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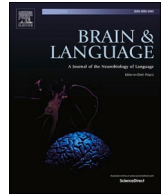
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Between bodily action and conventionalized structure: The neural mechanisms of constructed action in sign language comprehension

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ARTICLE INFO

ABSTRACT

Sign languages (SLs) are expressed through different bodily actions, ranging from re-enactment of physical events (constructed action, CA) to sequences of lexical signs with internal structure (plain telling, PT). Despite the prevalence of CA in signed interactions and its significance for SL comprehension, its neural dynamics remain unexplored. We examined the processing of different types of CA (subtle, reduced, and overt) and PT in 35 adult deaf or hearing native signers. The electroencephalographic-based processing of signed sentences with incongruent targets was recorded. Attenuated N300 and early N400 were observed for CA in deaf but not in hearing signers. No differences were found between sentences with CA types in all signers, suggesting a continuum from PT to overt CA. Deaf signers focused more on body movements; hearing signers on faces. We conclude that CA is processed less effortlessly than PT, arguably because of its strong focus on bodily actions.

1. Introduction

Human interaction is a multimodal experience with the body at its core (Ferrara & Hodge, 2018; Streeck et al., 2011). This is the case with sign languages (SLs), the linguistic systems that use the body to produce structures with different degrees of conventionalization. Of particular empirical interest is constructed action (CA), a type of language use in which signers depict events (e.g., actions, feelings, thoughts, and speech) through enactment with different parts of their body (i.e., hands, face, torso, and facial expressions) with or without strings of co-occurring signs[1] (Cormier, Smith, & Sevcikova, 2015; Hodge & Cormier, 2019). By contrast, signing without CA (henceforth plain telling [PT]) consists of highly conventionalized signs that require knowledge of the lexical repertoire of the language, without enactment. Here, we explore how the use of CA might influence SL comprehension.

Compared to PT, CA in its strongest (overt) form is a very different way of expressing linguistic meaning. One way to characterize this difference is to say that, with lexical and grammatical units (i.e., PT), meanings are essentially told, whereas with overt CA, meanings become shown instead (e.g., Clark & Gerrig, 1990; Ferrara & Johnston, 2014; Jantunen, 2022). This means, for example, that all articulators in a token of overt CA enact, and no lexical material is present (Cormier et al., 2015). Moreover, in CA, the signers' actions represent the character they are narrating about, not the actions of the actual narrator (Cormier et al., 2015). Articulatorily, the body movements in CA take up more space (i.e., more movement is involved) than when signing with lexical signs and clauses (Jantunen, De Weerdt, Burger, & Puupponen, 2020). Prototypically, the number of active articulators, especially the non-manual ones,

[1] Traditionally, CA has been defined as gestural enactment (e.g. Cormier et al., 2015) and many linguistic theories demarcate gesture from language. However, as more psycholinguistic and interaction-oriented studies have started to increase, researchers have become more aware that a sharp distinction between language and gesture cannot be made (e.g. Friederici, 2018). Recently, this has led to completely new models of language where gesture is seen as an integral part of linguistic competence, not an add-on to language (e.g. Kendon, 2017; Friederici, 2018). In this paper, we follow this latter, more recent tradition.

is larger in CA than in PT[2] (Cormier et al., 2015; Puupponen, 2019).

Moreover, the two meaning-making strategies, PT and CA, can also be mixed into a hybrid. In the literature, signing with CA and PT has been seen as opposite ends of a continuum (Cormier et al., 2015; Jantunen et al., 2020). In the middle of the continuum, researchers have postulated the existence of subtle and reduced subtypes of CA (Cormier et al., 2015; Jantunen et al., 2020; Puupponen, Kanto, Wainio, & Jantunen, 2022). In subtle CA, lexical material and clauses are still present, but the eyes and typically some other articulators (e.g. face, head) behave in an enacting manner, adding some aspects of the character's viewpoint to the utterance. In reduced CA, the lexico-grammatical material remains in the utterance, but unlike subtle CA, more enacting articulators are present, and the character's viewpoint is more salient than the narrator's viewpoint (Cormier et al., 2015; Jantunen et al., 2020; Puupponen et al., 2022).

The structural differences between sentences with CA and PT could help to disentangle the influence of CA (and its three types) on SL comprehension. In the brief history of sign neurolinguistics, studies have primarily focused on lexical processing (e.g., Gutiérrez-Sigut & Baus, 2021) and differences between speech and signing (e.g., MacSweeney et al., 2002). The structural differences between sentences with CA and PT present a unique opportunity to shed light on the processing of signed sentences. The reliance on enactment in CA and on lexical signs in PT would suggest different processing demands that have yet to be explored. Following the time course of the processes involved in language comprehension is possible using functional neuroimaging techniques such as electroencephalography (EEG). Due to its excellent temporal (millisecond [ms]) resolution, the EEG can be used to study electrical brain activity resulting from the processing of different linguistic units. Using a violation paradigm (e.g., using sentences where words/signs/CA tokens are semantically incongruent with the context), we can contrast sentences produced in the PT–CA continuum and reveal neural processes underlying language comprehension.

The visual processing of sentences whose meaning is violated triggers a sequential cascade of event-related potentials (ERPs, see Fig. 2) that, after the initial basic perceptual processing, begins with the N300 (Federmeier & Kutas, 2001; McPherson & Holcomb, 1999), which has been shown to be indicative of pre-lexical perceptual processing. This is followed by the N400, which is thought to reflect lexical and semantic processing. It then culminates with the P600, indicating syntactic and semantic re-analysis, and integration into the sentence context (Friederici, 2002). The N300 (200–300 ms), which is a negativity with a maximal distribution in frontal electrodes, may be attributed to the processing of visual stimuli (Federmeier & Kutas, 2001; McPherson & Holcomb, 1999). Although the exact nature of the processing before 300 ms is still debated (see Willems and Hagoort, 2007), the existing literature suggests a connection to modality-specific (McPherson & Holcomb, 1999; Vartiainen, Parviainen, & Salmelin, 2009) or phonological (Hagoort & Brown, 2000; Kujala, Alho, Service, Ilmoniemi, & Connolly, 2004) processes, depending on the task demands. Both types of processing are thought to involve similar neural populations and to reflect pre-semantic (phonological and object-based) processes that facilitate the subsequent semantic evaluation of a stimulus (Steinhauer & Connolly, 2008). The N400 (300–500 ms; Kutas & Hillyard, 1980) is a negativity with a maximum peak at centroparietal electrodes and is considered an index of meaning processing in the brain. It has been further subdivided into early (300–400 ms) and late N400 (400–500 ms) periods, indicating lexical (Pylkkänen, Stringfellow, & Marantz, 2002;

Pylkkänen & Marantz, 2003) and semantic (Kutas and Federmeier, 2000) processing, respectively, although this distinction remains controversial (Lau, Phillips, & Poeppel, 2008). Finally, the P600 (Osterhout & Holcomb, 1992), a positivity with a maximum at approximately 600 ms after target onset, is widely distributed across the scalp and extends to centroparietal areas.

