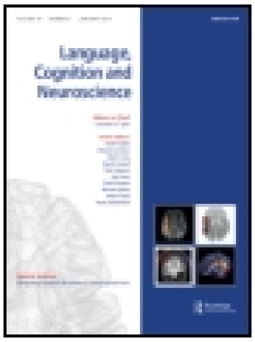

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Phonological and semantic priming in American Sign Language: N300 and N400 effects

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ABSTRACT
This study investigated the electrophysiological signatures of phonological and semantic priming in American Sign Language (ASL). Deaf signers made semantic relatedness judgments to pairs of ASL signs separated by a 1300 ms prime-target SOA. Phonologically related sign pairs shared two of three phonological parameters (handshape, location, and movement). Target signs preceded by phonologically related and semantically related prime signs elicited smaller negativities within the N300 and N400 windows than those preceded by unrelated primes. N300 effects, typically reported in studies of picture processing, are interpreted to reflect the mapping from the visual features of the signs to more abstract linguistic representations. N400 effects, consistent with rhyme priming effects in the spoken language literature, are taken to index lexico-semantic processes that appear to be largely modality independent. Together, these results highlight both the unique visual-manual nature of sign languages and the linguistic processing characteristics they share with spoken languages.

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American Sign Language; phonological priming; semantic priming; ERPs; N300; N400

An increasing number of studies have begun using sign languages to determine which of the psycholinguistic phenomena established in spoken language research are specific to the auditory-vocal modality versus representative of general language processing (see, e.g. Carreiras, 2010; Emmorey, 2002, for reviews). These studies have confirmed the intuition that some aspects of language, including semantics, are similar across spoken and signed languages (e.g. Capek et al., 2009; Kutas, Neville, & Holcomb, 1987). Here, the primary focus was on the extent to which phonological priming effects that are well documented in the spoken language literature (e.g. Coch, Grossi, Coffey-Corina, Holcomb, & Neville, 2002; Grossi, Coch, Coffey-Corina, Holcomb, & Neville, 2001; MacSweeney, Goswami, & Neville, 2013; Praamstra & Stegeman, 1993; Rugg, 1984a, 1984b; Rugg & Barrett, 1987) extend to languages that involve different articulators and a distinct phonological system (for reviews of sign language phonology, see Brentari, 2011; Sandler & Lillo-Martin, 2006). Specifically, we used event-related potentials (ERPs) to better characterise how semantic and phonological overlap between pairs of signs in American Sign Language (ASL) influences sign recognition.

Meaning is one subdomain of language that appears to be processed similarly across linguistic modalities. In ERP studies, semantic processing of spoken and written words is associated with the N400 component. Sentence-final words that fit with the preceding context elicit smaller amplitude N400s than those that are unexpected or anomalous (e.g. Kutas & Hillyard, 1980) and single word targets preceded by semantically related primes elicit smaller amplitude N400s than those preceded by semantically unrelated primes (see, e.g. Kutas & Federmeier, 2011, for a review). These priming effects are typically strongest across right hemisphere centroposterior sites in visual word studies in both hearing and deaf readers (e.g. Meade, Midgley, Sevcikova Sehyr, Holcomb, & Emmorey, 2017), and have a more bilateral frontal distribution in studies on auditory word processing (see Kutas & Federmeier, 2011; Kutas & Van Petten, 1994, for reviews). The smaller amplitude N400s in semantically related conditions are typically accompanied by faster reaction times (RTs; e.g. Bentin, McCarthy, & Wood, 1985; Holcomb, 1988) and have been associated with both ease of semantic access (e.g. Kutas & Federmeier, 2011) and integration (e.g. Brown & Hagoort, 1993; Hagoort, Baggio, & Willems, 2009).

Similar N400 semantic priming effects have been observed during sentence processing in sign language, with slight variations in distribution (Capek et al., 2009; Grosvald, Gutiérrez, Hafer, & Corina, 2012; Gutiérrez,

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Williams, Grosvald, & Corina, 2012; Hänel-Faulhaber et al., 2014; Hosemann, Herrmann, Steinbach, Bornkessel-Schlesewsky, & Schlesewsky, 2013; Kutas et al., 1987; Neville et al., 1997). For example, Capek et al. (2009) found that expected ASL target signs elicited smaller negativities than semantically anomalous signs between 300 and 875 ms after sign onset, especially over bilateral centro-posterior sites. Neville et al. (1997) also found widespread differences in N400 amplitude (300–600 ms) between sentence-final signs that fit with the preceding context and those that were semantically anomalous. The semantic effect began on the negativity preceding the N400 in deaf signers, which the authors referred to as an N250. However, the component they measured bears similarity with the N300 component that has since been observed in picture and gesture studies and has been associated with processing of early visual semantic features (e.g. Schendan & Kutas, 2003; Wu & Coulson, 2007). Focusing on the similarities in time course and distribution of semantic priming across auditory and visual modalities, some authors concluded that the N400 reflects access to a modality-independent semantic store (Capek et al., 2009; see also Holcomb & Anderson, 1993). Others have assigned greater importance to the minor differences in distribution across modalities, suggesting instead that the N400 effect reflects "modality sensitive but not modality specific" semantic processing (Kutas & Federmeier, 2011, p. 628). In other words, the N400 might reflect a similar process in all modalities (e.g. the transition to amodal semantic processing), but the specific topographical distributions of N400 semantic priming effects in various modalities reflect meaningful differences in how this process is implemented.

Outside of sentential contexts, there is behavioural evidence of semantic priming between pairs of ASL signs (e.g. Bosworth & Emmorey, 2010; Corina & Emmorey, 1993; Mayberry & Witcher, 2005), but no ERP evidence to our knowledge. Electrophysiological investigations of single target sign processing more often employ a cross-modal prime context (e.g. Leonard et al., 2012; Zachau et al., 2014). For example, Leonard and colleagues used magnetoencephalography to compare processing of ASL signs preceded by pictures representing the same concept or an unrelated concept. They found decreased activity within the N400 time window (300–350 ms) for sign targets in related pairs within the same left hemisphere fronto-temporal network that was also identified in a semantic priming paradigm with hearing participants (pictures followed by spoken words). Using ERPs, Zachau et al. investigated how Finnish auditory primes affected processing of antonymous (i.e. semantically related) and semantically unrelated word or sign targets in hearing signers. When the targets were also auditory words, they found smaller amplitude N400s for semantically related targets compared to semantically unrelated targets, as expected. However, when the target was a sign from Finnish Sign Language, the effect went in the opposite direction. Thus, N400 effects of semantic priming in sentences are similar across modalities, but it is unclear whether these effects also hold at the lexical level for pairs of signs.

In contrast to semantics, the phonological system of sign language is clearly distinct from that of spoken language. Phonological units (parameters) in sign language are visual-manual in nature, encompassing handshape, movement, and location (place of articulation). For example, the signs UGLY and SUMMER are minimal pairs in ASL because they share handshape and movement, but differ in location (see Figure 1). Moreover, whereas phonemes in spoken language are generally produced sequentially, phonological units in sign language are often produced simultaneously. These differences lead to questions about the extent to

Figure 1. Example stimuli. The top panels show an example of a phonologically related pair. In ASL, UGLY and SUMMER share both handshape and movement, but differ in location. The bottom panels show an example of a semantically related pair.

which analogies can be drawn between phonological processing in signed versus spoken languages.

