequencies: 80; number of timepoints: 230; Delorme & Makeig, 2004). We analysed alpha and beta range frequencies at all scalp electrodes (rather than focusing only on the mu rhythm at central electrodes) to assess whether the effects seen at central electrode sites are a result of sensorimotor activity (Arnstein et al., 2011), or are reflecting an alpha/beta-range effect present across the scalp. Here, we primarily refer to alpha and beta frequency activity, while acknowledging that the alpha-range activity occurring primarily in the central region is likely "mu" activity reflecting activity in the pre-and-post-central regions (Bowman et al., 2017). Study scripts are available at https://osf.io/6rtqf/.

2.7. Statistical analysis

We analysed the data using both the full-scalp time-bin analyses and the time-frequency plots at individual electrodes over the central region, in order to best capture the richness of the information present in time-frequency EEG analyses (Cohen, 2017). For the full-scalp analyses, the data was analysed in a number of predefined time bins, so that the distribution of effects over the scalp could be visualised. For the analyses at individual electrodes over the central region, we analysed the time-frequency dynamics of oscillatory activity across the continuous time and frequency ranges we defined *a priori*. Details of these two analyses approaches, which were all planned prior to data collection in order to test specific hypotheses, are given below.

2.7.1. Full scalp analysis

A 2×2 ANOVA with one paired condition (1H signs; 2H signs) and unpaired groups (Deaf; Hearing) was performed on two different time-windows for each trial. First, a window during the observation of the sign, and second, a window while participants started to produce their own imitation of the sign. This statistical comparison was performed across the full scalp to observe any significant differences in the amplitude of the frequencies of interest. The ANOVA was run as described and planned within group t-test comparisons of the 1H and 2H conditions for each group were analysed to test the *a priori* predictions of the study. We focused our analysis on four frequency bands: low alpha (8-10 Hz), high alpha (11-13 Hz), low beta (14-17 Hz), and high beta (18–25 Hz). Those frequencies were selected based on previous work analysing sensorimotor activity during action processing (Denis et al., 2017; Quandt & Marshall, 2014; Simon & Mukamel, 2016). Prior to running any analyses, the epoch from 0 to 2000 ms (time 0 = onset of sign) was divided into 8 different time bins. The first four time bins (0-250s,

250-500, 500-750, and 750-1000 ms) were assessed as part of the "observation" window, during which time the signing model was producing a sign. The last four time bins (1000-1250, 1250-1500s, 1500-1750, and 1750-2000ms) constituted the "production" window, during which time the sign video was ending, and the participant started to produce his or her imitation. Due to the variation in the sign clip length, the production window reflects a variety of processes. We analysed the length of the ASL videos to map out the content of the production window in the following way. The first guartile of elapsed time between sign onset and GO appearing on the screen was 1059 ms, the median elapsed time was 1251 ms, and the third quartile was 1401 ms (all times relative to sign onset, time 0). Thus, the production window used in this analysis encompassed participants' initiation of movement, as well as some preparatory time in advance of action production. This approach was used, as opposed to analysing data locked to participant's actual movements, because many sign productions, particularly those by the Hearing Non-Signers group, had ill-defined sign onsets. Visual inspection of recording revealed that Hearing Non-Signers' productions included more hesitant sign onset, multiple errors, and production of movements that appeared to be a mixture of sign and gesture (for related discussion, see Ortega & Morgan, 2015).

In an effort to limit spurious findings occurring at a single electrode on the scalp, we decided *a priori* that for analyses across the full scalp, a statistically significant effect would be included in our results only if it occurred within a cluster of three or more adjacent electrodes. We used an adjusted *p* value of .016 (.05/3) as the significance threshold for this determination to further control for the effect of carrying out multiple comparisons. This statistical approach has been used in prior work (Kubicek & Quandt, 2019; Quandt & Kubicek, 2018).