Identifying whether CA might selectively influence the perceptual, lexical, semantic, and integration processes (i.e., a combination or all of them) underlying SL comprehension would provide finer-grained insight into the functional significance of CA. The reduction of all the ERPs in the sequence has previously been reported to index the ease of processing (Hamm, Johnson, & Kirk, 2002; Kutas & Federmeier, 2011; Ovans et al., 2022; Peeters, Dijkstra, & Grainger, 2013; Szewczyk & Schriefers, 2011). In other words, a higher amplitude correlates with greater difficulty in processing the linguistic unit at each stage (i.e., the perceptual, lexico-semantic, and integration stages).

To the best of our knowledge, this is the first study to investigate CA in SLs from a neurophysiological perspective. However, the convergence between actions and meaning processing has been approached in gesture studies (Kelly, Kravitz, & Hopkins, 2004; Özyürek, Willems, Kita, and Hagoort, 2007; Wu & Coulson, 2005). N400 reductions have been described when hand gestures matched (versus mismatched) speech in naturalistic contexts (Kelly et al., 2004) or comics (Wu & Coulson, 2005). By contrast, no differing N400 effects were reported when comparing the simultaneous processing of (matched and mismatched) gestures and words in a sentence context (Özyürek et al., 2007). These studies show that, regardless of the modality (speech, gesture, or print), semantic violations elicit a negative-going inflection in the N400 component. A unique contribution of the current study is whether these violations are present within the same modality (manual–visual) in different types of signed sentences (i.e., the PT–CA continuum).

The current study also builds on prior research on embodied language cognition. Brain responses to observed human actions indicate an interconnection between motor and language systems during action comprehension (Desai, Conant, Binder, Park, & Seidenberg, 2013; Monaco et al., 2023; Tian et al., 2020, 2023). However, the nature of this interconnection is not fully understood, as research has evinced contradictory findings. While some studies do find support for the participation of the motor system in language comprehension (Fargier et al., 2012; Klepp et al., 2014; Levänen, Uutela, Salenius, & Hari, 2001; Moreno, de Vega, & León, 2013), others have failed to observe this association (Emmorey, Xu, Gannon, Goldin-Meadow, & Braun, 2010; Maieron, Marin, Fabbro, & Skrap, 2013). The study of CA in SL comprehension among deaf and hearing native (expert) signers may reveal the timing and principles of the neural computations underlying the interconnection between CA and language functions in meaning comprehension.

Many factors may lead to differences in a signer's brain dynamics. For instance, the literature suggests that exposure to signs or speech (from birth or early childhood) can lead to functional reorganization of the brain due to neuroplasticity (Levänen et al., 2001). Furthermore, as multimodal bilingual/multilingual individuals, deaf and hearing native signers might differ in the environments in which signed and spoken languages are used. SLs / spoken languages might be used in varying proportions by deaf and hearing signers (Emmorey, Borinstein, Thompson, & Gollan, 2008; Kanto, 2022). Therefore, studying both groups (deaf and hearing native signers) is theoretically significant due to the potential to uncover distinctions linked to brain plasticity or language use, regardless of the age of acquisition. These groups, considered separately, might show different patterns in the modulatory effect of CA on the neurophysiological processing of meaning.

Our aim in the present study was to explore how CA (in general) and its three types can modulate the functional brain processing of meaning in native Finnish SL (FinSL) signers. To answer these questions, we recorded EEG-based brain responses to a violation paradigm using

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[2] Although tokens of CA, especially overt ones, prototypically include more active articulators than PT, in some cases a token of PT can include as much (or more) non-manual articulation as a token of CA. However in this case, non-manual articulations are not enacting a referent, but have other functions (e.g. non-enacting depiction or indication of referents; see, e.g. Puupponen et al., 2019).

naturalistic videotaped signed sentences[3] and including varying levels of CA in deaf and hearing native signers. If all sentences exert the same processing demands, regardless of their degree of CA, then we would expect them to elicit the same amplitude in the incongruent conditions (i.e., no significant differences across sentences). However, if sentences with different degrees of CA rely on different degrees of embodiment, then a reasonable expectation is that they will display a gradient in processing costs, as they are integrated in the sentential context. We posit that sentences with overt CA stand out for their higher enactment with the body, the prominent use of facial expressions, and the absence of lexical signs (Cormier et al., 2015). Thus, we expect that they will be easier to process because they are more on par with bodily actions. We predict that sentences that consist of sequences of lexical signs (PT) without enactment will be the most difficult to process because the integration of this type of sentence requires more intensive processing of conventionalized linguistic structures (e.g., specific handshapes for lexical access) (Gutiérrez, Müller, Baus, & Carreiras, 2012). Overall, the largest difference in amplitude in the N400 component will occur between sentences with PT and sentences with overt CA (i.e., the highest negative amplitude will appear with PT sentences), whereas sentences with subtle and reduced CA will fall within these two.

2. Methods

2.1. Participants

Native signers were invited to participate in the study through calls sent to deaf and hearing signer associations in Finland. Some participants were also recruited through personal contacts made by the authors of this study. Thirty-five signers volunteered to participate, all of whom had acquired SL from birth or early childhood. Twenty-one of these signers were deaf (10 females), and 14 were hearing (12 females). The deaf and hearing signer groups did not differ in age ($t_{(33)} = 0.68$, $p = 0.50$, deaf 441.05 ± 89.33 months, hearing 415.43 ± 132.95 months). Thirty-three participants were right-handed, one was left-handed, and one reported using both hands indiscriminately. The participants did not report any neurological disorders or the use of medications that influence the central nervous system. All participants reported having normal or corrected-to-normal vision. All participants signed an informed consent form before participating in the study, which was previously approved by the Ethical Committee of the University of Jyväskylä to be conducted following the tenets of the Declaration of Helsinki. All participants received a small gift for their participation.

2.2. Stimuli and task

Participants were shown videos of an adult male (standing with face and hands toward the camera) signing 5 types of sentences (43 sets of 5 sentences each). The sentences included 2–3 items (signs / CA tokens) so that each sentence ended with a sentence-final predicate. In each set, four of the five sentence types were similar in meaning and included a semantic violation in the last sign / CA token. In the first sentence, the semantic violation was expressed through PT (Fig. 1b), and in the other three sentences through subtle (Fig. 1c), reduced (Fig. 1d), and overt CA (Fig. 1e). The semantic violation and CA started at the same time sentence-finally. All four sentences were compared with a neutral sentence that did not include semantic violation or CA (Fig. 1a). Table 1 summarizes the main characteristics used to differentiate the sentence endings with PT–overt CA within each set. An example showing the different types of CA used in the sentence endings is illustrated in Fig. 1 (see supplementary material for more examples).

