NeuroImage 195 (2019) 38–47

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

The facilitative effect of gestures on the neural processing of semantic complexity in a continuous narrative

Paulina Cuevas [a,b,*], Miriam Steines [a,b], Yifei He [a,b], Arne Nagels [c], Jody Culham [d], Benjamin Straube [a,b]

[a] Translational Neuroimaging Marburg, Department of Psychiatry and Psychotherapy, Philipps-University Marburg, Rudolf-Bultmann-Straße 8, 35039, Marburg, Germany
[b] Center for Mind, Brain and Behavior - CMBB, Hans-Meerwein-Straße 6, 35032, Marburg, Germany
[c] Department of General Linguistics, Johannes Gutenberg University Mainz, Jakob-Welder-Weg 18, 55128, Mainz, Germany
[d] The Brain and Mind Institute, University of Western Ontario, London, Ontario N6A 3K7, Canada

ARTICLE INFO

Keywords:
Co-speech gestures
Semantic complexity
Default mode network
Idea density
Discourse perception

ABSTRACT

Gestures are elemental components of social communication and aid comprehension of verbal messages; however, little is known about the potential role of gestures in facilitating processing of semantic complexity in an ecologically valid setting. The goal of this study was to investigate whether cognitive load, as indexed by semantic complexity, is modulated by the presentation of gestures accompanying speech. Twenty healthy participants watched 16 video clips of a short narrative while instructed to carefully listen to and watch the narrator while functional magnetic resonance imaging (fMRI) data were acquired. The videos contained passages with and without various co-speech gestures, as well as passages where the semantic complexity was either low or high, as measured by the metric of idea density. Increasing semantic complexity led to reduced activation within the default mode network (DMN); whereas, presents of gestures decreased activation in language-related regions (left middle temporal gyrus and left inferior frontal gyrus) and increased activation in high-level visual and multimodal regions of occipitotemporal cortex. Most interestingly, an interaction between semantic complexity and gestures was observed in a language-related area in left anterior temporal cortex; specifically, increasing gestures led to a greater drop in activation with high vs. Low semantic complexity. These results provide evidence that the facilitation of gestures on semantic processing, particularly for complex narratives, is reflected in the neural substrates of language processing.

1. Introduction

Complexity is an abstract concept associated with numerous systems in our everyday life. One of these systems is language. However, the calculation of complexity in language represents a challenge. To achieve this task, different metrics have been developed. The clear majority of complexity metrics has focused on syntactic complexity (Cheung and Kemper, 1992). In contrast, there are few metrics with a focus on the complexity of the *content*, which may be especially relevant for the detection of mental disorders (Snowdon et al., 1996). One metric for content complexity is idea density (hereafter ID)[1], which measures the quantity of ideas expressed with a specific number of words in spoken and written language (Spencer et al., 2012). Ideas represent elementary propositions such as predicates, adjectives, or connectives (Snowdon et al., 1996). Propositions are described as semantic units, which contribute to building the general meaning of a sentence (Bryant et al., 2013). Thus, they not only represent the content but also the relationship between the elements of a phrase (Farias et al., 2012). Currently, different methods for the calculation of ID exist, some of which are based on Turner and Greene's (1977) described methods. However, the majority of recent studies utilized an automatic program for the calculation of ID in English language texts: Computerized Propositional Idea Density Rater (CPDR) (Brown et al., 2008). Moreover, ID has been adopted in various studies that analyzed the complexity of produced speech of diverse populations: patients with dementia (Engelman et al., 2010; Iacono et al., 2009; Kemper et al., 2001; Mortimer and Borenstein, 2012; Riley et al., 2005; Sirts et al., 2017), older subjects (Farias et al., 2012; Ferguson et al., 2014; Kemper et al., 2001; Mitzner and Kemper, 2003;

* Corresponding author. Rudolf-Bultmann-Str.8, 35039, Marburg, Germany.
E-mail address: cuevas@staff.uni-marburg.de (P. Cuevas).

[1] Also known as propositional idea density, proposition density and P-density.

https://doi.org/10.1016/j.neuroimage.2019.03.054
Received 1 March 2019; Accepted 25 March 2019
Available online 28 March 2019
1053-8119/

Spencer et al., 2012, 2014), patients with aphasia (Bryant et al., 2013; Fromm et al., 2016), patients with schizophrenia (Cohen et al., 2014; Covington et al., 2007; Moe et al., 2016), and people with mild cognitive impairment (Roark et al., 2011). High ID values are associated with intact cognition despite Alzheimer's disease (Iacono et al., 2009), whereas low values are related to greater cognitive impairment (Snowdon et al., 1996). Evidence in the literature suggests that ID is a reliable metric for the assessment of semantic complexity, a practical tool for the early diagnostic and prediction of mental disorders and pathology, and an indicator of language deterioration (Ferguson et al., 2014). Thus, the metric gives an insight into the expressivity of language and the cognitive reserves of participants. Moreover, ID has the advantage of being easy to calculate even for non-experts users and presents an ecologically valid method (Chand et al., 2012a; Farias et al., 2012). Despite growing research estimating semantic complexity in the produced texts of specific populations, little is known with regard to the neurobiological correlates of ID, especially during the processing of naturalistic stimuli.

In general, the activation of default mode network (hereafter DMN) is associated with the complexity of a given task. The DMN (also called "resting state network" or "task negative network") comprises a group of functionally connected brain regions, known to be active during the absence of goal-directed or cognitively demanding tasks (Raichle et al., 2001). DMN activation is associated with internal tasks such as self-reflection, thinking, remembering, planning, social cognition, and passive states (Andrews-Hanna et al., 2007; Fransson and Marrelec, 2008; Hu et al., 2017; Mazoyer et al., 2001; Supekar et al., 2010). Some postulate that the DMN is deactivated if the task provokes no self-related mental processing (Fransson and Marrelec, 2008). Alternatively, there is evidence suggesting that the DMN remains active, although attenuated, during diverse activities, which may be not cognitively demanding for the subjects (Bosch et al., 2010; Mazoyer et al., 2001; Wilson et al., 2008). Thus, there seems to be a relation between the attenuation of the DMN and the difficulty and requirements of the task (Broyd et al., 2009; Esposito et al., 2006; Greicius and Menon, 2004). In fact, in several studies, the DMN remained active, at least partially, during language-related tasks, e.g., the perception and production of discourse (AbdulSabur et al., 2014; Binder et al., 1999; Seghier and Price, 2012; Wilson et al., 2008; Xu et al., 2005). Additionally, the network was found to be associated with semantic processing (Wilson et al., 2008). Despite the putative relation between DMN activity and complexity measures and its involvement during the perception of discourse, a study measuring the complexity in terms of ID is still missing. In particular, the relationship between DMN and semantic complexity has not yet been examined in "real-life situations" in which auditory-visual information such as co-speech gestures are presented in a natural and coherent context.

Social communication is a complex process that requires simultaneous integration of multisensory cues like gestures, facial expressions and lip movements with auditory speech signals (Dick et al., 2009; Goldin-Meadow and Alibali, 2013; Hostetter, 2011; Hubbard et al., 2009; Kelly et al., 2004). Comprehension of language is incremental and dynamic in nature. It also depends on the integration of additional information, such as meaningful hand and arm movements (McNeil et al., 2000). In this respect, gesture provides the interlocutor with useful (extralinguistic) material and increases the probability of interpreting the message in accordance with the intent of the speaker (Dick et al., 2009; Goldin-Meadow and Alibali, 2013). Gestures also provide insight into the thoughts and points of view that remain unspoken (Goldin-Meadow, 2006; McNeill, 1992). In fact, gestures influence the way in which we express ourselves because they allow the speaker to send information in a more efficient way, because not all kinds of gestures are bound by rules, unlike speech, and because gestures express information that may not be possible to code through words (McNeill, 1992). Thus, gestures impact communication by helping with the disambiguation of the message (Dick et al., 2009; Holle and Gunter, 2007), organizing and stressing important features of a narrative (Goldin-Meadow and Alibali, 2013; McNeill, 1992) and even retaining the attention of the listener (Hostetter, 2011). Moreover, they enhance the performance in memory tasks (Goldin-Meadow et al., 2001; Straube et al., 2009) and have an important role in language acquisition and foreign language learning (Goldin-Meadow and Alibali, 2013; Macedonia, 2014).

