Suppression of Non-Selected Meanings Via Hippocampal Inhibition as a Possible Brain Mechanism For Ambiguity Resolution: An fMRI Study Using The Word Fragment Completion Task

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Research Article

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Suppression of non-selected meanings via hippocampal inhibition as a possible brain mechanism for ambiguity resolution: an fMRI study using the word fragment completion task

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Abstract

Dealing with ambiguity, one usually selects one meaning unconsciously and remains unaware of the alternative meanings. The brain systems dealing with multiple meanings of ambiguous stimuli are relatively well studied, while the brain processing of their non-selected meanings is relatively less investigated. The current functional MRI event-related study used a modified version of the word fragment completion task to reveal possible brain mechanisms involved in processing the non-selected meaning of ambiguous stimuli. Some noun stimuli were ambiguous, and the others were not. Adjectives created contexts strongly biasing the choice of the noun meaning in one or the other way. All ambiguous and unambiguous noun stimuli were presented twice during the experiment. It was revealed that ambiguity resolution was associated with a decrement in the BOLD signal within the right and left hippocampi. This finding supported one of the tested hypotheses assumed that non-selected meanings are actively suppressed. The similarity between this result and BOLD signal changes observed for suppression-induced forgetting for purging unwanted memories from awareness allows suggesting the general neurophysiological basis for voluntary and automatic inhibitory awareness control.

Keywords: ambiguity resolution; non-selected meaning; memory suppression; fMRI; hippocampus; retrieval induced forgetting

1. Introduction

We live in a world where many visual images, linguistic expressions and other objects have more than one meaning. Therefore, we are constantly engaged in the process of ambiguity resolution, and different aspects of this process are extensively studied in psychology, linguistics and other cognitive sciences. Many important questions are still unresolved, and in the present paper we focus on the one concerning the status of non-selected meanings.

Dealing with ambiguity, we usually select one meaning unconsciously (relying on the context, as well as on its frequency and other factors) and remain unaware of the alternative meanings. Some authors assume that when one meaning is selected, nothing in particular happens to the alternative ones (e.g.[1,2]). The other theories claim that they must be actively suppressed (e.g.[3–6]) For instance, semantic ambiguity is associated with disadvantage caused by multiple-meaning competition for selection or retrieval[7] and possible suppression of the non-selected meaning to avoid interference in subsequent processing for repeated occurrence of the same ambiguous stimulus. These two

approaches were tested in many behavioral experiments (most often, the possible aftereffects of selecting one meaning and not selecting the others were assessed[7,8]), but the results were inconclusive. We present the results of a functional MRI event-related study that may shed new light on this question.

Neuroimaging studies focusing on ambiguity resolution are much less numerous than behavioral ones. For instance, it was found that processing of ambiguous sentences is associated with involvement of the left inferior frontal gyrus (LIFG) and the posterior part of the left inferior and middle temporal gyri[7,9]. The activity of these regions was increased when highly ambiguous sentences were compared with low-ambiguous ones. Different authors considered the possible role of the LIFG in processing multiple meanings to be related to conflict monitoring between these meanings or to combinatorial processing associated with selecting contextually appropriate ones. The posterior temporal region activity was attributed to the reinterpretation process needed to disambiguate and to select the meaning most relevant for the current context.

However, while these experimental results significantly furthered our understanding of which brain systems deal with multiple meanings of ambiguous stimuli and how they do so, much less is known about the processing of non-selected meanings. A potentially similar phenomenon based on suppressing alternative memories is retrieval-induced forgetting (RIF), when selective retrieval causes forgetting of a memory competing for awareness[10]. Notably, this effect was observed for various stimuli ranging from visual objects and actions to autobiographical memories and word fragment completion[11].

An important brain activity effect associated with effective forgetting based on repeated retrieval practice is the decrement of the local activity in the anterior cingulate and dorsal and ventral lateral prefrontal cortex[12]. This phenomenon is considered to be a reflection of suppressing competing memories and demonstrates the role of the inhibitory control in reducing the conflict arising after the initial retrieval. Such activity in prefrontal regions was positively correlated with the local hippocampal activity supporting the idea of controlling appearance of memories in awareness[13]. Experimental data demonstrating the relationship between the hippocampus deactivation and purging memories from awareness were presented in the studies using the Think/NoThink paradigms[11,13]. Such paradigms assume voluntary control over the awareness content, so this leaves an open question whether the downregulation of the hippocampal activity supports awareness while processing ambiguous stimuli in an automatic mode, being unaware of different options.

To address these questions, we conducted a functional MRI event-related study using a modified version of the word fragment completion task. Participants were asked to complete combinations of Russian adjectives and nouns with missing letters. Some noun stimuli were ambiguous, the others were not. Adjectives created contexts strongly biasing the choice of the noun meaning in one or the other way. All ambiguous and unambiguous noun stimuli were presented twice during the experiment.

Thus, during the first occurrence, ambiguous stimuli could be compared to unambiguous ones to look for possible evidence of inhibiting alternative meanings. We expected to observe brain activity similar to the effects found in the studies revealing brain signatures of suppressing memories from intruding to awareness. When ambiguous stimuli were presented for the second time, the context strongly favored the choice of previously non-selected meaning, so we could look for possible aftereffects of suppression. We hypothesized that such aftereffects may be similar to negative priming effects, which were demonstrated to be associated with a greater activity in the prefrontal and temporal brain regions (including the right dorsolateral prefrontal cortex, the left and right inferior frontal gyrus, the orbitofrontal cortex, or the left middle temporal gyrus[8]).

To sum up, based on the previous research, processing multiple meanings of ambiguous stimuli might be associated with a greater activity of selection- or inhibition-related brain regions, or even with the deactivation of memory-related structures, as a reflection of their downregulation to

control the content of awareness. Using these data, we hoped to shed new light on one of the basic questions concerning ambiguity resolution that could not be solved relying only on behavioral data.

2. Materials and Methods

2.1. Participants

Seventeen volunteers (seven males, ten females) with the mean age of 26.3 ± 4.5 took part in the study. All participants were right-handed native Russian speakers with no history of psychological or neurological diseases. Their handedness was assessed with the Edinburgh Handedness Inventory[14]. The study and all methods were carried out in accordance with the relevant ethical guidelines and regulations. All volunteers gave a written informed consent before the beginning of the study. The Ethics Committee of the N.P. Bechtereva Institute of the Human Brain (Saint Petersburg, Russia) approved all procedures.

