The Left Angular Gyrus Is Causally Involved in Context-dependent Integration and Associative Encoding during Narrative Reading

Francesca M. Branzi[1] , Gorana Pobric[2], JeYoung Jung[3], and Matthew A. Lambon Ralph[1]

Abstract

■ The role of the left angular gyrus (AG) in language processing remains unclear. In this study, we used TMS to test the hypothesis that the left AG causally supports the processes necessary for context-dependent integration and encoding of information during language processing. We applied on-line TMS over the left AG to disrupt the on-line context-dependent integration during a language reading task, specifically while human participants integrated information between two sequentially presented paragraphs of text ("context" and "target" paragraphs). We assessed the effect of TMS on the left AG by asking participants to retrieve integrated contextual information when given the target condition as cue in a successive memory task. Results from the memory task showed that TMS applied over the left AG during reading impaired the formation of integrated context-target representation. These results provide the first evidence of a causal link between the left AG function, on-line information integration, and associative encoding during language processing. ■

INTRODUCTION

The left angular gyrus (AG) is implicated in a wide range of cognitive activities including memory retrieval, language and semantic processing, numerical processing, spatial cognition, attention, and theory of mind (Bonnici, Cheke, Green, FitzGerald, & Simons, 2018; Humphreys & Lambon Ralph, 2015, 2017; Bonnici, Richter, Yazar, & Simons, 2016; Hartwigsen, Golombek, & Obleser, 2015; Seghier, 2013; Ciaramelli, Rosenbaum, Solcz, Levine, & Moscovitch, 2010). Among these activities, its specific role during semantic and language tasks is still not well understood. Recent neuroimaging evidence suggests that this region may support the integration of contextual information during language processing (Branzi, Humphreys, Hoffman, & Lambon Ralph, 2020; Ramanan, Piguet, & Irish, 2018; Humphreys & Lambon Ralph, 2015, 2017; van der Linden, Berkers, Morris, & Fernandez, 2017; Bonnici et al., 2016). For instance, the left AG, differently from other regions within the semantic network such as the anterior temporal lobes, is engaged in language and semantic tasks but only when information can be integrated into a contextual support (e.g., Branzi et al., 2020). Furthermore, the left AG responds more to stimuli with strong rather than weak contextual or thematic associations (Bar, Aminoff, & Schacter, 2008; Davey et al., 2015), and finally, it is involved in reactivation and recombination of information presented in a given context (Jonker, Dimsdale-Zucker, Ritchey, Clarke, & Ranganath, 2018; Ramanan et al., 2018; Bonnici et al., 2016; Wagner et al., 2015; Shimamura, 2011).

Although these fMRI investigations have advanced our understanding of the left AG's role in different aspects of cognition, to date, no study has provided evidence for a causal link between processes supporting on-line contextual integration during naturalistic language processing and the functioning of the left AG. Some previous studies have assessed the causal role of left AG for processing two-word combinations (e.g., student–pupil; Koen, Thakral, & Rugg, 2018; Sliwinska, James, & Devlin, 2015). Going beyond two-word combinations is critically important because two-word combinations do not engage the left AG to the same extent as language tasks involving multi-item context integration (e.g., sentence processing; see Humphreys, Hoffman, Visser, Binney, & Lambon Ralph, 2015; Humphreys & Lambon Ralph, 2015; Humphries, Binder, Medler, & Liebenthal, 2007), suggesting that this brain region may be particularly important for multi-item and time-extended integration of information (e.g., Ramanan et al., 2018; Humphreys & Lambon Ralph, 2015).

In this study, we evaluated the causal role of the AG for context-dependent integration of information using TMS during naturalistic reading. On-line TMS was applied over the left AG to temporarily interrupt the AG integration function while participants read narratives composed of two consecutive passages ("context" and "target" conditions). We hypothesized that if the left AG is necessary for continuous integration of information, AG TMS applied between context and target presentation should affect the encoding of an integrated context-target representation.