As gestures and their neural processing have been investigated extensively in recent years, there is mounting evidence that they influence the perception of language positively (Beattie and Shovelton, 1999; Dick et al., 2009; Holle and Gunter, 2007; Hostetter, 2011; Kelly et al., 2004; Kircher et al., 2009; McNeill, 1992), complementing the spoken message through visual information, which clarifies the meaning for the recipient (Straube et al., 2013b). Studies have mostly investigated three types of gestures: iconic gestures, which refer to concrete entities or physical properties (Green et al., 2009; Holle and Gunter, 2007; Özyürek et al., 2007; Wu and Coulson, 2005); metaphoric gestures, which are descriptive and refer to abstract speech units (Kircher et al., 2009; Schülke and Straube, 2017; Straube et al., 2011, 2013b); and beat gestures, which stress speech prosody and emphasize relevant features of the sentence (Bernard et al., 2015; Biau and Soto-Faraco, 2013; Dimitrova et al., 2016; Hubbard et al., 2009). The focus of recent neuroimaging analysis into gestures was on the integration of speech and one specific kind of gesture, investigating how the combination of semantic and audiovisual information blends into one representation (Green et al., 2009). The studies suggest that iconic, metaphoric, and beat gestures preferentially activate, respectively, the left temporo-occipital cortex (Green et al., 2009), the left fronto-temporal cortex (Straube et al., 2013b) and the left superior temporal gyrus, STG (Hubbard et al., 2009). Furthermore, the first studies combining EEG and fMRI techniques have provided a more holistic perspective on the integration of gestures, as temporal and spatial aspects of speech-gesture processing can be assessed simultaneously (He et al., 2015, 2018b). As previous studies mostly used artificial stimuli, including short sentences, unimodal gesture or mismatch conditions, to examine speech-gesture integration, investigations on the effect of gestures on the neural processing of continuous narratives with varying semantic complexity are still missing so far.

Several studies have analyzed co-speech gestures and specific complex linguistic structures (He et al., 2018a; Kircher et al., 2009; Straube et al., 2009, 2013b). The authors of these studies focused on processing of abstract vs. Concrete speech and gestures. Similar to the processing and integration of complex information of other kinds, the interpretation of abstract metaphoric material was found to require the recruitment of additional cognitive resources, likely for several reasons (Straube et al., 2013b). First, a semantic conflict between the literal and the abstract level has to be detected. Second, certain properties from one element have to be transferred to the other in order to interpret the meaning of a metaphoric construction in a given context or situation. McNeil et al. (2000) also investigated the influence of gestures depending on the complexity of the language in a group of infants. The authors concluded that gestures had a positive impact on comprehension when the content was complex for the children. There are also studies analyzing gestures in a narrative context (Wilson et al., 2008), and although the complexity is thought to have an influence on the processing, it was not assessed in a standardized manner.

In summary, in contrast to the assessment of language production, the perception of language has not been intensively studied with respect to semantic complexity. Although a negative relationship between DMN activation and the complexity of a task can be assumed, an empirical investigation using standardized procedures for the assessment of semantic complexity is missing to date. Furthermore, the facilitative role of gestures has been demonstrated in several studies, however, little is known about how gestures influence the perception of language depending on semantic complexity. Therefore, the purpose of the current study is to investigate the neural correlates of semantic complexity and the gesture-related neural facilitation while processing a narrative with varying degrees of complexity. To this end, we present an audiovisual continuous story to the subjects without any explicit task. This paradigm allows us to approach these questions and to analyze speech perception within an ecologically valid context (Hasson et al., 2018). For the semantic complexity analysis of the story, we examine segments of ten words each, which were categorized depending on their semantic complexity and the number of gestures presented concurrently. Through this method we were able to form trials without interfering with the continuous presentation of the video. There was no manipulation depending on the type of gesture, but the different gestures were randomly distributed across the story and importantly, the frequency of the different gesture types did not differ between segments with high or low ID (further details in the method section) and all gestures were naturally produced and therefore matching the sentence context. We had four main hypotheses. First, we hypothesize a reduction of DMN activation for segments with high compared to low semantic complexity (ID), due to the increased processing effort. Second, increase of activation in bilateral occipital and temporal regions due to the processing of co-speech gestures in addition to speech. Third, reduced neural activation for speech accompanied by gestures (compared to speech only episodes) in language related areas (e.g. left temporal and inferior frontal cortices). Fourth, the increase in activation in language-related areas for highly complex speech is expected to be modulated by the presentation of gestures, as we hypothesize that processing of ideas is facilitated, maintained, and associated to other ideas, when they are represented in both speech and gestures.

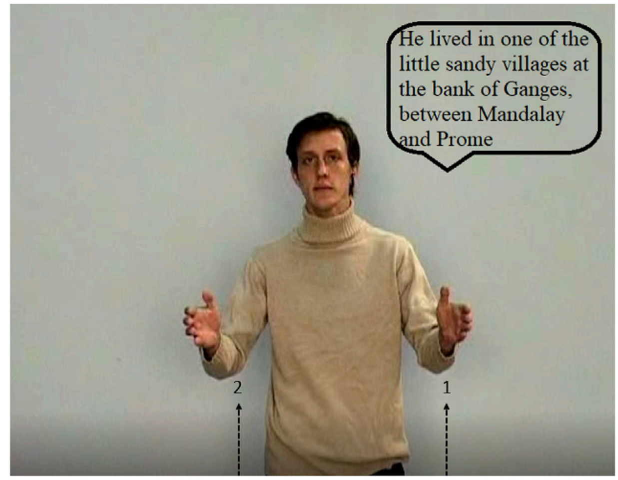

Fig. 1. Example of the stimuli videos. A sentence of the story was translated into English and depicted in the speech bubble for illustrative purposes. The still frame from the video shows the actor gesturing the last part of the sentence: "between Mandalay and Prome", represented by the left and right hand, respectively. The arrows indicate the direction of the hand movements, and the numbers indicate the order of the movements.

2. Methods

2.1. Participants

Twenty right-handed subjects (Oldfield, 1971) took part in the experiment (13 males and 7 females). All participants were native speakers of German and had normal or corrected-to-normal vision and none reported any hearing deficits. The mean age of the participants was 25.4 years and the range was 22–35 years. None of the participants reported any relevant medical or psychiatric illnesses. All subjects gave written informed consent prior to participation in the study. Permission for the study was obtained from the local ethics committee at Philipps University Marburg.

2.2. Stimuli

A set of 16 video clips were presented to the subjects. The videos showed an actor narrating a slightly modified version of the short story "Der Kuli Kimgun" (Dauthendey, 1909). For better comprehension of the story, foreign words were replaced by common German equivalents. The story was unknown to all of the subjects. The actor presented in the videos was asked to tell the story as naturally as possible and to include gestures of any kind using hands and arms. The actor decided freely when and how to make the gestures, which were all matching the semantic content of the story. The presentation of the videos lasted 32:12 min, with individual clips lasting between 1:02 and 3:31 min. An example of the stimuli is presented in Fig. 1.

2.3. Experimental design and procedure

After acquisition, the entire story was examined in segments of 10 words each for the semantic complexity analysis. A total of 330 segments were defined. Through this method, it was possible to identify passages of the story that were less complex than others, facilitated the calculation of the trial's onsets (milliseconds needed to utter the ten words of each segment), and we did not interfere with the continuous presentation of the videos. After the division of the story, the segments were analyzed to calculate their ID. The manual by Chand et al. (2012b) was used as an orientation for the analysis. The rules for the identification of ideas were adapted as much as possible for the German language. For example, comparisons are not included in the manual by Chand et al. (2012b), but for this analysis they were counted, given that they modified the phrase. Other categories not present in the German language such as the gerund *-ing* were left out. Ideas that were part of two segments were counted both in the segment in which they started and in the segment in which they ended. The calculation of the ID value proposed in the manual is estimated as follows: counting all propositions in a text, then dividing them by the number of total words and multiplying the result by 10. The subsequent result is the number of ideas expressed per 10 words (Chand et al., 2012b). Through this method, the semantic complexity of the whole text is independent of the length of the sentences. But, since in our case the segments of the story always consisted of 10 words, the number of ideas identified in a segment was automatically the ID value of the respective segment (no division by the number of total words). Table 1 shows the procedure of the calculation of the ID. Each segment of our story had an ID between two and nine. Segments that included the end of one video and the start of the next were not analyzed, since a pause of 6–14 s between videos (jitter period) would be modulated. After the complexity analysis, the number of gestures that appeared in each segment were counted. All kinds of gestures (metaphoric, iconic and beat gestures) were equally weighted because we hypothesize a general facilitative effect of gestures irrespective of gesture type[2]. Each segment had between zero and four gestures. Gestures that started in one segment and concluded in the next, were also counted in both segments.

Table 1
Example of the calculation of idea density within a segment.

[Samir war ein armer indischer Junge, so arm wie der] Staub auf der Landstraβe.	
'Samir was a poor, Indian boy, as poor as the dust on the country road'	
No. Of ideas	1. War, Samir, ein Junge
	*Samir was a boy
	2. Junge, armer
	*boy, poor
	3. Junge, indischer
	*boy, Indian
	4. So arm wie der Staub
	*as poor as the dust
ID = 4	

The square brackets show the limits of the segment, always encompassing ten words. Ideas between segments (as idea number 4) were counted in the segment where they started, and in the segment where they ended.

[2] The frequency of the different kinds of gesture did not differ significantly in the low- and high-ID conditions $\chi^2 = 5.1959$, p-value = 0.267781.

