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Brain correlates of constituent structure in sign language comprehension

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ABSTRACT

During sentence processing, areas of the left superior temporal sulcus, inferior frontal gyrus and left basal ganglia exhibit a systematic increase in brain activity as a function of constituent size, suggesting their involvement in the computation of syntactic and semantic structures. Here, we asked whether these areas play a universal role in language and therefore contribute to the processing of non-spoken sign language. Congenitally deaf adults who acquired French sign language as a first language and written French as a second language were scanned while watching sequences of signs in which the size of syntactic constituents was manipulated. An effect of constituent size was found in the basal ganglia, including the head of the caudate and the putamen. A smaller effect was also detected in temporal and frontal regions previously shown to be sensitive to constituent size in written language in hearing French subjects (Pallier et al., 2011). When the deaf participants read sentences versus word lists, the same network of language areas was observed. While reading and sign language processing yielded identical effects of linguistic structure in the basal ganglia, the effect of structure was stronger in all cortical language areas for written language relative to sign language. Furthermore, cortical activity was partially modulated by age of acquisition and reading proficiency. Our results stress the important role of the basal ganglia, within the language network, in the representation of the constituent structure of language, regardless of the input modality.

Introduction

Does language processing recruit a universal set of brain mechanisms, regardless of culture and education? In the past twenty years, this important question, initially posed solely throughout linguistic and behavioral studies in the context of Chomsky's Universal Grammar hypothesis, has begun to be investigated at the brain level (Moro, 2008). Several brain-imaging studies have homed in on a consistent network of brain regions in the superior temporal sulcus and inferior frontal gyrus, lateralized to the left hemisphere, which are systematically activated whenever subjects process sentences in their native language (Mazoyer et al., 1993; Marslen-Wilson and Tyler, 2007; Pallier et al., 2011; Friederici, 2012). Neuroimaging studies of language comprehension suggest that essentially the same left-lateralized perisylvian network is engaged by the processing of spoken or written language (Vagharchakian et al., 2012). Those regions respond to manipulations of syntactic complexity (Marslen-Wilson and Tyler, 2007; Pallier et al., 2011; Shetreet and Friedmann, 2014) and activate to natural but not unnatural linguistic constructions (Musso et al., 2003). Intracranial recordings in adults indicate that their activation varies monotonically with the number of words that can be integrated in a phrase or sentence (Fedorenko et al., 2016; Nelson et al., 2017). Remarkably, those regions are already active when 2-month-old babies listen to their native language (Dehaene-Lambertz and Spelke, 2015), and already exhibit hemispheric asymmetries that are unique to the human species (Leroy et al., 2015), further comforting the hypothesis that they may host a specific and universal mechanism for language acquisition.

The existence of sign languages presents a significant challenge for this hypothesis. Several researchers have presented data supporting the idea that, even though sign languages are based on an entirely distinct output modality, they are full-fledged natural languages and are governed by the same linguistic constraints as spoken languages (Klima and Bellugi, 1979; Sallandre and Cuxac, 2002; Sandler, 2003, 2010; Cuxac and Sallandre, 2007; Brentari, 2010; Pfau et al., 2012; Börstell et al., 2015). The acquisition of sign language also follows a time course similar to that of spoken language, with deaf babies undergoing an early stage of sign overproduction and “babbling” in the first year of life (Petitto and Marentette, 1991; Cheek et al., 1998; Cormier et al., 1998; Petitto et al., 2001, 2004). Moreover, consistent with neuroimaging studies of language comprehension, neuropsychological studies have revealed

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classical patterns of aphasia for sign language, due to similar brain lesions (Hickok et al., 2002; Pickell et al., 2005; Hickok and Bellugi, 2010; Rogalsky et al., 2013). Finally, neuroimaging studies of sign language (SL), when disregarding the low-level differences due to input modalities, have also converged on a classical network of left-hemispheric regions similar to spoken language (for reviews, see Campbell et al. (2007), Rogalsky et al. (2013), Corina et al. (2013b)). Nevertheless, a few studies have reported stronger responses to sign language in the right, or left, parietal regions, which have been hypothesized to reflect the spatial content of sign languages (Emmorey et al., 2002; Newman et al., 2002, 2010a; MacSweeney et al., 2008; Courtin et al., 2010; Newman et al., 2010b; Emmorey et al., 2013; Newman et al., 2015).

In summary, in the present state of knowledge, it seems plausible that sign language should rely on the same brain areas as spoken language, but the data is not fully convergent. Furthermore, most neuroimaging studies of sign language have only mapped the entire language system, from lexical to morphological, syntactic, semantic and pragmatic components, by using basic contrasts such as viewing full-fledged movies of people signing versus "backward layered" movies, i.e. 3 different semi-transparent ASL sentence video clips superimposed and played backwards (Newman et al., 2010a, 2010b; 2015). Furthermore, the comparison of the brain areas activated by sign language and by spoken or written language has typically been performed at the group level, by comparing a group of signers with another group of non-signers (Corina et al., 2013a). In the present work, our goals were to go beyond this state of knowledge in two distinct ways. First, our experimental design attempted to specifically isolate the cortical representation of the constituent structure of sign language. Second, we aimed to compare sign language with written language processing *within* the same subjects, by scanning deaf subjects who were native signers and who could also read written sentences fluently.