[1]University of Cambridge, [2]The University of Manchester, [3]University of Nottingham

We also used this new TMS exploration to test a more specific hypothesis that the AG is particularly engaged when integration involves ongoing coherently related content (Branzi et al., 2020; Humphreys & Lambon Ralph, 2015, 2017; van der Linden et al., 2017). For instance, recent neuroimaging evidence has shown that AG activity is positively engaged during information processing and is predictive of better memory retention, only when this information fits with a knowledge-based schema or semantic context (van der Linden et al., 2017). Thus, in the current experiment, an AG TMS effect should be observed only when context and target passages are semantically coherent (i.e., same schema or semantic context), but not when the semantic context changes between the passages (and thus, there is need to reset or update the current schema). To test this hypothesis, AG TMS was applied during two narrative conditions in which the same target paragraph was preceded by different types of context: (i) a highly congruent context (high congruent [HC]), which maximized the information contained in a single coherent story assimilated across both passages, versus (ii) a low-congruent (LC) paragraph with a divergent meaning, thus requiring updating the semantic context (see Figure 1A). In the subsequent memory task, participants were presented with the target condition (both HC and LC) as a cue and asked to retrieve context-related information that required access to an integrated representation ("Cue

Target" trials; see Figure 1B). We expected AG TMS to impair behavioral performance in HC conditions, but to have no effect on the retrieval of LC conditions.

Furthermore, the literature suggests that memory representations that include elements following and preceding the update of information are harder to retrieve than representations that require retrieval of associations within the same event (Swallow, Zacks, & Abrams, 2009; Speer & Zacks, 2005). Accordingly, we expected to find increased RTs and error rates for low over high context-to-target congruency under standard conditions (i.e., no AG TMS), and that AG TMS would diminish this effect given the AG's role in contextual integration. To rule out the possibility that TMS was affecting encoding in general, rather than the encoding of context-target integrated representations specifically (i.e., associative memory), we employed a control condition in the memory task. In "Cue Context" trials, participants were required to retrieve the same context-related information as in the Cue Target conditions (Figure 1B). However, they were provided with some contextual information as cue.

METHODS

Participants

Participants were selected from an existing database of volunteers that have been screened for contraindications
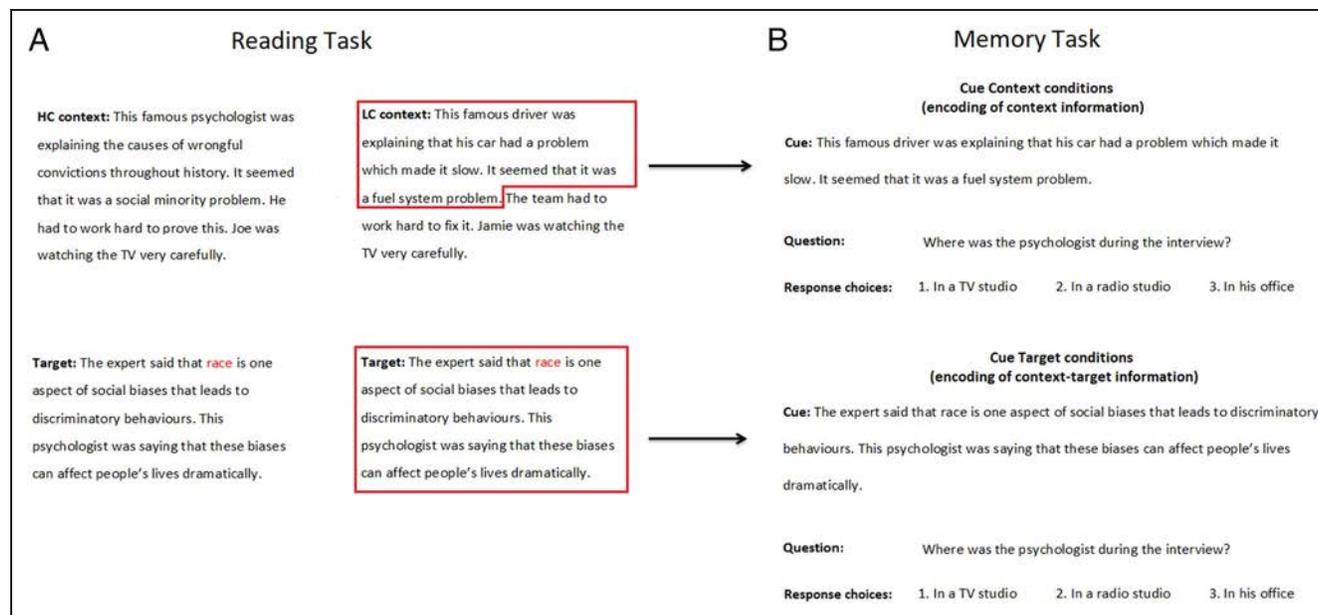