For spoken and written language, there is both behavioural and ERP evidence to suggest that target words are easier to process following a rhyming (i.e. phonologically related) prime word than following a phonologically unrelated prime word. Behaviourally, targets in rhyme pairs elicit faster RTs than targets in phonologically unrelated pairs, particularly when the task involves overt phonological judgments (e.g. Coch et al., 2002; Dumay et al., 2001; Grossi et al., 2001; MacSweeney et al., 2013; McPherson, Ackerman, Holcomb, & Dykman, 1998; Perre, Midgley, & Ziegler, 2009; Polich, McCarthy, Wang, & Donchin, 1983; Praamstra & Stegeman, 1993; Rugg, 1984a, 1984b; Rugg & Barrett, 1987). Electrophysiologically, phonology affects N400 amplitude such that targets in rhyme pairs elicit smaller amplitude N400s that peak earlier when compared to targets in phonologically unrelated pairs (e.g. Coch et al., 2002; Grossi et al., 2001; MacSweeney et al., 2013; Perrin & García-Larrea, 2003; Weber-Fox, Spencer, Cuadrado, & Smith, 2003). There is also evidence that the rhyme effect onsets before the N400 window, as early as 100–150 ms post target onset in some auditory studies (e.g. Coch et al., 2002). Akin to the semantic priming effect, the N400 rhyme effect across centro-posterior sites tends to be more right lateralised when the words are presented visually (e.g. Grossi et al., 2001; Rugg, 1984a, 1984b; Rugg & Barrett, 1987), including in deaf readers (e.g. MacSweeney et al., 2013), and more bilateral when the words are presented auditorily (e.g. Coch et al., 2002; Dumay et al., 2001; Perre et al., 2009; Praamstra & Stegeman, 1993, Experiment 1). Indeed, in a direct comparison between the semantic priming effect and the rhyme effect in an auditory lexical decision task, Radeau, Besson, Fonteneau, and Castro (1998) failed to find significant distributional differences.

Behavioural effects of phonological priming in sign language are less consistent, with reports of facilitation, null effects, and interference across a handful of studies (e.g. Baus, Gutiérrez, & Carreiras, 2014; Baus, Gutiérrez-Sigut, Quer, & Carreiras, 2008; Carreiras, Gutiérrez-Sigut, Baquero, & Corina, 2008; Corina & Emmorey, 1993; Corina & Knapp, 2006; Dye & Shih, 2006; Mayberry & Witcher, 2005). The current evidence suggests that the nature of phonological priming may vary depending upon which parameters are shared by the prime-target pairs. For example, when only location is shared, interference effects appear to dominate (e.g. Carreiras et al., 2008; Corina & Emmorey, 1993), possibly due to lexical competition between location "neighbours" (see also Caselli & Goldberg, 2014). In contrast, when prime-target pairs share only handshape or only movement, either facilitation or null effects have been found (e.g. Carreiras et al., 2008; Corina & Emmorey, 1993; Dye & Shih, 2006). In general, studies that have presented prime-target pairs that overlap in two out of three phonological parameters report facilitation rather than interference, but it is not clear whether facilitation effects vary depending upon which two parameters are shared (e.g. Baus et al., 2014; Corina & Knapp, 2006; Dye & Shih, 2006).

ERP investigations of phonological priming in sign language have yet to clarify how phonological overlap influences sign recognition, as the few extant studies to pursue this question have also yielded varying results (Gutiérrez, Müller, Baus, & Carreiras, 2012; Gutiérrez, Williams, et al., 2012; Meade et al., 2017). In a delayed lexical decision task, Gutiérrez, Müller, et al. (2012) compared processing of targets in pairs of Spanish Sign Language (LSE) signs that shared location only, pairs that shared handshape only, and pairs that were phonologically unrelated. They reported a *larger* negativity within the N400 window (300–500 ms) for targets preceded by prime signs with the same location compared to targets in the phonologically unrelated condition, but no effect of handshape overlap. The authors associated the larger amplitude negativity with the behavioural interference effects observed for signs pairs that overlap in location and suggested that lexical competition made location-related targets more effortful to process.

In contrast, evidence from a recent implicit phonological priming paradigm suggests that two-parameter overlap between pairs of ASL signs *decreases* N400 amplitude (300–500 ms; Meade et al., 2017). We presented deaf bimodal bilinguals with pairs of English words and asked them to decide whether the meanings of the two words were semantically related or not. When translated into ASL, half of the semantically unrelated pairs overlapped in two of three phonological parameters (handshape, movement, or location) and half were phonologically unrelated. For example, the ASL translations of *ugly* and *summer* overlap in both handshape and movement (see Figure 1), whereas the ASL translations of *poison* and *summer* are phonologically unrelated. Phonological relatedness attenuated N400 amplitude, especially over right anterior sites and when participants were unaware of the phonological manipulation. Thus, these two ERP studies converge in suggesting that N400 amplitude is sensitive to sign phonology, but the effects went in opposite directions, possibly due to differences in the type of phonological overlap.

Another critical difference between these two studies is that Gutiérrez, Müller, et al. (2012) presented the signs directly to participants, whereas English words that had phonologically related ASL translations were presented in the implicit priming study reported by Meade et al. (2017). In order to determine whether explicit priming generates an effect similar to that obtained in implicit priming, in the current study we presented the stimuli from the implicit priming study by Meade et al. (2017) explicitly as ASL sign pairs and asked participants to perform the same semantic relatedness judgment task. Half of the semantically unrelated pairs shared two phonological parameters and half shared no parameters.[1] Based on behavioural facilitation effects (e.g. Baus et al., 2014; Corina & Knapp, 2006; Dye & Shih, 2006; Giezen & Emmorey, 2016) and rhyme effects in spoken and visual word processing (e.g. MacSweeney et al., 2013; Perrin & García-Larrea, 2003; Weber-Fox et al., 2003), we predicted that targets preceded by signs that shared two phonological parameters would elicit smaller amplitude N400s (i.e. priming) than those preceded by phonologically unrelated signs. Together with our previous results (Meade et al., 2017), this would suggest that two-parameter overlap between pairs of signs decreases N400 amplitude irrespective of whether the signs are presented explicitly or activated implicitly. We were particularly interested in the topographical distribution of this effect given that the implicit priming effect with the same stimuli was uniquely restricted to right anterior sites (which was not the case in previous studies of implicit phonological priming in spoken languages; e.g. Thierry & Wu, 2007). Finally, we expected that phonological relatedness would interfere with the semantic relatedness decision. This interference would be reflected in slower "no" responses for phonologically related trials compared to phonologically unrelated trials, as found in previous studies of implicit phonological priming in ASL that used a semantic relatedness decision task (Meade et al., 2017; Morford, Kroll, Piñar, & Wilkinson, 2014; Morford, Wilkinson, Villwock, Piñar, & Kroll, 2011; Villameriel, Dias, Costello, & Carreiras, 2016).