Six different conditions were established based on the aforementioned calculations of ID and number of gestures. All the segments with an ID equal to or below five, were counted as less complex and segments which had an ID value equal to or above six were counted as highly complex. This division was made in relation to our values (ranging from two to nine), given that there is no established value which can be seen as a standard or reference of average complexity. This is due to the fact that in the case of language production ID values are influenced by the size of the analyzed text and the number of subjects participating in a study (Spencer et al., 2012). Other studies concerning ID in language production have defined high values as the top two-thirds and low values as the bottom third (Snowdon et al., 1996). However, we decided to divide the values into just two categories to create an equal split of four values each (i.e., 2–5 and 6–9). This approach (instead of a parametric) has been chosen to facilitate the interpretation of the complex interaction between the factors gesture and ID. To calculate this interaction, the low and high ID segments were further separated according to the number of gestures presented in the segment: no gestures (high_ID_noG, low_ID_noG), one gesture (high_ID_1G, low_ID_1G) and two or more gestures (high__ID_2G, low_ID_2G). This division, depending on the number of gestures, was chosen in order to investigate whether the reduction of cognitive load was related to the number of gestures presented. There was no significant interaction in numbers of trials ($\chi^2 = 3.058$; $p = 0.214$; frequency: 17 low_ID_noG, 13 high_ID_noG; 91 low_ID_1G; 53 high_ID_1G; 83 low_-ID_2G; 73 high_ID_2G) and segment duration ($F\ (1{,}324) = 0.410$, $p = 0.664$, eta-square $= 0.003$; Average durations: 4.46 low_ID_noG; 5.10 high_ID_noG; 4.60 low_ID_1G; 4.87 high_ID_1G; 4.87 low_ID_2G; 5.20 high_ID_2G) between the factors gesture and ID. However, we had fewer trials without gesture and longer duration for the high complexity conditions (main effect complexity; $F\ (1,\ 324) = 13.355$, $p < 0.005$; high: mean = 5.07sec., SD = 1.05; low: 4.71sec., SD = 0.92). We regarded these differences in main effects as unproblematic as our analyses are focused on the interaction between both factors.

During the scanning process, the participants were instructed to pay attention to the video, watch the movements of the actor and listen carefully to the story. The avoidance of using an artificial task enabled us to analyze the perception of language and gestures in a more naturalistic way. The participants observed the video through a mirror mounted on the head coil. In order to make sure that the subjects listened to the narrative, they were asked to answer a questionnaire containing details of the story (e.g. critical moments, narrative shifts etc.).

2.4. fMRI data acquisition

MRI data acquisition was performed on a 3-T scanner (Siemens MRT Trio series). The functional images were obtained using a T2*-weighted echo-planar image sequence (TR = 2 s, TE = 30 ms, flip angle = 90°, slice thickness = 4 mm, interslice gap = 0.36 mm, field of view = 230 mm, matrix = 64 × 64, voxel size = 3.6 x 3.6 × 4.0 mm, 30 axial slices orientated parallel to the AC-PC line). The images were acquired in two runs. During the first run 450 functional images were obtained (15 min) and in the second run 520 (17 min, 20 s). This was due to the varying lengths of individual videos.

2.5. Data analysis

The MRI images were analyzed using Statistical Parametric Mapping (SPM12; www.fil.ion.ucl.uk) implemented in MATLAB 7.9 (Mathworks Inc. Shevorn, MA). The first two volumes were discarded from the analysis to minimize T1-saturation effects. Afterwards, all images were registered to the first image of the first run and co-registered to the anatomical volume, normalized into MNI space and smoothed with an eight mm isotropic gaussian filter. A high-pass filter (cut-off period 128 s) was used. Statistical analysis was performed in a two-level procedure. The design matrix for the modulation of single-subject BOLD responses at the first level comprised the onsets and durations of all six conditions, as well as the six movements parameters of each subject. The hemodynamic response function (HRF) was modeled by the canonical HRF. A standard full factorial second level analysis was then performed.

A Monte Carlo simulation of the brain volume of the current study was employed to determine an adequate voxel contiguity threshold (Slotnick et al., 2003). It is suggested that this correction provides sensitivity to smaller effect sizes and also corrects for multiple comparisons across the whole brain volume (Slotnick, 2017). Assuming an individual voxel type 1 error of $p < 0.001$, a cluster extent of 87 contiguous resampled voxels was indicated as necessary to correct for multiple comparisons at $p < 0.05$. Thus, voxels of clusters with at least 87 voxels and a significance level of $p < 0.001$ are reported for all contrasts. All described coordinates of activation are located in MNI space. For the anatomical localization of the clusters, the AAL toolbox was employed (Tzourio-Mazoyer et al., 2002).

3. Contrasts of interest

To test for the main effect of ID, the differential contrasts of low_ID > high_ID and high_ID > low_ID were computed. For the main effects of speech (conditions noG) and speech with gesture (conditions 1G and 2G), the two contrasts speech > gestures + speech and gestures + speech > speech were computed. Finally, the interaction between complexity and gestures was also assessed in order to investigate the reduction of activation depending on the complexity of the story. For these analyses, a linear effect of number of gestures was assumed leading to the following contrast weights: −1 for noG, 0 for 1G and +1 for 2G. Weights for all high ID conditions were further multiplied by −1 (−1, 0, 1, 1, 0, −1). However corresponding analysis with the noG and 1G condition only led to comparable effects.

4. Results

Comparing low with high complexity conditions independently of the number of gestures, we observed stronger activation for the low complexity conditions in classic DMN regions. (for details see Table 2; Fig. 2). In contrast, no regions reached the significance threshold for the high conditions as compared to the low conditions.

For the contrast speech > gestures + speech, we observed two clusters of activation within perisylvian regions: the first one localized in the pars orbitalis of the left inferior frontal gyrus (IFG) and the second cluster localized within the left superior temporal gyrus (STG) and the anterior part of the middle temporal gyrus (MTG). Thus, these areas showed reduced activation for the presentation of gestures (see Fig. 3B and C). Exploratory analyses revealed that this effect was reliable across runs (see supplemental material, Fig. 2) and already present in segments with meaningless gestures (see supplemental material, Fig. 3). For the contrast gestures + speech > speech, we observed stronger bilateral activation in the middle occipital gyrus, in the posterior MTG and left precuneus, regions likely including areas thought to be involved in the processing of visual motion: middle temporal visual area (MT; Tootell et al., 1995.), the visual presentation of hands: left lateral occipitotemporal cortex (LOTC; Bracci et al., 2012) and bodies: extrastriate body area (EBA; Downing, 2001). The extent of activation was increased for a higher number of gestures (see Fig. 3E and F). This gesture related effect also included regions of the posterior temporal lobe which had previously been related to speech and gesture integration (see supplemental material, Fig. 4). The interaction analysis of gestures x complexity revealed complexity dependent activation decrease in the left anterior MTG (see Fig. 4).

Exploratory analyses across runs revealed no significant interactions with the factors ID and Gesture, suggesting that the time course of the story did not influence the reported effects. Only, a main effect in the bilateral temporal lobes, were found indicating a BOLD reduction in the second part of the narrative (see supplemental material, Fig. 1).

Table 2
Activation peaks and cluster extents for the contrasts low_ID > high_ID, speech > gestures + speech and gestures + speech > speech as well as the interaction of gestures and complexity.

Contrast	Anatomical region	Cluster extent	Hem.	MNI Coordinates			t-value	No. Voxels
				x	y	z		
low complexity > high complexity								
	Supramarginal	Middle occipital gyrus, middle temporal gyrus, superior temporal gyrus, angular gyrus	L	−56	−50	26	4.69	990
	Anterior cingulate	Superior frontal gyrus, middle frontal gyrus	R	10	44	10	4.57	1406
	Middle temporal	Angular gyrus, middle occipital gyrus, superior temporal gyrus	R	56	−50	14	4.53	910
	Precuneus	Posterior cingulate cortex, middle cingulate	L	6	−56	34	4.52	871
speech > gestures + speech								
	Pars orbitalis	Pars triangularis	L	−50	30	−8	4.94	261
	Middle temporal	Ssuperior temporal gyrus, hippocampus	L	−44	−36	−2	4.58	402
gestures + speech > speech								
	Middle occipital	Middle temporal gyrus, superior occipital gyrus, calcarine, inferior occipital gyrus, middle	L	−46	−74	6	14.36	5039
	Middle temporal	occipital gyrus, inferior temporal gyrus, fusiform	R	48	−68	2	12.31	5430
	Precuneus	Superior parietal gyrus, inferior parietal gyrus	L	8	−72	56	4.20	161
interaction (gestures x complexity)								
	Middle temporal	superior temporal gyrus, superior temporal pole	L	−52	−2	−20	4.01	96

Voxel activations were thresholded at $p < 0.001$ uncorr. and only clusters bigger than 87 voxels are reported (montecarlo cluster corrected at $p < 0.05$). Lateralization of the activation clusters is indicated by L (left) and R (right).