When recording the sentences, attention was paid to the consistency

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[3] For the rationale for using this kind of stimulation, see Hernández, Puupponen, Keränen, Wainio, Pippuri, Ortega, and Jantunen, 2022a.

of the visual properties. The luminance, colors, and appearance of the video and the location of the signer were kept constant. The sentences were articulated, and the stimuli were designed so that the signing was naturalistic (i.e., the speed of the signing was not artificially controlled) but controlled in a way that optimized the editing of the videos to the standard used in our lab (see Hernández, Puupponen, and Jantunen, 2022b).

High-definition silent videos were recorded for each sentence and saved in mp4 format with a resolution of 1080p. The frame rate (25 fps) and aspect ratio (16:9) were kept constant across the videos. The recorded videos were edited so that each sentence in a set (a-e in Fig. 1) included an identical frame-setting part and then the varying sentence-final targets. The cut-off point of the two sentence parts coincided with the onset of the target (see Fig. 1). In connected or continuous signing, the signs follow one another, just like words in the speech stream (for a full discussion, see Jantunen, 2015). In the phonetic framework of Kita, van Gijn, and van der Hulst (1998), the onset of the target signs aligns with the beginning of the preparation phase, during which the formational characteristics of signs are first visible. Only the subsequent stroke phases are fully specified in terms of linguistic form (see Arendsen, van Doorn, & de Ridder, 2007; Jantunen, 2015; Kita et al., 1998).

The duration of the videos differed between conditions ($F_{(4, 210)} = 182.97$, $p < 0.001$, PT = 5.02 s (s) SE = 0.02 s; subtle CA = 5.28 s SE = 0.06 s; reduced CA = 6.30 s SE = 0.08 s; overt CA = 7.70 s SE = 0.14 s; neutral = 4.79 s SE = 0.07 s). We consider that this difference reflects the motor component of CA, as larger motor actions need longer times for expression. Thus, the differences in duration are an essential part of the phenomenon that we are studying. However, the differences in duration were compensated by the way the videos were edited and synchronized with the EEG data. First, we controlled for the duration of the videos by adding black screens (at the beginning of the sentence) so that all (43×5) videos were identical in duration. To ensure an exact synchronization with the EEG data, we checked that the most expressive part of the target (stroke) started similarly across conditions. This procedure has been used before in other studies using naturalistic stimuli (Drijvers and Özyürek, 2018; Momsen, Gordon, Wu, & Coulson, 2021; Wu & Coulson, 2005). On average, the preparation phase of the targets lasted 7.5 frames (i.e., 300 ms from the video cut-off point). We estimated that all targets were recognized by the beginning of the stroke (Jantunen, 2015), which, in our stimuli, is always 2.727 s from the beginning of the sentence/video. Because this time denotes the earliest point at which the sign / CA token is understood, it was used as the 0 point for the ERPs.

Participants watched silent videos of the signed sentences. No response was needed from them. Signed instructions (highlighting the passive viewing and avoidance of eyes and body movements) were provided to the participants in person by a researcher. In addition, pre-recorded videos with instructions in FinSL were shown at the beginning of the task. In the lab, all communication with the participants was done in FinSL.

In the task, the videos of sentences were presented one by one, with the same appearance probability and in random order, with an inter-stimulus interval of 500 ms. The task was administered in two blocks. Between blocks, the participants had a short break (around 1–3 min) to rest their eyes or move slightly in the chair. The total duration of the task was 30 min. The task was programmed and controlled using PsychoPy software (Peirce et al., 2019).

The use of naturalistic sentences in the task would elicit quite complex responses that can be challenging to explain. To assist in the interpretation of the EEG results, a two-question interview was performed after the EEG measurements. At the end of the task, the participants were asked two questions: 1) What is your opinion about the sentence you just saw? What was your experience with the task? 2) What were you focusing on when viewing the sentences? Answers were collected (as written texts) and further analyzed.
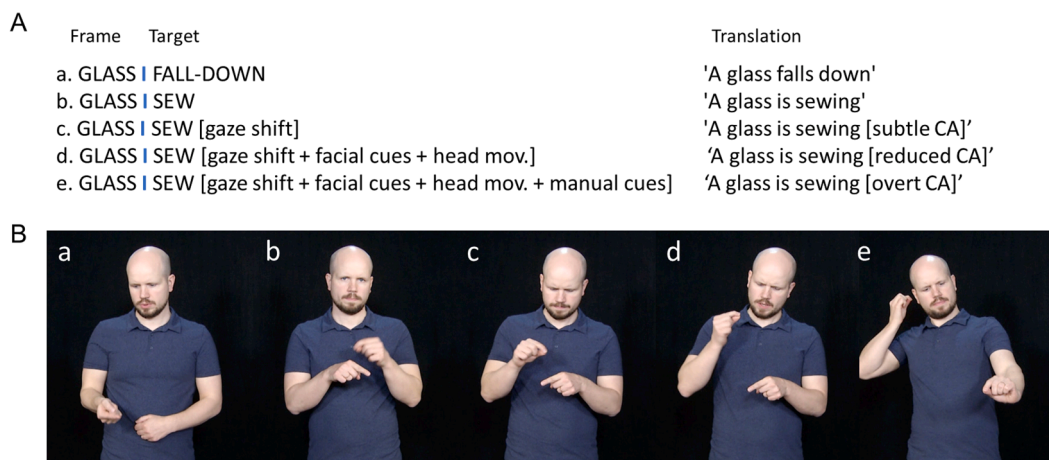
Fig. 1. (A) Example of last signs/CA tokens (targets) for one set of sentences. (a) neutral sentence: congruent target with PT, (b) incongruent target with PT, (c) incongruent target with subtle CA, (d) incongruent target with reduced CA, (e) incongruent target with overt CA. (B) Still images depicting the targets of sentence a-e. See the online article for the color version of this figure.

Table 1

Characteristics of the CA types used in the sentence endings within each set. The absence of horizontal lines indicates that the types and features are not categorical, but continuous.

CA type	Lexical unit	Viewpoint	Enacting articulator	Motion
PT	yes	Full narrator	none	least
subtle CA	yes	Narrator with character	face	some
reduced CA	yes	Character with narrator	face + head and/or body	more
overt CA	no	Full character	face + head/body + hands	most

2.3. ERP recording and analysis

Participants were seated inside an acoustically isolated room in a comfortable chair located approximately 1.5 m from a monitor in front of them. The room lights were turned off to avoid reflections in the monitor, following general recommendations from our lab (Hernández, Puupponen, and Jantunen, 2022b).

The EEG data were recorded using the Bittium NeurOne Tesla EEG system (Bittium Corporation, Oulu, Finland). A 64-electrode EEG cap (ActiCAP 32, Easycap GmbH, Herrsching, Germany) was adjusted to the participant's head according to the international 10–20 system. Impedances were kept below 5 kΩ. An electrode located in FCz was used as a reference during the recordings, and the ground electrode was in AFz.

