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Three-dimensional grammar in the brain: Dissociating the neural correlates of natural sign language and manually coded spoken language

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ABSTRACT

In several countries natural sign languages were considered inadequate for education. Instead, new sign-supported systems were created, based on the belief that spoken/written language is grammatically superior. One such system called SJM (system językowo-migowy) preserves the grammatical and lexical structure of spoken Polish and since 1960s has been extensively employed in schools and on TV. Nevertheless, the Deaf community avoids using SJM for everyday communication, its preferred language being PJM (polski język migowy), a natural sign language, structurally and grammatically independent of spoken Polish and featuring classifier constructions (CCs). Here, for the first time, we compare, with fMRI method, the neural bases of natural vs. devised communication systems. Deaf signers were presented with three types of signed sentences (SJM and PJM with/without CCs). Consistent with previous findings, PJM with CCs compared to either SJM or PJM without CCs recruited the parietal lobes. The reverse comparison revealed activation in the anterior temporal lobes, suggesting increased semantic combinatory processes in lexical sign comprehension. Finally, PJM compared with SJM engaged left posterior superior temporal gyrus and anterior temporal lobe, areas crucial for sentence-level speech comprehension. We suggest that activity in these two areas reflects greater processing efficiency for naturally evolved sign language.

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1. Introduction

Research on sign languages of the deaf has greatly enriched our understanding of the neural representation of human language. For example, it has provided important evidence for modifying the classical view of the neural linguistic specialization, where the left hemisphere is specialized for language processing whereas the right for visuo-spatial abilities. Given the fact that sign language uses space, movement and visual imagery in ways not available to spoken language, the discovery of uniformity in the neural systems that mediate both sign and spoken language processing was an important, and largely unexpected finding (for review see MacSweeney et al., 2008).

At first, it might appear that differences between the two language types are likely to be driven by their respective modalities. Lesion and neuroimaging studies (Atkinson et al., 2005; Hickok et al., 1998; Marshall et al., 2004) indicate that it is predominantly the left-lateralized perisylvian network that supports both visual and auditory linguistic communication. Differences between the two language types are relatively minor: while sign language elicits more activation in the movement processing regions of the middle temporal gyri, spoken language activates to a greater extent the auditory processing regions of the superior temporal gyri (MacSweeney et al., 2002; Söderfeldt et al., 1997).

However, additional differences between the two language types arise from the fact that grammars of individual sign languages include structures and categories unattested in oral communication. For instance, sign languages can encode spatial

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Abbreviations: PJM, (polski język migowy), a natural Polish Sign Language; SJM, (system językowo-migowy), devised system, Signed Polish; CC, classifier construction

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information linguistically via complex predicates usually referred to as classifier constructions, CCs (Emmorey, 2003). A CC is typically based on a particular handshape referred to as a "classifier" because its choice is driven by the most general physical properties of certain classes of entities, especially their shape and size. In contrast to regular lexical signs (e.g. nouns like MAN, WOMAN or CAR), classifiers do not denote specific entities but rather refer to broad and underspecified categories, such as vehicles, flat objects, thin objects, pipe-like objects, graspable objects etc. A CC is a combination of a classifier handshape and a three-dimensional component, such as motion or relative location (typically, a certain type of hand movement imitating the real-world movement of the entity referred to). For instance, if a signer produces two classifiers representing human beings and then moves his/her hands apart horizontally, the intended meaning is likely to be as follows: 'two people walked away in opposite directions'. Importantly, the exact form of a CC is determined by the spatial and dynamic properties of the three-dimensional aspect that is being mimicked (e.g. the motion of a vehicle will be represented differently from the way an instrument, such as a screwdriver, is handled by a human being). Unlike regular lexical verbs (like GO or DRIVE), CCs are subject to a wide range of modifications, reflecting the dynamics of the actions referred to (e.g. driving slowly vs. driving rapidly). Since CCs mime real-world activities visually, the phenomenon in question is very productive in sign languages, and has no direct equivalent in spoken communication.

Previous lesion studies suggest a specific role of the right hemisphere in both comprehension and production of CCs. Right hemisphere damaged signers performed well on tests of noun, verb and sentence comprehension, whereas they were impaired on locative sentences and CC comprehension (Atkinson et al., 2005). Along the same lines, Hickok et al. (2009) found that such patients made significantly more errors producing CCs than lexical errors in a narrative production task. Further evidence for the special role of classifier constructions in sign language comes from neuroimaging studies, which suggested the role of parietal cortices as markers of this spatial mode of communication. MacSweeney et al. (2002) showed that viewing topographic sentences which included CCs, compared to non-topographic sentences (without CCs) elicited greater activation in posterior middle temporal cortices bilaterally and left inferior and superior parietal lobules. These findings were extended by McCullough et al. (2012), who showed that sentences with motion CCs engaged motion sensitive posterior middle temporal cortices bilaterally (MT+), whereas left inferior and superior parietal lobules were specifically engaged by sentences with locative CCs. On the other hand, production of CCs compared to lexical signs has been shown to activate parietal lobes bilaterally (Emmorey et al., 2002) and this activity seems to be particularly robust for location and motion CCs, whereas the activity for object CCs was more similar to that elicited by lexical signs (Emmorey et al., 2013). The latter engaged anterior temporal lobes to a greater extent than CCs, which was interpreted as resulting from increased semantic processing required in the context of naming individual objects.