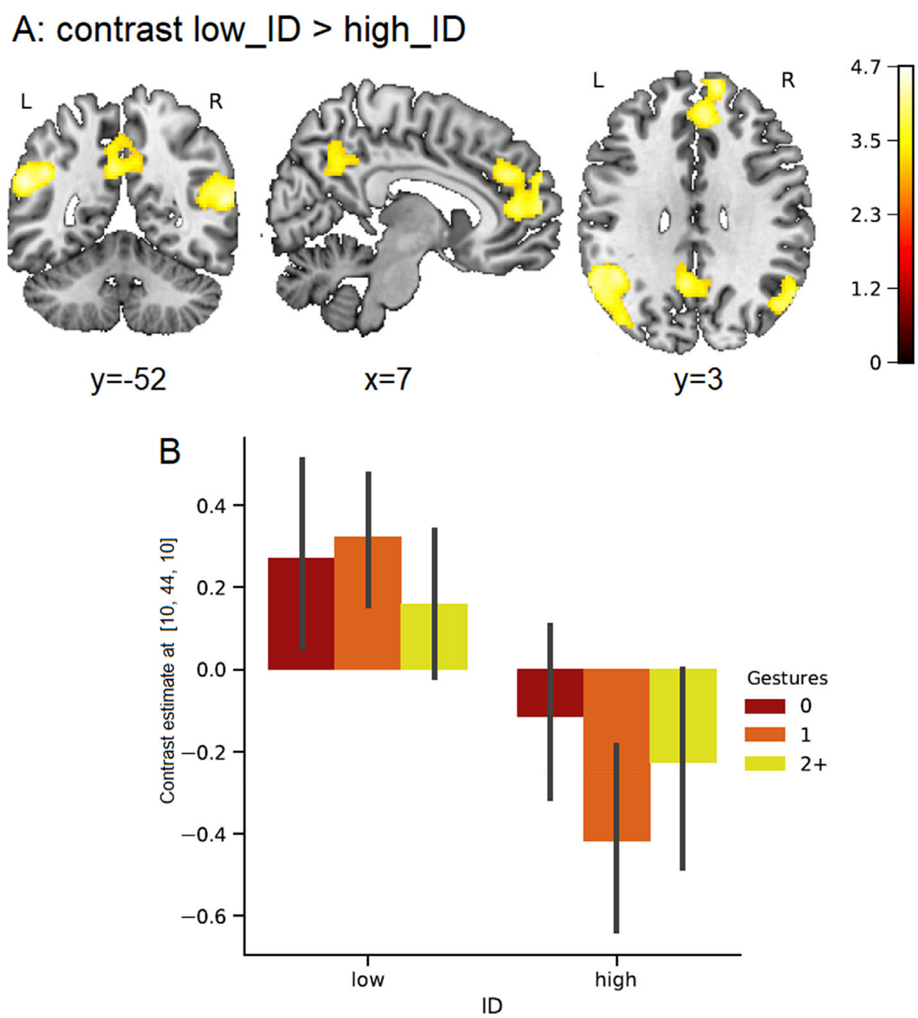

Fig. 2. Activation increase for low complexity. The clusters of activation showed in A cover the anterior cingulate/middle prefrontal cortex, posterior cingulate cortex/precuneus, bilateral middle temporal and angular gyrus, and left supramarginal gyrus. The bottom of the panel (B) the bar graph shows the activation pattern of the cluster localized at the anterior cingulate/middle prefrontal cortex, indicating strongest activation during the low complexity conditions.

5. Discussion

In our study, we investigated the extent to which co-speech gestures facilitate processing of natural stories with varying degrees of semantic complexity. More specifically, we examined whether passages of low and high ID within a natural story elicit different neural correlates during comprehension. In addition, we investigated whether gestures modulate the cognitive load induced by the sequential presentation of numerous

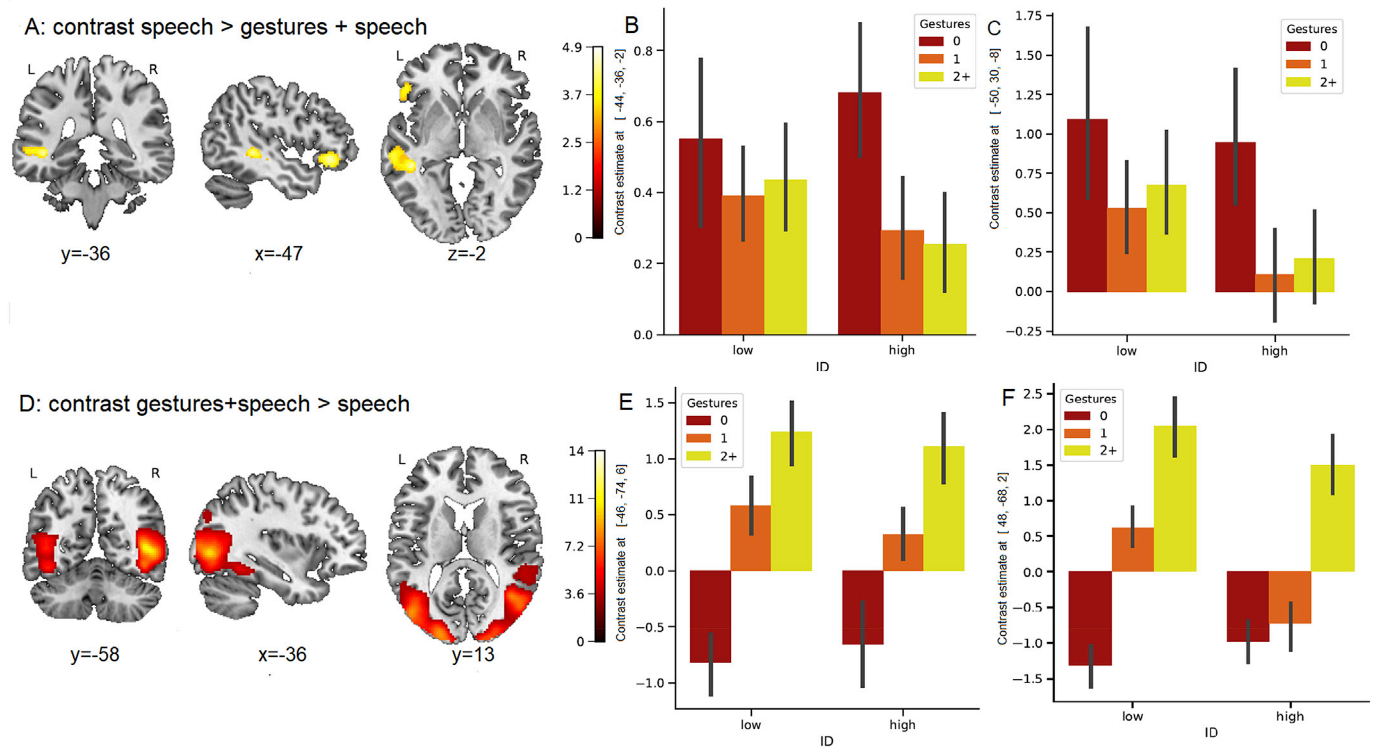

Fig. 3. Gesture related activation decrease (speech > gestures + speech) and increase (gestures + speech > speech). B shows the activation of the cluster localized in the left anterior MTG and C shows the cluster localized in the left IFG. E shows the activation of the cluster localized in the left posterior MTG and F the cluster localized in the right posterior MTG.

propositions. This follows the notion that utterances containing several propositions require more cognitive resources and cause more cognitive load for the interlocutor (Kintsch and Keenan, 1973). As hypothesized, we found reduced BOLD signal in DMN regions during high compared to low complexity conditions. Furthermore, gestures reduced activation for speech processing within the left MTG and left IFG (speech > gestures + speech), while activation of occipital regions and posterior MTG was related to gesture processing (gestures + speech > gesture). Finally, the interaction analysis indicated that gesture related activation reduction in language areas was strongest for high complex passages.

5.1. *Discourse perception and default mode network*

A direct comparison between low- and high-complexity conditions, independently of the number of gestures, revealed greater activity for the low conditions in the anterior cingulate cortex, middle prefrontal cortex (mPFC), MTG, supramarginal gyrus, angular gyrus, precuneus, and posterior cingulate cortex (PCC)– regions that, with the exception of the MTG, are known to be part of the DMN (Chen et al., 2017; Raichle et al., 2001).

Previous research findings further point to a relationship between the DMN and language-related tasks (Binder et al., 1999; Seghier and Price, 2012; Wilson et al., 2008; Xu et al., 2005). For example, Binder et al. (1999) observed that regions involved in semantic retrieval were similar to the regions activated during resting conditions. Another approach which presented similar results to ours are reported by Wilson et al. (2008). The authors postulate that the DMN is intrinsically involved in semantic processing, especially during the interpretation of discourse. For example, the authors explain the activation of the PCC/Precuneus as to these regions linking the perceived information with previously acquired knowledge. Interestingly, the authors also lightly touched upon the subject of semantic complexity, and they hypothesized that regions that are involved in the semantic processing should be more active during the perception of complex structures. Similarly, Xu et al. (2005) investigated the influence of contextual complexity on language processing and stressed the activation of DMN regions when a narrative was processed in comparison to the presentation of single sentences. These interpretations are, to some extent, in accordance with our results. During the low ID conditions, it might be speculated that the DMN supports the processing of the utterances and that the available resources are sufficient with respect to task performance. But, if the DMN is involved in semantic processing in general, one would expect an involvement of the DMN during the processing of the high ID conditions as well, which is not supported by our results. Despite the intrinsic involvement of the DMN in the semantic processing, given that thinking and planning require the interpretation of concepts (Binder et al., 1999; McKiernan et al., 2006), it might be the case that when semantic complexity increases the resources available for the interpretation of narratives do not suffice and other regions may be involved in order to meet the demands. Similarly, Seghier and Price (2012) linked the DMN to semantic processing and reported stronger deactivation in the PCC and mPFC due to severe demands on semantics. These findings are consistent with our results since both regions were deactivated potentially driven by semantic complexity effects. Nevertheless, the authors stressed that the semantics affect the activation of diverse parts of the DMN differently. They conclude that, if attention is focused on external stimuli, which impose severe demands on semantic processing, the regions which are involved with internal activities deactivate in order to accomplish the task. This explanation would support the attenuation of the DMN in our experiment.