2.2. Stimuli and Procedure

The experimental task was to complete Russian adjective-noun fragments with missing letters. For example, the fragments like *s-hoe vi-o* or *s-hoe -ino* were shown on the screen, and participants had to identify the missing letters by saying the complete phrase aloud: *suhoe vino* 'dry wine'. For adjectives, there was always only one completion option. For nouns, there were one or two, depending on the experimental condition, but the adjective strongly favored one of them in each fragment. In the examples above, *vi-o* can be completed only as *vino* 'wine' (control condition), while *-ino* can also be completed as *kino* 'movie' (ambiguous condition).

Adjective-noun phrases used as stimuli were created in the following way. At first, using the StimulStat database[15], we selected pairs of nouns that differed only by one letter, as in *vino* 'wine' and *kino* 'movie'. All nouns were 4–5 letters long, their frequency ranged from 5 to 100 ipm (according to the frequency dictionary[16]. In every pair, the difference in frequency between the two nouns was never greater than 50 ipm. For every noun, we selected an adjective that frequently cooccurs with it and is incompatible with the other noun in the pair. For example, *suhoe* 'dry' was selected for the noun *vino* 'wine', and *interesnoe* 'interesting' for *kino* 'movie'.
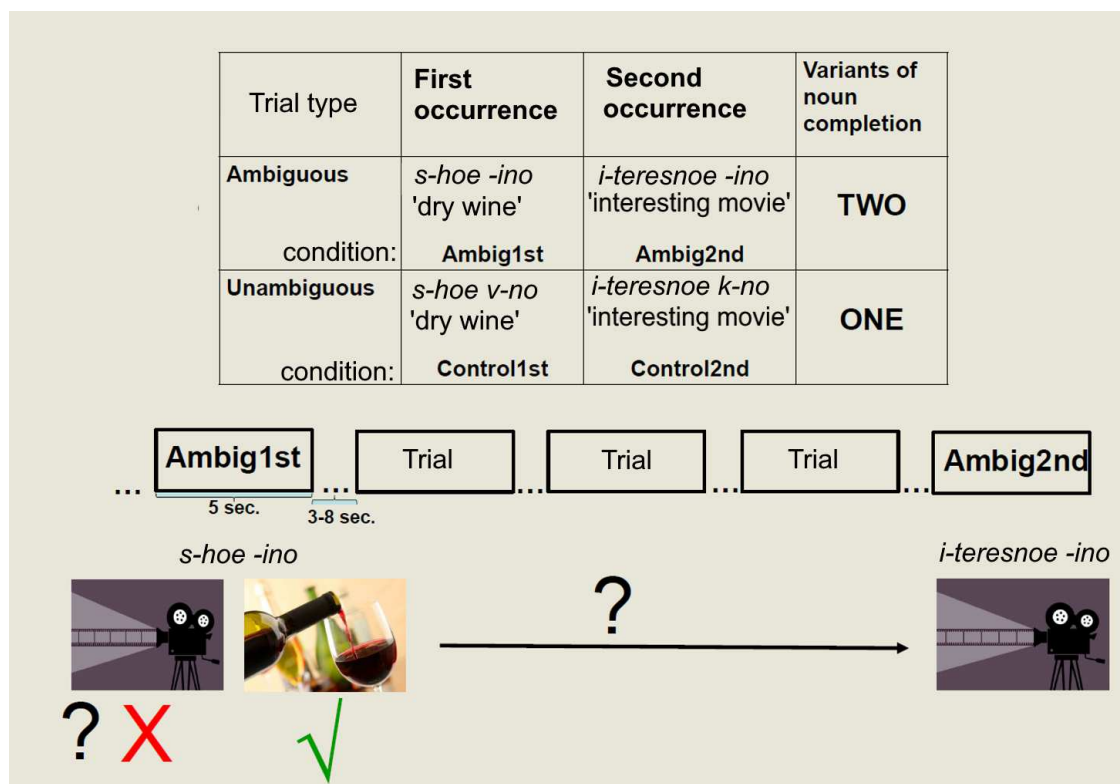
To check that the selected adjectives are indeed strongly associated with one noun in the pair, but not with the other, we conducted a pilot study with 22 volunteers (adult healthy speakers of Russian who provided an informed consent). They did not take part in the main experiment. In this study, adjective-noun fragments in the ambiguous condition were shown on the computer screen one by one in a random order. Participants were asked to complete them as fast as possible, though we did not include time limits in the experimental procedure. As a result, we selected 48 stimulus sets (consisting of two nouns and two adjectives) relying on the following inclusion criteria: more than 70% of correct completions for both adjective-noun combinations within the 5 s time interval after the fragment presentation.

Out of these 48 sets, 15 included noun pairs differing by the first letter. In seven sets, the last letters of the nouns were different; in the remaining 26 sets, the difference was in the middle of the nouns. For every set, we created four stimulus fragments, two in the ambiguous condition (e.g. *s-hoe -ino, i-teresnoe -ino*) and two in the control condition (e.g. *s-hoe vi-o, i-teresnoe ki-o*). In the two ambiguous fragments, the noun stimuli were identical (e.g. *-ino*). So if one of them is presented after the other, we can study how one and the same ambiguous stimulus is processed for the first and for the second time in two different contexts (created by adjectives).

In the fMRI study, every participant was asked to complete 96 fragments, i.e. all adjective-noun combinations we created (in one of the two experimental conditions). Two combinations from the same set were always separated by three other trials and were shown in the same condition. I.e.

those participants who saw *s-hoe vi-o* also saw *i-teresnoe ki-o* (both fragments in the control condition), those who were presented with *s-hoe -ino* were also presented with *i-teresnoe -ino* (both fragments in the ambiguous condition). This gives us four options for every stimulus set: e.g. presenting the 'wine' fragment before or after the 'movie' fragment in the ambiguous or in the control condition. Using the Latin square principle, we created four experimental lists. For every list, we generated three different stimulus presentation sequences making sure that two fragments from every set are separated by three trials.