Beyond CCs, sign language offers a unique opportunity to study whether devised versus natural communication systems are processed differently in the human brain. In many countries around the world, natural sign languages of the deaf were (or still are) considered inadequate for education and interpretation purposes. This linguistic discrimination has its roots in the belief that spoken/written language is grammatically superior to visual-spatial communication. In the 20th century, many artificial sign-supported systems were therefore created, with the underlying idea that linguistic communication of the deaf should be based on the grammar of the spoken language used in a particular country. The situation in Poland is a vivid example of this historical development: independent of the naturally evolved Polish Sign Language (*polski język migowy*, PJM), the artificial Signed Polish (*system językowo-migowy*, SJM) was created in the 1960s and has since then been in use in schools and on public Television. SJM is a manually coded variety of spoken Polish. SJM borrows most of its vocabulary from PJM, i.e. the two communication systems use the same content signs (nouns, verbs, etc.). Additionally, the lexicon of SJM includes invented signs for functional (grammatical) elements that exist in Polish, but not in PJM. SJM preserves the grammatical and lexical structure of spoken Polish (with respect to, among others, word order, syntactic constructions, lexical collocations). For instance, the SJM verb 'lie' ('to be at rest in a horizontal position') – similarly to its Polish equivalent '*leżeć*'-'to lie' – combines with both human and non-human referents. In contrast, the same-looking sign cannot be used in the case of inanimate objects in PJM as it iconically represents two legs (with the pointing and middle fingers extended); the use of this sign in the context of objects leads to a semantic (visual) anomaly, which is ignored in SJM. Contrary to SJM, PJM is a full-fledged natural language, structurally and grammatically independent of Polish. The Deaf community has been very reluctant in adopting SJM, not least because it's much less efficient (slower) than PJM. SJM, as opposed to PJM, contains several features that are cumbersome in the context of a sign language, such as the use of prepositions, which are normally redundant in the three-dimensional signing space (spatial relations such as "under" or "above" are manifested visually, i.e. there is no need for prepositions). The underlying idea of sign-supported communication, namely the one-to-one correspondence between spoken/written Polish and SJM, makes SJM sentences longer to articulate and more difficult to comprehend than their PJM equivalents. Similar phenomenon could be observed in other sign languages, where artificially created signing systems, usually by non deaf people for educational purposes, are less effective in information transfer rate when compared to naturally evolved sign languages (Wilbur, 2009). Unnaturalness of SJM for native, fluent PJM users could originate not only from lower efficacy but also from lower learnability specific to modality (for e.g. manually coded languages have strictly sequential inflectional morphology borrowed from spoken language). In consequence, deaf children exposed solely to manually coded language resort to creating their own linguist structures to meet the modality constraints on signed languages (Supalla, 1991).

Here, for the first time, we compared the neural bases of a manually coded spoken language (SJM) as compared to a natural sign language (PJM). Our prediction was that the difference between the natural (PJM) and the devised (SJM) modes of communication should be visible in the perisylvian regions of the left hemisphere, since the two languages differ in their efficiency of visuo-semantic integration supported by these areas. Second, we also exploited the fact that PJM offers two grammatical options: the same intended meaning may be conveyed either with or without the use of classifier constructions. This allowed us to tease apart responses to CCs by contrasting SJM and PJM sentences that are structured linearly, i.e. do not employ CCs (SJM and PJM without classifier constructions, Fig. 1), and PJM sentences that are structured three-dimensionally (PJM with classifier constructions, Fig. 1). PJM without CCs was, therefore, a very important condition in this study. It was included not only to see if CCs affect the neural processing of signed sentences, but also to check if it is possible to trace any neural correlates of those grammatical differences between PJM and SJM that go beyond the use of CCs. Based on the literature, we predicted that sentences with CCs will activate parietal cortices to a greater extent than sentences without CCs. The reversed comparison should show the engagement of the anterior temporal cortex. In order to test for possible visual differences between the sentence types, such as amount of motion, a

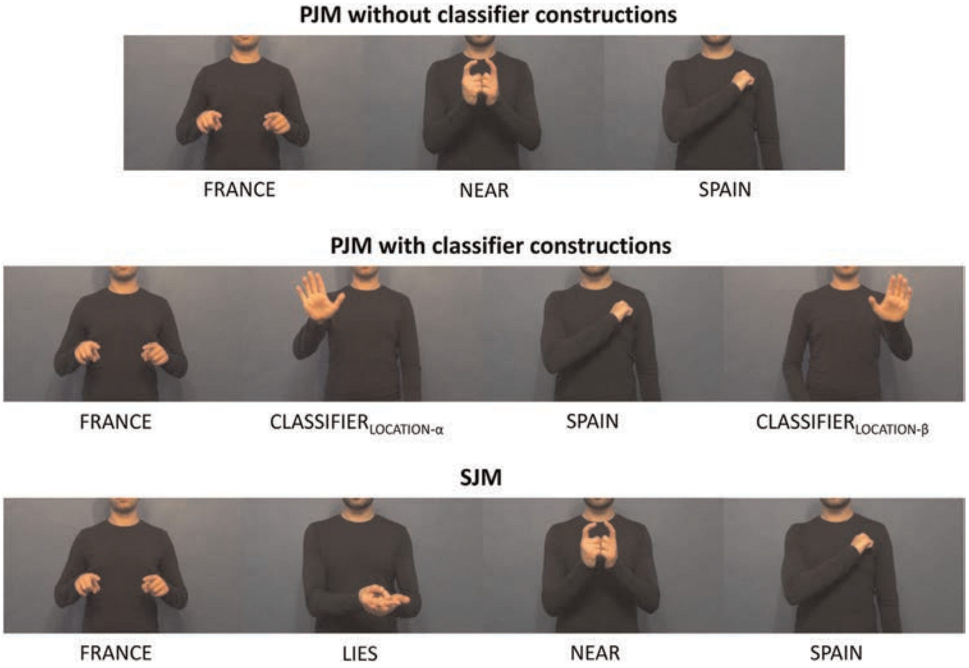

Fig. 1. Still images of the PJM, PJM_CC and SJM sentence "France lies next to Spain".

hearing sign naïve group was also included.