Alternatively, it could be argued that the specific properties or characteristics of the DMN regions allow the recipient to interpret the story. For example, the PCC and precuneus are associated with the processing of episodic memory and with the management of attentional resources according to the demands of the task (Mazoyer et al., 2001). Likewise, the involvement of the dorsal part of the mPFC is connected to the deduction of the communicative intent of utterances (Willems et al., 2010) and the interpretation of the intentions and motivations of the characters in a

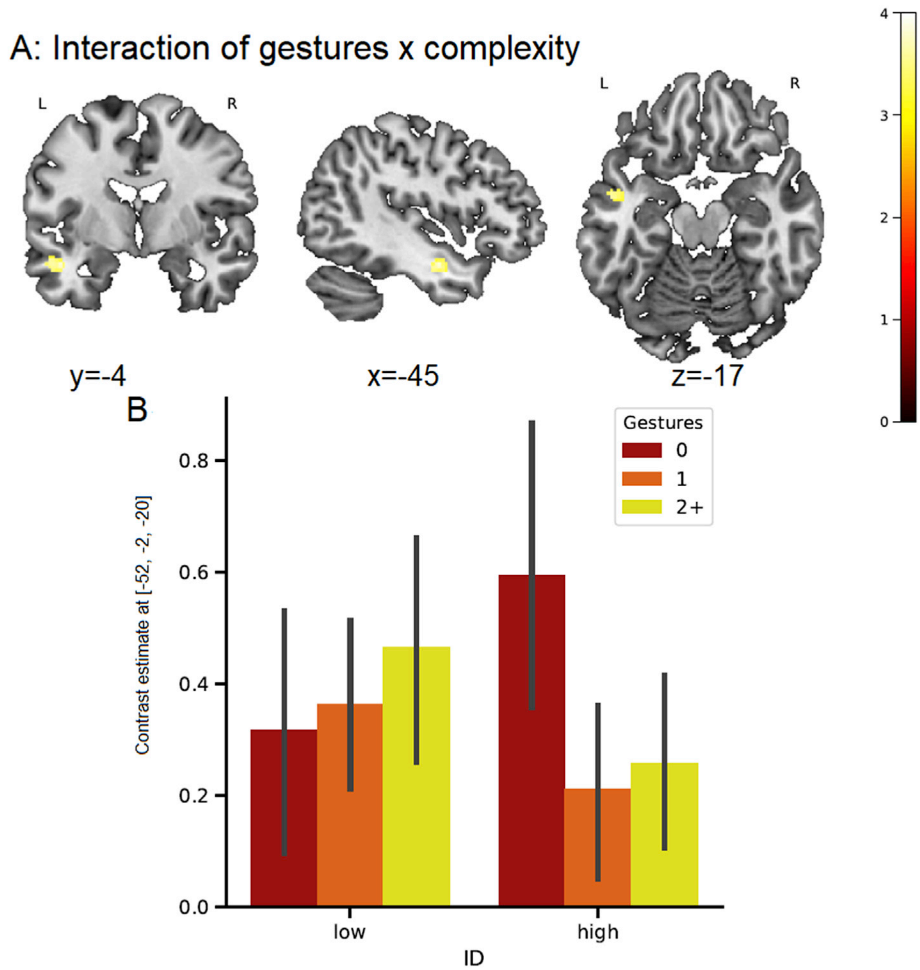

Fig. 4. Interaction analysis of gestures and complexity. The top of the panel (A) shows the cluster of activation covering the left MTG, STG and superior temporal pole. At the bottom of the panel (B), the bar graph shows the activation pattern of the cluster showed in A.

narrative (Xu et al., 2005). AbdulSabur et al. (2014) conclude that the network seems to help with inferring the mental states of others and building a situation model of the narrative and the characters, providing the demands allow it (AbdulSabur et al., 2014). This interpretation is in line with our results, but only with respect to the low complexity conditions. Here, the complexity or the demands of the narrative might allow the involvement of the DMN regions in these functions. But when complexity increases this seems not to be the case anymore.

In sum, the activation of the DMN during the low ID conditions supports our original hypothesis linking increasing semantic complexity to higher cognitive load. As stated above, the number of propositions presented probably increase the cognitive demands for the interpretation of the narrative (Kintsch and Keenan, 1973). In other words, more resources are needed for the interpretation of complex structures which contain numerous propositions. Since the attenuation of the DMN depends directly on the cognitive load of the task (Broyd et al., 2009), we found no attenuation of the DMN during the low conditions. Following this, minimal resources seem to suffice to process utterances with low ID. In contrast, for the processing of complex structures, the increased demand is reflected in a stronger attenuation of the DMN and might indicate the effective management of resources in order to realize a task (Dick et al., 2010) and the motivation to focus on the content and at the same time block internal thoughts (Spreng et al., 2009). This activation pattern supports the validity of ID as suitable measure of semantic complexity, not only for the quantification of the ideas produced by subjects themselves, as used in the majority of the previous studies, but also for the perception of complex structures used as stimuli.

5.2. Modulation of speech-related activation through the presentation of gestures

Another important focus of the current study was the effect of gestures on the neural processing of complex speech. As expected, we found stronger activation of the left MTG and IFG for speech-only conditions in contrast to co-speech gestures. In these regions, the addition of gestures makes the narrative easier to understand, thus requiring less effort to interpret the speech. Besides, the presentation of gestures elicited, as expected, increased activation in the occipital regions and the posterior MTG bilaterally. These activations can simply be attributed to the increased visual input when gestures are present. However, areas relevant for integrating speech and gestures are also likely to be involved. For example, similar results concerning the STS/MTG and their involvement in the integration of visual and auditory information are also reported in other studies (Dick et al., 2009; Green et al., 2009; He et al., 2015, 2018b; Holle et al., 2008; Kircher et al., 2009; Straube et al., 2011, 2018). Straube et al. (2011) found activation within the posterior MTG bilaterally during the perception of iconic gestures. In contrast, the IFG seemed to be involved in the integration of metaphoric gestures. Additionally, He et al. (2018b) focused on the temporal integration of gestures. In their two-stage model of integration, it is stressed that the STS/MTG play a fundamental role in the integration of inputs from multiple modalities at the first step of the model.

5.3. Interaction gestures x complexity

The main focus of this study was on the interaction between the facilitating effect of gestures and semantic complexity. In fact, we found that activation of the left MTG for highly complex sematic structures was specifically reduced when gestures were presented. Thus, our results highlight the potential role of the MTG in processing complex semantic information. Accordingly, subjects seem to profit from the additional visual information provided by co-speech gestures especially in highly demanding conditions. Similar results have been reported by Kircher et al. (2009), for the interaction of speech and metaphoric gestures. The authors described activation reductions related to the presentation of gestures in a cluster encompassing the STS and the left insula - adjoining regions of the MTG. The activation decreases in the study were related to semantics, given that the reduction was not found in the unknown language condition. Therefore, the presentation of metaphoric gestures led to more efficient processing. Thus, the decrease of activation in the left MTG caused by the presentation of gestures can be seen as a sign of lower processing demands when interpreting high proportions of ideas in a narrative. In addition, there is further evidence signaling a facilitation effect of gestures indicated by reduced functional connectivity between the involved regions (Skipper et al., 2007).

However, as Hostetter (2011) has postulated, the degree of influence of gestures depends on three factors: 1. the type of information they convey (concrete vs. abstract), 2. the information content of the gestures (redundant vs. new) and 3. the age of the listeners (children profit more from visual information than adults). With regard to the first factor, the story contained concrete and abstract speech as well as gestures, since the narrative consisted in large parts of figurative language. Concerning the information the gestures conveyed, it could be argued that the information was mostly redundant, because the actor only expressed information contained in the story itself. In other words, it was not spontaneous speech in which the speaker relied on gestures to cover additional information. Besides, it could be speculated that the function of the gestures in our experiment was not to express additional information, but rather to reinforce or illustrate the information uttered by the actor. Finally, in respect to the third factor, all the subjects of our experiment were adults. But despite these characteristics, we could observe reduction in activation for some regions when information was presented in combination with visual cues. We hypothesize that gestures had a facilitating effect because the story was completely new to the subjects and during the high conditions much information was coded, which was relieved by the reinforcement or redundant sending of information. McNeil et al. (2000) also stated that the effect of gestures depends not only on the relation between speech and gesture, but also on the complexity of the message. This conclusion is in accordance with our results as the effect of gestures was stronger in high-complexity conditions than in low-complexity conditions, at least in the left MTG. Thus, it could be the case that subjects profit more from visual gesture information when numerous propositions are presented. In the low complexity conditions, on the other hand, subjects could interpret the gestures as too redundant, leaving little space for improvement (Hostetter, 2011). These results stress the importance of treating comprehension as a dynamic phenomenon, which depends on the demands of the task and also on the external contextual cues supporting it (McNeil et al., 2000).