Because so little is known about the electrophysiological correlates of sign language processing, we also compared processing of semantically related and unrelated sign pairs. Here, we predicted a semantic priming effect (i.e. smaller negativity for targets in semantically related pairs than semantically unrelated pairs) with a more typical centro-posterior distribution within the N400 window and possibly within the N300 window (as in Neville et al., 1997). Behaviourally, semantic relatedness should facilitate semantic judgments, leading to faster responses for semantically related trials compared to semantically unrelated trials.

Method

Participants

Participants included 20 severely-to-profoundly deaf adults (mean age = 29.4 years; *SD* = 4.9). All participants were exposed to ASL before the age of seven (13 of them from birth), reported having normal or corrected-to-normal vision, and provided informed consent in accordance with the Institutional Review Board at San Diego State University.[2] Three of the participants were left-handed (as in Meade et al., 2017). Two of the left-handed signers had been exposed to ASL from birth and one had not. Data from one additional participant (a right-handed, native signer) were excluded from analyses because too many trials were rejected for blink artefacts (>20%).

Stimuli

Stimuli consisted of 90 triplets of ASL signs drawn from our previous study on implicit ASL phonological priming (Meade et al., 2017). The primary difference between studies was that English words were presented in that study, whereas ASL videos were presented in the present study, which made the ASL phonological manipulation explicit. Each triplet (e.g. POISON, UGLY, SUMMER) was used to form two ASL pairs with the same target (e.g. UGLY-SUMMER, POISON-SUMMER) for a total of 180 sign pairs. A native ASL signer (see Figure 1) was filmed producing each of the signs at a natural rate. Each video was clipped to begin two frames before sign onset and end at sign offset. Sign onsets and offsets were determined as in previous studies (e.g. Caselli, Sevcikova Sehyr, Cohen-Goldberg, & Emmorey, 2016; Crasborn et al., 2015; Johnson & Liddell, 2011). Specifically, for body-anchored signs, sign onset was defined as the first frame in which the fully formed handshape contacted the body and sign offset was defined as the last frame in which the hand contacted the body. For signs with no contact, sign onset was defined as the first frame in which the handshape was fully formed and arrived at the target location near the body or in "neutral space" in front of the signer. Sign offset for the no contact signs was defined as the last video frame before a hold was broken and the hands transitioned to rest position. A native signer and a fluent L2 signer each coded onsets and offsets for a randomly selected 20% of the stimuli with high interrater reliability (93% agreement for onsets and 80% agreement for offsets with a three-frame margin). Each of them then coded sign onset and offset for half of the remaining signs.

Half of the ASL sign pairs ($N = 90$) were semantically related and half of them were semantically unrelated (see Figure 2). In order to determine semantic relatedness, we used ratings from a previous norming study in which hearing participants judged the English glosses of each pair on a Likert scale from 1 (no semantic relationship) to 7 (very strong semantic relationship; Meade et al., 2017). Semantically related pairs had average semantic relatedness ratings at or above 5.3 (mean 6.16, *SD* .36), whereas semantically unrelated pairs had average ratings at or below 2.3 (mean 1.35, *SD* 0.34). As expected, semantic ratings for the semantically related pairs were significantly higher than for the semantically unrelated condition, $t(178) = 92.43$, $p < .001$. However, the video length of semantically related targets (mean 723 ms, *SD* 162 ms) and semantically unrelated targets (mean 670 ms, *SD* 160 ms) did not significantly differ, $t(88) = 1.57$, $p = .120$. Moreover, the average number of shared phonological parameters did not differ between the semantically related pairs (mean 0.90, *SD* .74) and the semantically unrelated pairs (mean 1.00, *SD* 1.00), $t(178) = .84$, $p = .400$.

The critical phonological manipulation happened on the semantically unrelated trials. Half ($N = 45$) of the semantically unrelated pairs were phonologically related in ASL (e.g. UGLY-SUMMER), operationalised as sharing two out of the three phonological parameters of handshape, movement, and location. The other half ($N = 45$) did not share any phonological parameters (e.g. POISON-SUMMER). Semantic ratings did not significantly differ between the phonologically related condition (mean 1.35, *SD* .28) and the phonologically unrelated condition (mean 1.35, *SD* .40), $t(88) = 0$, $p = 1.00$. The length of the prime videos in the phonologically related (mean 653 ms, *SD* 172 ms) and phonologically unrelated (mean 631 ms, *SD* 181 ms) conditions also did not differ significantly, $t(88) = .60$, $p = .552$. Finally, a subset of 20 semantically related pairs were also phonologically related in ASL (see Figure 2). Although 20 trials do not constitute an analysable condition, it was important to include these trials so that the phonological relationship between signs was not predictive of their semantic relationship (i.e. without these trials, all phonologically related trials would have been semantically unrelated).

Procedure

The experiment took place in a dimly lit room, with the participant seated in a comfortable chair about 140 cm from the stimulus monitor. Instructions were provided both in English and ASL, and a native deaf signer was present to answer any questions. Participants were informed that they would be seeing pairs of ASL signs and that some of the pairs would overlap in handshape, movement, or location. They were asked to focus on the meaning of the signs and to respond using a videogame response box, pressing one button if the meanings were related and a different button with the other hand if they were not, as quickly and accurately as possible. Response hand was counterbalanced across participants.

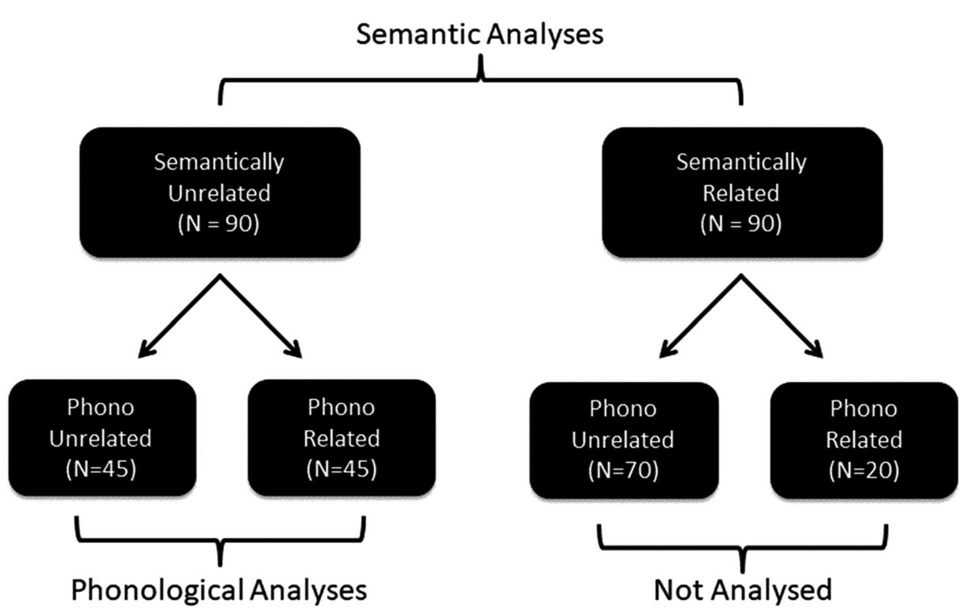

Figure 2. Experimental design. Prime-target pairs were either semantically related or unrelated. Half of the semantically unrelated pairs were phonologically related in ASL and half of them were phonologically unrelated in ASL. A subset of the semantically related pairs were also phonologically related in ASL, but there were too few of them to constitute an analysable condition.