Figure 1. (A) Examples of stimuli for HC and LC conditions (context and target paragraphs). Homonym word is colored in red. For a complete list of the stimuli, see Branzi et al. (2020). (B) Examples of stimuli for Cue Context (LC only in this example) and Cue Target conditions, assessing the encoding of context and context-target information, respectively. In Cue Context conditions, the cues for LC and HC conditions are identical to the LC and HC contexts, except for some information that was removed because it contained the answer to the questions in the memory task. For instance, the cues for LC and HC conditions in Figure 1B would correspond to the LC and HC contexts presented in Figure 1A, except for the final sentences *"The team had to work hard to fix it. Jamie was watching the TV very carefully."* and *"He had to work hard to prove this. Joe was watching the TV very carefully."*, which were removed from the Cue Context conditions because they contained the answer to the question (i.e., location of the interview). Questions for Cue Target and Cue Context conditions were the same *across* participants. However, for each narrative item, a given participant was asked different questions for Cue Target and Cue Context conditions. For instance, if in the Cue Context condition we were asking the question about the location of the interview (as in Figure 1B), in the Cue Target condition, we would have asked the question about who was listening to the interview (and vice versa).

to TMS. Specifically, participants were excluded if they had a current or previous neuropsychiatric or neurological illness, were taking any psychoactive medications, had a prior head injury that required hospitalization/surgery, if they had cardiac pacemaker and/or cochlear implants fitted, had any joint replacements or metal implants in any part of their body including the head, had a prior experience of a seizure, had a diagnosis or family history of epilepsy, and finally, if they might be pregnant. Eighteen volunteers took part in the study (average age = 22 years, standard deviation [SD] = 3 years; 12 women). All participants were right-handed (Oldfield, 1971), native English speakers with no history of neurological or psychiatric disorders and normal or corrected-to-normal vision. The participants included in the study were also screened for any developmental or acquired language impairments. Written informed consent was obtained from all participants. The experiment was approved by the local ethics committee.

Stimuli

Reading Task

The experimental stimuli used in the reading task were the same as in a previous study (Branzi et al., 2020). Thus, a total of 40 narrative paragraph pairs were employed in the reading task. For each narrative pair, the same second paragraph (target) was preceded by different first paragraphs (contexts) that could be either HC or LC with the target in terms of meaning. Both HC and LC context paragraphs could be integrated with the target paragraphs, though a reworking of the evolving semantic context was required after LC contexts (see Figure 1A for an example of the stimuli; for the full list of the stimuli used in the reading task, see Branzi et al., 2020). Homonym words (race, bank, etc.), presented at the beginning of the target paragraph, were employed to determine the exact point in the paragraph in which the shift in the semantic context should have been experienced. Finally, the "No Context" (NC) condition, where the target (the same as in HC and LC conditions) was preceded by a string of numbers, was employed as a control condition. The NC condition allowed us to verify that any TMS effect in the HC and LC conditions was due to integration processes and not to bottom–up attention triggered by the presentation of the target paragraph.