As a result, we had four types of experimental trials (see Figure 1): 1) *Ambig1st* – the first fragment from the set in the ambiguous condition (for example, *s-hoe -ino*); 2) *Ambig2nd* – the second fragment from the set in the ambiguous condition (for example, *i-teresnoe -ino*); 3) *Control1st* – the first fragment from the set in the control condition (e.g. *s-hoe vi-o*); 4) *Control2nd* – the second fragment from the set in the control condition (e.g. *i-teresnoe ki-o*). In the *Ambig1st* trials, the noun can be completed in two different ways, but the context (i.e. the adjective) facilitates the unconscious choice of one variant (e.g. the word *vino* 'wine' in Figure 1). We aimed to test whether the second variant (the word *kino*) is inhibited during this choice. To do so, we compared *Ambig1st* trials to *Control1st* ones in which no inhibition could be expected (but the same adjectives and nouns were used to avoid any confounding factors). We also wanted to test if the selection process during the *Ambig1st* trial complicates the selection of the supposedly inhibited variant during the following *Ambig2nd* trial. To do so, *Ambig2nd* trials were compared to *Ambig1st* ones in which no effects of earlier inhibition could be expected. The interval of three trials was selected as relatively short, but not instantaneous.

Figure 1. The experimental design of the fMRI study. The table illustrates four different trial types. The pictures in the lower part illustrate two variants of completion of the noun *-ino* (*vino* 'wine' or *kino* 'movie').

Each adjective-noun fragment was presented on the screen for 5 s. During this time, a participant had to press the MR-compatible controller button and to say aloud the completed phrase. Reaction times were measured. Oral answers were recorded and subsequently analyzed. The stimulus did not disappear after the button was pressed, always remaining on the screen for 5 s. During

interstimulus intervals, a fixation cross was presented on the screen. To improve the sample rate of the hemodynamic response function (HRF) their length randomly varied between 3 s and 8 s with the 500 ms equiprobable step. The total duration of one fMRI session was 16.8 min.

After the experiment was over, participants received a printed list of all stimuli (following the presentation order) and were asked to indicate for which ambiguous fragments they realized that two completion options were possible. Participants reported a small number of such cases. Of course, we could not guarantee that they remembered all such cases accurately, but wanted to do as much as we could to exclude them, since we were specifically interested in the unconscious processes of meaning selection in this study.

2.3. fMRI Image Acquisition Procedure and Image Processing

All structural and functional images were acquired using a 3T Phillips Achieva scanner with the 8-channel receiving coil (Philips Medical Systems, Best, Netherlands). Stimuli were presented using the specialized system for presenting visual stimuli NordicNeurolab, which allows synchronizing stimulus presentation (using E-prime) with participants' responses (button presses) and BOLD signal registration in the scanner. Oral responses were recorded via an MR-compatible microphone with a noise reduction system.

To obtain structural images of each participant's brain T1-weighted pulse sequences of high resolution were used (T1W-3D-FFE; [TR] = 2.5 ms; [TE] = 3.1 ms; flip angle = 30°; 130 slices, [FOV] = 240 × 240 mm; matrix = 256 × 256, slice thickness = 0.94 mm). Functional images of BOLD signal changes were registered with echo-planar imaging (EPI) sequences (so-called dynamic scans): the registration time of 32 axial slices was 2 s (TE = 35 ms) with the FOV 208 × 208, flip angle = 90° and pixel size 3 × 3 mm. The thickness of the slices was equal to 3 mm. Structural MRI images were used in the analysis of fMRI-data in two cases: 1) for spatial normalization of individual data into a standard stereotactic space; 2) for creating a mean grey matter image used as an "explicit mask" in the fMRI-data analysis — this allowed performing the statistical analysis only for those voxels, which were localized in the grey matter for all participants.

Prior to the statistical analysis individual dynamic scans were preprocessed in the following stages: 1) realignment of all images relative to the first dynamic scan with the calculation of head movement parameters; 2) slice-time correction; 3) normalization of functional images into a standard stereotactic space with the coregistration of structural T1-image with the first dynamic scan and its segmentation; 4) Gaussian smoothing (8 mm, FWHM). Preprocessing and statistical analysis were performed using the SPM12 software package (Statistical parametric mapping 12) running in Matlab (2012b, Mathworks Inc., Natick, MA, USA).

2.4. Statistical Analysis of fMRI data

On the first level of the statistical analysis, the brain activity associated with the experimental task was estimated individually for each participant. The generalized linear model (GLM) (Friston et al., 2007) included regressors corresponding to the four experimental conditions: *Ambig1st, Ambig2nd*, *Control1st* and *Control2nd*. Trials in which participants gave incorrect responses or did not respond at all constituted the regressor «Mistake». Ambiguous trials for which participants subsequently reported recognizing two completion options were also removed from the analysis by modeling a separate regressor («DoubleMeaning»). On average, 4 (SD 3.5) out of 48 ambiguous fragments were identified as «DoubleMeaning» regressors. Additionally, to account for head movements, the GLM included six regressors representing movement parameters, calculated on the realignment stage of preprocessing.

The standard hemodynamic response function and stimulus onset times were used to calculate regressors. Beta-coefficients, obtained for linear contrasts between compared experimental conditions on the individual level, were used in the second (group) level of the statistical analysis. They represented BOLD signal changes in relative units. The group analysis was performed in a voxel-wise manner using the GLM model for the random effect analysis.

