Regionally specific cortical lateralization of abstract and concrete verb processing: Magnetic mismatch negativity study

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ABSTRACT

The neural underpinnings of processing concrete and abstract semantics remain poorly understood. Previous fMRI studies have shown that multimodal and amodal neural networks respond differentially to different semantic types; importantly, abstract semantics activates more left-lateralized networks, as opposed to more bilateral activity for concrete words. Due to the lack of temporal resolution, these fMRI results do not allow to easily separate language- and task-specific brain responses and to disentangle early processing stages from later post-comprehension phenomena. To tackle this, we used magnetoencephalography (MEG), a time-resolved neuroimaging technique, in combination with a task-free oddball mismatch negativity (MMN) paradigm, an established approach to tracking early automatic activation of word-specific memory traces in the brain. We recorded the magnetic MMN responses in 30 healthy adults to auditorily presented abstract and concrete action verbs to assess lateralization of word-specific lexico-semantic processing in a set of neocortical areas. We found that MMN responses to these stimuli showed different lateralization patterns of activity in the upper limb motor area (BA4) and parts of Broca's area (BA45/BA47) within ~100–350 ms after the word disambiguation point. Importantly, the greater leftward response lateralization for abstract semantics was due to the lesser involvement of the right-hemispheric homologues, not increased left-hemispheric activity. These findings suggest differential region-specific involvement of bilateral sensorimotor systems already in the early automatic stages of processing abstract and concrete action semantics.

1. Introduction

Brain mechanisms for encoding and storage of linguistic information, such as different word meanings (semantics), remain a poorly understood and hotly debated topic. One of the major questions in cognitive psycho- and neurolinguistics concerns identifying the mechanisms specialized in the processing of abstract vs. concrete semantics. This particular issue originates from the studies of the so-called "concreteness effect" (Paivio, 1991) and extends to the grounded and embodied nature of speech and language processing (Barsalou, 2008). In brief, this effect implies facilitated processing of concrete words/concepts, as opposed to abstract semantics (James, 1975). Concrete words (i.e., those related to

specific referents in the physical world, e.g., *dog, house,* or *run, cry*) are faster learnt, more easily identified and responded to in various tasks than the abstract ones, which have no clear referents in the physical/sensorimotor domain (e.g., *love, freedom, hesitate, dream*; see (Mkrtychian et al., 2019). On the other hand, some studies found that the reverse effect might also take place, for instance, in patients with semantic dementia (a variant of fronto-temporal lobar degeneration, (Kindell et al., 2014) whose concrete semantic knowledge degrades while the abstract one is still preserved (Bonner et al., 2009). In any case, a substantial body of evidence shows that there is a basic distinction between semantic processing of concrete and abstract concepts that emerges at both the cognitive and neural levels.

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1.1. Theoretical accounts of processing abstract vs. concrete semantics

Different conceptual approaches have been proposed to explain the underpinnings of this distinction. For instance, the dual coding theory (Paivio, 1991) postulates that abstract semantic concepts are purely verbal, while concrete ones rely on both sensorimotor (i.e., related to physical referents) and verbal mechanisms. Therefore, functionally, the processing of these two types of semantics is supported by two interrelated representational systems that can act either separately or together (Mkrtychian et al., 2019). This availability of two vs. one processing mechanisms facilitates concrete over abstract semantics processing. Importantly, from the point of view of the dual coding theory, concrete semantics is based on a wider network of associated representations, resulting in more robust storage and enhanced processing mechanisms, also possibly suggesting the involvement of the right-hemispheric language-subdominant circuits in concrete semantics (Eviatar et al., 1990), as opposed to the abstract concepts confined to the core language networks of the left hemisphere. However, other experimental studies have provided evidence against such a basic bihemispheric explanation of differences between concrete and abstract language processing, highlighting the need for more research (Josh Cuevas, 2016).

Indeed, such inconsistencies led to further development of the dual coding framework into a range of models (Bi, 2021; Paivio, 2013). Among the most influential models attempting to explain word representations in the brain the so-called hub-and-spoke model suggests that words are processed in complex networks composed of interconnected modal (sensorimotor) nodes linked to an amodal hub (Patterson and Lambon Ralph, 2016). This amodal hub is often placed in the left anterior temporal lobes (ATL), and might also include the surrounding cortical temporoparietal regions. At the functional level, the processing of concrete semantics is therefore supported by the interaction of modality-specific 'spokes' with the amodal 'hub'. In turn, the processing of abstract semantics within this model is associated only with amodal hub(s), even though this still remains a matter of debate (Dove, 2021). Another major framework postulates even more widely distributed cell assemblies (CAs) as a neural mechanism through which lexico-semantic representations are implemented in the brain (Pulvermüller, 1999, 2023); this approach also relies on a hub-like function of the core language areas in temporal and inferior-frontal cortices (not necessarily limited to ATL). The reliance of abstract semantics on this left-lateralized core language system has been partially supported by asymmetrical brain activity patterns (Pexman et al., 2023).

In sum, the above models point to the structural and functional differences of the brain systems that support the processing of concrete and abstract semantics. Generally, they agree that concrete semantics relies on the modality-specific distributed sensorimotor cortical networks, while abstract semantics is more dependent on the amodal networks. Whereas the hub-and-spoke and the cell assembly frameworks are more specific in describing these cortical networks and the interactions that underlie the processing of different types of semantics, the dual coding approach generally emphasizes an unequal involvement of the cerebral hemispheres: left-hemispheric dominance for the processing of abstract semantics or symbolic information and the right-hemispheric processing for the concrete semantics (Paivio, 1991).

Alternatively, the context availability theory suggests that facilitated processing of concrete concepts might be caused by greater context-related activation associated with them, as compared to the abstract semantics (Jessen et al., 2000). In contrast, embodied (or grounded) cognition approaches postulate that semantic memory either does not rely on amodal representations at all, or is at least tightly interconnected with modality-specific representations that form the basis of cognitive processes (Farina, 2021; Foglia and Wilson, 2013; Paco Calvo, 2008). There are different conceptualizations of this claim within this broad field of theories (Barsalou, 2008), which make their major focus on simulation as a core mechanism of cognition. This implies that the initial sensorimotor experience (e.g., hearing and pronouncing words in conjunction with the objects/actions they mean) produces multimodal conceptual representations that are then stored in the semantic memory in the form of distributed neural networks (Beilock, 2009; Kumar, 2021). When needed, these action-perception networks become activated (hence the term "simulation") for the current cognitive/behavioral performance (Gallese, 2005). The special role of motor simulations has been emphasized for speech and language processing, particularly for action-related semantics (Gallese, 2007; Pulvermüller, 2005). For instance, TMS studies have provided evidence that cortical motor areas are causally involved in the processing of lexical semantics and acquisition of action-related words (Buccino et al., 2005; Vukovic et al., 2017; Vukovic and Shtyrov, 2019).

Particularly, recent findings in embodied theories have pointed out that processing of abstract semantics might be tightly connected with the purely verbal aspects of processing of words *per se* serving as labels for meanings (Borghi, 2023; Dove, 2022); that is, in the same say as representations of words with clear physical referents involve modality-specific sensory and motor areas, those with more abstract meanings may only have articulatory processes as their main sensorimotor anchor (Borghi et al., 2018). Speech, both overt and inner speech, might be therefore tightly involved in conceptual abstract knowledge processing (Borghi and Fernyhough, 2023). Consequently, the core language areas that are typically left-lateralized (Knecht et al., 2000), would become crucial neural nodes for the abstract semantics, with a particular role for the left inferior-frontal gyrus as a hub for speech production. Remarkably, this view converges with the other models described above on the role of the left-hemispheric core language areas in abstract semantic information processing.

1.2. Clinical data

A body of clinical data points to the specific links between brain lesion sites and particular semantic impairments. For instance, lesion studies show that lesions affecting frontal and, particularly, inferior frontal areas of the left hemisphere mostly impact the verbal semantics (i.e., motor/action-related verbs), while noun semantics (i.e., object-related nouns) remains less affected in these patients (Damasio and Tranel, 1993; Daniele et al., 1994). This is paralleled by the effects found in primary progressive aphasia: non-fluent patients are impaired mostly in verbal semantics, while fluent patients are impaired in object semantics (Hillis et al., 2004). Moreover, patients with Broca's aphasia caused by the left frontal lesions produce words having a lower degree of semantic abstractness in comparison to healthy controls (Roll et al., 2012). In contrast, concrete semantic processing impairments are associated with various lesions affecting the bilateral temporal, particularly the anterior temporal areas, and also temporoparietal and temporooccipital areas (Gainotti, 2000; Tranel et al., 1997). Generally, the results of clinical studies support the theoretical frameworks described above in that abstract semantics is processed in the left-lateralized networks that include inferior frontal areas, while concrete semantics is processed by bilateral multimodal networks, including posterior sensory cortical areas. Whereas studies on patients do not allow for unequivocal conclusions regarding the processes taking place in an intact healthy brain, non-invasive neuroimaging techniques have provided some evidence on the patterns of neural activity that underlie semantic processing.