6. Limitations

Notably, the present study has some limitations. First, there is no control condition where the actor performed the exact same story completely devoid of gestures or a gesture only condition. All our comparisons were made between different passages of the same story. Thus, it would be interesting to compare exactly the same passage with and without the presentation of gestures and observe whether the activation of the DMN is stronger in this scenario. However, since direct repetitions are not common in real life communication, we decided to present the story only once to avoid any habituation effects and maintain the model as naturalistic as possible. Besides, the presentation of gestures in isolation is not common in real life communication (except for emblems in specific contexts). Despite the fact that number of trials per conditions and duration are not exactly matched in this naturalistic approach, there was no significant interaction between our factors of interest (gesture and ID). Furthermore, those differences we found in the main effects (lower number of trials in the no-gesture condition and longer durations in the high complexity conditions) do not offer an explanation for our results as we found for example more activation in the no-gesture condition in the left IFG and MTG and higher activation of the DMN network regions for low complexity conditions. Second, all kinds of gestures (metaphoric, iconic, emblematic and beat) were treated equally for the present analysis, as it is the first study investigating the interaction of semantic complexity and gesture. Exploratory analysis suggest that the facilitative effect of gesture might be related to gesture meaning, however, the results remain inconclusive due to insufficient power. Therefore, it would be interesting to further analyze whether the facilitative effect of gestures varies depending on the kind of gesture presented in larger studies or with longer videos and higher gesture frequency. Finally, no established method or manual for the analysis of ID for the German language exists. It would be helpful to have a reference in order to make comparisons between studies or even to have an equivalent of the current automatic program for the calculation of ID (CPDR, Brown et al., 2008) for other languages.

7. Further research

Future investigations employing the same paradigm could be conducted with a different target population. It could be useful to investigate whether the DMN is also active during low ID conditions in patients with schizophrenia since there is evidence that the network is activated differently in these patients (Broyd et al., 2009; Fransson and Marrelec, 2008; Hu et al., 2017). Additionally, patients with schizophrenia exhibit difficulties with regard to the interpretation of complex constructions such as metaphors (Bonis et al., 1997; Kircher et al., 2007; Straube et al., 2013a), which are numerous in the story. Furthermore, they have problems in relating speech and gesture semantics (Nagels et al., 2019; Schülke and Straube, 2018), which might weaken the potential facilitating effect of gestures in these patients. Moreover, the same experiment could be conducted with an older group of subjects, since the mean age of our subjects was very low (24.5 years) and there is evidence that ID could be perceived differently by older subjects (Spencer et al., 2012). On the other hand, the DMN could show different patterns of activation within a group of older subjects (Andrews-Hanna et al., 2007). Finally, it might be interesting to analyze whether there are specific gender differences in respect to the perception of complex structures, since most ID studies examined a group of either women or men, and our study was performed with a mixed group.

8. Conclusion

Three notable conclusions can be drawn from this study. First, the DMN attenuated during high complexity conditions, indicating that activation of the DMN depends on the complexity of a narrative. Second, activation of language-related areas was modulated through the presentation of gestures, indicating the facilitation of speech processing through complementary visual information. Last, the left MTG played a fundamental role in processing highly complex semantics and benefitted the most from the visual information from gestures, suggesting that the supporting effect of gestures is particularly pronounced when cognitive demands are high.

Acknowledgements

This research was funded by the International Research Training

Group, IRTG 1901, "The Brain in Action'' by the German Research Foundation (DFG) and by the von Behring-Röntgen-Stiftung (vBR 59-0002 and 64-0001). The study was also supported by the Core Facility Brain Imaging, Faculty of Medicine, University of Marburg, Rudolf-Bultmann-Str. 9, 35039, Marburg, Germany. We also thank Lisa Friederich for the recommendations concerning idea density and the adaptation to the German language.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.03.054.

Declaration of interests

Declaration of interests: none.

References

AbdulSabur, N.Y., Xu, Y., Liu, S., Chow, H.M., Baxter, M., Carson, J., Braun, A.R., 2014. Neural correlates and network connectivity underlying narrative production and comprehension: a combined fMRI and PET study. Cortex; A J. Devoted Study Nervous Sys Behavior 57, 107–127. https://doi.org/10.1016/j.cortex.2014.01.017.

Andrews-Hanna, J.R., Snyder, A.Z., Vincent, J.L., Lustig, C., Head, D., Raichle, M.E., Buckner, R.L., 2007. Disruption of large-scale brain systems in advanced aging. Neuron 56 (5), 924–935. https://doi.org/10.1016/j.neuron.2007.10.038.

Beattie, G., Shovelton, H., 1999. Mapping the range of information contained in the iconic hand gestures that accompany spontaneous speech. J. Lang. Soc. Psychol. 18 (4), 438–462. https://doi.org/10.1177/0261927X99018004005.

Bernard, J.A., B Millman, Z., Mittal, V.A., 2015. Beat and metaphoric gestures are differentially associated with regional cerebellar and cortical volumes. Hum. Brain Mapp. 36 (10), 4016–4030. https://doi.org/10.1002/hbm.22894.

Biau, E., Soto-Faraco, S., 2013. Beat gestures modulate auditory integration in speech perception. Brain Lang. 124 (2), 143–152. https://doi.org/10.1016/j.bandl.2012.10.008.

Binder, J.R., Frost, J.A., Hammeke, T.A., Bellgowan, P.S.F., Rao, S.M., Cox, R.W., 1999. Conceptual processing during the conscious resting state: a functional MRI study. J. Cogn. Neurosci. 11 (1), 80–93. https://doi.org/10.1162/089892999563265.

Bonis, M. de, Epelbaum, C., Deffez, V., Féline, A., 1997. The comprehension of metaphors in schizophrenia. Psychopathology 30 (3), 149–154. https://doi.org/10.1159/000285041.

Bosch, B., Bartrés-Faz, D., Rami, L., Arenaza-Urquijo, E.M., Fernández-Espejo, D., Junqué, C., Solé-Padullés, C., Sánchez-Valle, R., Bargalló, N., Falcón, C., Molinuevo, J.L., 2010. Cognitive reserve modulates task-induced activations and deactivations in healthy elders, amnestic mild cognitive impairment and mild Alzheimer's disease. Cortex; A J. Devoted Study Nervous Sys Behavior 46 (4), 451–461. https://doi.org/10.1016/j.cortex.2009.05.006.

Bracci, S., Cavina-Pratesi, C., Ietswaart, M., Caramazza, A., Peelen, M.V., 2012. Closely overlapping responses to tools and hands in left lateral occipitotemporal cortex. J. Neurophysiol. 107 (5), 1443–1456. https://doi.org/10.1152/jn.00619.2011.

Brown, C., Snodgrass, T., Kemper, S.J., Herman, R., Covington, M.A., 2008. Automatic measurement of propositional idea density from part-of-speech tagging. Behav. Res. Methods 40 (2), 540–545. https://doi.org/10.3758/BRM.40.2.540.

Broyd, S.J., Demanuele, C., Debener, S., Helps, S.K., James, C.J., Sonuga-Barke, E.J.S., 2009. Default-mode brain dysfunction in mental disorders: a systematic review. Neurosci. Biobehav. Rev. 33 (3), 279–296. https://doi.org/10.1016/j.neubiorev.2008.09.002.

Bryant, L., Spencer, E., Ferguson, A., Craig, H., Colyvas, K., Worrall, L., 2013. Propositional idea density in aphasic discourse. Aphasiology 27 (8), 992–1009. https://doi.org/10.1080/02687038.2013.803514.

Chand, V., Baynes, K., Bonnici, L., Farias, S.T., 2012b. Analysis of Idea Density (AID): A Manual. Department of Neurology, Center for Mind and Brain, Department of Linguistics, University of California.

Chand, V., Baynes, K., Bonnici, L.M., Farias, S.T., 2012a. A rubric for extracting idea density from oral language samples. Curr. Protoc. Neurosci. https://doi.org/10.1002/0471142301.ns1005s58. Chapter 10: Unit 10.5.

Chen, J.E., Glover, G.H., Greicius, M.D., Chang, C., 2017. Dissociated patterns of anti-correlations with dorsal and ventral default-mode networks at rest. Hum. Brain Mapp. 38 (5), 2454–2465. https://doi.org/10.1002/hbm.23532.

Cheung, H., Kemper, S., 1992. Competing complexity metrics and adults production of complex sentences. Appl. Psycholinguist. (13), 53–76.

Cohen, A.S., McGovern, J.E., Dinzeo, T.J., Covington, M.A., 2014. Speech deficits in serious mental illness: a cognitive resource issue? Schizophr. Res. 160 (1–3), 173–179. https://doi.org/10.1016/j.schres.2014.10.032.

Covington, M.A., Riedel, W.J., Brown, C., He, C., Morris, E., Weinstein, S., Semple, J., Brown, J., 2007. Does ketamine mimic aspects of schizophrenic speech? J. Psychopharmacol. 21 (3), 338–346. https://doi.org/10.1177/0269881107077729.

Dauthendey, M., 1909. Der Kuli Kimgun. Lingam: Zwölf Asiatische Novellen. Projekt Gutenberg-DE.

Dick, A.S., Goldin-Meadow, S., Hasson, U., Skipper, J.I., Small, S.L., 2009. Co-speech gestures influence neural activity in brain regions associated with processing semantic information. Hum. Brain Mapp. 30 (11), 3509–3526. https://doi.org/10.1002/hbm.20774.