To test the hypothesis concerning the involvement of neural mechanisms responsible for processing non-selected meanings of an ambiguous stimulus, two contrasts of experimental conditions were analyzed: *Ambig1st > Control1st* and *Ambig1st < Control1st*. The t-contrasts between *Ambig2nd* and *Ambig1st* were analyzed to test the assumption regarding the aftereffect of ambiguity resolution. Bayesian inference was applied to revealed beta coefficients at the group levels of analysis to estimate the planned contrast (as implemented in the SPM12). In accordance with Bayesian statistics, the conclusion about the presence or absence of the effect of interest in a group of participants is based on the calculation of the posterior probability for obtaining the effect. The posterior probability refers to the probability of the difference between conditions (i.e. the contrasts obtained during the first level analysis) to be greater than zero. Posterior probability map threshold was defined as a log posterior odds threshold > 5 (posterior probability > 0.99) with the effect size >0 Hz.
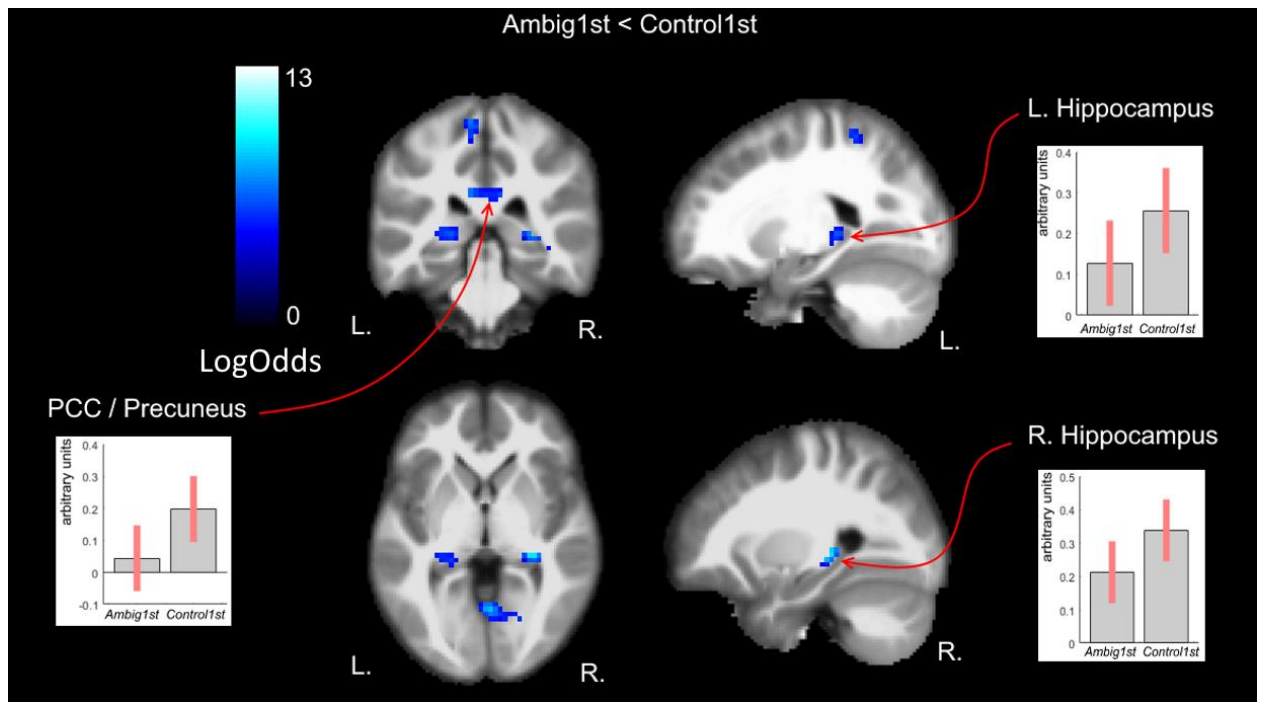
3. Results

3.1. Behavioral data

There were no significant differences in reaction times (RT) between *Ambig1st* and *Control1st* trials (group RT means: 1843 ms and 1786 ms, Mann-Whitney U Test, p=0.63), as well as between *Ambig1st* and *Ambig2nd* trials (group RT means: 1843 ms and 1984 ms, Mann-Whitney U Test, p=0.51).

3.2. Neuroimaging results

Significant BOLD signal changes were revealed in the *Control1st > Ambig1st* t-contrast. Ambiguous conditions were characterized by a decrement of the BOLD signal within the left superior parietal lobule, the right posterior cingulate cortex, the right lingual gyrus, and in the hippocampus bilaterally (Figure 2, Table 1). The reversed *Ambig1st > Control1st* contrast did not reveal any significant changes in the BOLD signal.
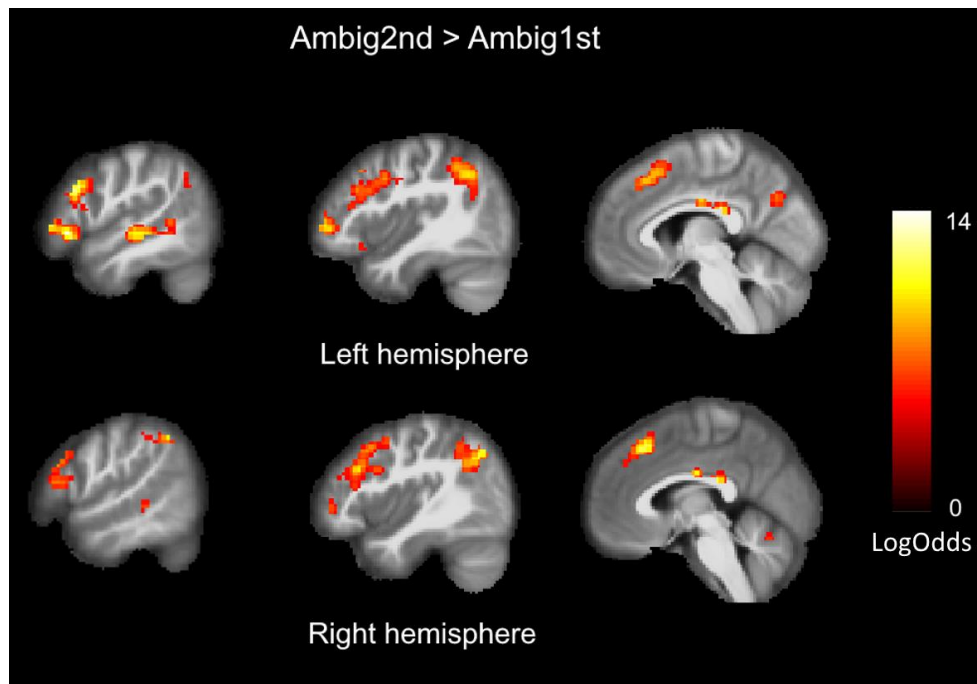
Figure 2. Decrement of the BOLD signal associated with processing of a non-selected meaning. Clusters of significant t-contrast *Control1st > Ambig1st* presented over a template brain image. Blue color bar represents the value of Log Odds Bars represented the sizes of effect in arbitrary units describing the PPI-parameters.