1.3. Neuroimaging evidence

A body of data on the neural architecture of concrete and abstract semantic processing has been provided by studies on healthy individuals with different types of language tasks. The results have been systematically analyzed in several reviews that show that differently lateralized, although partially overlapping, networks support the processing of abstract and concrete semantics. For instance, a seminal meta-analysis (Binder et al., 2009) revealed two broad neural networks, covering

both hemispheres of the cortical surface, as being involved in the processing of concrete (perceptual) and abstract (conceptual) information in language tasks. These two networks seem largely distinct from each other, with some overlap in the inferior and superior temporoparietal and inferior frontal areas. Strikingly, the network processing internal, conceptual information (i.e., abstract semantics) turned out to be more left-lateralized, while the network processing the external, perceptual information (i.e., concrete semantics) was bilateral.

Another work (Wang et al., 2010) specifically investigated the neural representations of abstract and concrete concepts elicited in various speech tasks across studies using the multilevel kernel density method (Wager et al., 2007). It was found that abstract word processing networks have stronger responses in the left inferior frontal areas, as well as left anterior temporal cortex whereas concrete word processing networks have stronger responses in posterior multimodal and multidomain areas (left precuneus, posterior cingulate, parahippocampal gyrus, fusiform gyrus as well as cerebellum).

Finally, a recent meta-analysis (Bucur and Papagno, 2021) addressed some of the confounds presented in previous works by including only studies with abstract and concrete word stimuli. The results showed partially overlapping yet distinct cortical clusters supporting the processing of abstract and concrete semantics. Importantly, among these clusters, the left IFG showed responses that were more associated with the processing of abstract nouns and verbs, while the bilateral posterior temporoparietal and occipital regions were more associated with the processing of concrete words.

These findings show a fairly specific and consistent pattern of differential responses in language tasks. Thus, abstract semantic processing networks are more left-lateralized than those for concrete language. Moreover, virtually all the studies emphasize the greater involvement of the left IFG in abstract semantics. In contrast, concrete semantic networks are more bilateral and include posterior multisensory and multidomain areas (Bucur and Papagno, 2021). Hence, one key pattern of distinct abstract and concrete semantic processing might be the hemispheric laterality of the processing-related responses. Importantly, the abstract semantic processing patterns are more focused around the left IFG (Vigneau et al., 2006), also including adjacent cortical areas (e. g. (Fletcher et al., 1997),). Indeed, as described above, the left IFG (LIFG) has been argued to be a hub for abstract semantics processing on the basis of our experience with abstract word being predominantly verbal (see, e.g. (Borghi et al., 2019),), which resonates well with the dual-coding approach (Paivio, 1991).

When investigating the LIFG function, we should consider that this area is structurally and functionally heterogeneous. Anatomically, it includes three subregions (Petrides and Pandya, 2002): *pars opercularis* (BA44), *pars triangularis* (BA45) and *pars orbitalis* (BA47). Various studies have revealed different roles of these areas in speech and, particularly, in semantic processing. For instance, Heim and colleagues (Heim et al., 2005) found that activity in the left BA45 might be more specific to lexical comprehension tasks than phonological ones, while the left BA44 activation might be observed in both types of tasks. Moreover, in both speech comprehension and speech production contexts, BA44 was shown to activate more for phonological than for semantic or syntactic fluency tasks (Heim et al., 2009). Within such an approach, the left BA44 (and adjacent premotor areas) might be considered as a crucial node for phonological and/or syntactic processing. Other studies showed that semantic processing is predominantly associated with both BA45 and BA47 areas (Poldrack et al., 1999; Skeide and Friederici, 2016). Supporting this view, the study by Fiebach and colleagues (Fiebach et al., 2003) showed that cortical memory traces associated with learned lexical items involve BA45 and BA47/12. Among them, BA45 and its activity have been shown to be associated with the processing of words of different semantic categories (Carota et al., 2017). Furthermore, a more detailed investigation of category-specific semantic processing shows differential roles for areas within the left IFG: for instance, action words are more strongly

associated with BA45 than with other IFG areas, which is in line with existing evidence that BA45 shows more specificity for verb, rather than noun, processing (Perani et al., 1999). Taken together, various findings suggest that different (combinations of) Brodmann areas within the left IFG might support different aspects of linguistic processing (Hagoort, 2005). Particularly, the left BA45 and BA47 together are more specific for semantics processing, the left BA44 and BA45 together are involved in syntactic processing, while BA44, possibly together with BA6, also contributes to the phonological processing.

Importantly, in most of the studies mentioned above semantic-related responses in the left IFG were strongly task-dependent, and their authors emphasized that the factor of specific task used might impact the results to a large extent. To avoid the confounds related to experimental tasks (which, in an extreme case, might lead to the specific area response being task-driven and not semantically specific) task-free paradigms are needed. That is, recording automatic brain activity arising in the absence of any stimulus-related task might shed extra light on different semantic processing effects, including contrasts between neural activation patterns induced by abstract and concrete lexicon and their spatial localization.

1.4. Task-free mismatch negativity paradigm

Contrary to the active-task approaches discussed above, task-free paradigms typically implemented using neuroimaging techniques with high temporal resolution (such as MEG or EEG) might provide more objective evidence regarding the neural patterns associated with online linguistic processing, including their spatio-temporal dynamics and its lateralization across the two hemispheres. A widely used task-free experimental approach is to use the *oddball mismatch negativity (MMN) paradigm* (Naatanen, 2001).

The oddball MMN design typically includes frequent repetitive (so-called "standard") stimuli, randomly interspersed with rare "deviant" stimuli, usually presented without any stimulus-related task under the condition of attention withdrawal to a competing visual input. Since this design is focused on difference responses (deviant minus standard ERP/ERF), it allows for a uniquely complete control over acoustic/auditory/phonological stimulus confounds, which is achieved by including physically identical contrasts within the context of otherwise different standard/deviant sets. This type of paradigm makes it possible to study the spatial and temporal dynamics of activation of both short-term auditory memory processes and long-term memory traces of individual phonemes and syllables (Näätänen et al., 1997; Shtyrov et al., 2000), to detect long-term memory traces of stimulus words (Pulvermüller et al., 2001), to quantify differences in neural responses depending on their psycholinguistic features (Alexandrov et al., 2011), and to scrutinize neuroanatomical specificity of memory trace distribution to different word classes (Pulvermüller et al., 2004; Shtyrov et al., 2014). The potential of the mismatch paradigm to provide fine-grain details of word-specific memory traces in the brain has been shown in several studies. For instance, EEG and MEG studies of word-elicited MMN responses) demonstrated that stimulus words in the mismatch negativity paradigm cause asymmetrical left-lateralized responses (Pulvermüller et al., 2001; Shtyrov et al., 2005). Their results revealed that meaningful words caused a significant increase in the left hemispheric MMN response when compared to pseudowords, whereas no significant response differences were found in the right hemisphere, and no similar left-hemispheric specificity could be seen in foreign-language participants unfamiliar with the stimulus words.

Moreover, semantic features of the meaningful word stimuli might impact the spatial patterns of the bilateral MMN responses. These stimulus-related effects are distributed and might be found outside the superior temporal and inferior frontal areas, the core MMN generators. For instance, topographically differential involvement of cortical regions into the processing of hand- and leg-related action verbs (i.e., regional specificity of the semantic MMN responses) was shown in an

EEG MMN study of English verbs (Shtyrov et al., 2004). More precise localization of such semantically-related memory traces in the cortex was achieved in an MEG study of Finnish verbs (Pulvermüller et al., 2005), in which two action words (face- and leg-related) elicited somatotopically distinct activation within frontocentral motor cortices. This association of motor system with word comprehension function was more deeply investigated in an MEG study using an MMN paradigm comprising a set of stimuli varying in their lexical (nouns and verbs) and semantic (leg-, hand-, and mouth-related words) categories (Shtyrov et al., 2014). Analysis of the magnetic MMN sources elicited by semantically different types of stimuli within the left motor cortex demonstrated that each specific category elicited greater responses in the respective area of the somatotopically organized motor cortex (i.e, leg, hand, or mouth-related motor representations) than the other two. This result showed the semantically specific functional topography of the MMN responses that exist in the left motor cortex. Notably, these differential activations occurred rapidly, starting from ~80 ms of the semantic disambiguation point during the auditory presentation of spoken words. However, only the areas in the language-dominant left hemisphere were analyzed in this research, and no right-hemispheric data were reported; consequently, no conclusions could be drawn of the hemispheric lateralization of word processing. Monitoring the activity of broader neural networks spanning across both the left and the right hemispheres would be extremely important in the light of the existing theoretical accounts, which predict different neural networks for abstract and concrete (including action-related) semantics, as already discussed above.