The raw EEG data were pre-processed and analyzed with Meggie (CIBR, Jyväskylä, Finland; Heinilä & Parviainen, 2022), a graphical user interface for MNE-Python (Gramfort et al., 2014). Bad channels were excluded after visual inspection of the recordings. The data were resampled to 250 Hz and re-referenced to the average mastoids. Subsequently, the data were bandpass filtered between 1 and 40 Hz. Artifacts from eye movements and heartbeats were determined and removed using Independent Component Analysis (ICA; Hyvärinen & Oja, 2000). Clean data were epoched based on each sentence type, with a baseline of 200 ms before the beginning of the target in each sentence and 800 ms post-target. Residual artifacts exceeding ± 100 μV in amplitude were removed. Epochs per target type (sentence endings with semantic violations and overt, reduced, and subtle CA, and PT; sentence endings without violation and PT) were obtained. The average of rejected epochs did not differ between conditions ($F_{(4, 165)} = 0.05$, p = 0.99, PT: 38.41 epochs, subtle CA: 37.79 epochs, reduced CA: 38.00 epochs, overt CA: 37.85 epochs, neutral: 38.15 epochs). Epochs for the same target type

were averaged together. Specific time-windows for each ERP in the sequence were identified as: 200–300 ms (N300), 300–400 ms (early N400), 400–500 ms (late N400), and 500–700 ms (P600), see Fig. 2. The resulting variables (amplitude for each ERP) were inspected to identify outliers. The Z scores that exceeded 2.5 standard deviations were considered outliers (atypical) and were exchanged for the closest non-atypical values.

2.4. Interview analysis

The responses given by the participants after the EEG measurement for the questions regarding (1) their opinion about the sentences and (2) where they were focusing (when viewing the sentences) were further analyzed qualitatively. Based on the answers provided, the following categories were identified for question 1: sentences funny, sentences weird; and question 2: movement, specific parts of the body, semantics, whole body per participant.

2.5. Statistical analysis

The EEG data were analyzed in MNE Python (Gramfort et al., 2014) with the within-group differences in the whole sample, as well as for the groups of deaf and hearing signers with cluster-based permutation tests across time and space (Maris & Oostenveld, 2007). In all tests, the cluster threshold was 0.05, the cluster significance was set under 0.05, and 1000 permutations were computed. Time and location were not limited. The use of permutation tests allowed us to avoid the multiple comparisons problem (Maris, 2012). The obtained *p*-values were corrected for multiple comparisons with the Bonferroni correction.

The remainder of the statistical analysis was performed with SPSS (IBM SPSS Statistics for Windows, Version 26.0; IBM Corp., Armonk, NY, USA). The relationships between CA and the amplitude of each ERP were assessed with simple regression analysis of the two groups of signers. The continuum between PT and overt CA was used as an
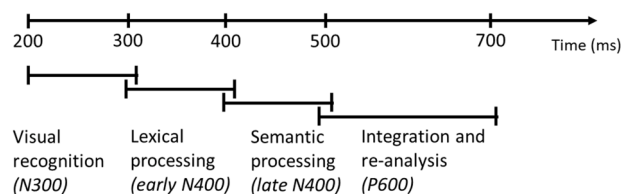

Fig. 2. Diagram of the ERP sequence underlying sentence understanding in terms of its temporal extent (in ms).

independent variable in all the analyses. The assumptions of linearity, normality, and homogeneity of variances of the residuals were checked with residual and Q-Q plots. The means of the residuals in all models were close to zero.

The interview responses that participants provided after the EEG measurements were analyzed with the Fisher–Freeman–Halton exact test in SPSS (IBM SPSS Statistics for Windows, Version 26.0; IBM Corp., Armonk, NY, USA) with a significance level of 0.05.

3. Results

3.1. Neural correlates of CA and PT

A within-subjects permutation test was run for all participants (deaf and hearing signers), comparing the difference waves obtained by subtracting the brain response to the neutral sentences from sentences ending with PT and with any kind of CA averaged together. No

significant difference was revealed by this analysis (Fig. 3A, B). This suggests that sentences with incongruent endings produced with PT (mean = -1.01) and the sentences whose endings were performed with any degree of CA (mean = -0.52) elicited similar N400 effects in the whole group.

A similar within-subjects permutation test performed for each group separately revealed significant differences between sentence endings performed with PT and those performed with CA for the group of deaf signers (Bonferroni-corrected p = 0.048, see Fig. 3C, D). This effect, which was widespread over the scalp covering the central line, was observed in the time window 228–320 ms post-stimulation. This significant difference suggests that stronger N300 and early N400 negativities are elicited by sentence endings produced with PT (mean = -1.17) than with CA (mean = -0.49) in the group of deaf signers. This suggests that CA endings are more easily processed despite their violation. No significant differences were found for the group of hearing signers (see Fig. 3E, F).
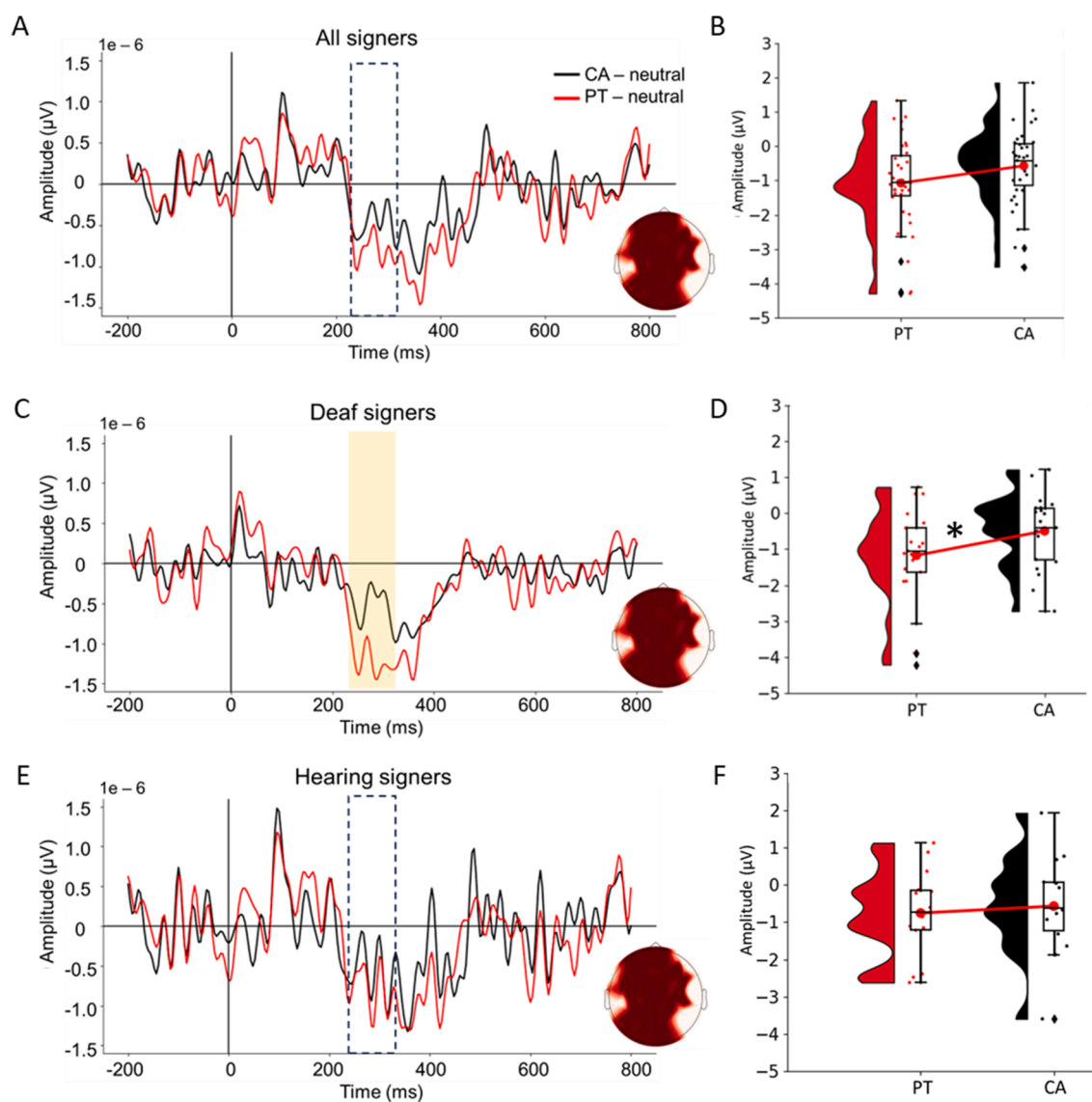