Memory Task

Seventy-five experimental stimuli were employed. In the memory task, the presentation of a cue displayed on the screen was followed by a question about the context of the narrative along with three possible response choices (see Figure 1B). Importantly, in the memory task, there were different types of conditions. These conditions did not differ with respect to the type of information that participants had to retrieve (the same contextual information); rather, they differed in the type of cue (see below).

Cue target conditions. In this condition, the cues contained the information presented in the target paragraph for both HC and LC narratives (i.e., HC Cue Target conditions [n = 25] and LC Cue Target conditions [n = 25]). This condition tested participants' ability to retrieve target-context integrated representations.

Cue context conditions. In this condition (n = 25), the cues contained only a part of the context paragraph (see an example in Figure 1B). Thus, participants were presented with this information as a cue and then had to retrieve the "missing" contextual information. Therefore, unlike the Cue Target condition, this condition did not require participants to retrieve the integrated representation of the two sequential paragraphs, but only tested participants' ability to retrieve the context-paragraph representation.

In both conditions, the type of contextual information to be retrieved during the memory task covered a variety of episodic details (e.g., who, where, when; Figure 1B).

Task Procedures

Structure of the Experimental Sessions

Before starting the experimental study, all participants signed an informed consent and were given written and oral instructions. A PC running ePrime (Psychology Software Tools, Inc.) was used to present the stimuli and record participants' behavioral responses. The participants completed three sessions on different days. During two out of three sessions, participants received TMS (TMS over the left AG and TMS over the vertex). In one session, TMS was not used. The sessions were at least 1 week apart (average days between sessions = 12, SD = 3), and the order of sessions was counterbalanced across participants.

In each session, participants performed two different tasks: a reading task and a memory task. Both reading and memory tasks were divided into two blocks (i.e., "Reading Task 1" and "Reading Task 2"; and "Memory Task 1" and "Memory Task 2"), which were presented in an interleaved fashion (see Figure 2A). Each session started with Reading Task 1 (see Figure 2A), in which participants read half of the narrative stimuli. This was followed by a memory task (i.e., Memory Task 1), composed of questions about the narratives presented in Reading Task 1. After a short break (10 min), the remaining narratives were presented (Reading Task 2; see Figure 2A), which was followed by Memory Task 2, including questions relating to the narratives presented in Reading Task 2.