To sum up, memory representations of abstract and concrete semantics seem to differ in several ways, which may be due to differential impact of sensorimotor-associated content of concrete and abstract items. This view is partially supported by clinical data on patients with language and semantic memory deficits. Moreover, as reviewed above, neuroimaging data on language processing in healthy individuals generally confirm this distinction and suggest a specific pattern for the abstractness-concreteness difference: more left-lateralized response patterns with the involvement of regions in left IFG is more typical for abstract semantics, while more bilateral response patterns that involve multimodal posterior cortical areas, are more typical for concrete semantic processing. However, more specific patterns of the semantic-related responses, particularly, the localization of the abstract semantics processing within IFG, remain controversial. Also, the existing data have been mostly obtained in fMRI studies using different types of language tasks, which, on the one hand, do not allow to disentangle task-independent semantic activation from task-specific activity, and, on the other hand, do not have the temporal resolution to track the rapid automatic neural activity unfolding during online language comprehension. The use of task-free oddball mismatch negativity MEG/EEG approach could allow us to probe the dynamics of semantically specific neural activity in question with excellent temporal resolution by employing a variety of semantically different language stimuli. Moreover, such an approach has been proven to be beneficial for studying functional lateralization. For instance, it has been demonstrated that it is the meaningful linguistic features of speech sounds presented in an oddball paradigm that drive the leftward lateralization of otherwise bilateral or even right-lateralized MMN (Shtyrov et al., 2005, 2008). Furthermore, source analysis of neuromagnetic MMN responses allows for detailed scrutiny of language-specific neuronal circuits within specific cortical regions of both hemispheres (Pulvermuller and Shtyrov, 2009). Whereas the left superior-temporal increase in MMN amplitude was associated with lexical-semantic memory traces activation in general, the laterality of inferior-frontal responses appeared to depend on the lexical and morphological features of the stimuli presented. The lateralized MMN activity of action-perception circuits was also shown to be linked to novel wordform acquisition processes (Pulvermüller et al., 2012). All in all, a number of extant works have shown bilateral distribution of the lexical-semantic MMN responses (Endrass et al., 2004;

Naatanen, 2001; Pulvermüller et al., 2001, 2004), mostly indicating relatively greater contribution of the left-hemispheric activity into the processing of different linguistic features.

With respect to processing concrete action semantics, one previous MEG experiment successfully used the MMN paradigm to address the contribution of the left-hemispheric motor cortex to the processing of different action-related verbs and nouns (Shtyrov et al., 2014). While showing somatotopic specificity of motor-cortex activation to the effectors implied by the action-word stimuli, that study, however, omitted the right-hemispheric from activity from analysis altogether. In light of the evidence reviewed above, the lateralization of neural responses might be the key factor that distinguishes the neural responses associated with these two different types of semantics. Still, the latter has not been demonstrated yet. To our knowledge, there is only a single EEG study that attempted to find such differences but was unsuccessful (Brunellière et al., 2011), which is unsurprising given the poor spatial resolution of EEG.

1.5. Present study

The present study aimed to fill this gap by implementing an improved lexical MMN paradigm and fine-grain data analysis approaches to disentangle the hemispheric effects associated with the processing of concrete and abstract semantics, namely concrete and abstract action verbs. To minimize confounds, we used verbs of two types – abstract and concrete – rather than verbs vs. nouns, as used in many previous studies (which also introduces word class differences in addition to semantic ones). We tested the following hypothesis: the lateralization of the mismatch negativity responses in modality-specific and amodal cortical areas will depend on their relation to the processing of specific semantic information, abstract vs. concrete.

The choice of verbs as stimuli in our study was due to their various crucial features. There is a phylogenetic approach that considers language as a result of evolution of communication from manual gestures to vocal motor acts (De Stefani and De Marco, 2019; McNeill, 2012). In this sense, action-related semantics, and above all, verbal semantics, becomes a fundamental constituent of the language structure, which motivates research on the neural mechanisms of verbs representations in the brain. Moreover, the link between the motor systems and action-related language, developed in evolution and reinstated in individual language acquisition, has been a subject or particular scrutiny in human cognitive neuroscience. For instance, the mirror neuron hypothesis postulates a highly specific system of cortical neurons in humans, which might mediate the links between motor execution and the processing of action-related semantics (De Stefani and De Marco, 2019; Rizzolatti and Arbib, 1998). The tight neural links between verbal domain of language and cortical neural networks have also been linked to fundamental neural principles, such as associative learning (Hebb, 2005) that leads to formation of distributed cell assemblies functioning as word-specific memory traces: during language acquisition, neurons within different brain areas coactivate forming such distributed neural networks (Pulvermüller, 1999). Particularly, reciprocal connections between motor and language neural systems are considered as a substrate for action-related semantic processing (Hauk et al., 2008), further highlighting the need for the study of verbs as a neurolinguistic phenomenon. The specific role of verbs in language processing at the neural level has also been confirmed by clinical studies comparing the neurophysiological mechanisms underpinning verb processing against other lexical classes, typically noun stimuli (Damasio and Tranel, 1993; Perani et al., 1999). These studies have shown a double dissociation indicating that lexical deficits in verbs and nouns have different bases at the brain level. Further highlighting this dissociation, there are findings that point to a strong involvement of the prefrontal and premotor cortical areas specifically in processing of verbs (Berlingeri et al., 2008; Tranel et al., 2001, 2003). In sum, the existing evidence and theoretical frameworks point to a very specific verbal-related language substrate that makes

studying verb processing a relevant task for the understanding of the human language system and the neural mechanisms that underlie it.

Based on the available evidence, we hypothesized that concrete words will yield more bilateral responses mostly in the sensorimotor areas known to be specifically related to their semantic processing. Conversely, abstract words could be expected to elicit more left-lateralized responses primarily in the left inferior frontal area (Broca's area, BA45/47 in particular), which has been suggested to be specific to abstract semantics storage and processing. We selected a restricted but strictly controlled set of verb stimuli to be presented in the mismatch negativity paradigm; these stimuli only differed in their semantics while the rest of the phonological and lexical features were matched, with identical standard-deviant contrasts across all conditions. The stimulus set included a verb associated with upper extremities' movement activity (hand-related), an abstract verb not directly associated with movements, and a control condition with a pseudoword stimulus, phonologically and phonotactically similar to the real verbs. Given the lack of semantic specialization, we did not expect the pseudowords to provide any specific pattern of laterality.

2. Material and methods

2.1. Participants

A group of 30 healthy adults (mean age 20.4 years, SD = 2.6; 18 females) participated in the study. All of them were native Russian speakers, right-handed (mean handedness score of 87% according to the Edinburgh handedness inventory (Oldfield, 1971), and had not been diagnosed with any mental or neurological impairments prior to the study. All participants had normal hearing and normal or corrected-to-normal vision.

The sample size was calculated with G*Power 3.1.9.7 (Faul et al., 2007). To the best of our knowledge, there have been no previous studies that investigated a similar complex interaction effect (see the "Statistical analysis of region-specific lateralization effects" section below). Thus, we assumed a moderate effect size: partial eta squared 0.03 that corresponds to Cohen's f = 0.18 (α = 0.05, 1-β = 0.8). The statistical power analysis revealed that a sample size of 19 participants would be adequate. For a more conservative partial effect size level with partial eta squared = 0.02, Cohen's f = 0.14 (α = 0.05, 1-β = 0.8), a sample of 28 participants would be required. To account for the possibility of excluding participants due to a possible poor data quality, we recruited more participants, which led to the final choice of N = 30.

2.2. Stimuli and paradigm

The following auditory linguistic stimuli were used in three oddball experimental conditions:

i) a concrete hand-action imperative verb, "лепи" ("lepi" [lʲɪpʲⁱi] – Eng. sculpt, mould, glue, stick/glue) was used as a random deviant stimulus presented among acoustically similar pseudo-words "лепе" ("lepe" [lʲɪpʲⁱɛ]);

ii) an abstract imperative verb, "копи" ("kopi" [kɐpʲⁱi] – Eng., save up, accumulate, amass) was used as a deviant and a pseudoword "копе" ("kope" [kɐpʲⁱɛ]) was used as a standard;

iii) a deviant pseudoword "ропи" ("ropi" [rɐpʲⁱi]), phonologically closely resembling the two verbs above and a pseudoword "ропе" as a standard ("rope" [rɐpʲⁱɛ]), but devoid of any meaning.

We also attempted to achieve the highest phonological similarity possible across all three sets with identical disyllabic CVCV structure, as well as the identical standard-deviant contrasts between the stimulus-final vowels: [ɛ] vs. [i]. All the stimuli were generated by using Julia deep neural network for speech synthesis (Speech Technology Center, Saint Petersburg, Russia; https://cp.speechpro.com/service/tts). The

duration of all sound files was matched across the conditions and was set to 432 ms.