Each trial consisted of a prime sign and a target sign, separated by a 1300 ms stimulus onset asynchrony (SOA; i.e. the prime video and a blank screen of variable duration). Videos were presented on a black screen and subtended a visual angle of 4.0 degrees in the vertical direction and 5.4 degrees in the horizontal direction. A black screen appeared immediately after the target video and remained until 750 ms after the response. In between trials, a purple fixation cross appeared for 1500 ms, a white fixation cross appeared for 500 ms, and a blank screen appeared for 500 ms. Participants were asked to blink during the purple cross in between trials and during longer blink breaks that occurred approximately every 12 trials.

Each participant saw all 180 pairs of signs. As in our previous study (Meade et al., 2017), the presentation order of two pseudorandomized lists was counterbalanced across participants to minimise the effect of target repetition. Each target appeared once in each list and all four prime conditions were equally distributed between the two lists. For example, some of the participants saw UGLY-SUMMER in the first half of the experiment and POISON-SUMMER in the second half, whereas others saw these pairs in the reversed order. The session began with 10 practice trials, five of which were semantically related and five of which were phonologically related in ASL. None of the targets were repeated within the practice and none of the practice items occurred during the real experiment.

EEG recording and analysis

EEG was recorded from 29 active electrodes (see Figure 3) in an elastic cap (Electro-Cap) with a left mastoid reference. Additional electrodes were placed below the left eye and on the outer canthus of the right eye to identify blink and horizontal eye movement artefacts, respectively. Scalp and mastoid electrode impedances were maintained below 2.5 kΩ and eye electrodes below 5 kΩ. EEG was amplified with SynAmpsRT amplifiers (Neuroscan-Compumedics) with a bandpass of DC to 100 Hz and was sampled continuously at 500 Hz.

Offline, ERPs were time-locked to the onset of the target signs with a 100 ms pre-stimulus-onset baseline. ERPs from individual sites were processed with a 15 Hz low-pass filter and averaged to create the same five ROIs as in our previous study (Meade et al., 2017) in order to make the results directly comparable across studies. The left anterior (LA) ROI included sites F3, F7, FC5, and T3; the right anterior (RA) ROI included sites F4, F8, FC6, T4; the middle (M) ROI included sites FC1, FC2, Cz, CP1, and CP2; the left posterior (LP) ROI included sites CP5, T5, P3, and O1; the right posterior (RP) ROI

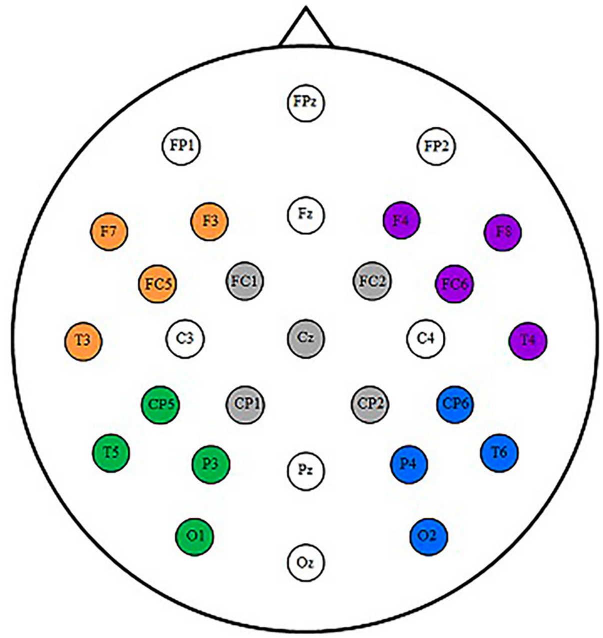

Figure 3. Electrode montage and ROIs. The left anterior (LA) ROI is indicated in orange, the right anterior (RA) ROI is indicated in purple, the left posterior (LP) ROI is indicated in green, the right posterior (RP) ROI is indicated in blue, and the middle (M) ROI is indicated in grey.

included sites CP6, T6, P4, and O2. Trials contaminated by eye movement or drift artefacts within 900 ms of target onset were excluded from all analyses (9.3 trials, or 5%, on average). Trials with reaction times shorter than 200 ms and longer than 2500 ms were also removed.

Mean N400 amplitude was calculated between 325 and 625 ms after target onset separately for each subject, each condition, and each ROI.[3] Given the variability in N400 epochs among the few ERP studies of sign processing, this window was based on visual inspection of the componentry of the grand mean waveforms and is similar to previous ASL studies (e.g. Neville et al., 1997). The fact that it differs from our previous study (300–500 ms) likely reflects differences in processing of signs versus printed words. Mean N300 amplitude was calculated between 225 and 325 ms after target onset (e.g. McPherson & Holcomb, 1999). A repeated-measures ANOVA with factors Phonology (Related, Unrelated), Hemisphere (Left, Right), and Anterior/Posterior (Anterior, Posterior) was used to assess the effect of phonological overlap on sign processing at the lateral ROIs within each time window. A similar analysis was also conducted for the middle ROI. Note that this analysis compares processing of the exact same target signs (e.g. SUMMER) preceded by phonologically related (e.g. UGLY) versus phonologically unrelated (e.g. POISON) primes. Parallel analyses were also used to compare semantically related and unrelated trials (i.e. semantic priming) with correct semantic judgments within the N300 and N400 time windows. The targets in this semantic analysis were not identical across the related and unrelated conditions. However, they were controlled on a number of factors, as detailed in the Stimuli section.

Results

Reaction times

Trials with incorrect responses (25 trials, or 14% on average) or RTs shorter than 200 ms or longer than 2500 ms (4 trials, or 2% on average) were excluded from behavioural analyses. As in our previous implicit study (Meade et al., 2017), we used a linear mixed effect model with items and participants as random intercepts to compare processing of phonologically related and unrelated trials. A significant main effect of Phonology indicated that phonologically related trials (mean 1288 ms; $SE = 57$ ms) elicited slower RTs than phonologically unrelated trials (mean 1230 ms; $SE = 61$ ms), $t = 2.63$, 95% CI = [15.69, 107.38]. In a similar linear mixed effects model focused on semantic relatedness, there was a main effect of Semantics such that semantically related trials (mean 1155 ms; $SE = 51$ ms) elicited faster RTs than semantically unrelated trials (mean 1259 ms; $SE = 58$ ms), $t = 2.34$, 95% CI = [14.08, 159.98].