2. Methods

2.1. Participants

Fifteen right-handed deaf signers aged 20–36 years (mean age=28.4 years, SD=4.4) participated in the study (seven women). Thirteen were congenitally deaf, whereas the other two lost their hearing in the first two years of their lives. All deaf participants began learning SJM in primary school at age of 7. Eight were native signers, born into deaf families, whilst seven had hearing parents and acquired PJM at a later stage (in primary school). They all used PJM as their primary and preferred language, but were also fluent in SJM to which they had been exposed for many years, both at school and by watching TV programs for the deaf. The participants' signing proficiency could not be measured directly with a quantitative test as there are no PJM tests comparable to, for instance, the Sentence Reproduction Task (SRT) developed for American Sign Language (Hauser et al., 2008). However, after the fMRI experiment, the participants were asked to complete an additional on-line questionnaire, showing their understanding of all signs used in the study. The questionnaire included the following questions presented after each video clip: *1. Do you understand this clip?* (answers: *Yes*/*No*); 2. *Do you know every sign used by the signer?* (answers: *Yes*/*No*); 3. *Do you use these signs?* (answers: *Yes, all of them*/*Yes, most of them*/*No*); 4. *If you don't use any of these signs, explain why.*

Fourteen hearing non-signers were matched to the deaf signers with respect to age (mean age=27.8 years, SD=4.0), gender, handedness (all participants were right-handed) and years of education (mean=15). All participants gave informed consent in accordance with national and institutional guidelines. Study was approved by the local ethical committee at the University of Social Sciences and Humanities, Warsaw.

2.2. Materials and task

Based on grammaticality judgments elicited from 6 PJM signers, we selected 20 sentences which could be produced in PJM in two equally acceptable versions: with and without CCs. For example, the meaning 'France is next to Spain' may be conveyed by the following two sequences of signs: 1) FRANCE NEAR SPAIN (PJM), 2) FRANCE CLASSIFIER$_{\text{LOCATION-}\alpha}$ SPAIN CLASSIFIER$_{\text{LOCATION-}\beta}$ (PJM_CC). Additionally, each of such pairs was translated into SJM, following the grammar of spoken Polish. For example, the SJM equivalent of the above PJM sentences consists of the following signs: FRANCE LIE NEAR SPAIN (SJM), corresponding to the Polish sentence *Francja leży obok Hiszpanii* – literally 'France lies near Spain' (see Fig. 1 for still images of the PJM, PJM_CC and SJM examples). For some of the sentences used in this study, the difference between the version in SJM and the one in PJM without CCs was minimal (as in the example illustrated in Fig. 1); still, each SJM-PJM pair was meant to reflect a typical grammatical contrast between the two communication systems. For instance, the PJM sentence BIRD TREE SIT ('A bird sat on a tree') was juxtaposed with its SJM equivalent BIRD SIT ON TREE. Although the difference between the two may seem insignificant, it illustrates that the grammar of PJM differs from that of SJM (and spoken Polish) with respect to the basic word order and the use/lack of prepositions.

Once 20 appropriate triplets of sentences have been selected, they were all recorded as 60 video clips (20 clips per condition). An additional clip with the signer at rest was also recorded to serve as the baseline condition. Participants were instructed to watch passively all the sentences and pay attention to their meaning. In order to focus their attention on the manual code, clips were recorded with the signer visible from neck down, with his face outside the frame. The face was not included as there are clear differences between the PJM and SJM in how the face is used in communication, that would likely affect brain activity. In PJM, facial expressions are important parts of the grammar and convey information about emotion or intonation, whereas in SJM the signer clearly articulates whilst simultaneously sending messages of signs corresponding to individual words. At the same time, face being a salient stimulus, would likely capture the attention of the hearing sign naïve participants more that the manual code. The recordings were re-evaluated by 5 PJM signers in order to double-check that both CC and CC-less sentences were perceived as grammatically acceptable. The PJM signers who provided grammaticality judgments and who re-evaluated the recordings did not participate in the fMRI study.

2.3. Procedure

Videos were presented using Presentation software (Neurobehavioral Systems). A hybrid design was chosen with 6 linguistic blocks containing 10 sentences, alternated by 6 baseline blocks where a video of the signer resting was shown. In the linguistic blocks the order of three conditions was pseudorandomized with a constraint of no more than 2 presentations of the same type of sentence in sequence. However, each condition within the block was modeled independently. The sentences within each triplet (PJM, SJM and PJM_CC) were counterbalanced between the blocks. The mean duration of sentences varied from 4 to 10 s (mean time=6 s) and did not differ between the three conditions. These videos were presented with various inter stimulus intervals ranging from 5 to 7 s. The duration of baseline block was held constant at 10 s.

2.4. Image acquisition

Structural and functional MR data were acquired using a 3 T Trio TIM Siemens scanner equipped with a 32-channel head coil at the Laboratory of Brain Imaging at Nencki Institute, Warsaw. For anatomical reference and spatial normalization, high resolution T1-weighted images were acquired with the following specifications: FOV=256; TR=2530, TE=3.32, flip angle=7; voxel size=$1 \times 1 \times 1$ mm^3.

For functional images, 33 EPI axial slices were acquired in interleaved ascending order, covering the whole brain, with repetition time (TR) of 2190 ms, an echo time (TE) of 30 ms, flip angle=90, FOV=192, 64×64 matrix, 3×3 mm^2 in-plane resolution and 3.6 mm slice thickness (no gap).

2.5. Image analysis

For data preprocessing and analysis we used BrainVoyager Q.X 2.8 software (Brain Innovation, Maastricht, The Netherlands). Preprocessing of the functional data included interleaved slice time correction (using cubic spline interpolation), 3-dimensional rigid-body motion correction (using trilinear-sinc interpolation), linear trend removal, temporal high-pass filtering (using frequency-space filter with a cutoff of 0.008 Hz) and spatial smoothing (FWHM 5-mm Gaussian kernel). Estimated motion plots were examined for each participant in order to identify movement and eliminate runs with head motion greater than 3 mm of translation in any direction or 3 degrees of rotation about any axis (for which no runs were eliminated). For each participant, functional images were coregistered to the T1 anatomical images. Subsequently, anatomical images were transformed into Talairach stereotaxic space, and this transformation was applied to the aligned functional data.