During the TMS sessions, on-line TMS was delivered during each trial in the reading tasks (for details, see Figure 2B and Stimulation Parameters and Stimulation Sites section). TMS was not applied during the memory task. We did not apply TMS during the memory task because the goal of this study was to measure the contribution of the left AG to context integration during language comprehension. Because the left AG is implicated not only in language
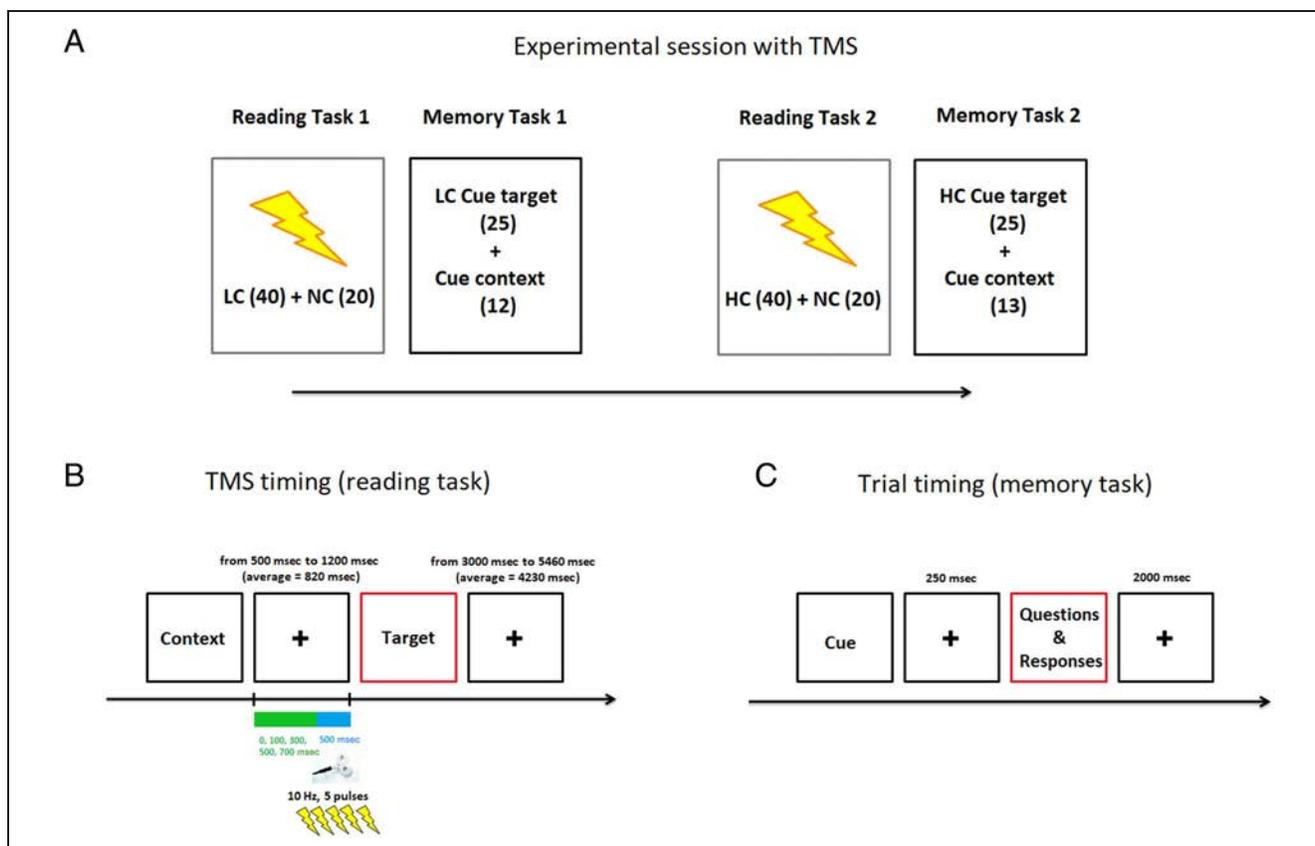
Figure 2. (A) An example of the structure of a session in which TMS was used. (B) Trial timing in the reading task. (C) Trial timing in the memory task.

processing but also in memory retrieval (Rugg & King, 2018; Humphreys & Lambon Ralph, 2015; Rugg & Vilberg, 2013), avoiding TMS during the memory task ensured that any observed TMS effect reflected the contribution of the AG for integrating information during the reading task. At the end of each TMS session, participants completed a questionnaire in which they reported the extent to which TMS was perceived as uncomfortable and distracting (scales from 1 = *not very* to 7 = *very*).

Reading task. As noted above, the reading task was divided in two blocks (Reading Task 1 and Reading Task 2). In total, participants were presented with 40 narrative items per condition (HC, LC, and NC). As in our previous study (Branzi et al., 2020), each trial consisted of two text paragraphs (context and target) that participants had to read silently (verbal material and numbers). Contexts and targets were displayed on the screen until participants pressed a button to indicate that they had finished reading the paragraph (for both contexts and targets). The instruction emphasized speed, given the limited amount of time for reading (max duration for context was 12 sec and for targets was 7.5 sec), but also the need to understand and encode the information presented in the narratives. We informed participants that, at the end of each reading task, they would perform a memory task, requiring them to answer questions on the content of the narratives. We also specified that, in order to perform the task, it would be

necessary to integrate the information presented in context and target paragraphs. Rest time was varied between context and targets (range between 500 msec and 1200 msec, average time = 820 msec) and between trials (range between 3000 msec and 5460 msec, average time = 4230 msec) during which a black fixation cross was presented.