2.7.2. Central region analysis

We performed a time-frequency analysis at electrodes falling within our region of interest: the 21 electrodes that lay over the central region of the scalp, above the primary sensorimotor region of the brain: FC5, FC3, FC1, FCz, FC2, FC4, FC6, C5, C3, C1, Cz, C2, C4, C6, CP5, CP3, CP1, CPz, CP2, CP4, and CP6. We opted to focus analyses on these electrodes since alpha and beta rhythms at central electrodes are associated with activity in preand post-central gyri, which are key regions of the mirroring system (Arnstein et al., 2011; Perry & Bentin, 2009; Ritter et al., 2009). For each electrode, we computed time-frequency transforms from 8 to 25 Hz for observation and production windows. For these central region analyses, the observation window extended from -750 to 1500 ms and the production window extended from 1000 to 3000 ms. The longer time windows, which included the time prior to sign onset as well as extending well into the participants' own imitations, allowed us to more fully visualise the oscillatory dynamics unfolding over the course of the task. A 2×2 ANOVA design was implemented for the central region analyses, with one paired condition (1H signs; 2H signs) and unpaired groups (Deaf; Hearing). For these analyses, a *p* value threshold of .05 was used at each electrode, with a false detection rate (FDR) correction applied (Benjamini & Hochberg, 1995).

3. Results

3.1. Observation with intent to imitate

3.1.1. Comparing deaf vs hearing groups

There was no main effect of group during the observation window using any analysis approach. Overall sensorimotor EEG responses to ASL signs (both 1H and 2H stimuli combined) were not significantly different between Deaf and Hearing participants during the observation window. No significant differences were found using either full-scalp analyses or time–frequency visualisations at the electrodes overlying the sensorimotor ROI.

3.1.2. Sensitivity to sensorimotor characteristics

3.1.2.1. Time-frequency analyses across the scalp. For the Hearing Non-Signer group, there were no significant differences between conditions (1H and 2H) at any of the four time bins time during the observation window in any frequency band.

For the Deaf group, there were no significant differences between conditions in the lower alpha (8–10 Hz) or the upper beta (18–25 Hz) bands at any time. In the upper alpha (11–13 Hz) band, time bins 250–500, 500–750, and 750–1000 ms showed more ERD in response to 2H signs compared to 1H signs (p < .016). From 250 to 500 ms, the effect was seen a cluster of three electrodes (C2, CP2, and CP4) in the right central-parietal region (p < .016). In the 500–750 ms bin, the effect was seen in a cluster of three electrodes (F6, AF8, and AF4) in the right frontal region (p < .016). From 750 to 1000 ms, ten electrodes over the right posterior parietal region (CPz, CP2, CP4, TP8, P2, P4, P6, P8, POz, and PO4) showed significantly more alpha ERD in response to 2H signs (p < .016).

Scalp activity in the lower beta (14-17 Hz) band also showed greater ERD (p < .016) in response to 2H signs in the Deaf group during the last three time bins. Topographic patterns of responses can be seen in Figure 2.



Figure 2. Low beta EEG power (14–17 Hz) during observation of signs with the intent to imitate, 250–1000 ms following onset of the sign in the video stimulus. Data are analysed at 64 electrodes sites for Deaf and Hearing groups, in response to seeing one-handed (1H) and two-handed (2H) signs. Cool colours indicate desynchronisation while warm colours show synchronisation.

3.1.2.2. Central region analyses. We conducted targeted analyses at the electrodes overlying the central, fronto-central, and centro-parietal regions in order to assess the temporal dynamics of the responses to 1H and 2H signs while observing with the intent to imitate. Deaf and Hearing groups both showed greater ERD in response to 2H signs (p < .05, FDR corrected), although the profile of those responses showed a fair degree of variability. For example, at electrode CPz (see Figure 3), while both groups showed significantly more alpha and beta ERD in response to 2H signs, that difference was seen much earlier, and with more continuity, in the Deaf Signers compared to the Hearing Non-Signers. Eight electrodes within the central region showed the same pattern of earlier and more robust discrimination (p < .05, FDR corrected) of 1H vs. 2H conditions for Signers: C1, C2, C4, Cz, CP1, CP2, CP4, and CPz (pictured). In the other 13 electrodes in the ROI, the groups did not show a distinct difference in onset of discrimination between 1H and 2H signs. In all cases, for both groups, observation of 2H signs elicited greater alpha/beta ERD.