Data were analyzed using the general linear model (GLM). For each participant, we calculated the GLM including experimental conditions (SJM, PJM, PJM_CCs, baseline) and six motion correction parameters (x, y, z for translation and for rotation). Predictors' time courses were modeled with a linear model of hemodynamic response using two-gamma function. Beta values of baseline condition were subtracted from each condition of interest (SJM, PJM, PJM_CCs). Next, resulting beta values were entered into 2 (deaf and control) × 3 (SJM-baseline, PJM-baseline, PJM_CCs-baseline) random-effects ANOVA for group-level comparisons. Areas of activation were identified at a voxel-wise uncorrected level of $p < 0.005$. A cluster threshold was used to correct for multiple comparisons (Forman et al., 1995; Xiong et al., 1995). It was calculated using Brain Voyager's Cluster Threshold Estimator, which employs a bootstrapping procedure to calculate the minimum cluster size that yields a corrected threshold of $p < 0.05$. Applying the cluster threshold resulted in a $< 5\%$ chance of discovering false-positive voxels in the key analyzes.

Region of interest (ROI) analysis was performed for detailed comparisons between the three experimental conditions in both deaf and hearing subjects. ROIs were defined as 10mm spheres around peaks of activation in (SJM+PJM+PJM_CCs) – (baseline) contrast, calculated for all subjects ($p < 0.005$, uncorrected). Importantly, contrast used for ROIs definition is orthogonal to comparisons performed in further ROI analysis. Thus, our analysis was not affected by double-dipping effect (Kriegeskorte et al., 2009). NeuroElf (www.neuroelf.net) and Talairach Daemon (http://www.talairach.org/daemon.html) software was used to identify local maxima of activation and ROIs were defined around peaks within the classic language regions in the left hemisphere (Broca's area in the inferior frontal gyrus, anterior and posterior STG, anterior temporal lobe) and parietal cortices, bilaterally.

Standard BrainVoyager routines were used to calculate beta weight for each ROI, condition and subject, using the same GLM model as in the whole-brain analysis. Resulting beta weights were then used as dependent measures. All comparisons were done using two-tailed paired t tests.

3. Results

3.1. Behavioral results

The deaf participants' answers to the first three questions on the online questionnaire were analyzed with repeated measures ANOVA with factor signed communication on 3 levels (SJM, PJM and PJM_CC). In case of the first two questions measuring comprehension of presented sentences and knowledge of the used signs, there were no significant differences between the 3 conditions. However, consistently with predictions of greater reliance on PJM than SJM in every day communication, a significant difference between the conditions was found for the question "*Do you use these signs?*" ($F(2,13)=15.09$, $p < 0.001$). Deaf participants declared that they use more PJM than SJM signs ($p < 0.001$), there was also a trend for PJM_CC > SJM difference ($p=0.059$).

3.2. FMRI results

Table 1 shows a list of brain areas that increased their activity for each type of signed communication against baseline, for both deaf and hearing subjects. In both subject groups the activity patterns between conditions were largely overlapping, and included mainly the motion sensitive inferior temporal areas (MT+) and postcentral gyri in the case of control subjects and additionally the bilateral perisylvian language areas and parietal lobes in the case of deaf subjects (Fig. 2).

To uncover activations specific for each type of signed communication, direct comparisons between 3 conditions: SJM, PJM and PJM_CC were performed for the deaf participants (Table 2). First, stronger activation for PJM than SJM was found only a in a single cluster in the left posterior STG (Fig. 3, upper panel). The reverse comparison produced no significant results even at an exploratory threshold of $p=0.01$, uncorrected. Second, PJM_CCs compared to either SJM or PJM recruited the parietal areas (bilateral inferior parietal lobule, IPL and right superior parietal

Table 1
The local maxima of brain areas of increased activity for each type of signed communication against baseline for deaf and hearing subjects.

Region	Brodmann's area	*x*	*y*	*z*	T stat	Voxels
Deaf signers						
PJM > baseline						
RH Middle Occipital Gyrus	BA37	51	−70	4	11.94	1183
RH Superior Temporal Gyrus	BA22	63	−37	13	9.51	
RH Fusiform Gyrus	BA37	42	−43	−14	5.71	
LH Middle Occipital Gyrus	BA37	−48	−70	4	11.15	1396
LH Middle Temporal Gyrus	BA22	−48	−40	7	10.65	
LH Middle Temporal Gyrus	BA21	−57	2	−8	7.39	
LH Fusiform Gyrus	BA37	−45	−40	−11	5.77	
LH Superior Frontal Gyrus	BA6	−3	−1	64	7.10	147
LH Precentral Gyrus	BA6	−48	2	49	6.55	528
LH Middle Frontal Gyrus	BA9	−54	20	28	5.37	
LH Inferior Parietal Lobule	BA40	−33	−37	43	4.82	
LH Inferior Frontal Gyrus	BA9	−48	8	28	4.27	
LH Superior Parietal Lobule	BA7	−30	−58	40	3.92	
RH Middle Temporal Gyrus	BA22	54	5	−11	5.80	53
RH Precentral Gyrus	BA9	36	5	34	5.19	307
RH Middle Frontal Gyrus	BA46	48	29	25	5.07	
PJM_CC > baseline						
RH Middle Occipital Gyrus	BA37	51	−70	4	12.77	1113
RH Superior Temporal Gyrus	BA22	63	−37	13	9.97	
RH Superior Temporal Gyrus	BA41	45	−34	7	8.63	
RH Fusiform Gyrus	BA37	42	−43	−14	5.86	
LH Middle Occipital Gyrus	BA37	−48	−70	4	11.13	905
LH Middle Temporal Gyrus	BA22	−48	−40	7	8.99	
LH Fusiform Gyrus	BA37	−42	−46	−11	5.14	
LH Inferior Parietal Lobule	BA40	−33	−37	43	7.81	816
LH Precentral Gyrus	BA6	−48	−1	52	6.09	
LH Inferior Frontal Gyrus	BA9	−51	5	31	5.21	
RH Postcentral Gyrus	BA3	27	−34	43	5.86	279
RH Superior Parietal Lobule	BA7	24	−58	61	5.65	
RH Inferior Parietal Lobule	BA40	33	−37	52	5.38	
RH Precentral Gyrus	BA6	42	−4	52	5.38	265
RH Inferior Frontal Gyrus	BA9	36	5	31	4.23	
SJM > baseline						
RH Middle Occipital Gyrus	BA37	51	−70	4	11.44	1020
RH Superior Temporal Gyrus	BA22	63	−37	10	8.74	
RH Superior Temporal Gyrus	BA41	45	−34	7	8.57	
RH Fusiform Gyrus	BA37	42	−43	−17	5.19	
LH Middle Occipital Gyrus	BA37	−48	−70	4	10.53	1218
LH Middle Temporal Gyrus	BA22	−48	−40	7	9.91	
LH Superior Temporal Gyrus	BA21	−54	−22	1	6.31	
LH Precentral Gyrus	BA6	−51	−1	49	6.68	526
LH Middle Frontal Gyrus	BA9	−54	20	31	5.92	
LH Inferior Frontal Gyrus	BA9	−48	8	25	5.11	
LH Inferior Parietal Lobule	BA40	−33	−37	43	4.75	
LH Medial Frontal Gyrus	BA6	−3	−1	61	6.18	107
RH Middle Frontal Gyrus	BA46	51	29	22	4.57	59
RH Inferior Frontal Gyrus	BA9	36	8	31	4.23	148
Hearning nonsigners						
PJM > baseline						
RH Inferior Temporal Gyrus	BA37	45	−64	−2	10.61	316
LH Inferior Temporal Gyrus		−48	−70	1	10.02	514
LH Inferior Parietal Lobule	BA40	−48	−34	25	4.88	
RH Postcentral Gyrus	BA5	30	−43	58	5.33	136
LH Postcentral Gyrus	BA3	−51	−19	37	4.68	82
LH Inferior Parietal Lobule	BA40	−33	−37	46	4.39	71
PJM_CC > baseline						
RH Inferior Temporal Gyrus	BA37	45	−64	−1	10.96	368
LH Inferior Temporal Gyrus		−48	−70	1	10.23	617
LH Inferior Parietal Lobule	BA40	−51	−37	25	5.88	
RH Postcentral Gyrus	BA5	30	−43	58	6.31	238
RH Insula	BA13	51	−34	22	4.61	94
LH Inferior Parietal Lobule	BA40	−33	−40	46	4.49	108
RH Cuneus	BA31	24	−82	28	4.45	62
LH Middle Occipital Gyrus	BA18	−27	−91	13	4.08	46
LH Postcentral Gyrus	BA2	−60	−22	34	3.75	50
SJM > baseline						
RH Middle Temporal Gyrus	BA37	45	−61	4	9.63	296
LH Inferior Temporal Gyrus		−48	−70	1	9.26	477
LH Insula	BA13	−48	−37	25	4.51	
RH Postcentral Gyrus	BA5	30	−43	58	5.48	161
LH Inferior Parietal Lobule	BA40	−36	−43	55	4.97	87
LH Inferior Parietal Lobule	BA40	−63	−25	34	4.57	99