Importantly, HC and LC narrative stimuli were presented separately (see Figure 2A). This was because HC and LC conditions terminated with the same target paragraph, and therefore, mixing them during the reading task would have created confusion during the memory task. Thus, in each session, Reading Task 1 included either HC trials (40) or LC trials (40), and half of the NC trials (20; see Figure 2A). Reading Task 2 included the remaining narratives (either LC trials or HC trials, and the remaining 20 NC trials). The order of LC and HC conditions (i.e., whether they were assigned to Reading Task 1 or 2) was counterbalanced across participants and sessions. The stimuli presented in the reading task were the same across all three sessions.

Memory task. The memory task was divided in two blocks (Memory Task 1 and Memory Task 2). In total, participants were presented with 25 items per condition (Cue Context, LC Cue Target, and HC Cue Target). Memory was probed using a three-alternative forced-choice task. Each trial started with the presentation of a cue displayed on the screen until participants made a button response. This was followed by the presentation of the questions

and response choices, which were displayed until the participants made their selection by button response, up to a time limit of 8.5 sec (see Figure 2C). The instruction emphasized speed, given the limited amount of time for responding. Rest time (black fixation cross) was presented between cue and questions/response choices and between trials (fixed time intervals: 250 and 2000 msec, respectively).

Importantly, Cue Context, LC Cue Target, and HC Cue Target were presented in the following way: In Memory Task 1, LC Cue Target trials (25) were presented with half of the Cue Context trials (12 or 13), always after reading the LC narratives. In Memory Task 2, HC Cue Target trials (25) were presented with the remaining Cue Context trials (13 or 12), always after the HC narratives (see Figure 2A). The order of presentation of LC and HC conditions (i.e., whether they were assigned to Memory Task 1 or 2) was counterbalanced across participants and sessions. Note that, for each participant, HC Cue Target trials (25) and LC Cue Target trials (25) referred to different narratives. Although the question stimuli for Cue Target and Cue Context trials were the same *across* participants, for the same narrative item, each participant was asked different questions in Cue Target (HC or LC) and Cue Context conditions (see Figure 1B). Finally, the stimuli presented during the memory task were always different across the three sessions.

Stimulation parameters and stimulation sites. TMS was delivered using a Magstim Rapid2 stimulator (Magstim Co.) and a figure-of-eight coil with a diameter of 70 mm. Stimulation was performed at 120% of the individual's motor threshold, measured before the start of the first session (mean stimulation intensity = 71, $SD = 8$, range = 54–84). The resting motor threshold of the relaxed contralateral abductor pollicis brevis muscle was measured as the lowest stimulation intensity able to cause a visible twitch in the muscle 5 out of 10 times (Sandrini, Umiltà, & Rusconi, 2011).

For each trial, one train of five pulses (10 Hz for 500 msec) was delivered. This stimulation protocol has already been used over the inferior parietal cortex to induce inhibitory effects during language (Capotosto et al., 2017; Sliwinska et al., 2015; Hartwigsen et al., 2010) and nonlinguistic processing (Riddle, Scimeca, Cellier, Dhanani, & D'Esposito, 2020), which is consistent with the inhibitory theory related to alpha oscillations in parietal-occipital areas (Klimesch, 2012). The first pulse was administered before the presentation of the target to avoid disrupting reading (TMS to the AG can induce eye twitches; see Figure 2B). A pilot study confirmed that this procedure was successful for obtaining the expected (inhibitory) TMS effect on behavior. The rest time between the context and target phases was variable and randomized (see Figure 2B). Thus, participants were not able to anticipate when they would receive TMS. Finally, the TMS frequency, intensity, and duration were well within established international safety limits (Rossini et al., 2015).