ERPs: phonological priming effects

N300 (225–325 ms)

Lateral ROIs. Targets in phonologically related pairs elicited smaller amplitude N300s than targets in phonologically unrelated pairs (see Figure 4). Interactions with distributional factors suggested that this effect was especially strong over the left anterior ROI, Phonology × Anterior/Posterior, $F(1,19) = 5.02$, $p = .037$, $\eta_p^2 = .21$, Phonology × Hemisphere × Anterior/Posterior, $F(1,19) = 5.77$, $p = .027$, $\eta_p^2 = .23$. However, in follow-up analyses that included only the left anterior ROI, the phonological priming effect only approached significance, Phonology, $F(1,19) = 3.18$, $p = .090$, $\eta_p^2 = .14$.

Middle ROI. The effect also failed to reach significance at the middle ROI, Phonology, $F(1,19) = 2.51$, $p = .130$, $\eta_p^2 = .12$.

N400 (325–625 ms)

Lateral ROIs. A main effect of Phonology indicated that target signs elicited smaller amplitude N400s following phonologically related primes than phonologically unrelated primes, $F(1,19) = 13.56$, $p = .002$, $\eta_p^2 = .42$. Interactions with distributional factors indicated that the N400 phonological priming effect was strongest for the right hemisphere and anterior ROIs, Phonology × Hemisphere, $F(1,19) = 9.98$, $p = .005$, $\eta_p^2 = .34$, Phonology × Anterior/Posterior, $F(1,19) = 27.08$, $p < .001$, $\eta_p^2 = .59$. In follow-up analyses that included only the two right ROIs, there was a significant effect of phonology that was stronger at the right anterior ROI than at the right posterior ROI, Phonology, $F(1,19) = 17.92$, $p = .001$, $\eta_p^2 = .48$, Phonology × Anterior/Posterior, $F(1,19) = 9.98$, $p = .005$, $\eta_p^2 = .34$. In a second round of follow-ups including only the right anterior ROI, there was a significant phonological priming effect, Phonology, $F(1,19) = 27.82$, $p < .001$, $\eta_p^2 = .59$.

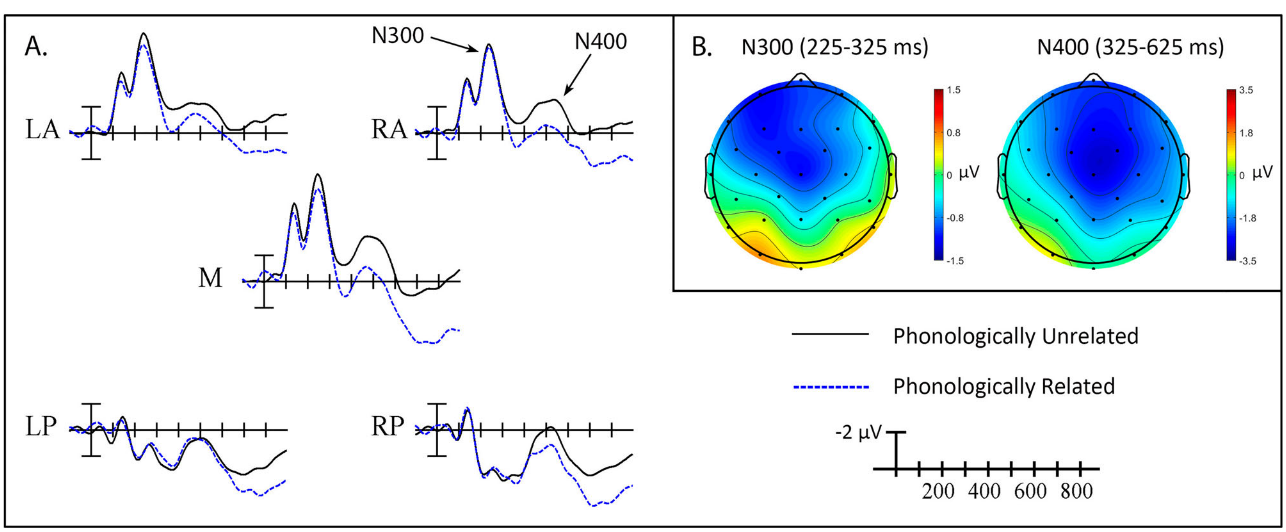

Figure 4. Phonological priming effects. (A) Grand average ERP waveforms elicited by targets in phonologically unrelated pairs (black solid line) and phonologically related pairs (blue dotted line). Each vertical tick marks 100 ms and negative is plotted up. The calibration bar marks 2 µV. (B) Scalp voltage maps showing the distribution of the phonological priming effects (unrelated-related) on mean amplitude within the N300 and N400 windows.

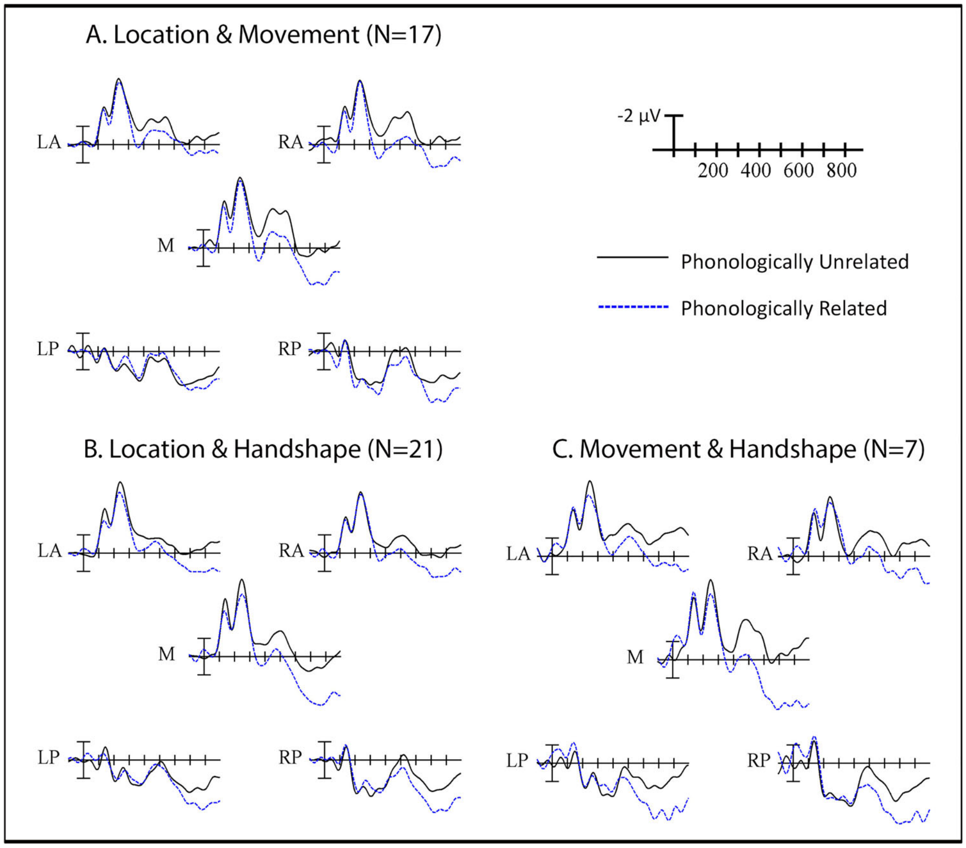

Figure 5. Exploratory plots of phonological priming with different two-parameter combinations. Grand average ERP waveforms for targets overlapping in (A) location and movement, (B) location and handshape, and (C) movement and handshape. Targets in related pairs (blue dotted lines) elicited smaller negativities than targets in unrelated pairs (black solid lines) similarly across the three combinations of two-parameter overlap. Each vertical tick marks 100 ms and negative is plotted up. The calibration bar marks 2 µV.