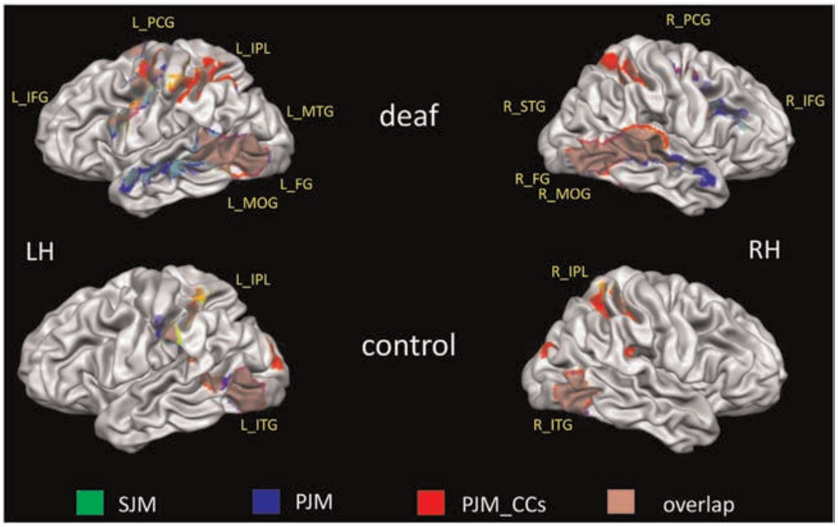

Fig. 2. Brain activity overlap between conditions in deaf and control subjects. IFG-inferior frontal gyrus, PCG-postcentral gyrus, IPL-inferior parietal lobule, STG-superior temporal gyrus, MTG-middle temporal gyrus, ITG-inferior temporal gyrus, FG-fusiform gyrus, MOG-middle occipital gyrus. Thresholds: $p < 0.005$ voxel-wise, $p < 0.05$ cluster-wise.

lobule, SPL) to a greater extent, whereas both SJM and PJM elicited more activation in the anterior temporal lobes (bilateral MTG and STG) and the left cingulate gyrus compared to PJM_CCs (Fig. 3, middle and lower panels).

To test whether these differences were specific to deaf signers and thus, were not a result of visual differences between the analyzed types of signed sentences (the amount of space and motion used by the signer), we performed similar comparisons in the control group. We found that in those sign-language naïve subjects, the only significant differences between the conditions were present for the PJM_CCs comparison with PJM and SJM, with greater activity mainly in the visual areas (bilateral lingual gyri, left inferior occipital gyrus and right fusiform). This confirms that the effects described in the previous paragraph were not due to the types of motion used by the signer, but to the actual linguistic form of the signed sentences.

We further explored language related regions of the left hemisphere and the bilateral parietal cortices in an ROI analysis in both hearing and deaf subjects (Fig. 4). Again, we confirmed that there were no differences in activation between the experimental conditions in hearing participants. In case of deaf subjects, differences between conditions were found in anterior and posterior STG, anterior temporal lobe and bilateral parietal cortices. In the anterior STG, viewing PJM and SJM resulted in higher activity than in the case of PJM_CCs ($t(14)=2.97$, $p=0.01$ and $t(14)=2.56$, $p=0.023$, respectively), whereas in the posterior STG there was a significant difference only between PJM and SJM with higher signal for the former ($t(14)=3.76$, $p=0.002$). In the left anterior temporal lobe, all conditions differed significantly with the highest contrast estimated in PJM then SJM and PJM_CC (PJM > SJM-$t(14)=2.61$, $p=0.021$, PJM > PJM_CC-$t(14)=4.47$, $p=0.001$, SJM > PJM_CC – $t(14)=2.69$ $p=0.018$). Finally, PJM_CCs activated both left and right inferior parietal lobules to a greater extent than PJM and SJM (left-$t(14)=3.83$, $p=0.002$ and $t(14)=2.99$, $p=0.01$, right-$t(14)=2.46$, $p=0.027$ and $t(14)=2.38$, $p=0.032$, respectively). On the whole, ROI analysis largely confirmed the results obtained on the whole brain, providing additional information on the difference between PJM and SJM in the left anterior temporal lobe.