3.2. Producing ASL signs

3.2.1. Comparing deaf and hearing groups

3.2.1.1. Time-frequency analyses across the scalp. There was no main effect of group during the production window for the first three production time bins (1000–1250, 1250–1500, or 1500–1750 ms). However, from 1750 to 2000 ms, at all four frequency bands, Deaf Signers showed significantly lower EEG



Figure 3. Comparison of alpha and beta activity during observation of signs with the intent to imitate, from -750 to 1500 ms (time 0 = onset of sign) at channel CPz for both groups. Deaf signers show earlier and more consistent differentiation between 1H and 2H signs. Cool colours refer to event-related desynchronisation relative to baseline.

power (p < .016) compared to Hearing Non-Signers across a wide swath of electrodes including frontal, central, and right posterior scalp regions (see Figure 4 for visualisation of the scalp distribution).

3.2.1.2. Central region analysis. There was a main effect of group during the production window at several central region electrodes. The time–frequency analyses at the following eight electrodes showed significantly greater ERD in alpha/beta bands (p < .05, FDR corrected) in Deaf Signers compared to in Hearing Non-Signers: FC1, FCz, C1, C2, Cz, CP1, CP2, and CP6 (see Figure 4(B) for one representative plot).

3.2.2. Sensitivity to sensorimotor characteristics 3.2.2.1. Time-frequency analyses across the scalp. In

the lower alpha (8–10 Hz) band, Hearing Non-Signers showed stronger alpha ERD at five right parieto-occipital electrodes (P4, P6, P8, P08, O2) when producing a 2H sign during the 1000–1250 ms time bin (p < .016). No other differences were seen at any time for the Deaf or Hearing groups in the low alpha range.

In the upper alpha (11–13 Hz) band, both the Deaf and Hearing groups showed significantly more alpha ERD as they produced 2H signs during all four time bins (p < .016). See Figure 5 for the topographical distribution of these effects across the scalp across the latter three time bins.

In the lower beta (14–17 Hz) band, both the Deaf Signers and Hearing Non-Signers showed significantly different neural activity while producing 1H and 2H signs. These effects were present across vast regions of the scalp more beta ERD during 2H sign production compared to 1H sign production across fronto-central, central, parietal, and occipital regions from 1000-1250 to 1250-1500 ms (p < .016). During these time bins, effects were present for both groups at more than 50% of the electrodes, spanning broad regions of the scalp. From 1500 to 1750 ms, the differences became less widespread and were apparent at seven parietal electrodes in the Deaf Signers and 17 right frontal and parietal electrodes for the Hearing Non-Signers. From 1750 to 2000 ms, there were no significant differences for the Hearing Non-Signers, while the Deaf



Figure 4. Alpha and beta frequency responses while participants imitate the signs. (A) EEG responses across the scalp from 1750 to 2000 ms following the onset of the sign in the stimulus video. (B) Time-frequency plot of activity at electrode Cz from 1000 to 3000 ms. The 1750–2000 ms period that is depicted in part A is marked with dotted lines.



Imitation: High Alpha EEG Power (11-13 Hz)

Figure 5. High alpha EEG power (11–13 Hz) while participants imitate one-handed (1H) and two-handed (2H) signs, from 1250 to 2000 ms following onset of the sign in the video stimulus. Data are analysed at 64 electrodes sites for Deaf and Hearing groups, in response to seeing one-handed (1H) and two-handed (2H) signs. Cool colours indicate desynchronisation while warm colours show synchronisation.

Signers showed more beta ERD during the production of 2H signs at 14 bilateral centro-parietal electrodes (p < .016).

In the upper beta band (18–25 Hz), both groups displayed greater beta ERD during the production of 2H signs at centro-parietal electrodes from 1000 to 1250 ms (p < .016). For Hearing Non-Signers this effect was seen across 18 bilateral central, parietal, and occipital electrodes, whereas for Deaf Signers the effect was present at 6 right parietal electrodes only. From 1250–1500 to 1500–1750 ms, the Hearing group showed significantly lower beta power for 2H signs at more than 50% of scalp electrodes, and the Deaf group showed no differences. There were no beta ERD differences in the last time bin.