Fig. 3. Results of the cluster-based permutation test contrasting targets with PT (red) and CA (black) for all (A), deaf (C), and hearing (E) signers. Time courses were obtained by averaging over the electrodes comprising the cluster identified by the permutation test. The yellow box indicates the time window in which a statistically significant difference was observed. The dashed box indicates that significance was not reached in that time window. The colored head in the lower-right corner shows the topographic map representing the electrodes contributing to the cluster (red). Raincloud plots show the distributions and differences in the strength of responses to PT (red) and CA (black) in the cluster identified by permutation tests for all (B), deaf (D), and hearing (F) signers. See the online article for the color version of this figure. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2. Neural correlates of CA types and PT

A within-subjects permutation test was performed for all signers to compare the difference waves obtained by subtracting the brain response to the neutral sentences from sentences ending with PT and with each kind of CA. No significance was found for all signers, suggesting that PT and the three types of CA elicit similar ERPs for all signers.

A similar within-subjects permutation test performed for each group revealed no significant differences between conditions in either group (see Fig. 4E, F for the group of hearing signers). However, a tendency to significance was observed between the four types of sentence endings (PT and the three types of CA) for the group of deaf signers (Bonferroni-corrected p = 0.072; see Fig. 4C, D). The potential effect, which was widespread over the scalp covering the central line, was observed in the time window 222–373 ms post-stimulation (consistent with N300 and early N400).

3.3. PT–CA continuum

We further explored whether the association between CA and sentence comprehension follows a continuum by running simple regression analyses (one per ERP) in each group. Fig. 5 shows how the PT–CA continuum modulates the functional processing of meaning in the brain in native signers. In view of the absence of significant differences between the four ending types (see section 3.2), topographic regions of interest (ROI) were selected, representing the typical frontocentral topography of the N300 (Fig. 5A) and the centroparietal topography of the N400 (Fig. 5B). The amplitude trajectory of the PT–CA continuum is also shown individually for the N300 (Fig. 5E) and the early (Fig. 5F) and late (Fig. 5G) N400 amplitudes. Neither group of signers showed P600; thus, this ERP was excluded from further analyses.

Simple linear regression analyses revealed significant positive relationships between CA and the amplitudes of the N300 and the early N400 for deaf signers. For the N300 amplitude, the regression model
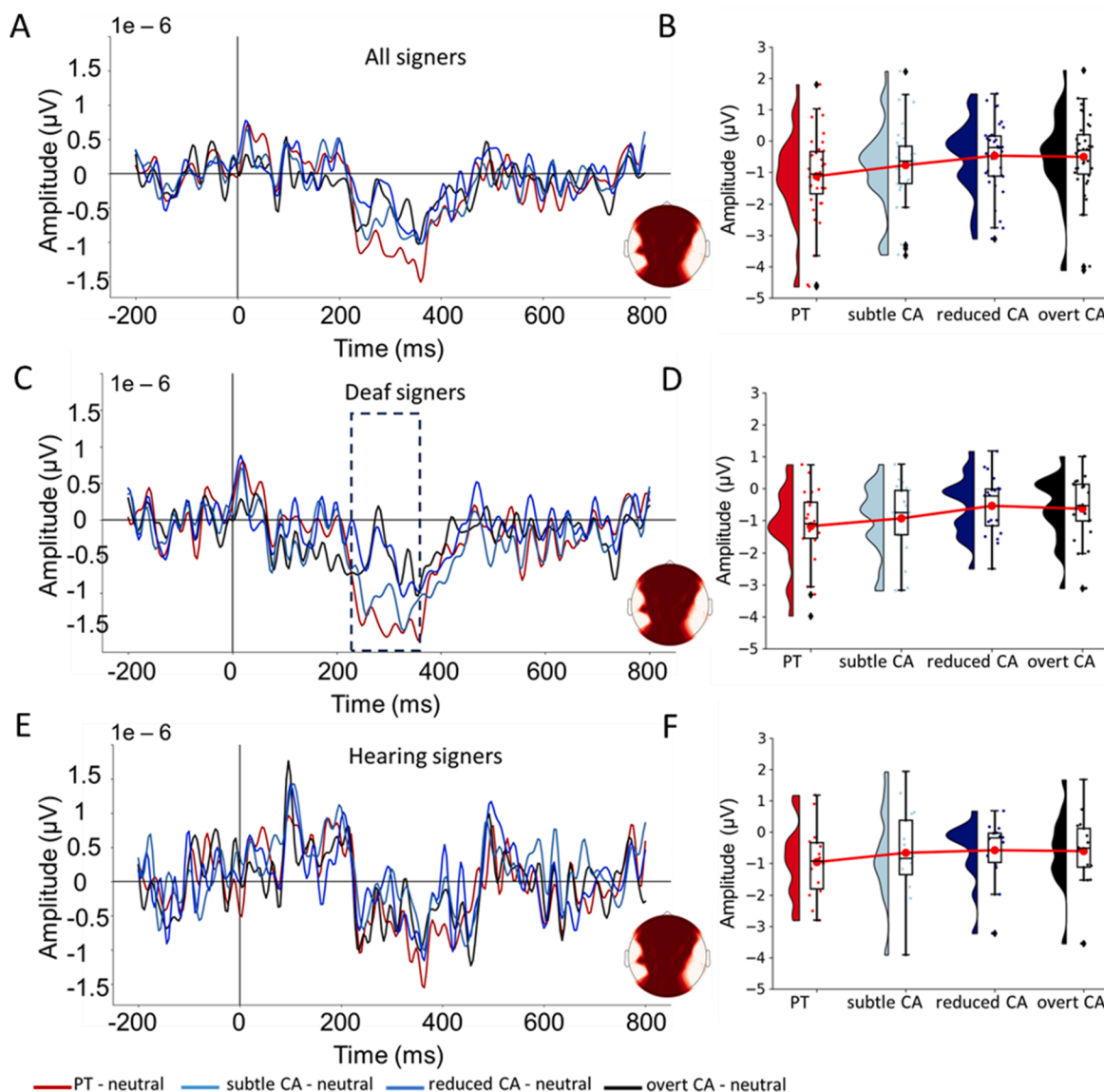