4. Discussion

A typical Polish deaf person is able to communicate in both PJM and SJM. However, many individual signers and organizations oppose the use of SJM in educational and interpreting services. Being a one-to-one calque of spoken Polish, SJM is often perceived as unnatural and less efficient. This perception may be related to the fact that it lacks classifier constructions altogether, and contains several features that are cumbersome in a sign language, such as the above-mentioned use of prepositions. Still, numerous educators and interpreters prefer to use SJM because of its alleged precision (i.e. structural closeness to Polish). Additionally, SJM is often considered an efficient tool in teaching Polish to the deaf. Here, we were interested whether the comprehension of PJM and SJM produces similar patterns of brain activity in the deaf or whether there are specific brain areas that can differentiate between these two communication types, due to, for example, differences in the efficiency of their visuo-semantic integration. In addition, we were interested in the neural representation of classifier constructions, a linguistic phenomenon of key importance to the grammatical structure of PJM and other natural sign languages.

In agreement with our hypothesis and in line with many previous studies (Capek et al., 2008; Petitto et al., 2000; Sakai et al., 2005), all three signed communication modes engaged left and right perisylvian language areas (IFG, MTG and STG) in the deaf, together with parietal, motor/premotor and temporal motion sensitive areas. This pattern was largely overlapping and restricted to parietal and temporal motion sensitive areas in the control hearing non-signers.

When deaf participants were watching sentences involving classifier constructions (PJM_CCs) they engaged the inferior parietal lobules bilaterally and the right superior parietal lobule to a greater extent than when watching sentences constructed with lexical signs. This finding is in line with previous studies, which showed a specific involvement of the parietal areas during either comprehension (MacSweeney et al., 2002, McCullough et al., 2012) or production (Emmorey et al., 2002, 2013) of classifier constructions. However, in contrast to both MacSweeney et al. (2002) and McCullough et al. (2012), and in line to Emmorey et al. (2013), the activity found in the present study was bilateral with a stronger engagement of the right hemisphere. MacSweeney et al. (2002) suggested that the left parietal lobe is specifically involved in processing the precise configuration of the hands in space in order to represent objects, agents and actions. Whereas McCullough et al. (2012) argued that this brain area may be particularly

Table 2
The local maxima of brain areas of increased activity for direct comparisons between 3 conditions in deaf and hearing subjects.

Region	Brodmann's area	x	y	z	T stat	Voxels
Deaf signers						
PJM > SJM						
LH Superior Temporal Gyrus	BA39	−54	−52	13	4.16	42
SJM > PJM						
–						
PJM_CC > SJM						
LH Middle Frontal Gyrus	BA6	−21	−10	55	5.45	86
LH Inferior Parietal Lobule	BA40	−36	−37	40	5.17	241
LH Precuneus	BA7	−18	−70	43	4.45	
RH Middle Temporal Gyrus	BA19	39	−58	13	5.08	198
RH Middle Occipital Gyrus	BA19	36	−73	19	4.54	
RH Superior Parietal Lobule	BA7	24	−55	58	4.78	226
RH Inferior Parietal Lobule	BA40	30	−40	37	4.47	
RH Middle Frontal Gyrus	BA6	24	−10	49	4.66	96
LH Middle Temporal Gyrus	BA37	−45	−61	−2	4.58	123
LH Cuneus	BA18	−27	−70	19	4.43	42
RH Insula	BA13	48	−37	19	4.14	107
RH Inferior Parietal Lobule	BA40	63	−31	25	3.75	
SJM > PJM_CC						
LH Middle Temporal Gyrus	BA21	−63	−16	−8	4.49	182
LH Superior Temporal Gyrus	BA21	−48	−25	−2	4.32	
LH Posterior Cingulate	BA23	−3	−28	25	4.41	118
RH Middle Temporal Gyrus	BA21	57	−22	−2	4.19	44
RH Insula	BA13	30	26	1	4.13	54
PJM_CC > PJM						
LH Precuneus	BA7	−18	−64	46	5.21	422
LH Inferior Parietal Lobule	BA40	−39	−31	37	4.74	
LH Postcentral Gyrus	BA5	−33	−43	58	4.60	
RH Inferior Parietal Lobule	BA40	63	−28	31	4.71	104
RH Superior Parietal Lobule	BA7	21	−58	61	4.58	227
RH Precuneus	BA7	15	−64	52	3.82	
LH Lingual Gyrus	BA19	−27	−67	−2	4.34	40
RH Middle Frontal Gyrus	BA6	24	−10	52	4.22	70
LH Middle Frontal Gyrus	BA6	−21	−10	55	4.22	84
RH Middle Occipital Gyrus	BA19	36	−73	19	4.04	50
PJM > PJM_CC						
LH Middle Temporal Gyrus	BA21	−63	−16	−8	5.86	465
LH Superior Temporal Gyrus	BA21	−57	−1	−5	5.83	
LH Cingulate Gyrus	BA23	0	−25	25	5.52	366
RH Precuneus	BA31	9	−70	28	5.24	
LH Precuneus	BA21	−9	−70	28	4.75	
RH Superior Temporal Gyrus	BA22	57	−7	−2	5.46	154
RH Middle Frontal Gyrus	BA9	39	20	31	4.52	58
Hearning nonsigners						
PJM > SJM						
–						
SJM > PJM						
–						
PJM_CC > SJM						
LH Inferior Occipital Gyrus	BA17	−15	−88	−5	5.26	238
RH Lingual Gyrus	BA17	15	−85	1	4.99	161
RH Fusiform Gyrus	BA19	24	−76	−11	4.27	
RH Inferior Temporal Gyrus	BA37	51	−70	1	4.22	49
SJM > PJM_CC						
–						
PJM_CC > PJM						
LH Lingual Gyrus	BA17	−6	−85	1	5.81	620
RH Lingual Gyrus	BA18	6	−82	1	5.71	
LH Thalamus (Anterior Nucleus)		−6	−4	13	4.04	58
PJM > PJM_CC						
–						