There were too few trials to statistically analyse individual combinations of parameters (i.e. handshape + location, location + movement, handshape + movement). However, given the mixed phonological priming results in the literature, we examined all three parameter combinations for possible qualitative differences. The general pattern of facilitation appeared to be the same for all combinations in this exploratory analysis (see Figure 5).

Middle ROI. The phonological priming effect was also significant within this window at the middle ROI, Phonology, $F(1,19) = 38.72$, $p < .001$, $\eta_p^2 = .67$.

ERPs: semantic priming effects

N300 (225–325 ms)

Lateral ROIs. A main effect of Semantics indicated that targets in semantically related pairs elicited smaller amplitude N300s than targets in semantically unrelated pairs, $F(1,19) = 6.84$, $p = .017$, $\eta_p^2 = .26$ (see Figure 6). An interaction with Anterior/Posterior indicated that the N300 semantic priming effect was especially strong at the two anterior ROIs, Semantics × Anterior/Posterior, $F(1,19) = 8.78$, $p = .008$, $\eta_p^2 = .32$. Follow-up analyses including only the two anterior ROIs confirmed that the semantic priming effect was significant at these sites, Semantics, $F(1,19) = 11.70$, $p = .003$, $\eta_p^2 = .38$.

Note that our semantic comparison was not completely orthogonal to the phonological comparison (see Footnote 1 and Figure 2), for which we also found an N300 effect with an anterior distribution. The mean number of shared parameters did not significantly differ between the semantically related and unrelated conditions, but the distribution of the number of shared parameters necessarily did. Semantically unrelated sign pairs either shared two or no parameters (because the phonological manipulation occurred on these trials), whereas the phonological relationship between semantically related sign pairs was less systematic. To ensure that the semantic N300 effect that we report was not due to the different distributions of

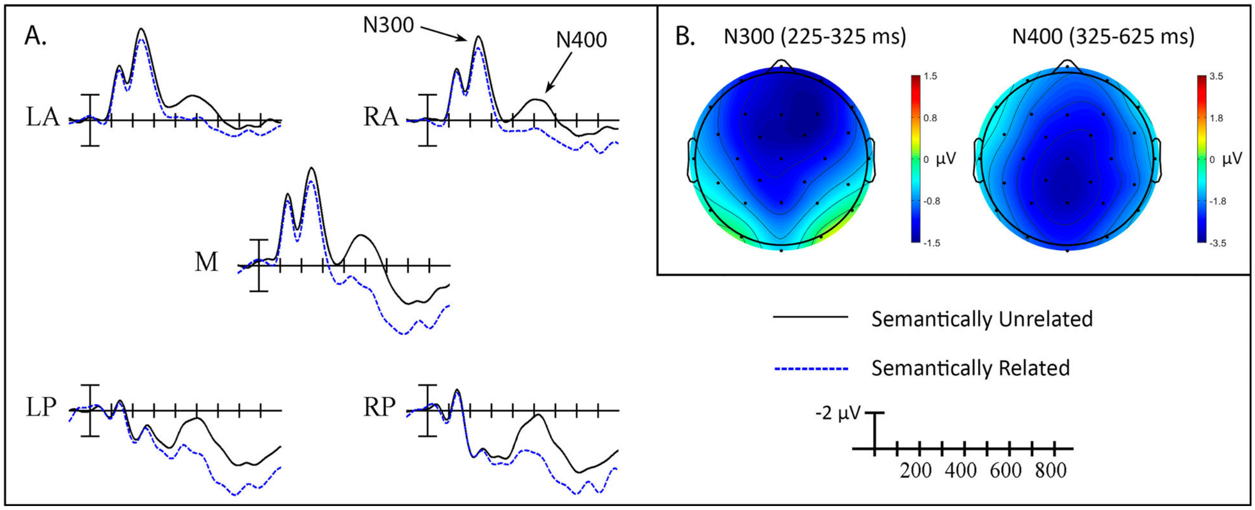

Figure 6. Semantic priming effects. (A) Grand average ERP waveforms elicited by targets in semantically unrelated pairs (black solid line) and semantically related pairs (blue dotted line). Each vertical tick marks 100 ms and negative is plotted up. The calibration bar marks 2 μV. (B) Scalp voltage maps showing the distribution of the semantically priming effects (unrelatedrelated) on mean amplitude within the N300 and N400 windows.

phonological overlap, we repeated the analysis on a randomly selected subset of 30 trials from each semantic condition that had no overlapping phonological parameters. The effect was still significant in this post-hoc analysis controlling for phonological overlap between the two conditions, suggesting that the N300 is sensitive to semantic priming in ASL, Semantics, $F(1,19) = 11.37$, $p = .003$, $\eta_p^2 = .38$, Semantics × Anterior/Posterior, $F(1,19) = 9.02$, $p = .007$, $\eta_p^2 = .32$. The effect also remained significant in analyses that only included the anterior ROIs, $F(1,19) = 6.51$, $p = .020$, $\eta_p^2 = .26$.

Middle ROI. The N300 semantic priming effect was also significant at the middle ROI in analyses including all trials, $F(1,19) = 22.40$, $p < .001$, $\eta_p^2 = .54$, and in analyses that included only the subset of phonologically unrelated trials, $F(1,19) = 20.70$, $p < .001$, $\eta_p^2 = .52$.

N400 (325–625 ms)

Lateral ROIs. A main effect of Semantics indicated that target signs in semantically related pairs continued to elicit smaller amplitude negativities than target signs in semantically unrelated pairs within the N400 window, $F(1,19) = 34.18$, $p < .001$, $\eta_p^2 = .64$. However, the distribution shifted from the preceding N300 window and became strongest at posterior ROIs, Semantics × Anterior/Posterior, $F(1,19) = 12.87$, $p = .002$, $\eta_p^2 = .40$. In analyses that only included the two posterior ROIs, the effect remained significant, Semantics, $F(1,19) = 43.54$, $p < .001$, $\eta_p^2 = .70$.

Middle ROI. The N400 semantic priming effect was also significant in analyses that included only the middle ROI, $F(1,19) = 38.12$, $p < .001$, $\eta_p^2 = .67$.