Fig. 4. Results of the cluster-based permutation test contrasting targets with PT (red), subtle CA (light blue), reduced CA (dark blue), and overt CA (black) for all (A), deaf (C), and hearing (E) signers. Time courses were obtained by averaging over the electrodes comprising the cluster identified by the permutation test for deaf signers. The dashed box indicates that significance was not reached in that time window. The colored head in the lower left corner shows the topographic map representing the electrodes contributing to the cluster. Raincloud plots show the distributions and differences in the strength of responses in the cluster identified by permutation tests to PT (red), subtle CA (light blue), reduced CA (dark blue), and overt CA (black) for all (B), deaf (D), and hearing (F) signers. See the online article for the color version of this figure. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
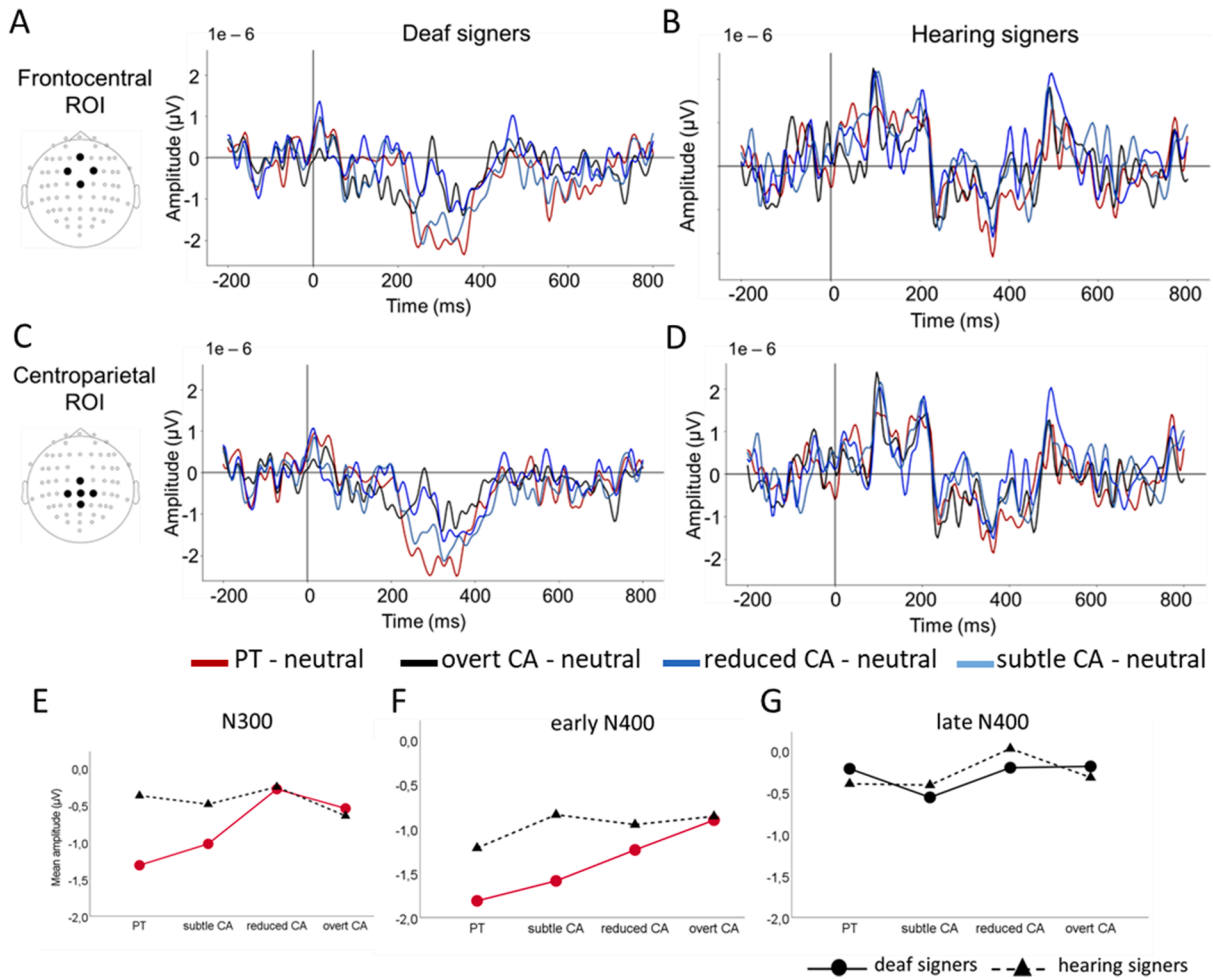
Fig. 5. Time-course of the responses obtained in the frontocentral (A and B) and centroparietal (C and D) ROIs for deaf (A and C) and hearing (B and D) signers. Schematic representation of the amplitude trajectory followed by the PT–CA continuum for deaf (solid line) and hearing (dashed line) signers for the sequence of ERPs: N300 (E), early (F) and late (G) N400. Red color denotes the significant models identified by the simple regression analyses. See the online article for the color version of this figure. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

predicted a 0.31 μV increase for each increment of CA in this violation paradigm (p = 0.04). This model explains 5 % of the variance in the N300 amplitude. For the early N400 amplitude, the regression model predicted a 0.31 μV increase for each increment of CA in this violation paradigm (p = 0.02). This model explains 6 % of the variance in the early N400 amplitude. No other significant associations were found for the group of deaf signers. No significant associations were found for the group of hearing signers.