The stimulation site for the left AG region corresponded to the Montreal Neurological Institute coordinates ($x = -48$, $y = -63$, $z = 36$; see Figure 3A) derived from our previous fMRI study in which the same experimental material was used and where, in accord with other studies (for a review see Ramanan et al., 2018), the left AG activity was modulated by context integration and was positively engaged (against rest) for coherent conditions only, that is, for HC conditions (Branzi et al., 2020; see Figure 3B). Anatomically, this peak falls within an area between posterior PGa and PGp, two subregions of the AG, as defined by cytoarchitectonic parcellation (Caspers et al., 2006, 2008).

During the AG TMS testing session, a Polaris Vicra infrared camera (Northern Digital) was used in conjunction with the Brainsight frameless stereotaxy system (Rogue Research) to register the participant's head to their own MRI scan to accurately target stimulation throughout the experiment. As in many previous studies that investigated the role of the AG in cognition, we selected the vertex as the control site (Thakral, Madore, Kalinowski, & Schacter, 2020; Bonnici et al., 2018; Koen et al., 2018; Thakral, Madore, & Schacter, 2017; Yazar, Bergström, & Simons, 2014, 2017; Davey et al., 2015). The vertex has also been used in many other TMS studies (Jung, Bungert, Bowtell, & Jackson, 2016; Silvanto, Cattaneo, Battelli, & Pascual-Leone, 2008) and is a suitable control site for the AG, because behavioral RT side effects induced by TMS over AG or vertex do not differ (Meteyard & Holmes, 2018). The location of the vertex was established for each participant by using the International 10–20 system (Steinmetz, Fürst, & Meyer, 1989). The halfway intersection of the two lines was marked using a skin marker.

Behavioral and Data Analysis

Discomfort/distractibility scores and reading times. To rule out the possibility that AG TMS effects measured in the memory task could be because of general disruption of reading processing induced by TMS, that is, nonspecific TMS effects, we obtained discomfort and distractibility self-report measures during each TMS session and assessed the impact of TMS on the reading task performance. At the end of each TMS session, participants completed a questionnaire in which they reported the extent to which TMS was perceived as uncomfortable and distracting (scales from 1 = *not very* to 7 = *very*). Thus, we conducted separate *t* tests for each measure (discomfort and distractibility), comparing ratings between sites (AG vs. vertex).