Table 1. Decreases in the BOLD signal associated with processing of a non-selected meaning revealed in the *Control1st > Ambig1st* contrast.

Brain Region	k	Log Odds	peak MNI coordinates		
			x	y	z
Contol1st > Ambig1st					
R. posterior cingulate cortex / Precuneus	207	13.70	6	-52	-36
R. hippocampus	47	9.67	27	-31	-1
R. Lingual gyrus (BA 19)	65	8.81	3	-64	-1
L. Superior parietal lobule / Precuneus (BA 7)	106	7.3	-9	-37	71
L. hippocampus	28	6.65	-21	-34	2

Denotations: L/R – left/right hemisphere; k – cluster size in voxels; BA – Brodmann area; SPL – superior parietal lobule

Assessment of the aftereffect of ambiguity resolution revealed greater increases in the BOLD signal for the *Ambig2nd* condition as compared to the *Ambig1st*. Revealed clusters were located bilaterally in the inferior frontal gyrus (IFG), the middle frontal gyrus (MFG), the angular gyrus (BA 40), the right caudate and lentiform nucleus, the left superior and middle temporal gyrus, the right middle temporal gyrus, the left precentral gyrus, the precuneus, the middle occipital gyrus and the cerebellum (Figure 3, Table 2).

Figure 3. Ambiguity disadvantage. Clusters of the BOLD signal associated with processing of the second occurrence of an ambiguous stimulus in the *Ambig2nd* trial as compared to the *Ambig1st* trial, in which this stimulus was presented for the first time.

Table 2. Increases of the BOLD signal associated with the aftereffect of ambiguity resolution revealed in the *Ambig2nd > Ambig1st* contrast.

Brain Region	k	Log Odds	peak MNI coordinates		
			x	y	z
Ambig2nd > Ambig1st					
L. inferior frontal gyrus (BA 10/47/45)	180	14	-51	29	-4
L. inferior frontal gyrus / middle frontal gyrus (BA 6/9/45/46)	319	13.3	-48	23	29
R. inferior frontal gyrus / middle frontal gyrus (BA 6/9/45/46)	417	12.3	48	29	29
Cingulate gyrus (BA 23)	92	12.2	-3	-28	23
R. caudate / Putamen	134	11.7	21	-1	20
R. / L. left superior medial frontal gyrus (BA 8/6)	256	11.7	3	29	47
R. angular / supramarginal gyrus (BA 7/39/40)	299	11.3	42	-64	41
L. middle occipital gyrus (BA 7/19/40)	323	11	-30	-70	41
L. middle temporal gyrus (BA 21/22)	137	10.5	-51	-22	-4
R. middle temporal gyrus (BA 22)	25	9.3	60	-34	-1
Right cerebellum	48	7.4	18	-73	25
L precuneus / posterior cingulate cortex (BA 7)	40	7.3	-6	-70	35
L cerebellum	25	5.8	-24	-64	28

Denotations: L/R – left/right hemisphere; k – cluster size in voxels; BA – Brodmann area

4. Discussion.

The main finding of the current study is that ambiguous trials are associated with a decreased BOLD signal in the right and left hippocampi as compared to unambiguous ones. The revealed deviation of the hippocampal activity can be considered a signature of suppressing a non-selected meaning while completing the ambiguous noun with a missing letter. This supports the idea that inhibiting the hippocampus is a critical neurobiological mechanism responsible for preventing competing or interfering memories from intruding to awareness. Such purging allows not only to select and fixate one meaning of an ambiguous stimulus, but also to avoid proactively the interference from competing memories in the forthcoming behavior. In this sense, the observed deactivation of the hippocampus is similar to analogous effects of retrieval-induced forgetting.

Moreover, a similar effect on brain activity was observed when some memories were effectively forgotten due to voluntary efforts to suppress them in the Think/NoThink paradigm[11]. Such suppression-induced forgetting of unwanted memories is positively associated with the downregulation of the hippocampal activity caused by the right dorsolateral prefrontal cortex (DLPFC), as demonstrated by several effective connectivity studies[17,18]. This downregulation can be exerted over the hippocampus or the motor cortex depending on the behavioral goal to suppress unwanted memories or actions, respectively[19]. All these findings point towards a critical role of the inhibitory control in controlling the content of awareness. For instance, the individual level of the hippocampal GABA concentration assessed by the MR spectroscopy was positively correlated with the degree of functional decoupling between the DLFPC and the hippocampus associated with effective forgetting[20]. Therefore, despite the apparent psychological differences between the willful forgetting and the automatic suppression of context-irrelevant meanings during ambiguity resolution, they may rely on very close neurophysiological mechanisms of inhibitory control. Although the nature of inhibitory control involvement in suppressing non-selected meanings of ambiguous stimuli should be further investigated in future research, the results of the current definitely study extend the view of the role played by inhibition in the automatic control of awareness.

The results of assessing the aftereffect caused by ambiguity resolution partly corroborated the possible involvement of non-selected meaning suppression. When seeing an ambiguous noun stimulus for the second time, participants needed to use the previously non-selected meaning of this stimulus. This led to the BOLD signal changes resembling the negative priming effect[8,21] observed as an increase of activity levels in the DLPFC, the angular gyrus, the superior and middle temporal cortex, and the basal ganglia. Although there were no significant changes in the reaction times, the revealed involvement of the frontoparietal brain cognitive control network possibly reflects the conflict between the dominant, but contextually irrelevant meaning and previously suppressed, but currently relevant one. Therefore, accessing a previously suppressed meaning is effortful since one needs to overcome the initial decision not to choose this meaning, i.e., to negatively select it[22].

However, the revealed BOLD-based negative priming effect[8] could also be explained as a negative aftereffect of positive selection. For instance, according to a version of the episodic retrieval theory[23], processing operations tend to be repeated if they were applied to the stimulus in the past. Likewise, another model, the theory of event coding[8,24], predicts that the second presentation of the same noun with a missing letter will induce an automatic retrieval of the response given to the previous presentation of such noun. This prediction was corroborated by an independent behavioral study using the same experimental design[25]. This study demonstrated that when subjects completed ambiguous nouns for the second time, they often repeated a previously chosen variant inappropriate in the current context. In this sense, revealed changes could be associated with greater efforts needed to select between two possible alternatives like it occurs in free choice deceptive paradigms, demonstrating the similar patterns of BOLD signal changes[26]. Therefore, the present study cannot fully disentangle possible effects of suppression of a non-selected meaning vs. a reinstatement of a previously performed response to a particular stimulus in the observed

negative aftereffect. We also cannot exclude the possibility that both processes are simultaneously involved in producing these NP-like effects, which should be addressed in future research.