The word stimuli had a lexical frequency above zero according to the Russian lexical frequency dictionary (http://dict.ruslang.ru/freq.php). Acoustic contrasts between the second syllables of the deviants and standards were identical across all three series, which was achieved using a cross-splicing procedure. Thus, the second syllables, both for the standards and deviants, were generated separately to avoid any impact of coarticulation and combined with the first syllables of the corresponding stimuli. All stimuli had their fundamental frequencies and loudness matched. The acoustic similarity of the standard and deviant stimuli across all series made it possible to compare the impact of the lexical and semantic features on the evoked responses produced by different types of stimuli unconfounded by acoustic factors (see Fig. 1).

To verify the degree of action-relatedness of the two verbs and to control the intended semantic distinctions between them, they were subjected to a rating study. After the MEG session, participants rated these stimuli on a scale 1 to 10 according to their relevance to any concrete motor action they may perform. The statistical analysis using non-parametric Wilcoxon sign rank test showed that participants gave a significantly higher average rating for the concrete than for the abstract stimulus (T = 253, Z = 4,12, p < 0.0001). In other words, for our participants the concrete stimulus "lepi" was much stronger associated with the concrete motor actions than the abstract stimulus "kopi", confirming the intended semantic distinction between these stimuli.

During the experimental session, participants were presented with silent video clips whose content was unrelated to the auditory stimuli, which were delivered via non-magnetic earplugs (3M E-A-RLINK, USA). Stimulus presentation was implemented using NBS Presentation Version 16.3 Build 12.20.12 software (Neurobehavioral Systems Inc, Berkeley, CA, USA, http://www.neurobs.com). Overall, each condition was presented with 600 standards and 120 deviants, with deviant stimulus probability of ~16.7%. Each of the three auditory series was broken into two subblocks (6 min each) with a short break in-between, to reduce the subjects' fatigue. The order of the blocks within a session was randomized across subjects. The interstimulus interval varied in the range of 900–1100 ms with steps of 50 ms, and the average value was 1000 ms.

2.3. MEG data collection and processing

Participants were seated in an acoustically and electromagnetically insulated room. Raw MEG signal was recorded continuously throughout each session using a 306-channel MEG setup (Neuromag, Helsinki, Finland) at a 1 kHz sampling rate with the online band-pass filter set in the 0.03–300 Hz range. Horizontal and vertical electrooculogram (EOG) and electrocardiogram (ECG) were recorded to detect physiological artifacts. Positions of four head position identification (HPI) coils, along with the fiducial points, were digitized using Fastrak 3D digitizer (Polhemus Digitizing Systems, USA). HPI signal was continuously recorded throughout the session to track any head movements for the subsequent offline correction.

To reduce the impact of external magnetic field noise and technical artifacts, raw MEG data were pre-processed using tSSS algorithm (Taulu and Simola, 2006) implemented in MaxFilter 2.0 software (Neuromag) with simultaneous correction for head movement. All the data were transformed to the standard head position (x = 0 mm, y = 0 mm, z = 45 mm). Band-pass filtering (0.5–45 Hz) was then applied to the signal. Physiological artifacts of cardiac activity and eye movements were removed by SSP (singnal-space projection), implemented in Brainstorm toolbox (Tadel et al., 2011) for Matlab (Mathworks, Natick, MA, USA). Thereby preprocessed and artifact-cleaned data were epoched into segments of −200 to 1000 ms relative to the stimulus onset. Baseline correction was applied using the 200 ms pre-stimulus interval. The baseline-corrected responses were averaged separately for deviant and standard stimuli in each condition to produce event-related fields (ERFs). The differential magnetic mismatch negativity response (MMN)
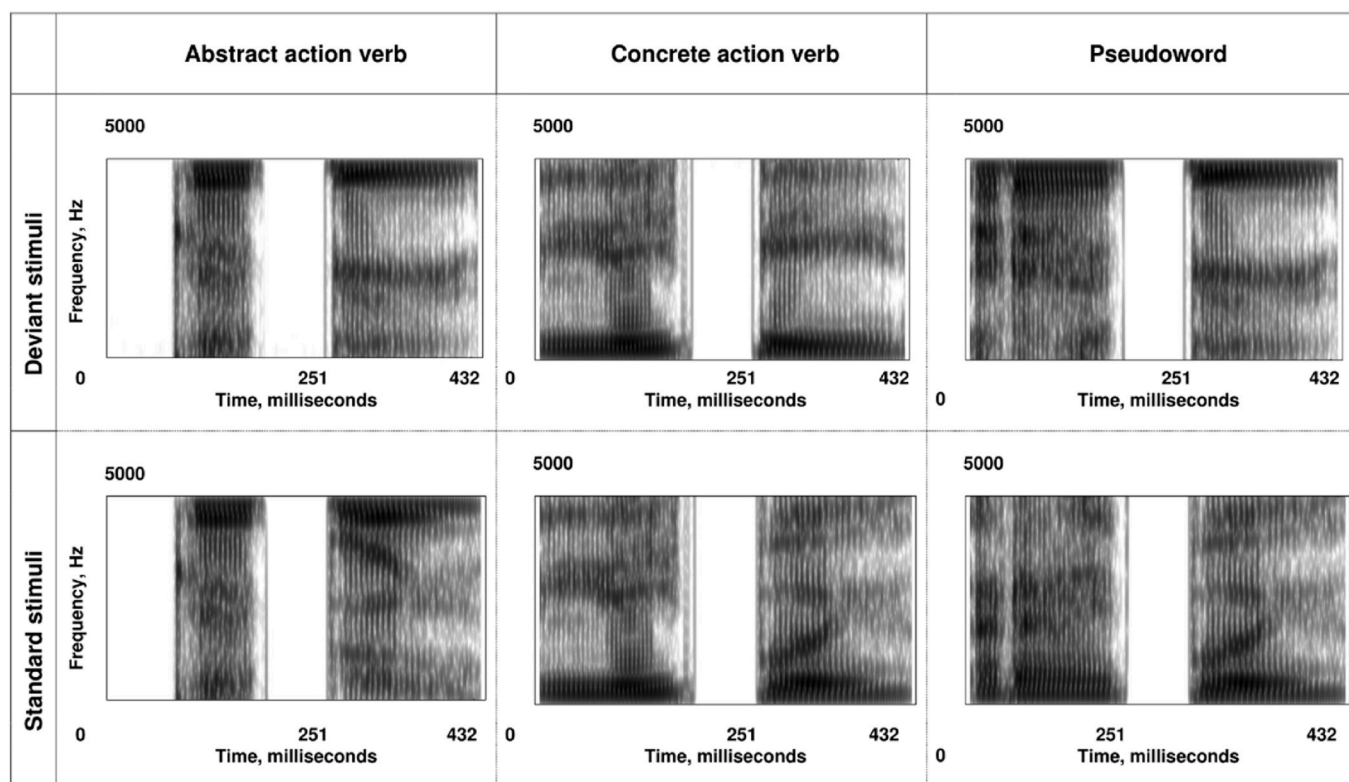
Fig. 1. Auditory stimuli: spectrograms of the spoken words and pseudowords used in the mismatch negativity experiment. Note the high degree of acoustic similarity across the three conditions and the identical acoustic-phonetic contrasts between the standard and deviant stimuli in each block.

was computed by subtracting the ERF to the standard stimulus from that to the deviant one separately for each subject and condition.

The global field power (GFP) of the resulting ERFs was computed for each stimulus type (standard and deviant), condition (abstract action verb, concrete action verb and pseudoword), and hemisphere (left, right). Visual inspection of the GFP responses comparison in both hemispheres for the standard and the deviant stimuli across all the stimuli types confirmed (see Supplementary Fig. 1) a clear MMN response.

Further, to study the regional specificity of the MMN responses for different conditions and particularly the putative lateralization effects that were the focus of this study, we conducted analysis of cortical generator sources of the observed ERFs. Forward modeling was performed using the overlapping spheres approach (Huang et al., 1999). To compute the forward model, noise covariance matrices were calculated based on the individual empty room recordings. Data covariance matrices were calculated for standard and deviant ERFs in each condition using full 1000-ms epochs, with baseline corrected for the 200 ms pre-stimulus interval. To estimate the brain activity sources, we constructed individual automatic surface-based cortical parcellations using Freesurfer 6.0 software (Martinos Center for Biomedical Imaging; (Fischl, 2012) based on the individual structural T1-weighted MRIs obtained with a 1.5 T Optima MR360 scanner (General Electric, USA; Spin Echo sequence, voxel size = 1 mm^3, slice thickness = 1 mm, field of view = 288 × 288, TR = 600 ms, TE = 13.5 ms). Area map was constructed using PALS-B12 (Van Essen, 2005) atlas which parcellates cerebral hemispheres into 79 areas (40 Brodmann areas in the left hemisphere, 39 in the right one). We focused our analysis of source activation dynamics on an a priori defined (based on previous literature, see Introduction) set of symmetrical regions-of-interest (ROIs) in both hemispheres. Based on previous research, the putative semantic effects may be underpinned by subregional functional activity rather than that of larger anatomical regions (for example, the upper limb motor area, rather than the entire motor cortex, for the action verb). Selected ROIs

(see Fig. 2) included the following areas in the left hemisphere and their right-hemispheric homologues: the primary auditory cortex (BA41, as the primary source of the auditory mismatch negativity response), the motor cortex, BA4, and the inferior frontal gyrus, IFG. Within these ROIs we further selected the subregions that included parts of the IFG (BA44, BA45, BA47) and the upper limb motor cortex (specified using anatomically more fine-grained Brainnettome atlas; Fan et al., 2016).