Discussion

In the present study, we used ERPs to clarify the effects of explicit two-parameter phonological priming and semantic priming between pairs of ASL signs. As predicted, targets in phonologically related pairs and semantically related pairs elicited smaller amplitude N400s (325–625 ms) than those in the respective unrelated pairs. This phonological priming effect suggests that explicit phonological overlap facilitates sign recognition, as has been reported for rhyming pairs of spoken and written words (e.g. Coch et al., 2002; Grossi et al., 2001; MacSweeney et al., 2013; Rugg, 1984a, 1984b). The semantic priming effect extends previous studies of sign semantic priming in a sentential context (e.g. Capek et al., 2009; Kutas et al., 1987) to the minimal context of sign pairs. Both effects were also significant within the preceding N300 window (225–325 ms). Whereas the phonological priming effect was consistently anterior across both windows, the semantic priming appeared to shift from being more anterior in the N300 window to being more centro-posterior in the N400 window. This distributional shift is consistent with the anterior-to-posterior shift reported between the N300 and N400 windows in studies on picture processing (e.g. McPherson & Holcomb, 1999), but this is the first report of this distributional shift for sign language processing to our knowledge. Together, these results emphasise both the similarities that sign language has with spoken language and its unique visual-manual nature.

As predicted, target signs in phonologically related pairs elicited smaller amplitude N400s and slower responses than those in phonologically unrelated pairs. This pattern replicates what we found in our previous implicit priming study (Meade et al., 2017) and confirms that two-parameter overlap reduces N400 amplitude irrespective of whether the signs are presented explicitly (as in the present study) or activated implicitly by the signer (as in the study reported by Meade et al., 2017). Although the effect was more widely distributed here than in the previous implicit study, the same general distributional features – strongest over the right anterior ROI and reversed over the left posterior ROI – held across both studies. This strengthens the claim that this distribution is linked to form processing in sign language more generally, rather than being tied to the specific mechanisms that underlie implicit priming. Moreover, the same qualitative N400 pattern held for all combinations of two-parameter overlap (refer to Figure 5), which suggests that the N400 may be a more reliable index of priming than the behavioural measures used in previous studies (e.g. Baus et al., 2014; Corina & Knapp, 2006). In the behavioural results of the present study, we observed a phonological interference effect on RTs, rather than a priming effect. This result is likely tied to the fact that participants needed to respond "no" in the semantic task and this decision process was disrupted when the sign pairs were related on another dimension, namely phonology (see, e.g. Meade et al., 2017; Morford et al., 2011; Morford et al., 2014; Villameriel et al., 2016).

Though internally consistent, the current findings and those in the implicit study reported by Meade et al. (2017) may appear to conflict with the study by Gutiérrez, Müller, et al. (2012), who found that targets in phonologically related LSE pairs elicited *larger* amplitude N400s. In fact, the results across all three ERP studies fit well with the general patterns in the behavioural literature in suggesting that location-only overlap (as in the Gutiérrez, Müller et al. study) increases processing difficulty, whereas two-parameter overlap facilitates processing. Recent fMRI results by Cardin et al. (2016) suggest that phonological processing is comprised of both parameter-specific perceptual regions and parameter-non-specific language regions, and this distinction could further constrain the interpretation of our ERP results. Adopting a multimodal imaging approach to investigating the role of each parameter (and the combination thereof) could have important implications for our understanding of sign recognition and the organisation of the sign lexicon.

Theoretically, the phonological priming ERP effect could originate at many different levels of processing. Indeed, to the extent that it is analogous to the rhyming effects observed in spoken languages, the priming effect likely has multiple sources ranging from perceptual facilitation to pre-activation at the sublexical and lexical levels to strategic attention (see, e.g. Coch, Grossi, Skendzel, & Neville, 2005; Dumay et al., 2001; Yoncheva, Maurer, Zevin, & McCandliss, 2013). The fact that we also observed an N400 phonological priming effect in the previous implicit priming study (i.e. when participants were not consciously aware of the phonological relationship in ASL; Meade et al., 2017) suggests that the priming effect cannot be entirely strategic. Nevertheless, in a qualitative comparison across studies, the explicit phonological priming effect in the present study appeared to begin almost 100 ms earlier than when sign representations were activated implicitly. This difference in timing indicates that additional mechanisms might underlie the explicit effect here. One possibility is that participants were more attentive to the phonological manipulation because it was overt. This increase in attention may have made the priming effect larger or shifted it earlier in time. Another possibility is that the earlier onset observed here reflects priming at processing levels that are not implicated in implicit priming, most likely perceptual or sublexical processing. To isolate the contribution of perceptual priming to these effects, a similar study could be conducted with participants who do not know ASL and are therefore immune to the linguistic aspects of priming (at both the sublexical and lexical levels). To differentiate sublexical from lexical effects, signers could be presented with pseudosign targets, which are not lexically represented and should therefore not be influenced by pre-activation of lexical representations. In fact, Gutiérrez, Müller, et al. (2012) found that the N400 modulation associated with location-only overlap did not occur for pseudosign targets, indicating a lexical level effect. Examining the time course of two-parameter phonological priming with sign-naïve participants and with pseudosigns would lend insight into the processes that are driving the earlier onset of the priming effect that we found here.

In addition, we note that this early phonological priming effect occurred during a marked negative peak that bears similarity with the N300 (or N350) reported in studies of both picture processing (e.g. Barrett & Rugg, 1990; Hamm, Johnson, & Kirk, 2002; Holcomb & McPherson, 1994; Maguire, Magnon, Ogiela, Egbert, & Sides, 2013; McPherson & Holcomb, 1999; Schendan & Kutas, 2002, 2003) and gesture processing (e.g. Özyürek, Willems, Kita, & Hagoort, 2007; Wu & Coulson, 2007, 2011). First, the component peaks within the same time window as previous studies, and second, the component and priming effects are largest across anterior sites, consistent with the picture and gesture studies. These studies can therefore serve as a foundation for our interpretation of the functional role of the N300 in sign language processing. Specifically, phonological overlap in sign language can be characterised as visual similarity (see Figure 1), and this similarity at the perceptual level might affect N300 amplitude. Few studies have investigated the effect of visual similarity on N300 (e.g. Barrett & Rugg, 1990; Kovalenko, Chaumon, & Busch, 2012). In one such study, Barrett and Rugg (1990) found that N300 amplitude did not significantly differ as a function of subjective ratings of visual similarity between picture pairs. However, the study was not designed to detect effects of visual similarity, and it is possible that there was not enough variation in the similarity ratings to observe an N300 effect (the mean rating of visual similarity for pictures in the highly similar condition was only 2.6 out of 5). Indeed, with a wider range of stimuli and a more objective measure of visual similarity, Kovalenko et al. (2012) found that target pictures in visually similar pairs elicited smaller negativities than those in visually dissimilar pairs within a time window that roughly corresponds to the N300. Further research is needed to ascertain whether visual similarity is associated with a reduced N300 response for either picture or sign stimuli.