Concluding remarks

The revealed decrement in the BOLD signal within the right and left hippocampi associated with ambiguity resolution while processing words with missing letters supports the hypothesis that non-selected meanings are suppressed. The similarity between this result and BOLD signal changes observed for suppression-induced forgetting for purging unwanted memories from awareness allows suggesting the general neurophysiological basis for voluntary and automatic inhibitory awareness control. This substantially extends the current view on the inhibitory control impact in the automatic processing of ambiguous information. Observed increased levels of local activity within the frontoparietal brain network, the temporal cortex and basal ganglia associated with the negative aftereffect of ambiguity resolution could be caused both by the non-selected meaning suppression and by the automatic retrieval of the previous response to the repeated ambiguous stimulus, or by the combination of these two processes.

References

1. Walley, R. & Weiden, T. Lateral inhibition and cognitive masking: a neuropsychological theory of attention. *Psychol. Rev.* **80**, 284–302 (1973).

2. Mcclelland, J. L. & Rumelhart, D. E. *An Interactive Activation Model of Context Effects in Letter Perception: Part 1. An Account of Basic Findings. Psychological Review VOLUME* **88**, (1981).

3. Allakhverdov, V. *The experience of theoretical psychology*. (Publishing house St. Petersburg State University, 1993).

4. Cleeremans, A., Allakhverdov, V. & Kuvaldina, M. *Implicit learning: 50 Years on*. (2019).

5. Kuvaldina, M., Chetverikov, A. & Andriyanova, N. Implicit learning from one's mistakes. in *Implicit learning: 50 years on* 108–132 (2019). doi:10.4324/9781315628905-5

6. Gernsbacher, M. Attenuating interference during comprehension: The role of suppression. (1997).

7. Rodd, J. *Lexical ambiguity. Oxford handbook of pycholinguistics* (2018).

8. Frings, C., Schneider, K. K. & Fox, E. The negative priming paradigm: An update and implications for selective attention. *Psychon. Bull. Rev.* **22**, 1577–1597 (2015).

9. Vitello, S. & Rodd, J. M. Resolving Semantic Ambiguities in Sentences: Cognitive Processes and Brain Mechanisms. *Lang. Linguist. Compass* **9**, 391–405 (2015).

10. Anderson, M. C., Bjork, R. A. & Bjotk, E. Remembering Can Cause Forgetting: Retrieval Dynamics in Long-Term Memory Article. *J. Exp. Psychol. Learn. Mem. Cogn.* **20**, 1063–1087 (1994).

11. Anderson, M. C. & Hulbert, J. C. Active Forgetting: Adaptation of Memory by Prefrontal Control. *Annu. Rev. Psychol.* **72**, (2021).

12. Kuhl, B., Dudukovic, N., Kahn, I. & Wagner, A. Decreased demands on cognitive control reveal the neural processing benefits of forgetting. *Nat. Neurosci.* **10**, 908–914 (2007).

13. Levy, B. & Anderson, M. Purging of memories from conscious awareness tracked in the human brain. *J. Neurosci.* **32**, 16785–16794 (2012).

14. Oldfield, R. C. The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* **9**, 97–113 (1971).

15. Alexeeva, S., Slioussar, N. & Chernova, D. StimulStat: A lexical database for Russian. *Behav. Res. Methods* **50**, 2305–2315 (2018).

16. Lyashevskaya, O. N. & Sharoff, S. A. *Častotnyj Slovar' Sovremennogo Russkogo Jazyka ('The Frequency Dictionary of Modern Russian Language')*. (Azbukovnik, 2009).

17. Gagnepain, P., Hulbert, J. & Anderson, M. C. Behavioral/Cognitive Parallel Regulation of Memory and Emotion Supports the Suppression of Intrusive Memories. *J. Neurosci.* **37**, 6423–6441 (2017).

18. Mary, A. *et al.* Resilience after trauma: The role of memory suppression. *Science (80-.).* **367**, (2020).

19. Apšvalka, D. *et al.* Dynamic targeting enables domain-general inhibitory control over action and thought by the prefrontal cortex. *bioRxiv* (2020). doi:10.1101/2020.10.22.350520

20. Schmitz, T., Correia, M. & Ferreira, C. Hippocampal GABA enables inhibitory control over unwanted thoughts. *Nat. Commun.* **8**, 1–11 (2017).

21. Yaple, Z. & Arsalidou, M. Negative priming: a meta-analysis of fMRI studies. *Exp. Brain Res.* **235**, 3367–3374 (2017).

22. Allakhverdov, V. M. *et al.* Consciousness, learning, and control: on the path to a theory. in *Implicit learning: 50 years on* 71–108 (Taylor & Francis, 2019).

23. Neill, W. Mechanisms of transfer-inappropriate processing. in *Inhibition in cognition* 63–78 (2007).

24. Hommel, B. Event files: feature binding in and across perception and action. *Trends Cogn. Sci.* **8**, 494–500 (2004).

25. Gershkovich, V. *et al.* Aftereffects of ambiguity resolution in the word fragment completion task. in *The Night Whites Language Workshop : The Fifth Saint Petersburg Winter Workshop on Experimental Studies of Speech and Language (Night Whites 2019)* 24 (2020).

26. Kireev, M., Korotkov, A., Medvedeva, N. & Medvedev, S. Possible role of an error detection mechanism in brain processing of deception: PET-fMRI study. *Int. J. Psychophysiol.* **90**, 291–299 (2013).

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Author contributions

MK, VA, TC, VG and NM designed the project. NS, VG and NM created a balanced list of verbal stimuli. AK, MZ, RM and DC performed the experiment. MK, RM and MZ analyzed the data. MK, VG, NS, NM co-wrote the manuscript. TC, VA, AK and DC revised the manuscript. All authors have read and approved the final version of the manuscript.