3.2.2.2. Central region analysis. The targeted central region analyses revealed that both Deaf and Hearing groups showed significant differences (p < .05, FDR corrected) in EEG activity between conditions over the central region during sign imitation. However, these differences came about as a result of starkly different profiles of activity in the sensorimotor cortices for the two groups. For the Hearing Non-Signers, much of the difference was driven by increases in EEG power across alpha and beta ranges, particularly when producing a 1H sign. For example, at electrode CPz (see Figure 6), while both groups showed significant differences in power between 1H and 2H signs, for the Deaf group that effect is driven by alpha/beta ERD, with more ERD in response to 2H signs. In contrast, for the Hearing Non-Signers, both conditions elicit an increase in EEG power, with higher power for 1H signs and lower power for 2H signs. For both groups these differences were apparent throughout the production window. These patterns were widespread across the ROI, with significant effects occurring in the same direction at all electrodes in the central region for the Hearing Non-Signers, and for 18 electrodes in the central region for the Deaf Signers.

4. Discussion

In the current study, we questioned whether Deaf Signers and Hearing Non-Signers would show similar or different sensorimotor EEG activity during an imitative signing task. This question was motivated by interests in how action experience influences the neurodynamics of action processing, and also by open questions about the sensorimotor processing of signed languages. We analysed sensorimotor EEG activity in alpha and beta frequency bands while participants watched and imitated individual ASL signs. We analysed data both from the period of time when participants were watching with the intent to imitate, and during the period of time when they were carrying out their imitation.

4.1. Watching with the intent to imitate

We predicted that during sign observation, Deaf Signers would show less sensorimotor system activity and less differentiation of sign types in the sensorimotor system, because of the likelihood that for signers the task would involve language systems of the brain more robustly than sensorimotor systems. This hypothesis was based both on related work from our lab in which the same stimuli as we used here were shown in a passive observation task, with no imitation required (Kubicek & Quandt, 2019), as well as other functional neuroimaging evidence suggesting more linguistic



Figure 6. Comparison of alpha and beta activity during imitation, from 1000 to 3000 ms (time 0 =onset of sign) at channel CPz for both groups. Cool colours refer to event-related desynchronisation relative to baseline.

processing and less sensorimotor involvement when signers process sign stimuli (Corina & Knapp, 2006; Emmorey et al., 2010; Okada et al., 2016; Rogalsky et al., 2013). However, in contrast to our prediction, we found no significant differences in overall alpha/beta ERD between the two groups while participants were observing the signs. This is likely due to the imitative context of the current study. Given that participants were all watching signs with an intent to imitate them, the typical neural response seen during action observation was likely overlaid with the neural substrates of motor preparation. This preparatory anticipation may have engaged Deaf Signers' sensorimotor systems more readily. Recent work comparing action experts and novices has shown greater alpha ERD when the experts anticipate upcoming actions, an effect seen over frontal, occipital, and parietal brain regions (Simonet et al., 2019). It is possible that the context of motor preparation in our task increased the signers' alpha/beta ERD due to their greater expertise with the signs, thus washing out any significant differences between the groups that would be seen in a non-imitative paradigm.

For the Hearing Non-Signers, the task of imitating signs is a complex motor imitation task – they are unfamiliar with the movements, lack conceptual understanding of their meanings, and thus they probably needed to focus on the basic physical parameters of the observed sign. This lies in contrast to the relatively simple wordimitation task which the Deaf Signers were engaged in, given their existing knowledge of the signs and experience producing them. We expected that both groups would show different sensorimotor EEG responses to one-handed and two-handed signs, but that the effect would be stronger in the Hearing Non-Signers, due to greater attention toward basic physical parameters of the signs. However, our data did not support this prediction. The Hearing Non-Signers showed no significant differences between conditions (1H and 2H) during the observation window in any frequency band. For these individuals, sensorimotor differentiation between conditions did not start until after our observation window was over. In contrast, deaf signers showed earlier and more consistent differentiation between one- and twohanded signs. Two-handed signs elicited greater alpha and beta ERD in Deaf Signers, as seen by the cluster of right-central electrodes which differentiated between stimulus types during the 250-500 ms time bin (see Figure 2). Taking a closer look at the temporal dynamics of neural oscillatory activity in the central region, we see that Deaf Signers' sensorimotor response differentiates extremely early between 1H and 2H signs - before the actual onset of the sign. Indeed, as seen at electrode CPz (in Figure 4), there is significantly greater ERD for two-handed signs starting ~300 ms before sign onset, while the model's hands are moving into place to begin producing the sign. Our data support the notion that fluent deaf ASL users engage mirroring-like processes earlier, and more continuously, than do hearing non-signers when seeing ASL signs in an imitative context.