The source reconstruction was performed using the LCMV beam-forming source estimation approach with constrained (normal to cortex) dipole orientations. Beamformer-type solutions are a group of spatial filtering methods that allow to focus on the local sources of interest, separating them from other generator sources (Hillebrand and Barnes, 2005). These features make beamforming an optimal approach for studying the cortical sources dynamics within specific areas of interest, which was the original aim of the present design. Individual cortical sources were calculated based on planar gradiometer data for each stimulus type (standard, deviant) and condition (abstract action verb, concrete action verb, pseudoword) separately with subsequent deviant-minus-standard sources' subtraction.

2.4. Statistical analysis of region-specific lateralization effects

Based on previous EEG and MEG mismatch negativity research, we chose a broadly defined 100–350 ms time window after the deviance point (corresponding to the word disambiguation point at the onset of the second syllable) for further statistical analysis of the magnetic MMN responses. Such a window covers the full range of MMN latencies, known for spoken stimuli, as reported in various prior studies (see, e.g. (McGee et al., 1997; Pettigrew et al., 2004; Pulvermüller and Shtyrov, 2003),). Fig. 3 illustrates that, for the present data, this window indeed covered the entire MMN response in each ROI, each hemisphere, and each condition.

We computed absolute values of mean source strength across the entire time window over all the vertices separately within each of the
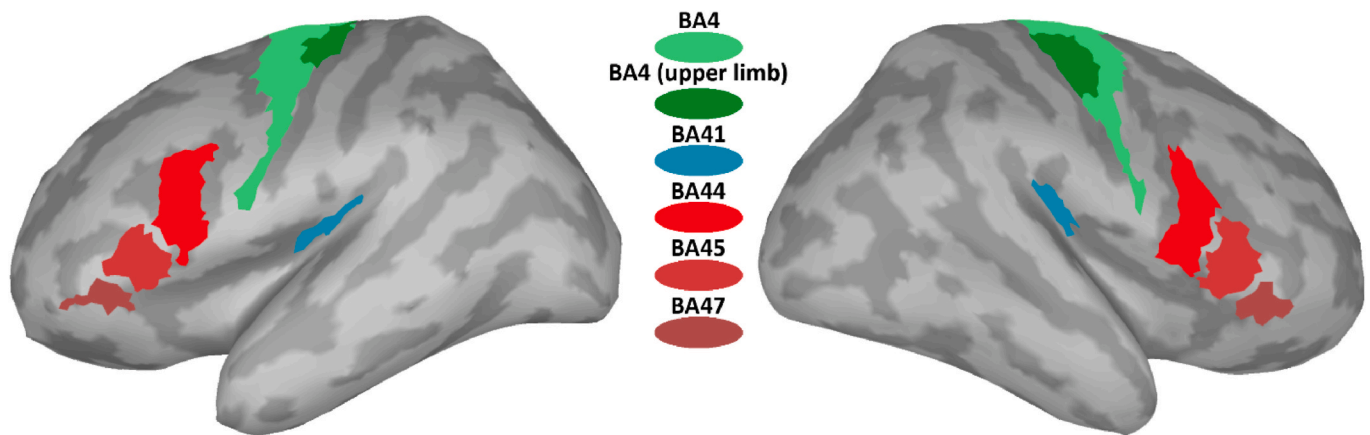
Fig. 2. The regions of interest in the left and the right hemispheres selected for sources analysis (single-subject inflated BEM given as an example): BA41 highlighted in blue, BA4 in green (with upper limb area in darker shade), IFG (BA44, BA45, BA47) in red.
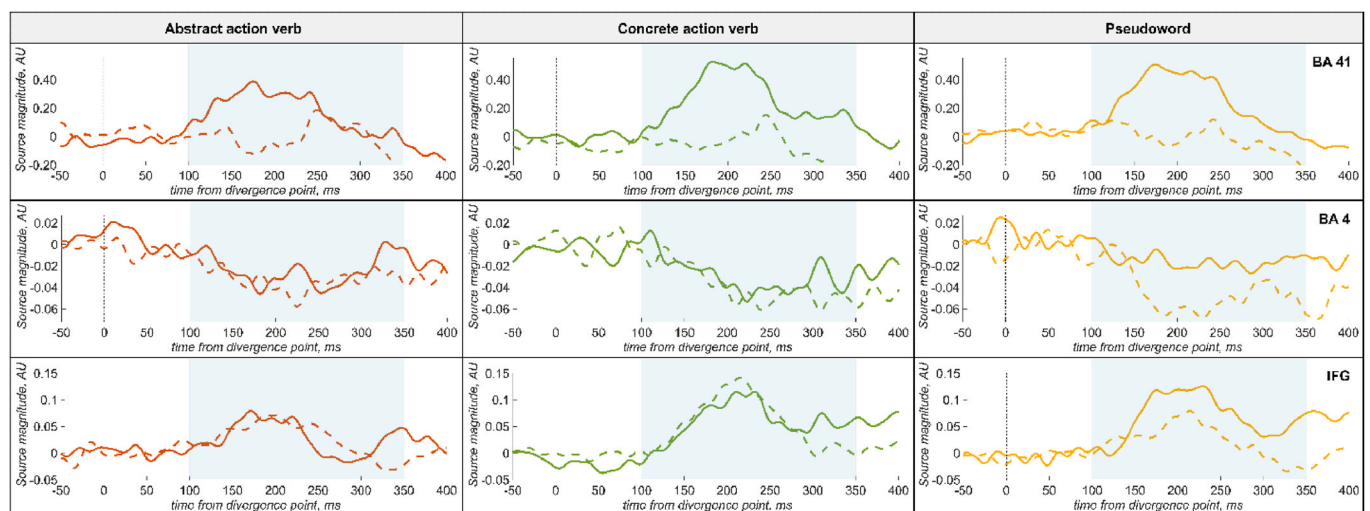

Fig. 3. Source time courses of the MMN responses to stimuli of different categories (concrete action verb, abstract action verb, pseudoword) within specific bilateral ROIs: BA41, BA4, IFG. Thick lines: left-hemispheric MMN responses, dashed lines: right-hemispheric MMN responses. Shadowed areas show the time window of interest (100–350 ms) that corresponds to the observed MMN responses.

selected ROIs, condition and hemisphere, using the R software package, version 4.2.0 (R Foundation for Statistical Computing, Vienna, Austria; https://www.R-project.org/). These source amplitude values were normalized using log transformation, which indeed led to their normal distribution, as assessed by Shapiro-Wilk normality test ($p > 0.05$). These were then submitted to further statistical analysis using a three-way repeated-measures ANOVA on the magnetic MMN source magnitudes with the factors of condition (three levels: abstract action verb, concrete action verb, pseudoword), cerebral hemisphere (two levels: left, right), and ROI (three levels: auditory cortex, motor cortex, IFG) in which the assumption of sphericity was met (Mauchly's test of sphericity, $p > 0.05$).

3. Results

GFP analysis showed that averaged ERFs were successfully obtained for all the conditions (abstract action verb, concrete action verb and pseudoword) in both hemispheres. For all three conditions in both hemispheres the averaged event-related responses produced by the deviant stimulus demonstrated a larger amplitude than the standard one (see Supplementary Fig. 1); therefore, neuromagnetic mismatch negativity responses could be successfully calculated.