important for comprehending static location expressions (as opposed to motion sentences) since in this case the precise configuration of the hands in space must be mapped to a conceptual representation of the spatial relationship between entities. Importantly, both studies required participants to make explicit judgments about the semantic correctness of presented sentences. It is therefore plausible that in such case the engagement of the left hemisphere is much more pronounced. In the present study, we looked at implicit language processing therefore the pattern of obtained results might be different. Further, the PJM_CCs condition included sentences with both locative and motion classifiers. Production of these two kinds of CCs compared with lexical signs resulted in greater activation of bilateral superior parietal cortex (Emmorey et al., 2013). Last but not least, right parietal cortex involvement in these functions may explain why signers with damage to the right hemisphere showed deficits on locative sentences and classifier comprehension (Atkinson et al., 2005).

We observed greater activation in the anterior temporal lobes for PJM and SJM sentences compared with PJM_CCs sentences. It has been shown previously (Rogers et al., 2004) that there is

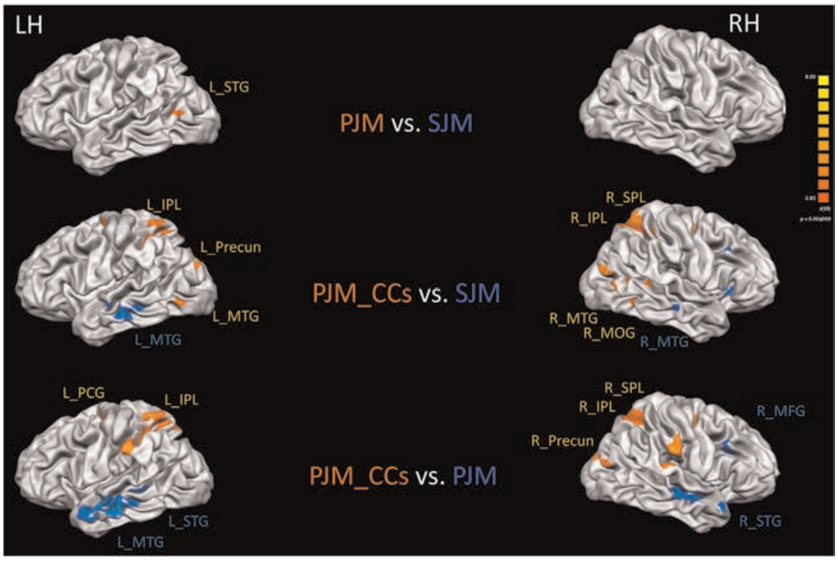

Fig. 3. Brain activity for direct comparisons between the 3 conditions in deaf subjects. MFG-middle frontal gyrus, IPL-inferior parietal lobule, SPL-superior parietal lobule, STG-superior temporal gyrus, MTG-middle temporal gyrus, Precun-Precuneus, MOG-middle occipital gyrus. Thresholds: $p < 0.005$ voxel-wise, $p < 0.05$ cluster-wise.

greater activation in anterior temporal lobes for specific-level concepts (e.g. a carrot), where increased semantic processing is required, than for basic level concepts (e.g. a vegetable). Further, Emmorey et al. (2013) showed that naming objects with more specific lexical signs compared to production of classifier constructions engaged anterior temporal lobes. However, in the present study PJM_CC condition, besides classifiers, included lexical nouns to convey object information, so in terms of semantic precision this condition was not different from PJM or SJM. A potential explanation of the difference in ATL activity observed in the current study might be related to basic semantic combinatory processes. Left ATL appears specialized to the combination of predicates with other predicates to derive more complex predicates (as in ‘red boat’) but not predicates with their arguments (as in ‘eats meat’) or numerical quantifications (as in ‘two boats’) (Bemis and Pylkkänen, 2011, 2012). When lexical items are brought together in relation to one another in sentences or discourses, it seems that the ATL activity reflects the greater extent to which lexical semantic representations can be refined. However, it remains to be determined whether PJM or SJM sentences produce more activity in left ATL than PJM_CC because of increased semantic combinatory processes. Additionally, there is an interesting debate whether anterior temporal lobes can serve as an amodal hub that integrates information associated with a concept (Patterson et al., 2007). Based on recent meta-analysis, it appears that this region may not be fully amodal, as visual object processing often recruits ventral anterior temporal lobe structures, while linguistic and auditory processing tend to recruit lateral anterior temporal lobe structures (Visser et al., 2009). The results of the present study may shed new light on this issue, as lateral anterior temporal lobe structures show higher brain activity for linguistic processing of PJM and SJM sentences than sentences with classifier