The Deaf Signers showed discrimination between observed one- and two-handed signs very early. Our findings complement prior work demonstrating that deaf signers discriminate between plausible and nonplausible signs quickly, within around 100 ms of seeing a still image representing a sign (Almeida et al., 2016). The timing of the effects we see in our study aligns with prior work as well. In one action production task, participants' beta ERD was seen within 110–120 ms of seeing a cue about the upcoming action (Tzagarakis et al., 2010). Our results suggest that signed language experience can recruit action mirroring processes in the brain to more quickly discriminate between the specific sensorimotor characteristics of observed signs. The patterns in the EEG of Deaf Signers suggest that signers do not necessarily process deep linguistic features of observed signs.

In many ways, our results echo prior findings from work looking at how action expertise changes the mirroring-related processing of others' actions. Recent work comparing action experts and novices sheds light upon the current findings. For instance, high alpha ERD is associated with the activation of specific sensorimotor characteristics of observed actions (Denis et al., 2017), likely because experts have greater access to calling upon the specific sensorimotor characteristics of an observed action than do non-experts. While our analyses did not reveal significant group differences in high alpha ERD during observation, Signers did show significantly more sensitivity to the specific sensorimotor characteristics of actions in the high alpha band, compared to Non-Signers. Specifically, our signing group showed early high-alpha and low-beta ERD in response to two-handed signs, compared to one-handed signs. This sensitivity to the motor characteristics of the observed action in these frequency bands suggests that signers are calling upon their prior sensorimotor experiences with the signs they are seeing, and invoking mirroring-like simulation as they see the action unfold.

As we speculated about earlier in this paper, the relationship between mirroring and experience with signed language may well be non-linear. In other domains of human action (e.g. dance, grasping), the action experts' sensorimotor cortex is more active while they see others perform actions with which they have experience, like we see in the current results. However, in the current study, there is a vast discrepancy between the amount of ASL experience that the Deaf Signers and Hearing Non-Signers have, and if we were able to compare sensorimotor reactivity across the full spectrum of ASL experience (e.g. including hearing fluent signers, and intermediate signers), it is very possible that a complex, non-linear relationship between sign experience and mirroring would emerge (Gardner et al., 2015, 2017a, 2017b).

Some of the key findings in this paper involve greater neural activity in response to two-handed signs over the right sensorimotor cortex (i.e. right central/centro-

parietal electrodes). Given that all our signers were right-handed, and the model was right-handed, this pattern suggests that participants were indeed simulating the production of action as they observed, or perhaps invoking preparatory motor plans in anticipation of imitation. One-handed signs in ASL are always produced with the dominant hand, which is associated with primarily contralateral sensorimotor cortex activity. Two handed signs, in contrast, invoke bilateral sensorimotor cortex (Emmorey et al., 2016). Thus, the predicted difference between two-handed and one-handed signs, if an observer is calling upon their own sensorimotor cortices to process observed actions, would be over the right-lateralised sensorimotor cortex. This is what we found in high alpha and low beta EEG rhythms during the observation window, particularly in early time bins (e.g. 250-500 ms) for Deaf Signers only.

It is likely that in the current study, those effects were heightened due to the imitative context in which the signs were observed. The task of preparing to imitate likely primed observers (from both groups) to prepare their own motor plans for reproducing the signs. Watching signed language has been associated with the generation of internal predicting coding models, as indicated by increased activity in the superior parietal cortex during sign viewing compared to speech listening in hearing bimodal bilinguals (Emmorey et al., 2014). Our current results suggest that indeed, fluent signers are encoding the articulatory specifications of observed signs from a very early time during sign viewing, a phenomenon which appears to be enhanced in an imitative context, where internal predictive models supporting comprehension may be working in parallel to motor planning in advance of producing one's own imitation.