3.4. Interview responses

The Fisher–Freeman–Halton exact test revealed no association between the groups based on hearing status and the answers to the first question about the participants' general opinion on the sentences (p = 0.21). The most common answer in both groups was that the sentences were weird (see Fig. 6A). Five of the 14 hearing signers reported, in answer to this question, that they translated the signed sentences into
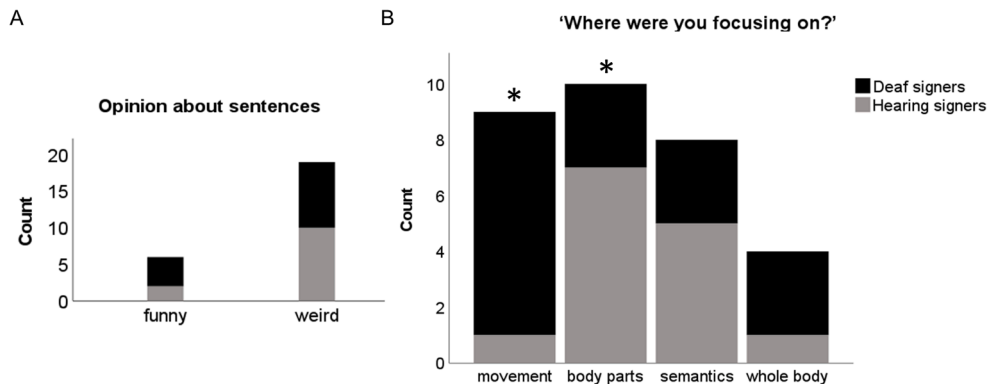

Fig. 6. Graph bars showing the count values per category in the groups of deaf (black) and hearing signers (gray) for questions 1 (A) and 2 (B). Significant associations from the Fisher–Freeman–Halton exact test are shown with asterisks.

spoken Finnish.

The Fisher–Freeman–Halton exact test on the answers to the second question ('*Where were you focusing on (when viewing the sentences)?*') revealed a significant association with the groups based on hearing status (p = 0.02). Deaf signers focused mostly on movements of the whole body, while hearing signers focused more on specific parts of the body (face = 6/14, body = 4/14, hands = 1/14, see Fig. 6B).

4. Discussion

The current study explored a potential CA modulation of SL sentential meaning processing in native signers. The results showed that semantically incongruent targets produced less negative N300 and early N400 effects when executed with CA than when produced with PT, but only for the group of deaf signers. The group of hearing signers did not show any of these effects. When PT and the three types of CA were contrasted, similar ERP amplitudes were observed for all signers, regardless of group. The CA increases, from PT until overt CA, predicted increases in N300 and early N400 amplitudes in deaf signers, but not in hearing signers. Interestingly, during sentence watching, the deaf signers reported focusing on movements of the body, while the hearing signers reported focusing on faces.

The more positive N300 and early N400 effects for CA tokens (averaged together) than for PT signs (without enactment) in the group of deaf signers indicate that CA might be used together with lexical information to process SL meaning. Thus, we interpret this finding as CA facilitating the comprehension process for deaf signers based on the lower processing costs suggested by the reduced negativities. This is in line with previous studies showing that gestures ease (spoken) language comprehension (Drijvers and Özyürek, 2018; Kelly et al., 2004; Momsen et al., 2021) and meaning processing in other contexts (Wu & Coulson, 2005). Consequently, these results also support (and extend to CA in SL) the idea that meaningful (and congruent) motor actions may interact to facilitate processing meaning across context and modality (For a review, see Kita & Emmorey, 2023).

Our results revealed significant differences in the brain responses to PT and CA during the initial stages of sentential meaning processing, as indicated by the N300 and early N400 components. Specifically, CA seemed to influence activations at the N300 time window, suggesting modulation at the pre-lexical activation (Federmeier & Kutas, 2001; McPherson & Holcomb, 1999; Vartiainen et al., 2009). The modulation exerted by CA in this time window reduced the neural processing costs associated with incongruent targets, perhaps making their processing more efficient. We argue that tokens of CA engaged the body more, so this might ease the form-based processing of the target. Some argue that the N300 reflects a bottom-up analysis of an incoming stimulus before it is integrated in the sentential context. For instance, the words *brush* and *brave* are likely to be similarly activated because they share the same syllable onset, but only the former would be semantically congruent when talking about paint (Van Den Brink, Brown, & Hagoort, 2001). In our study, we argue that the enhanced N300 indexes similar lexical processing. Relatedly, our finding regarding N300 supports prior research demonstrating enhanced visual abilities in deaf individuals, particularly in processes such as motion detection and localization (for a review, see Alencar, Butler, & Lomber, 2019). The N300 effect is also consistent with previous studies showing earlier and more efficient behavioral and brain answers from deaf individuals to human motions (Corina et al., 2007; Quandt, Kubicek, Willis, & Lamberton, 2021).

The CA modulation of the previous visual form-based processing (N300) in deaf individuals spreads into the next processing stage (early N400) related to meaning-based processing (Connolly & Phillips, 1994; Hagoort & Brown, 2000; Vartiainen et al., 2009). An association has been suggested between the early part of the visual N400 and the lexical evaluation of words (Pylkkänen et al., 2002; Pylkkänen & Marantz, 2003). We interpret our result (the smaller early N400 for CA than PT) as CA lowering the processing costs when retrieving (and comparing) signs

/ non-overt CA tokens from the stored lexicon. The literature has identified that signers make use of the sublexical structure of signs (e.g., location, handshape, and movement) to achieve lexical access (Gutiérrez-Sigut & Baus, 2021). Therefore, our results regarding the amplitude reduction of early N400 are in line with those studies showing facilitation of lexical access by a type of movement either in isolation (Emmorey & Corina, 1990) or combined with other sublexical parameters, such as handshape (Gutiérrez, 2008) and location (Dye & Shih, 2006). As overt CA does not include lexical content, its processing costs are presumably the lowest. Another explanation for the N400 decrease associated with CA found here could be related to the increased iconicity of CA as compared to PT, since N400 decreases have also been shown for more iconic signs (McGarry, Midgley, Holcomb, & Emmorey, 2023).

The current study provides evidence for CA modulation of the earliest two stages of the temporal unfolding of FinSL comprehension in deaf native signers. More specifically, CA seems to impact both the form-based and meaning-based phases of visual semantic processing between 200 and 400 ms post-target onset. This effect was not observed for the late N400, and the P600 was absent in any condition for either group of signers. This suggests that processing at the two early stages seems to resolve the cognitive demands posed by the incongruency. This would allow the semantic processing of signs / CA tokens and their integration into the overall meaning of the sentence to remain unaffected by the incongruity.

Interestingly, our findings that CA influences the perceptual and lexical processes (N300 and early N400) but not the semantic and integration steps (late N400 and P600) also suggest that CA could be specifically modulating bottom-up (but not top-down) information processing. Kutas and Federmeier (2011) have argued that bottom-up processes contribute to the early stages of meaning processing. Bottom-up and top-down mechanisms are used to prioritize relevant information according to saliency or goals, respectively (For a review, see Chica, Bartolomeo, & Lupiáñez, 2013). A bottom-up (or stimulus-driven) mechanism orients attention to external, salient, and behaviorally relevant stimuli to detect new objects or events. This idea raises additional questions regarding the cognitive strategies employed by deaf signers during SL and CA processing. Therefore, the electrophysiological responses observed in our study are likely linked to the motor aspect of CA or to the salience of the movement itself. This suggests two possible underlying explanatory mechanisms for the observed results: one involving the engagement of brain regions associated with motor processing, and the other activating bottom-up visual attention mechanisms that process salient information. Whether these associations primarily involve the motor component of CA, early cognitive (attentional) processing elicited by the salience of CA, or a combination of both factors remains to be determined.