Dick, A.S., Solodkin, A., Small, S.L., 2010. Neural development of networks for audiovisual speech comprehension. Brain Lang. 114 (2), 101–114. https://doi.org/10.1016/j.bandl.2009.08.005.

Dimitrova, D., Chu, M., Wang, L., Özyürek, A., Hagoort, P., 2016. Beat that word: how listeners integrate beat gesture and focus in multimodal speech discourse. J. Cogn. Neurosci. 28 (9), 1255–1269. https://doi.org/10.1162/jocn_a_00963.

Downing, P.E., 2001. A cortical area selective for visual processing of the human body. Science 293 (5539), 2470–2473. https://doi.org/10.1126/science.1063414.

Engelman, M., Agree, E.M., Meoni, L.A., Klag, M.J., 2010. Propositional density and cognitive function in later life: findings from the Precursors Study. J. Gerontol. Ser. B Psychol. Sci. Soc. Sci. 65 (6), 706–711. https://doi.org/10.1093/geronb/gbq064.

Esposito, F., Bertolino, A., Scarabino, T., Latorre, V., Blasi, G., Popolizio, T., Tedeschi, G., Cirillo, S., Goebel, R., Di Salle, F., 2006. Independent component model of the default-mode brain function: assessing the impact of active thinking. Brain Res. Bull. 70 (4–6), 263–269. https://doi.org/10.1016/j.brainresbull.2006.06.012.

Farias, S.T., Chand, V., Bonnici, L., Baynes, K., Harvey, D., Mungas, D., Simon, C., Reed, B., 2012. Idea density measured in late life predicts subsequent cognitive trajectories: implications for the measurement of cognitive reserve. J. Gerontol. Ser. B Psychol. Sci. Soc. Sci. 67 (6), 677–686. https://doi.org/10.1093/geronb/gbr162.

Ferguson, A., Spencer, E., Craig, H., Colyvas, K., 2014. Propositional idea density in women's written language over the lifespan: computerized analysis. Cortex; a journal devoted to the study of the nervous system and behavior 55, 107–121. https://doi.org/10.1016/j.cortex.2013.05.012.

Fransson, P., Marrelec, G., 2008. The precuneus/posterior cingulate cortex plays a pivotal role in the default mode network: evidence from a partial correlation network analysis. Neuroimage 42 (3), 1178–1184. https://doi.org/10.1016/j.neuroimage.2008.05.059.

Fromm, D., Greenhouse, J., Hou, K., Russell, G.A., Cai, X., Forbes, M., Holland, A., MacWhinney, B., 2016. Automated proposition density analysis for discourse in aphasia. J. Speech Lang. Hear. Res. : JSLHR (J. Speech Lang. Hear. Res.) 59 (5), 1123–1132. https://doi.org/10.1044/2016_JSLHR-L-15-0401.

Goldin-Meadow, S., 2006. Talking and thinking with our hands. Curr. Dir. Psychol. Sci. 15 (1), 34–39. https://doi.org/10.1111/j.0963-7214.2006.00402.x.

Goldin-Meadow, S., Alibali, M.W., 2013. Gesture's role in speaking, learning, and creating language. Annu. Rev. Psychol. 64, 257–283. https://doi.org/10.1146/annurev-psych-113011-143802.

Goldin-Meadow, S., Nusbaum, H., Kelly, S.D., Wagner, S., 2001. Explaining math: gesturing lightens the load. Psychol. Sci. 12 (6), 516–522. https://doi.org/10.1111/1467-9280.00395.

Green, A., Straube, B., Weis, S., Jansen, A., Willmes, K., Konrad, K., Kircher, T., 2009. Neural integration of iconic and unrelated coverbal gestures: a functional MRI study. Hum. Brain Mapp. 30 (10), 3309–3324. https://doi.org/10.1002/hbm.20753.

Greicius, M.D., Menon, V., 2004. Default-mode activity during a passive sensory task: uncoupled from deactivation but impacting activation. J. Cogn. Neurosci. 16 (9), 1484–1492. https://doi.org/10.1162/0898929042568532.

Hasson, U., Egidi, G., Marelli, M., Willems, R.M., 2018. Grounding the neurobiology of language in first principles: The necessity of non-language-centric explanations for language comprehension. Cognition 180, 135–157. https://doi.org/10.1016/j.cognition.2018.06.018.

He, Y., Gebhardt, H., Steines, M., Sammer, G., Kircher, T., Nagels, A., Straube, B., 2015. The EEG and fMRI signatures of neural integration: an investigation of meaningful gestures and corresponding speech. Neuropsychologia 72, 27–42. https://doi.org/10.1016/j.neuropsychologia.2015.04.018.

He, Y., Nagels, A., Schlesewsky, M., Straube, B., 2018a. The role of gamma oscillations during integration of metaphoric gestures and abstract speech. Front. Psychol. 9 (1348) https://doi.org/10.3389/fpsyg.2018.01348.

He, Y., Steines, M., Sommer, J., Gebhard, H., Nagels, A., Sammer, G., Kircher, T., Straube, B., 2018b. Spatial–temporal dynamics of gesture–speech integration: a simultaneous EEG-fMRI study. Brain Struct. Funct. 223 (7), 3073–3089.

Holle, H., Gunter, T.C., 2007. The role of iconic gestures in speech disambiguation: ERP evidence. J. Cogn. Neurosci. 19 (7), 1175–1192. https://doi.org/10.1162/jocn.2007.19.7.1175.

Holle, H., Gunter, T.C., Rüschemeyer, S.-A., Hennenlotter, A., Iacoboni, M., 2008. Neural correlates of the processing of co-speech gestures. Neuroimage 39 (4), 2010–2024. https://doi.org/10.1016/j.neuroimage.2007.10.055.

Hostetter, A.B., 2011. When do gestures communicate? A meta-analysis. Psychol. Bull. 137 (2), 297–315. https://doi.org/10.1037/a0022128.

Hu, M.-L., Zong, X.-F., Mann, J.J., Zheng, J.-J., Liao, Y.-H., Li, Z.-C., He, Y., Chen, X.-G., Tang, J.-S., 2017. A review of the functional and anatomical default mode network in schizophrenia. Neurosci. Bulletin 33 (1), 73–84. https://doi.org/10.1007/s12264-016-0090-1.

Hubbard, A.L., Wilson, S.M., Callan, D.E., Dapretto, M., 2009. Giving speech a hand: gesture modulates activity in auditory cortex during speech perception. Hum. Brain Mapp. 30 (3), 1028–1037. https://doi.org/10.1002/hbm.20565.

Iacono, D., Markesbery, W.R., Gross, M., Pletnikova, O., Rudow, G., Zandi, P., Troncoso, J.C., 2009. The Nun study: clinically silent AD, neuronal hypertrophy, and linguistic skills in early life. Neurology 73 (9), 665–673. https://doi.org/10.1212/WNL.0b013e3181b01077.

Kelly, S.D., Kravitz, C., Hopkins, M., 2004. Neural correlates of bimodal speech and gesture comprehension. Brain Lang. 89 (1), 253–260. https://doi.org/10.1016/S0093-934X(03)00335-3.

Kemper, S., Greiner, L.H., Marquis, J.G., Prenovost, K., Mitzner, T.L., 2001. Language decline across the life span: findings from the nun study. Psychol. Aging 16 (2), 227–239. https://doi.org/10.1037/0882-7974.16.2.227.

Kintsch, W., Keenan, J., 1973. Reading rate and retention as a function of the number of propositions in the base structure of sentences. Cogn. Psychol. 5 (3), 257–274. https://doi.org/10.1016/0010-0285(73)90036-4.

Kircher, T., Straube, B., Leube, D., Weis, S., Sachs, O., Willmes, K., Konrad, K., Green, A., 2009. Neural interaction of speech and gesture: differential activations of metaphoric co-verbal gestures. Neuropsychologia 47 (1), 169–179. https://doi.org/10.1016/j.neuropsychologia.2008.08.009.

Kircher, T.T.J., Leube, D.T., Erb, M., Grodd, W., Rapp, A.M., 2007. Neural correlates of metaphor processing in schizophrenia. Neuroimage 34 (1), 281–289. https://doi.org/10.1016/j.neuroimage.2006.08.044.

Macedonia, M., 2014. Bringing back the body into the mind: gestures enhance word learning in foreign language. Front. Psychol. 5, 1467. https://doi.org/10.3389/fpsyg.2014.01467.

Mazoyer, B., Zago, L., Mellet, E., Bricogne, S., Etard, O., Houdé, O., Crivello, F., Joliot, M., Petit, L., Tzourio-Mazoyer, N., 2001. Cortical networks for working memory and executive functions sustain the conscious resting state in man. Brain Res. Bull. 54 (3), 287–298. https://doi.org/10.1016/S0361-9230(00)00437-8.

McKiernan, K.A., D'Angelo, B.R., Kaufman, J.N., Binder, J.R., 2006. Interrupting the "stream of consciousness": an fMRI investigation. Neuroimage 29 (4), 1185–1191. https://doi.org/10.1016/j.neuroimage.2005.09.030.