4.2. Producing ASL signs

In the current paradigm, participants experienced a predictable imitative exchange. In each trial, they saw a sign, then produced the sign themselves. This consistency means that in this context there was no strict boundary between sign observation and when participants were preparing their own imitations. However, we opted to separately analyse the time while participants were initiating and carrying out their own productions of the signs. Our goal was to see whether mirroring systems would engage more greatly during this period for the expert signers, who have a great deal of sensorimotor experience to draw upon, but who may be processing the signs largely linguistically, or for the hearing novices, for whom the signs represent complex gestures they likely have never produced before.

There were stark differences in EEG activity during production between the two groups. Overall, the Deaf Signers showed a sustained ERD response across alpha and beta frequencies, whereas the Hearing Non-Signers showed increased power across these frequency bands (see Figure 4). This difference between the two groups during action production was in contrast to our expectations. We had expected that while imitating signs, Hearing Non-Signers would recruit sensorimotor regions more than Deaf Signers, as in our prior work wherein Hearing Non-Signers showed greater alpha/ beta ERD when passively observing signs, in comparison to Deaf Signers (Kubicek & Quandt, 2019). However, what we found suggests that instead, during the actual production of ASL signs, Deaf Signers recruit sensorimotor cortex in a typical way, exhibiting ERD over central sites, predictably differentiating between oneand two-handed signs. In contrast, Hearing Non-Signers show less ERD over central sites, and in fact show increases in alpha and beta EEG power as they carry out actions. Since this EEG was recorded during the production of manual actions, it is also possible that the oscillatory activity here is affected by movement artefacts, in a manner which differs between Deaf Signers and Hearing Non-Signers. For instance, Hearing Non-Signers may have been producing larger, less controlled movements, or movements with more self-correction. Future work would be needed to fully disentangle the brain-based and motion-based sources of this activity.

The observed pattern of results suggests that in this imitative paradigm, Deaf Signers are involving their sensorimotor cortices as they produce signs they are undoubtedly very familiar with. Thus, although the Deaf Signers know the semantic and other linguistic features of the signs, and have a lifetime of experience with both perceiving and producing the signs, their sensorimotor cortices are still underlying their sign productions. This should come as no surprise, given that signed communication requires coordinated movements of the fingers, hands, arms, and body. As well, our results align with prior PET findings of signers producing ASL signs (Emmorey et al., 2016). Both comprehending and producing ASL signs preferentially engages the premotor cortex, parietal cortices, and motion-sensitive areas of the middle temporal gyrus moreso than when speaking or comprehending speech (Emmorey et al., 2014). This pattern is likely due to the gross sensorimotor demands of coordinating and articulating language using the hands and body, and the demands of perceiving another person's complex hand and body articulations. Looking to the broader action-expertise literature, our current results may speak to the notion that in some circumstances, action experts exhibit greater involvement sensorimotor cortices during action than action novices, in contrast to the idea of neural efficiency (Babiloni et al., 2009, 2010).

The specific oscillatory activity within the four frequency bands we studied can yield further information about what characteristics of action were contributing to these effects. During sign production, low alpha power at central region electrodes did not differ between groups (although frontal regions differed), perhaps because the low alpha rhythm is thought to represent broad initiation of movement, without much differentiation between movement types (Denis et al., 2017; Pfurtscheller & Neuper, 2000). Greater ERD within the beta frequency band is thought to reflect a higher degree of certainty about how to produce an action (Palmer et al., 2016; Tzagarakis et al., 2010). In comparing beta ERD between the two groups (regardless of 1H/2H conditions) during the production window, Hearing Non-Signers exhibited a surge of higher power in the beta frequency band, which may be because of their uncertainty about how to proceed. In contrast, the Deaf Signers showed a clear beta ERD response, perhaps due to their certainty and existing knowledge about how to produce the sign they had just seen.

When comparing EEG activity between 1H and 2H conditions, Deaf Signers showed a predictable result: greater sensorimotor cortex activity (as shown by more alpha/beta ERD) while producing a 2H sign. As expected, this effect was evident over right centro-parietal electrodes, suggesting that the right sensorimotor cortex is particularly involved when carrying out a movement that includes the left hand and arm. However, the Hearing Non-Signers displayed an unexpected pattern of results. While EEG activity was significantly lower in the 2H condition than in the 1H condition, there were overall increases in EEG power for both conditions, and the difference appears to be driven by a marked increase in EEG power during the production of 1H signs (Figures 5 and 6).