We then further investigated the magnetic MMN lateralization

(regionally specific differences in the left and right hemispheres' responses) for the different stimuli (abstract and concrete action verbs and to the pseudoword) in the literature-based predefined ROIs: motor, ventrolateral prefrontal cortex (semantically non-specific responses in the auditory cortex were considered as baseline). We proceeded to analyze these differences in the selected zones within the regions of interest (BA41, BA4, and IFG combining BA44, 45 and 47). The initial ANOVA showed a significant interaction of three factors: condition, ROI and hemisphere ($F_{4,116} = 2.651$; $p = 0.037$; all the p-values presented here and below are Bonferroni-corrected for multiple comparisons). A follow-up analysis of this interaction showed no Condition x ROI interaction in the left hemisphere ($F_{4,116} = 2.45$; $p = 0.3$) and a marginally significant Condition x ROI interaction in the right one ($F_{4,116} = 3.38$; $p = 0.072$), which indicates differential hemispheric involvement. The manifestation of this trend may be limited due to the functional heterogeneity of the IFG area: as described in the Introduction, previous research has linked BA45 and BA47, but not BA44, to semantic processing. Therefore, we further analyzed the results using combined activation in BA45 and BA47 areas as a level in the ROI factor (along with BA41 and BA4), discarding BA44. This analysis indicated a significant interaction of all three factors ($F_{4,116} = 3.425$; $p = 0.011$). Furthermore, a follow-up analysis of this interaction showed significant Condition x ROI interaction in the right hemisphere ($F_{4,116} = 4.54$; $p =$

0.012), but not in the left one ($F_{4,116} = 1.75$; $p = 0.864$). Following up this interaction, we found that it was driven by a statistically significant main effect of Condition on source amplitudes being present only in the right BA45/47 ($F_{2,58} = 8.59$; $p = 0.0016$) but not in BA4 ($F_{2,58} = 0.45$; $p = 1$) or BA41 ($F_{2,58} = 1.6$; $p = 0.63$) regions. Investigating this further with post hoc comparisons, we found that right-hemispheric BA45/47 responses to the concrete action verbs were higher than to both abstract action verbs ($p = 0.019$) and pseudowords ($p < 0.001$). Interestingly, the same follow-up comparisons did not show any differences between responses to different stimuli in the motor cortex (BA4). Since previous fMRI and MEG studies (Hauk et al., 2008; Shtyrov et al., 2014) have clearly indicated somatotopic specificity of motor cortex responses to words, we focused our further analysis only on the upper limb motor area, discarding the rest of motor strip activity, as our concrete action verb stimuli were related to hand movements specifically. Using this approach, rmANOVA confirmed the significant three-way ROI × Hemisphere × Condition interaction ($F_{4,116} = 3.24$; $p = 0.015$), which was driven by a significant Condition x ROI interaction in the right hemisphere ($F_{4,116} = 5.39$; $p = 0.003$), but not in the left one ($F_{4,116} = 0.67$; $p = 1$). Crucially, using the specific motor area (upper limb area instead of the whole BA4), the Condition x ROI follow-up in the right hemisphere showed significant main effects of Condition not only in the BA45/47 ($F_{2,58} = 92.8$; $p = 0.0016$), but now also in the upper limb motor area *per se* ($F_{2,58} = 5.04$; $p = 0.03$). In each of these areas, significant differences were found between responses to stimuli with concrete and abstract semantics ($p = 0.019$ in BA45/47 and $p = 0.03$ in BA4 upper limb area) with stronger responses to concrete semantics in both cases. In addition, post hoc comparisons indicated stronger responses to concrete verb than to the pseudoword stimuli (BA45/47: $p = 0.0009$; BA4 upper limb area: $p = 0.016$)), but no similar differences between abstract action verbs and pseudowords ($p = 1$ in both areas). Fig. 4 shows the source strength within each ROI (BA41, BA4 upper limb area, BA45/47) and hemisphere (left, right) for each condition (abstract action verb, concrete action verb, pseudoword).

4. Discussion

4.1. Main findings

The present study aimed to explore putative differences in hemispheric involvement in the processing of abstract and concrete verbal semantics within key modality-specific and amodal cortical areas, selected based on previous findings. To that end, we employed a mismatch negativity paradigm, an established approach to tracking word-specific memory trace activation in the brain that allows for maximal balancing of stimuli's acoustic/phonetic features by introducing identical stimulus contrasts into lexico-semantically different contexts. Furthermore, it focuses on the earliest automatic stages of such activations that take place without a linguistic task under conditions of attention withdrawal to an irrelevant visual input. We expected that words with concrete motor and abstract action semantics would provide responses with differential contribution of the left and right hemispheric areas (motor and inferior frontal) into observed MMN patterns. More precisely, semantically concrete motor-related stimuli were expected to evoke more bilateral mismatch negativity responses, especially in the motor areas (particularly in the upper limb area, given the hand-related action verb stimuli employed here). In contrast, semantically abstract verb stimuli were expected to predominantly activate the left inferior frontal cortex (Broca's area).

The global field power analysis showed that all categories of deviant stimuli, presented among the corresponding standards, yielded mismatch negativity responses in both hemispheres. These responses were generally stronger in the left hemisphere for all conditions (as can be seen most clearly in Fig. 3), which is in line with the dominant role of the left hemisphere in speech information processing.

Cortical source dynamics of the mismatch negativity responses were computed for all the stimuli conditions, within all ROIs in both hemispheres. The source activations could be seen as most expressed in the time the 100–350-ms time window after the deviance point, when the critical deviant stimuli could be disambiguated from the frequent
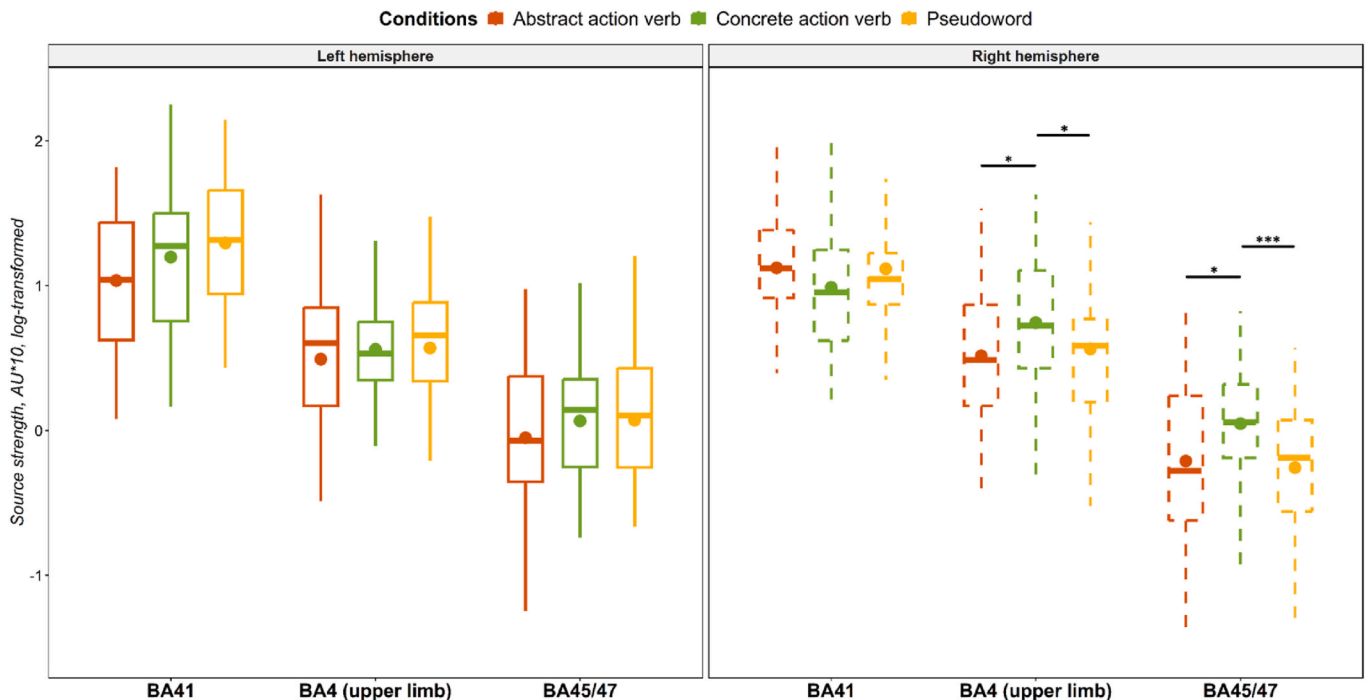

Conditions ■ Abstract action verb ■ Concrete action verb ■ Pseudoword

Fig. 4. The magnetic MMNs' source strength: log-transformed mean absolute values within the 100–350 ms time window after the disambiguation point in the left- and right-hemispheric ROIs (BA41: primary auditory area, BA4: upper limb area, IFG: combined BA45 and 47) for all the conditions (red: abstract action verb, green: concrete action verb, yellow: pseudoword; *p < 0.05, ***p < 0.001, Bonferroni corrected). Boxes represent first and third quartile, whiskers represent minimum and maximum values, horizontal line inside of the boxes represent median, dots inside of the boxes represent the mean.

standards, enabling access of corresponding lexical representations. This corresponds well with the data reported in the literature on the time windows for speech-induced MMN responses (McGee et al., 1997; Pulvermüller and Shtyrov, 2003). Early language-elicited MMN responses have been typically reported in the 100–200 ms range (Näätänen et al., 2007; Shtyrov et al., 2014). It has been emphasized that these components reflect the ultra-rapid neural mechanisms for the early lexical-semantic access when processing meaningful speech auditory stimuli.

Importantly, the patterns of mismatch negativity responses in the selected ROIs varied across the two hemispheres. For the primary auditory cortex (Brodmann area 41) the response patterns were the same, left-lateralized for all types of stimuli (see Fig. 3, ROI: BA 41). The absence of semantic condition-specific differences in BA41 responses is in line with this area's predominant function, i.e., acoustic and phonetic processing of incoming auditory signal, but not semantic analysis (Eggermont, 2001; Obleser and Eisner, 2009; Steinschneider, 2004). Leftward lateralization of the MMN response in the temporal areas is common for speech-induced mismatch negativity responses as opposed to right-lateralized MMN for non-speech contrasts (Naatanen, 2001), highlighting MMN's sensitivity to phonetic stimulus properties and phonological representations.