In studies of picture and gesture recognition, the N300 is more typically implicated in semantic processes. For example, Barrett and Rugg (1990) found that picture targets preceded by semantically related pictures elicited smaller amplitude N300s than those preceded by semantically unrelated pictures. The critical difference between N300 and N400 semantic priming effects seems to be that N300 effects are specific to the visual modality, whereas N400 effects are modality-independent. More specifically, Wu and Coulson (2007, p. 242) hypothesised that the N300 reflects "image-specific semantic processes," which include matching the visual features of a stimulus (i.e. a picture or gesture) to those of a stored visual representation (e.g. Schendan & Kutas, 2003) or a broader conceptual representation (e.g. McPherson & Holcomb, 1999). This characterisation of the N300 was based on the finding that picture targets preceded by related iconic co-speech gestures were primed within the N300 window, but picture targets preceded by speech-only related primes were not. Wu and Coulson suggested that the visual aspects of the gesture prime cued more specific conceptual representations and triggered pre-activation of the visual-spatial features of the subsequent picture target, thereby facilitating picture recognition and reducing N300 amplitude.

Several characteristics of sign languages allow for a unique test of this hypothesis. For one, the arbitrary mapping between non-iconic signs[4] and the concepts they represent allows for a dissociation between the visual features of the stimulus and those of the concept. In the stimuli that we used here, there was little overlap in the visual characteristics of the semantically related signs themselves; they shared less than one phonological parameter on average and the N300 semantic priming effect held in post-hoc analyses including a subset of signs that shared no phonological parameters. As a result, if N300 amplitude was indexing similarity in visual semantic features in the present study, then it must have been at a higher conceptual level. For example, the ASL signs for *skunk* and *raccoon* are visually dissimilar, but the concepts they represent share many visual semantic features (e.g. black and white, similar size, four legs, etc.). Such shared visual semantic features could have facilitated processing among semantically related signs and led to a decrease in N300 amplitude. In picture studies, in contrast, it is very difficult to isolate visual similarity at the conceptual level in this way. Another unique property of sign languages is that signs can represent abstract concepts that are difficult to depict pictorially. Indeed, a handful of our targets had more abstract meanings (e.g. *HOT-COLD*, *ANGEL-HEAVEN*). If the N300 is only specific to visual features, we might not expect an N300 semantic priming effect for such signs. Although there were not enough abstract signs in the present study to address this question, the distinction between abstract and concrete signs could be exploited to better delineate the levels of representations to which the N300 is sensitive in future studies. Generally speaking then, the use of non-iconic signs allows for separate investigation of the role of the visual features of the stimulus versus those of the concept. The present results suggest that visual similarity at a conceptual level is sufficient to elicit N300 semantic priming effects.

It is also possible that the N300 priming effect in the present study does not depend on visual feature matching per se. An alternative explanation is that the semantic priming effect is due to strategic generation of "expectancy sets" (e.g. Neely, 1991); the N300 has also been proposed to index the search for "a stored structural description that matches the perceived image" (Schendan & Kutas, 2002, p. 943), or in this case the perceived sign. Reducing the number of conceptual representations to which the incoming stimulus could correspond is thought to decrease N300 amplitude. Thus, if participants were strategically biasing their search space to favour targets that were semantically related to the prime, this would have facilitated recognition of semantically related signs and led to a reduction in N300 amplitude. In contrast, such expectancy sets would have had little influence on processing of semantically unrelated signs because they would be unlikely to fall within that restricted search space. Adopting a strategy like this seems especially plausible given that (1) a considerable proportion of trials were semantically related, (2) the task emphasised meaning relationships, and (3) a long SOA separated the prime and target. Many of the picture semantic priming studies that have reported an N300 effect have also used a relatedness judgment task (e.g. Barrett & Rugg, 1990; Kovalenko et al., 2012; McPherson & Holcomb, 1999); it would be interesting to investigate N300 effects of semantic priming in ASL using a task that does not bias semantic processing in these ways. If this explanation proves to be true, however, the functional dissociation between the N300 and N400 effects is less clear cut, as similar task-specific strategies have also been proposed to contribute to the N400 semantic priming effect (e.g. Holcomb, 1988).

Finally, although previous sign language studies have demonstrated semantic priming behaviourally (e.g. Bosworth & Emmorey, 2010), and we replicated that facilitation effect here, to our knowledge this is the first study to demonstrate a reduced amplitude N400 for semantically related sign pairs. This finding indicates that lexicosemantic processing recruits the same neural systems around the same time for both signed and spoken languages, despite differences in how these languages are perceived and produced. In contrast to the right anterior distribution that we found for the phonological manipulation within the N400 window, the semantic priming effect had more of a typical bilateral centro-posterior distribution, as has been reported in previous sign sentence processing studies (e.g. Capek et al., 2009).

In conclusion, our results highlight how the study of sign languages provides insights into the neurobiology of language. Specifically, our findings confirm that semantic processing of lexical representations is associated with a centro-posterior N400 response that is independent of language modality. However, we also observed neural patterns that may be specific to the visual-manual modality of sign language. In particular, for semantically related sign targets, there was a shift from an earlier anterior N300 to the centro-posterior N400, which suggests parallels between sign and picture/gesture processing. Further research is needed to determine whether this semantic N300 priming effect arises from visual similarities at the conceptual level, from task-specific strategies, or from another source. Moreover, the ERP response to phonologically related sign targets points to neural generators that may be specific to form processing in sign language. In both the current study (explicit priming) and our previous study (implicit priming; Meade et al., 2017), we found an attenuated negativity in the N400 window for phonologically related targets, but with an anterior rather than a centro-posterior distribution. Together, these results suggest that a unique neural generator may underlie lexical-level form processing in sign language. Finally, the phonological N300 priming effect may also be unique to sign language, but its functional significance is much less clear. This early response could reflect visual overlap between phonologically related signs at the perceptual level or at the sublexical level. Future studies examining the neural response to visually similar pictures, gestures, pseudosigns, and signs will help to illuminate the functional nature and properties of the N300.

Notes

1. Ideally, we would have had a similar phonological manipulation within the semantically related condition in order to have a full 2×2 design. However, we were unable to find a sufficient number of semantically related and phonologically related pairs to implement the full design.
2. The pattern of results was very similar for both native signers (exposed to ASL from birth) and non-native signers.
3. Note that the same pattern of results is found with a shorter window (450–550 ms) that only encompasses the peak of the N400. Given the limited number of previous ERP studies with sign stimuli, and the variability in the N400 time windows that have been reported, we tried to choose windows that thoroughly and accurately reflect the data.
4. Iconicity is another property that might affect N300 amplitude because the visual features of iconic signs align better with those of the corresponding concept. To verify that iconicity was not driving the semantic priming effect that we observed here, we extracted iconicity ratings for the 82 target signs (out of 90) that were available in the ASL-LEX database (Caselli et al., 2016). Iconicity ratings did not significantly differ between targets in the semantically related (mean 3.54, *SD* 1.68) and semantically unrelated (mean 3.00, *SD* 1.82) conditions, $t = 1.37$, $p = .17$.

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