Supplementary video related to this article can be found at https://doi.org/10.1016/j.neuroimage.2017.11.040.

To achieve those goals, we adapted, to sign language, a paradigm previously developed to study the constituent structure of written language (Pallier et al., 2011), and in which the stimuli were lists of twelve words that ranged in complexity from a list of 12 unrelated words to phrases of 2 words, 3 words, 4 words, 6 words, or a full sentence of 12 words. Here, similarly, we presented deaf participants with sequences of 8 signs in which the size of syntactic constituents was systematically manipulated, from unrelated signs to phrases of 2, 4 or 8 signs. All participants were congenitally deaf adults who had acquired French Sign Language (LSF: Langue des Signes Française) as a first language and written French as a second language. With this design, our aim was to identify the brain regions involved in compositional processes in sign language comprehension (see Makuuchi et al. (2009), Goucha and Friederici (2015), Zaccarella et al. (2015), or Nelson et al. (2017) for similar approaches in written sentence processing). We also included a reading condition where participants watched sequences of words that formed either fully well-formed sentences or plain lists of words that could not merge into larger constituents, thus partially replicating the Pallier et al. (2011) experiment within the same subjects. Our main experimental questions were the following: (1) are the brain responses to the constituent size manipulation similar in sign language and in reading within deaf signers? (2) how do these responses compare to the ones in the native French speakers tested in Pallier et al. (2011)?

Materials and methods

Participants

Twenty signers of French sign language (8 men and 12 women, all right-handed) took part in the study (see Table 1 for details). All the participants had a binaural hearing loss of 75 dB or more. They were all born deaf except one, who lost hearing when she was 3 months old. All participants declared that sign language was their dominant language.

Table 1
Participants' profiles and behavioral data. The laterality quotient was obtained from the Edinburgh questionnaire (Oldfield, 1971) with one additional question about the dominant hand when signing. The participants self-reported the ages at which they started learning sign language and French (age of start of acquisition), the ages at which they considered having mastered sign language and French (age of mastering), their fluencies in sign language and French reading, on a scale from 1 (not good at all) to 7 (very good). The last rows describe the performance on three short behavioral tests of reading ability: semantic decision, lexical decision, and detection of grammatical anomalies. SD: standard deviation; Sign language: French sign language. * indicates significant values at p_{FWE}=0.05.

Deaf subjects (n = 20)		Mean	SD	Min–Max
Age (years old)		30.2	6.7	19.5–43
Laterality quotient (%)		93.6	8.6	64–100
Age of start of Acquisition (years)	Sign language*	2.5	4.0	0–16*
	French	6.3	2.9	2.5–16
Age of Mastering (years)	Sign language	12.8	6.2	4.5–25
	French	13.9	4.2	8–23
Self-rated fluency (1–7)	Sign language	6.5	0.6	5.5–7
	French reading	5.3	0.9	3.5–7
Semantic decision on French words	Time per word (s)	1.4	0.3	0.9–2.1
	Accuracy (%)	98.5	2.2	92.5–100
Lexical decision on French words	Time per word (s)	1.6	0.5	1–3
	Accuracy (%)	82	10.8	55–95
Detection of grammatical errors in French sentences	Accuracy (%)	80.5	8	62.5–95

Sixteen of them had started to learn sign language before age 5 (11 of them since birth). The remaining four participants started at the age of 5.5, 6, 8 and 16 years. 19 of them had been "oralized" (that is, they learned to lip read French and articulate it) so that they had all received linguistic input early in life. Moreover, all had received an education in French, and reached various degrees of proficiency. Our initial criterion for inclusion was to be native in sign language (age of acquisition = 0). However, in the course of recruiting participants we relaxed this criterion because, in France, it is very difficult to find true native signers as the education system still favors oralization.

In addition to their "age of acquisition", i.e. the age of start of exposure, we also asked the participants about the age at which they thought that they had reached proficiency in each language (sign language and French). We expected more variability in the amount of exposure to sign and written languages across participants than is typically the case when the question of age of acquisition is asked to native speakers of an oral language. Thus, our questionnaire aimed to capture this variability in the ages of reaching high proficiency, while acknowledging that this is a highly subjective judgment.

Background information on the participants is provided in Table 1. The experiment was approved by the regional ethical committee, and all subjects gave written informed consent and received 80 euros for their participation.

Behavioral data

Three short behavioral tests were administered to assess reading ability: semantic decision, lexical decision, and detection of grammatical anomalies. For the semantic decision task, participants were presented with a printed list of forty nouns and asked to classify each of them as quickly as possible as 'artificial' or 'natural'. All words were five letters long, had a lexical frequency above 10 ppm according to Lexique3 (see http://www.lexique.org); half of them represented man-made objects (such as radio, train) and half were natural objects (such as fruits). Accuracy and time to complete the test were recorded. For the lexical decision task, forty stimuli were used. Half were French nouns with a