In turn, given the present stimulus design, semantically specific response patterns were expected to occur in areas outside of the primary auditory cortex. Indeed, different hemispheric patterns were found in the a priori defined (based on previous studies, see Introduction) cortical areas of interest. Namely, these effects were found in the motor hand area for concrete action verbs and in the IFG for abstract verbs. These differences were predominantly driven by varying contribution of the right-hemispheric cortical areas into the bilateral magnetic MMN response. This contribution was the largest in the hand motor cortical area (and especially for the concrete action verb compared to the abstract action verb and pseudoword). Conversely, the right hemispheric contribution was the smallest for the BA45 and 47 areas in IFG (see Supplementary Fig. 1). This variability of the MMN response patterns possibly indicates the different modes of the bilateral areas of interest activity, specific for different semantics types: abstract and concrete. Those parts of the semantic processing networks that could be found in sensorimotor areas, are more specific for concrete semantics. They demonstrate more bilateral response patterns for verbs, whereas the semantic networks in the frontal association cortical areas (IFG, more specific to the abstract semantics) demonstrate more left-lateralized patterns of response.

4.2. The problem of semantic concreteness impact on MMN laterality

Previous studies have dealt with the subject of lateralization of lexical-semantic MMN responses (Hauk et al., 2008; Pulvermüller et al., 2004, 2012), though showing generally mixed results and not considering the impact of the semantic concreteness on the lateralization. At least one previous study (Brunellière et al., 2011) tried to specifically disentangle the variability in the mismatch negativity response pattern lateralization associated with differences in semantic concreteness. In that study, two French words varying in concreteness were presented as deviant stimuli to speakers of different French dialects. These words produced different soundforms thus leading to variation in semantic concreteness for the two groups of listeners. The authors expected to see an alteration of the EEG-recorded patterns of MMN responses: one showing the detection of soundform differences between dialectal groups and the other related to the concreteness of the semantic representation of these words. In the latter case, a greater right-hemispheric involvement was expected. In fact, the responses found in both groups for both types of stimuli involved frontocentral and right hemispheric clusters. Those who perceived the stimuli as phonologically different showed different ratio of the frontocentral and the right hemispheric activity peaks for two types of stimuli. In turn, the participants who

perceived them as phonologically similar showed no stimulus-related differences in the ratio of the right-hemispheric and frontocentral activity. The authors suggested that the absence of the clear concreteness effect in the first group was associated with an interference between the two factors: acoustic deviance between the stimuli, and the degree of concreteness, while the effect found in the second group might be explained by the lack of phonological difference between stimuli (dialect-specific). It may also be explained by the fact that both of the stimuli had a more abstract meaning for the second group of participants than for the first one. However, this absence of obvious semantic concreteness effects in the ERP patterns might also be due to certain limitations of that study. It employed a 64-channel EEG which is not known to be the optimal tool to study the lateralization effects in MMN responses. In EEG, MMN is well-known to produce a strong frontocentral signal surface distribution that is a composite of bilateral temporal source activity, obscuring any laterality effects and largely precluding lateralization analysis (Giard et al., 1995). Higher-density recording methods along with source analysis techniques are better suited for this. The other limitation of low-resolution EEG use in such studies may derive from the regional specificity of concrete and abstract semantics processing, which this method may not be sufficiently sensitive to, particularly in the absence of source reconstruction analysis. A number of aforementioned works (Binder et al., 2009; Bucur and Papagno, 2021; Wang et al., 2010) emphasize that the concrete semantics networks encompass bilateral sensorimotor areas, while abstract semantics networks are mostly centered around left inferior-frontal areas (i.e., Broca's area). On the other hand, these meta-analytic reviews generally include studies based on fMRI technique. Though having a perfect spatial resolution, this neuroimaging technique does not allow to study the fine temporal structure of task-dependent neural responses and cannot exclude that (at least some of) the obtained activations reflect task effects or secondary, post-comprehension processes, rather than the online parsing of linguistic input. The latter is of high importance when analyzing brain activity associated with linguistic tasks, considering the speed (within the range of tens of milliseconds) with which linguistic information unfolds at the input. The neuroimaging technique we used, high-density MEG, is more neuroanatomically accurate than conventional EEG, whilst at the same time has excellent temporal resolution, tracking neural activation with a millisecond precision, unattainable in fMRI. This combination of features makes it possible to select regions of interest using individual structural MRIs for the analysis of the local neuromagnetic activity dynamics. Crucially, the mismatch negativity paradigm employed here makes it possible to track early short-living and transient activation of lexico-semantic memory traces at the neural level (Näätänen et al., 2007; Pulvermüller and Shtyrov, 2006). This approach made it possible to reveal cortical region-specific modulations of magnetic MMN responses that were different for the words with abstract and concrete semantics.

4.3. Regional specificity of MMN response lateralization for abstract and concrete action words

We focused on two previously identified areas – the motor cortex and inferior frontal gyrus – known to be specifically activated for concrete hand action-related semantics (Carota et al., 2017; Vukovic et al., 2017) and abstract semantics (Bucur and Papagno, 2021; Wang et al., 2010), respectively. In the motor areas, we found differences between response lateralization patterns, which are in line with the general idea that concrete word representations, like that of the motor action verb used in the present study, are underpinned by more bilateral networks than abstract words. In turn, the left inferior frontal gyrus (pars triangularis and pars opercularis, in particular) showed stronger responses for the abstract condition.

Previous studies have suggested that pars triangularis (BA 45) of the left inferior frontal area may be a crucial hub for lexical-semantic processing (Heim et al., 2009). When comparing phonological and lexical

decision tasks, BA45 shows stronger association with lexical processing, as opposed to BA44 (Heim et al., 2005). In turn, a comparison of phonological and semantic tasks particularly links BA45/47 complex with semantic processing (Poldrack et al., 1999). Consequently, we might expect to see semantically specific distinctions between responses to abstract and concrete stimuli in BA45 and BA47, but not in BA44. Our results support this distinction. This finding might be, among other factors, related to cytoarchitectonic differences between areas: BA45 and BA47 have an extended granular Layer 4, unlike BA44 (Zilles and Amunts, 2018). This increased L4 in prefrontal cortical areas is believed to support higher-order cognitive processes (Nieder, 2009). Moreover, due to their extensive connections with temporal areas, BA45 and BA47 seem to support multimodal language-related processes (Friederici, 2009), which gives them another advantage in storing and processing abstract representations.

In addition, there are some structural anatomical asymmetries known to be specific to the Broca's area as a part of IFG which might have an impact on the functional laterality (Keller et al., 2009), although the extent of the leftward lateralization of the neural tissue density reported for these areas vary substantially (Uylings et al., 2006). Moreover, the impact of the structural anatomical factors on the neural responses' lateralization patterns is less clear for the other region of our interest, BA4 upper limb area. On the one hand, the stronger right-hemispheric contributions in the response patterns found there may seem to somewhat contradict the reported structural asymmetry of upper limb motor representation in right-handers (Rademacher, 2001; Volkmann et al., 1998). On the other hand, the present MMN response pattern in BA4 is more in line with the results of the previous functional neuroimaging studies (see Introduction), showing that the sensorimotor areas are involved bilaterally (or even have a stronger right-hemispheric response counterpart) for concrete motor semantics processing.

A study by Uddén and Bahlmann (Uddén and Bahlmann, 2012) provides a complex model to distinguish the portions of the IFG based on their relations to abstract linguistic information processing. The functional differences the authors reported point to heterogeneity of the left IFG areas. It might be suggested that rostral parts of IFG, i.e., BA45 and BA47, and caudal parts, i.e., BA44 and adjacent BA6 process linguistic items of different length, i.e., sentences, words and phonemes. This causes varying load on the processing of temporal features of these items, which is related to the extent of their abstractness. Alternatively, this rostro-caudal gradient might point to the different degree of concept generalization when processing linguistic items across different IFG subregions. Finally, the authors pointed out that this functional gradient in the IFG might be based on the local structural cytoarchitectonic differences between its subregions. The results found in the present study are in line with this model: the semantic abstractness effects were found in the rostral parts of IFG (BA45/47), but there were no such effects in the caudal part, BA44.