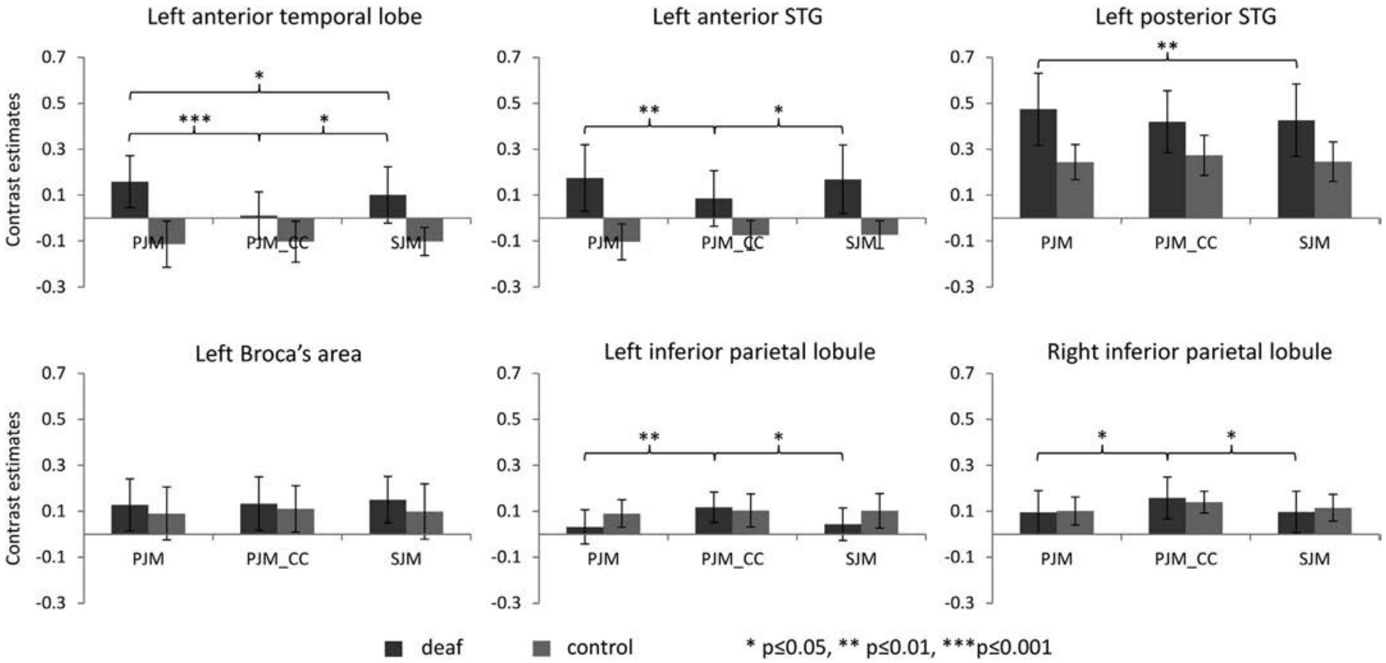

Fig. 4. Contrast estimates extracted from each of the selected regions of interest. Error bars represent standard deviation.

constructions (PJM_CCs).

It could be argued that some effects observed in our study are a consequence of visual differences between different types of signed utterances. Conveying information by means of classifier constructions may be claimed to involve greater amount of physical motion in space than composing sentences of lexical units only. In order to have a clearer view of this, we performed comparisons between the 3 conditions in the hearing control group. The only significant differences were found for PJM_CCs compared to PJM and SJM, with greater activity for PJM_CCs mainly in the visual areas. This confirms that the different responses to sentences with/without classifier constructions were not due to the types of motion produced by the signer, but to the actual linguistic form of the signed sentences.

Last but not least, we found that PJM, as compared to SJM, in a whole brain analysis, activated to a greater extent the left posterior part of the superior temporal gyrus. Historically, the left superior temporal gyrus (STG) was identified as crucial for understanding speech (Wernicke, 1874). This region shows greater activity associated with intelligible speech relative to a complex acoustic stimulus with speech-like characteristics (Zahn et al., 2000) even in a passive listening task (Narain et al., 2003). Left posterior superior temporal regions have been also identified as showing a relatively selective response to sentence stimuli over nonsentence stimuli (Vandenberghe et al., 2002). Further, in sign language studies, this structure has been found to be more active when deaf or hearing subjects are asked to pay attention to the meaning of sentences in British Sign Language (BSL), as compared to nonsensical "Tic Tac sentences" (a code used by bookmakers at the races to communicate about the odds on horses).

Although the peak activations for PJM and SJM in the STG had the same coordinates, the extent of the PJM cluster was larger than in the case of the SJM. The peak of the observed PJM > SJM difference [Talairach coordinates $x=-54$, $y=-52$, $z=13$] was located more posterior to the PJM > baseline and SJM > baseline peaks [Talairach coordinates $x=-48$, $y=-40$, $z=7$ for both contrasts]. The PJM > SJM difference was thus partially due to this greater extent of PJM activation. We thus think that PJM evokes greater activation than SJM either because the relationship between mastery/efficiency of language (greater for PJM than SJM) and neural activity in the STG might be linear, similar to the one described by Dehaene and colleagues (2010) for written language and by Wong et al. (2007) for spoken language. Thus, greater processing efficiency would lead to stronger activations. Secondly, studies of expertize in the sensory systems show cases of progressive, spatial shift in activations as expertize is acquired (reviewed by Ahissar and Hochstein, 2004). The difference in STG activation pattern for PJM might have emerged through such a spatial shift, a consequence of our subjects' superior experience in PJM language.

Additionally, in the region of interest analysis we found a significant difference between PJM and SJM not only in the posterior STG, but also in the left anterior temporal lobe. This structure besides it role in semantic combinatory processes described above, has been also implicated in sentence-level processing and syntax. Specifically the left anterior temporal lobe was found to be more active for sentences than random word lists either constructed from real words or pseudowords (Humphries et al., 2006); sentences presented in the listener's native language compared to an unfamiliar language (Schlosser et al., 1998) and sentences vs. other types of like environmental sound sequence events (e.g., tires squealing followed by a crash; Humphries et al. (2001)). Therefore, it has been proposed that the left anterior temporal is carrying out constituent and phrase structure analysis (Humphries et al., 2006).

We propose that PJM, a natural sign language, activates the posterior superior temporal regions and left anterior temporal lobe more strongly than SJM, because it is more effective in conveying information than the latter. If confirmed by further studies, this finding is of possible great importance to future education and interpreting practices. Going back to the exemplary sentence in the method section, the lexical verb LIE in the SJM sentence is a highly iconic sign, whose form (with the index and middle fingers extended) clearly alludes to a lying person. From a semantic point of view, the use of this sign in the context of a country is quite inappropriate. This kind of mismatches in the mapping of spoken Polish onto the visual modality of sign language has long been the focal point of criticism addressed at SJM. Our study shows that these concerns may find a reflection in the neural representation of sign language communication.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2015.03.031.

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