The difference between brain electrical responses to incongruent targets (PT vs. CA) was not replicated in the group of hearing signers. In this group, PT and CA elicited similar N400 effects, suggesting no modulation of meaning processing by CA. We don't have a full explanation for this unexpected result. Although both groups include multilingual individuals, who use multiple modalities in their everyday communication (e.g. Puupponen et al., 2022), one possible explanation could be related to differences in the proportion in which the modalities are present in their communication in daily life. The varying input, modalities, and usage contexts between spoken Finnish (majority) and FinSL (minority) may impact SL processing skills differently in deaf and hearing signers (For a review about acquisition in multilingualism, see Kanto, 2022). Empirical evidence indicates that hearing signers experience a strong cross-linguistic and cross-modal influence between speech and signing, which manifests in both online processing and production tasks (Manhardt, Brouwer, & Özyürek, 2021). In the two-question interview of the current study, some of the hearing signers reported on attempting to comprehend the sentences by translating them into Finnish, which was not reported by the deaf signers. Furthermore, according to the interviews the deaf signers reported on

integrating information from the whole body simultaneously, while hearing signers reported paying closer attention to the face of the signer (i.e. eye gaze, mouth actions, etc.). The aforementioned issues bring forth the question whether characteristics in the multilingualism and multimodality of the hearing and deaf signers' daily communicative practices may be connected to the difference we see in the data. However, one must take into consideration that we cannot be certain of this explanation as we did not collect information on the participants' daily language practices. Further studies are needed which compare the characteristics of the multilingualism of deaf and hearing signers, and whether this connects to the processing of iconic discourse strategies such as CA.

Another aim of this study was to examine how the three CA types could modulate the functional brain processing of meaning in native signers. When we unraveled and contrasted the neuroelectric responses to different types of CA, we did not find any significant difference between them in either group. This supports and adds neuroimaging evidence to the growing body of studies showing the existence of a continuum between PT and subtle, reduced, and overt CA (Cormier et al., 2015; Jantunen, 2017, 2020; Puupponen et al., 2022) rather than the existence of independent categories. Furthermore, simple regression analyses revealed a (modest) predictive relationship between CA intensity and the amplitudes of N300 and early N400 in deaf signers. Even though the models explained a small part of the amplitude variances (5 % for N300 and 6 % for early N400), this suggests that CA, together with other processes, may be influencing the form- and meaning-based processing of information in the brains of deaf native signers. More specifically, as CA increases from PT to overt CA, a corresponding decrease occurs in the neural resources allocated to processing meaning in the early stages indexed by those ERPs. These findings hint that high levels of CA could be a resource used in SL comprehension among deaf individuals.

The continuum from PT to overt CA in the form-based visual analysis showed an increasing pattern for the N300 amplitude from PT to reduced CA, which did not appear to be followed by overt CA. A plausible explanation is that overt CA does not contain lexical information (this can be seen in Fig. 1B-D & supplementary material). From PT to reduced CA, the signers use the sign's lexeme and its formal subcomponents (e.g., hand configuration) for identification (Cormier et al., 2015). However, the lexeme is no longer available in the signs produced with overt CA. In the subsequent (lexical) processing stage (as indexed by the early N400), the continuum from PT to overt CA showed a linearly increasing pattern of amplitude. We argue that the concept of the continuum, in its clearest form, seems to be in the meaning-based stage of analysis. Specifically, the most gradient meaning processing occurs when lexical items are selected and contrasted with (and selected from) their previously stored memory representations. This is an illustration of the cognitive–linguistic nature of the PT–CA continuum.

In principle, our finding that CA supports SL understanding in deaf signers suggests the involvement of the motor system in action-related meaning processing, as shown in previous studies (Desai et al., 2013; Monaco et al., 2023; Tian et al., 2020; 2023). However, establishing whether the brain activity results from the interconnection of motor and language brain areas can be challenging using EEG data. Indeed, the literature shows that, with the use of more structural methods, the activation of the mirror neuron system in deaf signers while passively viewing SL and pantomimes remains elusive (Corina et al., 2007; Emmorey et al., 2010; MacSweeney et al., 2004). The nature of this discrepancy may be elucidated in future studies of the effects of CA on the specific contributions of motor and language brain areas to SL comprehension.

One of the limitations of the current study resides in its small sample size, especially for the group of hearing signers. Thus, more statistical power may have been needed to detect an effect in this group. In that case, this result should be taken as preliminary until it is replicated in the future with larger sample sizes. However, if a smaller sample size was the reason for the failure to see an effect like that observed in the deaf participants, we should have seen a clearer effect when the brain responses of all signers were combined (Fig. 3A and 4A) than in the deaf signers (Fig. 3B and 4B). This was not the case, and the negativities in response to PT and CA became more similar for all signers than for the group of deaf signers. This reinforces the idea that hearing signers may show a different pattern of processing. The small sample size can also underlie the absence of significant differences between CA types in both groups. Thus, our results should be interpreted with caution until future studies clarify this point.

One important point to note is that our paradigm required only passive viewing of videos containing SL sentences. This was done to avoid a reduction in the amplitude of the N400 due to attention (Kutas & Hillyard, 1980). Therefore, we cannot infer that our results relate to more complex demands, such as active/attentive processing of the same stimuli. The modulation that CA would exert in an active paradigm in which CA would be consciously processed, as in a judging task, remains to be elucidated. We did not collect the behavioral responses of the participants (due to the passive nature of the paradigm); therefore, we were not able to confirm whether the brain effects observed here were indeed associated with improved performance. Future studies involving behavioral answers from the participants are needed to clarify this point.

We conclude that CA modulates the sentential processing of meaning in FinSL among deaf signers. This modulation seems to occur specifically at the bottom-up stages of meaning processing, comprising the visual processing of the forms and the lexical processing of signs. CA does not seem to influence the meaning processing of hearing signers, which may be connected to the characteristics of their multilingualism. These findings underscore the importance of considering sensory focus and individual differences in SL research. Our results confirmed the existence of a continuum between PT and subtle, reduced, and overt CA in deaf signers' visual perception and lexical processing. Overall, this study contributes to a better understanding of how the body is used to create meaning and how it differs from more conventionalized structures within the manual–visual modality.

CRediT authorship contribution statement

Doris Hernández: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft. **Anna Puupponen:** Conceptualization, Investigation, Methodology, Resources, Visualization, Writing – original draft. **Jarkko Keränen:** Investigation, Methodology, Resources, Visualization, Writing – review & editing. **Gerardo Ortega:** Supervision, Validation, Writing – review & editing. **Tommi Jantunen:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bandl.2024.105413.

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