Finally, the pseudoword stimuli in the present study showed an MMN response pattern close to that observed for the abstract action verb. The comparison between pseudoword and abstract verb responses provided additional insights on the neural processes underlying semantic access for different types of language stimuli, demonstrating a similarly strong involvement of the left IFG cortical areas in both cases. Besides its specific role in abstract semantics, the IFG is also considered as an important cortical hub for controlled semantic memory retrieval processes (Wang et al., 2010). The increased load on the retrieval processes (i.e., more effortful retrieval) might become manifest in the greater involvement of the left IFG in various linguistic tasks (Hirshorn and Thompson-Schill, 2006; Thompson-Schill et al., 1997), particularly when more cognitive effort is required (such as for ambiguous, rare or unknown stimuli). The similarity of abstract verbs and pseudowords responses we found in the left IFG might suggest that both types of linguistic information require a greater cognitive effort for the lexical search and retrieval. Particularly, the costs of greater retrieval effort might include a longer time required for the search in the mental lexicon

(Collins and Quillian, 1969). This time increase might derive, for instance, from longer processes of the target representation selection among potential semantic associations induced by a stimulus cue, i.e., greater uncertainty about the word meaning (Moss et al., 2005). Our findings on the responses similarities within the IFG are also well in line with some of the previous results (Goldberg et al., 2007) on the similar involvement of BA44 and BA45 both in abstract semantics and in pseudoword processing. Interestingly, a recent investigation of language learning processes has showed that across the acquisition of novel word forms, early neural activation for abstract items was more similar to that for pseudowords than for concrete items (Mkrtychian et al., 2019), which is also in line with our findings.

The similarity between abstract verbs and pseudowords was also observed in the lateralization of their response patterns. Previous findings on the laterality of the MMN responses elicited by pseudoword stimuli are mixed (Pulvermüller et al., 2001; Shtyrov and Pulvermüller, 2002), showing either no clear pattern of lateralization or left-hemispheric dominance, typical of language. For instance, (Pulvermüller et al., 2001) have reported that pseudowords-elicited MMN have diminished amplitudes and more bilateral response patterns, in contrast to left-lateralized meaningful word-elicited MMN responses. However, the latter difference was shown for the core MMN area, superior temporal cortex, while our finding is related to the extra-auditory areas: BA4, 45, 47. We suggest that this might be due to two reasons, not mutually exclusive. First, as the pseudoword stimuli we used here had a typical phonological structure of an imperative form or Russian verbs, possibly causing some verbal associations in participants leading to response patterns similar to the meaningful word. Second, the greater leftward lateralization in BA45 might point to the absence of the concrete associations for the pseudoword representation. In this case, the pseudoword response will not strongly involve the right-hemispheric counterpart (employed for existing concrete representations), whilst attempts at its parsing might still be undertaken by the core language areas of the left hemisphere.

Two main conclusions might be drawn here. First, the magnetic mismatch negativity responses lateralization for semantically different stimuli (abstract words, concrete words) is indeed regional-specific. Second, these region-specific differences in lateralization stem from differential contributions of the right-hemispheric, language-subdominant neuromagnetic activity rather than on left-hemispheric modulations. In other words, semantic concreteness and semantic specificity impact the neuromagnetic responses lateralization differently across cortical regions depending on the right-hemispheric contribution.

4.4. Theoretical implications

From the theoretical viewpoint, our results can be interpreted in terms of different approaches. In line with the dual coding theories (Paivio, 1991), we found that processing of concrete semantics requires a higher load in the right-hemispheric language-subdominant networks (Eviatar et al., 1990). Our results revealed that though there is some extent of specialization for different cortical areas, all the areas of interest show responses elicited by all types of semantic stimuli. This part of our results confirms that the concrete and abstract semantic processing systems are not fully distinct from each other and are interrelated, as the dual-coding approach suggests (Bi, 2021; Mkrtychian et al., 2019). Nonetheless, the finding that the processing of concrete semantics involves both amodal anterior Broca's area and modality-specific motor area might be better explained by distributed accounts of word representations. This includes both the embodied accounts positing involvement of modality-specific areas in word-specific cell assemblies (memory traces) formed in associative learning (Pulvermüller, 1999, 2023) and the hub-and-spoke model that postulates that concrete semantic processing is supported by cortical neural networks containing both modal and amodal nodes involved (Patterson and Lambon Ralph, 2016).

Remarkably, both the motor area (modality-specific) and anterior Broca's (amodal) were involved in generating responses elicited by both abstract and concrete stimuli, with differences in the lateralization of their processing patterns being of a gradual rather than an absolute nature. This important part of our findings might be explained in the context of the embodied or grounded theories, that claim that tightly interconnected modal and amodal representations exist in the semantic memory (Davis and Yee, 2021; Paco Calvo, 2008). In line with that, the lateralization effects and their association with abstract or concrete semantics might be interpreted from the point of view of the extended embodiment approaches. Particularly, the "words as tools" (WAT) approach says that conceptual abstract items might be considered as tools that are used to operate over the concrete sensorimotor experience in social interactions (Borghi et al., 2013; Kee, 2020). Other related works emphasize that such a conceptual, symbolic knowledge processing is tightly connected with speech and inner speech processes underpinned by the language-dominant left hemisphere (Borghi, 2023; Dove et al., 2022).

In sum, various theoretical accounts agree that semantic representations diverge between abstract and concrete linguistic items. Generally, this can be explained by the different weight of modal sensorimotor content in these two types of representations. However, the extent to which the sensorimotor experience impacts abstract and concrete semantic concept processing remains a subject of discussion. Our study demonstrates that the concrete and abstract semantic systems in the brain strongly overlap, although differ in the involvement of their key amodal (left-hemispheric Broca's area) and modal modes (semantically relevant sensorimotor regions) in the processing of particular types of semantic information.

4.5. Potential limitations

The paradigm used in the present study, the oddball mismatch negativity, has certain limitations that should also be considered. In particular, it uses only few highly controlled stimuli thus making the design not fully ecological (Sonkusare et al., 2019). This restricted design reflects only partially the natural conditions of speech (Verga and Kotz, 2019). Nonetheless, to some extent at least, this paradigm is relevant for modeling natural speech processing, as it provides a window onto the innate ability of the cortical neural networks to detect patterns of regularities and violations in the auditory input. Crucially, as shown in previous studies, including those reviewed in the Introduction, MMN response dynamics is reliably associated with lexical and semantic processes (Pulvermüller and Shtyrov, 2006; Shtyrov, 2010). Remarkably, this happens in spite of both attentional withdrawal from the stimulus stream and the strong habituation that is known to affect ERP amplitudes in repetitive stimulus presentation (Todorovic and de Lange, 2012). That is, despite the design limitations, the semantic effects produced by MMN are so robust that they can be picked up neurophysiologically, implying their high degree of automaticity. Indeed, one of the main reasons to choose the MMN paradigm is that it allows to study the automatic stages and types of language processing at the neural level.

However, future research should address the lack of ecological validity of this paradigm and verify our findings in more ecologically valid designs. For that, future studies might take into account previous research comparing naturalistic and controlled stimuli paradigms (Levy et al., 2021). For instance, a recent study by Jaaskelainen and colleagues (Jääskeläinen et al., 2021) on the use of movies and narratives has shown a number of advantages and drawbacks in using both well-controlled and naturalistic stimuli. Particularly the latter ones might cause significant effects in brain responses that can be attributed not only to the content of these stimuli (linguistic, emotional or social), but also to some of their perceptual features. As a solution, the authors suggested to use both types of stimuli in parallel or even as a continuum from well controlled stimuli to naturalistic, to account for the ecological validity as a factor on its own. Using this and possibly other approaches,

future studies could validate and extend the present results obtained with a more strictly controlled minimalistic design.

5. Conclusions

The results obtained in the present study confirm that cortical areas of the two cerebral hemispheres are differentially involved in processing abstract and concrete semantics. This differential pattern is shown here using magnetic mismatch negativity responses without language-oriented tasks under the conditions of attention withdrawal from the speech input; this implies a high degree of automaticity of the brain's semantically-specific mechanisms involved in word comprehension. Moreover, the results demonstrate that the response lateralization for semantically different stimuli is region-specific. Crucially, these regional-specific differences in lateralization stem from differential contribution of neural activity within the homologous cortical areas in the language-subdominant right hemisphere. Taken together, the results point to the presence of the overlapping cortical neural networks that differentially involve their bilateral nodes into the processing of specific types of semantics. Further studies are needed to investigate the topography and the spatio-temoral dynamics of these networks in greater detail, linking them to their neuroanatomical and cytoarchitectonic properties as well as structural and functional connectivity.

Authors' contributions

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Beatriz Bermudez-Margaretto: Conceptualization, Editing, Funding acquisition.

Ioannis Ntoumanis: Formal analysis.

Aleksei Gorin: Data acquisition, Software.

Olesya Moiseenko: Data acquisition.

Evgeny Blagovechtchenski: Methodology, Supervision.

Victoria Moiseeva: Funding acquisition, Resources.

Anna Shestakova: Conceptualization, Funding acquisition, Supervision.

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Yury Shtyrov: Conceptualization, Methodology, Investigation, Writing, Editing, Supervision.

Ethics approval statement

The study was approved by the local research ethics committee, decision No. 19–3 of December 9, 2019.

Data availability

Data will be made available on request.

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[1] Author IPJ contributed prior to 4/2022.

paper.

Appendix A. Supplementary data

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