Competing Interests Statement

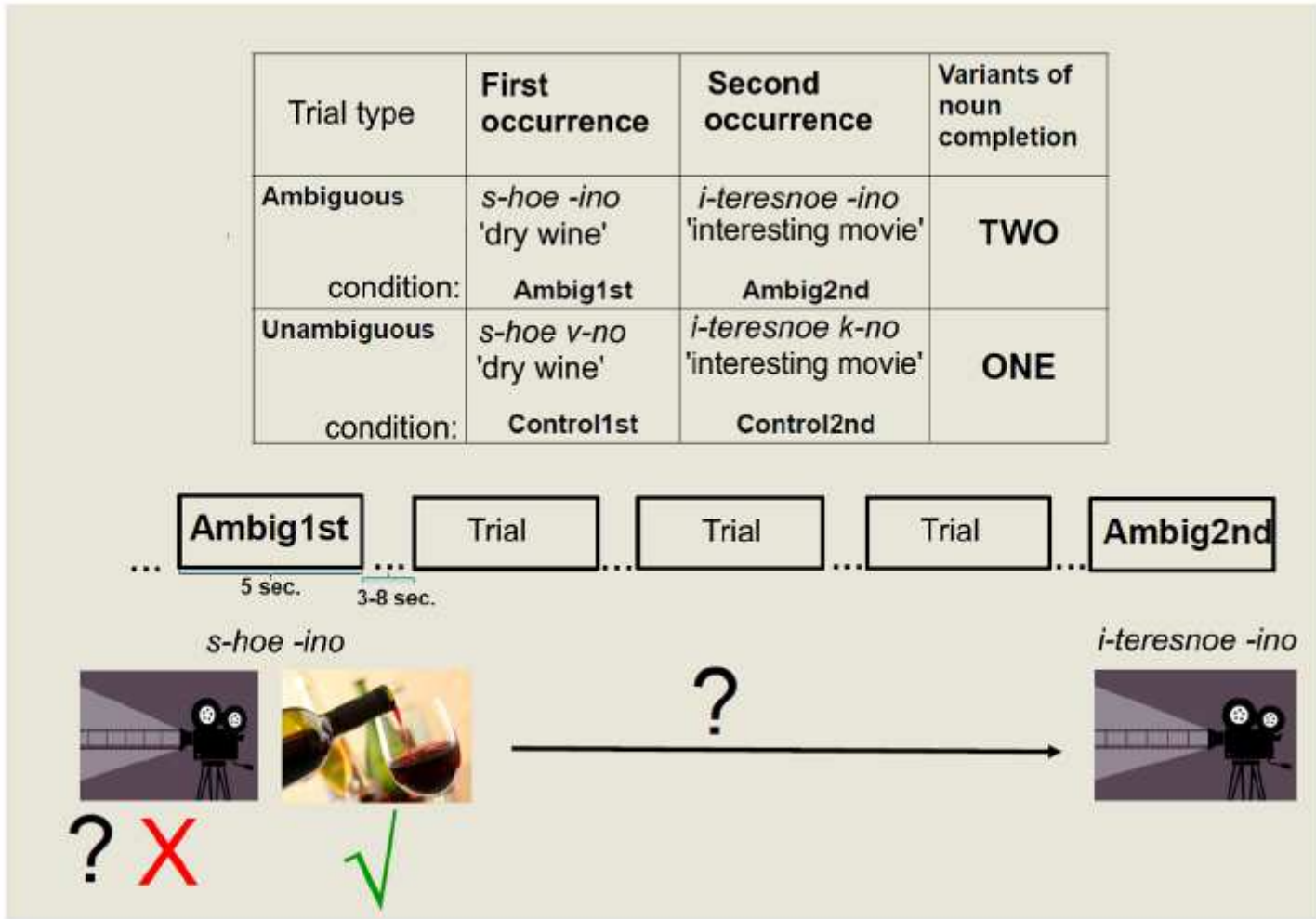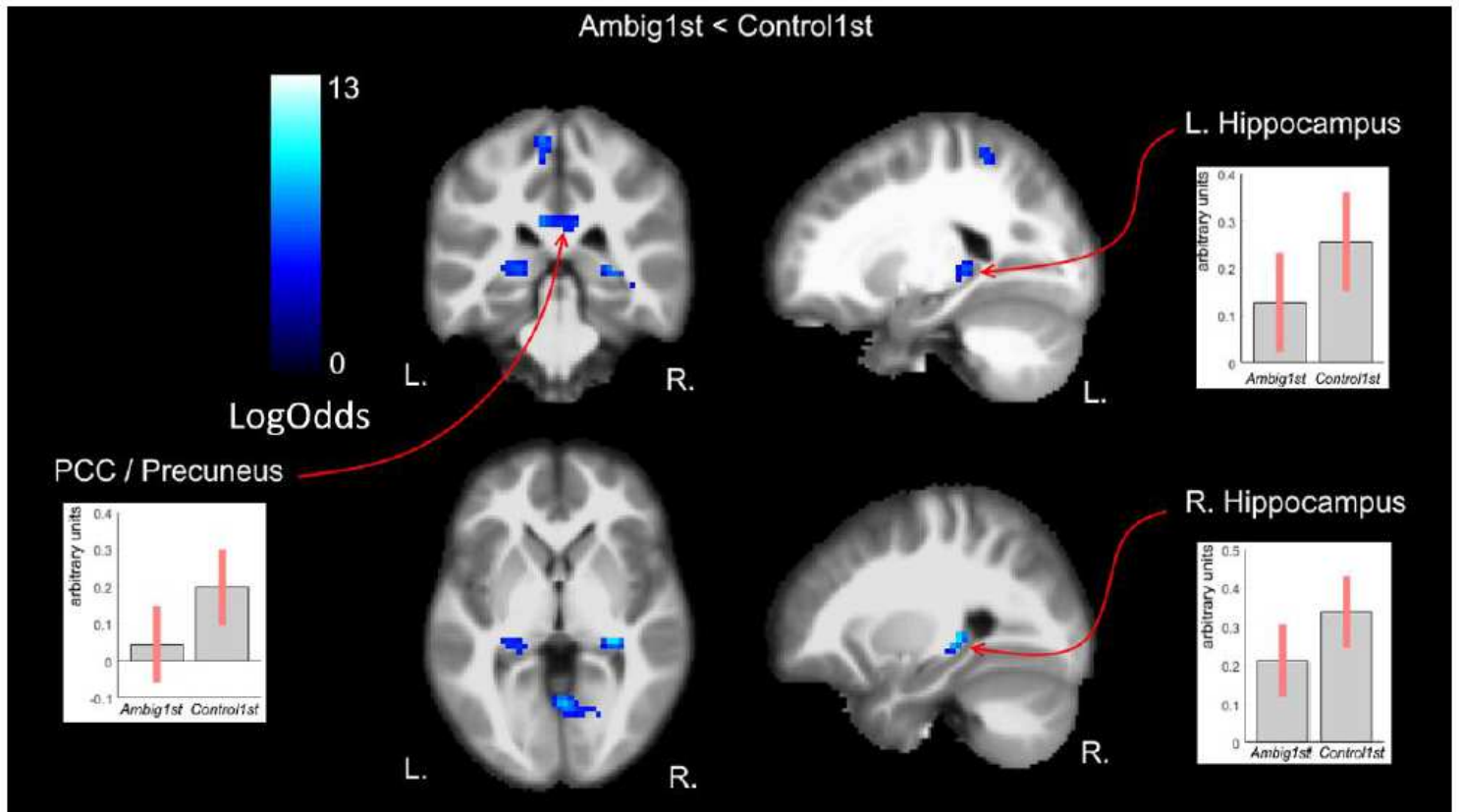The authors declare no conflict of interest.