McNeil, N.M., Alibali, M.W., Evans, J.L., 2000. McNeil et al. 2000 J. Nonverbal Behav. 24 (2), 131–150. https://doi.org/10.1023/A:1006657929803.

McNeill, D., 1992. Hand and Mind: what Gestures Reveal about Thought. University of Chicago Press, Chicago.

Mitzner, T.L., Kemper, S., 2003. Oral and written language in late adulthood: findings from the Nun Study. Exp. Aging Res. 29 (4), 457–474. https://doi.org/10.1080/03610730303698.

Moe, A.M., Breitborde, N.J.K., Shakeel, M.K., Gallagher, C.J., Docherty, N.M., 2016. Idea density in the life-stories of people with schizophrenia: associations with narrative qualities and psychiatric symptoms. Schizophr. Res. 172 (1–3), 201–205. https://doi.org/10.1016/j.schres.2016.02.016.

Mortimer, J., Borenstein, A., 2012. Idea density in early life is associated with APOE-ε4 but affects the risk of Alzheimer's disease independently. Alzheimer's Dementia 8 (4), P629. https://doi.org/10.1016/j.jalz.2012.05.1677.

Nagels, A., Kircher, T., Grosvald, M., Steines, M., Straube, B., 2019. Evidence for gesture-speech mismatch detection impairments in schizophrenia. Psychiatr. Res. 273, 15–21. https://doi.org/10.1016/j.psychres.2018.12.107.

Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9 (1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4.

Özyürek, A., Willems, R.M., Kita, S., Hagoort, P., 2007. On-line integration of semantic information from speech and gesture: insights from event-related brain potentials. J. Cogn. Neurosci. 19 (4), 605–616. https://doi.org/10.1162/jocn.2007.19.4.605.

Raichle, M.E., MacLeod, A.M., Snyder, A.Z., Powers, W.J., Gusnard, D.A., Shulman, G.L., 2001. A default mode of brain function. Proc. Natl. Acad. Sci. U. S. A 98 (2), 676–682. https://doi.org/10.1073/pnas.98.2.676.

Riley, K.P., Snowdon, D.A., Desrosiers, M.F., Markesbery, W.R., 2005. Early life linguistic ability, late life cognitive function, and neuropathology: findings from the Nun Study. Neurobiol. Aging 26 (3), 341–347. https://doi.org/10.1016/j.neurobiolaging.2004.06.019.

Roark, B., Mitchell, M., Hosom, J.-P., Hollingshead, K., Kaye, J., 2011. Spoken language derived measures for detecting mild cognitive impairment. IEEE Trans. Audio Speech Lang. Process. 19 (7), 2081–2090. https://doi.org/10.1109/TASL.2011.2112351.

Schülke, R., Straube, B., 2017. Modulating the assessment of semantic speech–gesture relatedness via transcranial direct current stimulation of the left frontal cortex. Brain Stimulation 10 (2), 223–230. https://doi.org/10.1016/j.brs.2016.10.012.

Schülke, R., Straube, B., 2018. Transcranial direct current stimulation improves semantic speech-gesture matching in patients with schizophrenia spectrum disorder. Schizophr. Bull. https://doi.org/10.1093/schbul/sby144.

Seghier, M.L., Price, C.J., 2012. Functional heterogeneity within the default network during semantic processing and speech production. Front. Psychol. 3, 281. https://doi.org/10.3389/fpsyg.2012.00281.

Sirts, K., Piguet, O., Johnson, M., 2017a. Idea density for predicting Alzheimer's disease from transcribed speech. In: Proceedings of the 21st Conference on Computational Natural Language Learning (CoNLL 2017). Proceedings of the 21st Conference on Computational Natural Language Learning (CoNLL 2017), Vancouver, Canada. Association for Computational Linguistics, Stroudsburg, PA, USA, pp. 322–332.

Sirts, K., Piguet, O., Johnson, M., 2017b. Idea density for predicting Alzheimer's disease from transcribed speech. Proceedings of the 21st Conference on Computational Natural Language Learning (CoNLL 2017) 322–332.

Skipper, J.I., Goldin-Meadow, S., Nusbaum, H.C., Small, S.L., 2007. Speech-associated gestures, Broca's area, and the human mirror system. Brain Lang. 101 (3), 260–277. https://doi.org/10.1016/j.bandl.2007.02.008.

Slotnick, S.D., 2017. Cluster success: fMRI inferences for spatial extent have acceptable false-positive rates. Cogn. Neurosci. 8 (3), 150–155. https://doi.org/10.1080/17588928.2017.1319350.

Slotnick, S.D., Moo, L.R., Segal, J.B., Hart, J., 2003. Distinct prefrontal cortex activity associated with item memory and source memory for visual shapes. Cogn. Brain Res. 17 (1), 75–82. https://doi.org/10.1016/S0926-6410(03)00082-X.

Snowdon, D., Kemper, S.J., Mortimer, J.A., Greiner, L.H., Wekstein, D.R., Markesbery, W.R., 1996. Linguistic ability in early life and cognitive function and alzheimer's disease in late life. J. Am. Med. Assoc. (275), 528–532.

Spencer, E., Craig, H., Ferguson, A., Colyvas, K., 2012. Language and ageing - exploring propositional density in written language - stability over time. Clin. Linguist. Phon. 26 (9), 743–754. https://doi.org/10.3109/02699206.2012.673046.

Spencer, E., Ferguson, A., Craig, H., Colyvas, K., Hankey, G.J., Flicker, L., 2014. Propositional idea density in older men's written language: findings from the HIMS study using computerised analysis. Clin. Linguist. Phon. 29 (2), 85–101. https://doi.org/10.3109/02699206.2014.956263.

Spreng, R.N., Mar, R.A., Kim, A.S.N., 2009. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. J. Cogn. Neurosci. 21 (3), 489–510. https://doi.org/10.1162/jocn.2008.21029.

Straube, B., Green, A., Bromberger, B., Kircher, T., 2011. The differentiation of iconic and metaphoric gestures: common and unique integration processes. Hum. Brain Mapp. 32 (4), 520–533. https://doi.org/10.1002/hbm.21041.

Straube, B., Green, A., Jansen, A., Chatterjee, A., Kircher, T., 2009. Social cues, mentalizing and the neural processing of speech accompanied by gestures. Neuropsychologia 48 (2), 382–393. https://doi.org/10.1016/j.neuropsychologia.2009.09.025.

Straube, B., Green, A., Sass, K., Kirner-Veselinovic, A., Kircher, T., 2013a. Neural integration of speech and gesture in schizophrenia: evidence for differential processing of metaphoric gestures. Hum. Brain Mapp. 34 (7), 1696–1712. https://doi.org/10.1002/hbm.22015.

Straube, B., He, Y., Steines, M., Gebhardt, H., Kircher, T., Sammer, G., Nagels, A., 2013b. Supramodal neural processing of abstract information conveyed by speech and gesture. Front. Behav. Neurosci. 7, 120. https://doi.org/10.3389/fnbeh.2013.00120.

Straube, B., Wroblewski, A., Jansen, A., He, Y., 2018. The connectivity signature of co-speech gesture integration: the superior temporal sulcus modulates connectivity between areas related to visual gesture and auditory speech processing. Neuroimage 181, 539–549. https://doi.org/10.1016/j.neuroimage.2018.07.037.

Supekar, K., Uddin, L.Q., Prater, K., Amin, H., Greicius, M.D., Menon, V., 2010. Development of functional and structural connectivity within the default mode network in young children. Neuroimage 52 (1), 290–301. https://doi.org/10.1016/j.neuroimage.2010.04.009.

Tootell, R.B., Reppas, J.B., Kwong, K.K., Malach, R., Born, R.T., Brady, T.J., Rosen, B.R., Belliveau, J.W., 1995. Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. J. Neurosci. 15 (4), 3215–3230. https://doi.org/10.1523/JNEUROSCI.15-04-03215.1995.

Turner, A., Greene, E., 1977. The Construction and Use of a Propositional Text Base (Technical Report 63). University of Colorado, Institute for the Study of Intellectual Behavior, pp. 1–81.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., Joliot, M., 2002. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. Neuroimage 15 (1), 273–289. https://doi.org/10.1006/nimg.2001.0978.

Willems, R.M., Boer, M. de, Ruiter, de, J.P., Noordzij, M.L., Hagoort, P., Toni, I., 2010. A dissociation between linguistic and communicative abilities in the human brain. Psychol. Sci. 21 (1), 8–14. https://doi.org/10.1177/0956797609355563.

Wilson, S.M., Molnar-Szakacs, I., Iacoboni, M., 2008. Beyond superior temporal cortex: intersubject correlations in narrative speech comprehension. Cerebral cortex (New York, N.Y. 18 (1), 230–242. https://doi.org/10.1093/cercor/bhm049, 1991.

Wu, Y.C., Coulson, S., 2005. Meaningful gestures: electrophysiological indices of iconic gesture comprehension. Psychophysiology 42 (6), 654–667. https://doi.org/10.1111/j.1469-8986.2005.00356.x.

Xu, J., Kemeny, S., Park, G., Frattali, C., Braun, A., 2005. Language in context: emergent features of word, sentence, and narrative comprehension. Neuroimage 25 (3), 1002–1015. https://doi.org/10.1016/j.neuroimage.2004.12.013.