4.2.1. Hearing non-signers imitating signs

In our task, the hearing non-signers seemed to experience a great deal of uncertainty, given the challenge of reproducing signs after only one viewing. The difficulty of the task for this group likely had a strong influence over these unexpected results. For hearing non-signers, learning ASL signs draws upon working memory capacity, particularly phonological short-term memory (Martinez & Singleton, 2018). Beta eventrelated synchronisation at frontal electrode sites is greater during simple working memory tasks compared to a more difficult task (Pesonen et al., 2007). Recent work also suggests that beta activity (14–20 Hz) in the parietal cortex serves as an episodic buffer, holding recent sensory input and linking it to executive commands to produce relevant actions (Gelastopoulos et al., 2019). It is possible that for Hearing Non-Signers, there was a difference in the degree of working memory and episodic buffering involved for the onehanded and two-handed signs, which could help explain the effects seen in that group.

The hearing non-signers in our experiment may have been stressed by the task at hand. While we did not collect formal measures of stress, our experimenters noted many informal comments made by participants, as well as non-verbal expressions, showing some degree of anxiety about the task. Participants who felt stressed may have developed various strategies to hold motor plans in place before imitation occurred, necessitating mental rotation-related skills due to the need to produce an action which had only been seen from the third-person perspective (Shield & Meier, 2018). Hearing participants' development, testing, and use of these various strategies (e.g. covert rehearsal, attempts to make semantic links, attempting to memorize motor sequences) may be a significant source of mental effort in a task such as ours (Martinez & Singleton, 2018), which likely influences the neural oscillatory patterns during sign production (Gelastopoulos et al., 2019). This aligns with other prior research showing that hearing non-signers show increased effortful attention during sign perception (Williams et al., 2016). The difficulty of the task for the hearing group stands in contrast to its ease for the Deaf Signers, who were essentially doing a word-shadowing task using words they were familiar with.

4.3. Future directions

While the results presented here contribute to our growing understanding of how deaf signers and hearing non-signers process visual stimuli differently, there are many questions left unanswered. One limitation of this study is the lack of different expertise levels with ASL, which would allow us to observe how the neural responses to perceiving and producing ASL change with expertise. Our group of Deaf Signers was quite heterogeneous – the group included native signers who grew up using ASL, as well as individuals who were fluent in ASL after learning it later in life. This heterogeneity provides strength to our findings, in that the effects were present even in such a diverse group, but it limits the ability to specify whether the

observed differences are due more to the physical experience of being deaf, or to long-term fluency with ASL. Future inclusion of other groups (e.g. hearing native ASL users, or deaf people who don't know any signed language) will significantly clarify this issue. More narrow recruitment criteria would likely yield more detailed information about how ASL perception in native signers may differ from those who became fluent later in life (Twomey et al., 2020). A more finegrained analysis of different sign types (e.g. symmetric vs. asymmetric signs) could also yield useful information about how different groups process sign stimuli, but that analysis was outside the scope of this investigation. Finally, the results we present here cannot differentiate precisely between the sensory plasticity arising from deafness and the effect of fluency in ASL. It is our hope that future work can further disentangle these complex, and likely overlapping, effects.

5. Conclusion

Fluent deaf signers have long-term experience with producing and perceiving the complex movements that constitute signed languages. To date, the research about whether, and how, signers may invoke the mirroring system during sign perception has yielded mixed results. We conducted this EEG study to assess the timing and presence of mirroring-like processes during the perception of American Sign Language signs, and the profile of sensorimotor involvement during the imitation of the observed signs. We present evidence that deaf ASL signers show earlier and more robust involvement of their own sensorimotor cortices to discriminate the sensorimotor characteristics of observed signs, in contrast to hearing non-signers. When producing their own versions of the observed signs, stark differences were apparent in the oscillatory responses across all measured EEG frequency bands. Together, this work demonstrates that in an imitative context, ASL users rapidly process others' signs by drawing upon their own sensorimotor representations of those signs. It appears that fluent deaf signers are particularly sensitive to the specific complex features of observed signs, which is yet another way in which deaf signers show enhanced motion perception.

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