Figures

Figure 1

The experimental design of the fMRI study. The table illustrates four different trial types. The pictures in the lower part illustrate two variants of completion of the noun -ino (vino 'wine' or kino 'movie').
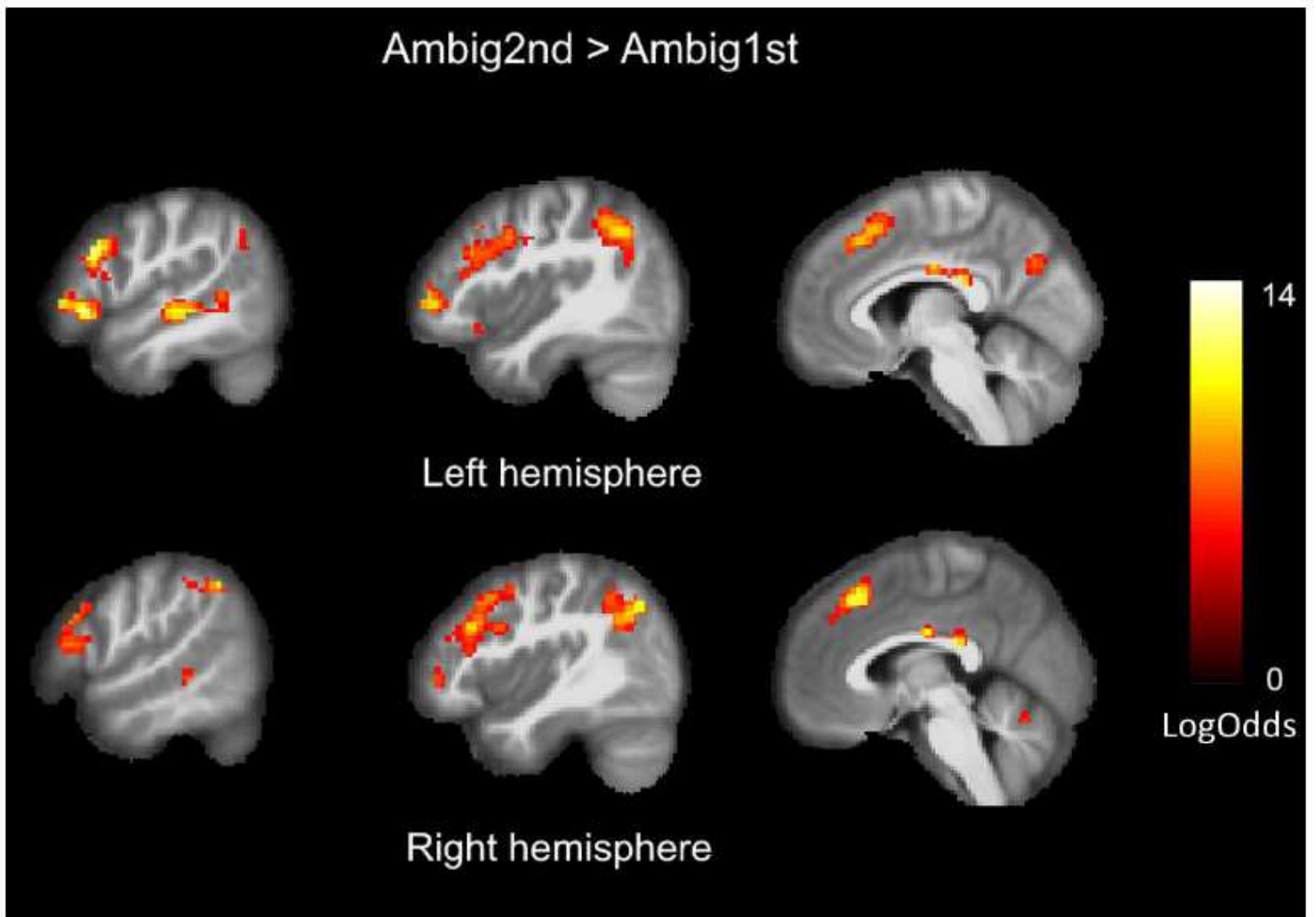
Figure 2

Decrement of the BOLD signal associated with processing of a non-selected meaning. Clusters of significant t-contrast Control1st > Ambig1st presented over a template brain image. Blue color bar represents the value of Log Odds Bars represented the sizes of effect in arbitrary units describing the PPI-parameters.

Figure 3

Ambiguity disadvantage. Clusters of the BOLD signal associated with processing of the second occurrence of an ambiguous stimulus in the Ambig2nd trial as compared to the Ambig1st trial, in which this stimulus was presented for the first time.