Behavioral analyses were also performed on reading times to quantify the impact of discomfort and distractibility induced by TMS on the reading task performance (as measured by reading times). Trials exceeding 3 *SD*s above or below a given participant's mean reading time were excluded from the analyses, causing a loss of 0.2% of data, across all task conditions and type of sessions. Then, the TMS effect was assessed by conducting a 3 × 3
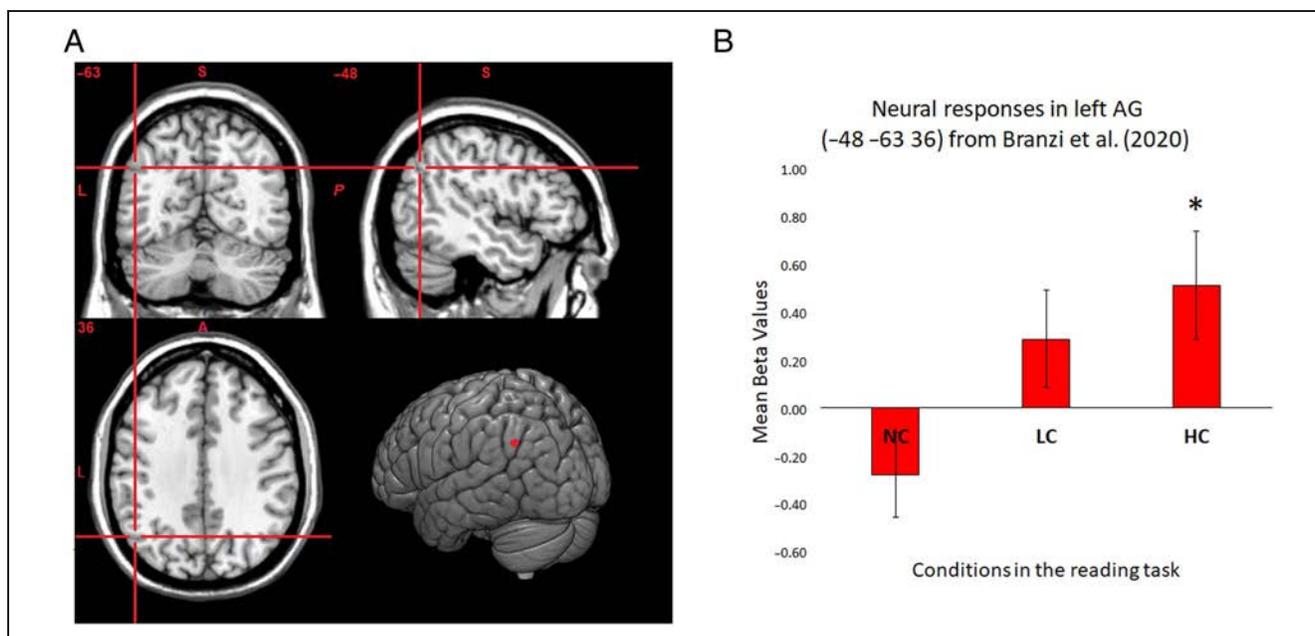
Figure 3. (A) The left AG stimulation site pinpointed on the Montreal Neurological Institute cortical template. (B) The neural data results are derived from Branzi et al. (2020), where the same stimuli and task were employed. The neural responses measured at the left AG stimulation site (sphere of 10-mm radius) reflect neural activity of left AG against rest during context integration, that is, measured at the onset of the target paragraph. Error bars correspond to standard errors (*SE*s). The neural activity measured at the stimulation site shows a context-dependent effect [main effect of condition: $F(1.663, 34.933) = 15.784$, $p < .001$, $\eta_p^2 = .429$, post hoc t test comparisons Bonferroni-corrected indicate that HC > NC and LC > NC ($p < .001$ and $p = .012$, respectively)] and that neural responses against the baseline are positively enhanced for HC conditions only [one-sample t test for HC conditions: $t(21) = 2.249$, $p = .035$; one-sample t test for LC conditions: $t(21) = 1.427$, $p = .168$].

within-subject ANOVA with the repeated-measures factors Condition (NC, LC, and HC) and Session Type (No TMS, TMS to left AG, and TMS to vertex). Bonferroni correction for multiple comparisons was applied on post hoc pairwise contrasts. Finally, correction for nonsphericity (Greenhouse–Geisser procedure) was applied to the degrees of freedom and p values associated with factors having more than two levels (i.e., Condition and Session Type).

Memory task. Behavioral analyses were performed on RTs and accuracy measures. RT analysis was conducted only for correct trials. Having eliminated error trials (see Table 1), trials exceeding 3 *SD*s above or below a given participant's mean were excluded from the RT analysis, causing a loss of 2% of data, across all task conditions and type of sessions. Thus, for each Session Type (No TMS, AG TMS, and Vertex TMS), the remaining set of data on which we performed the RT analysis consisted, on average, of

Table 1. Memory Task: Descriptive Statistics for RTs and Accuracy Measures

	No TMS			AG			Vertex		
	Cue Context	LC Cue Target	HC Cue Target	Cue Context	LC Cue Target	HC Cue Target	Cue Context	LC Cue Target	HC Cue Target
Descriptive Statistics RTs									
Mean	3134	3239	2950	2978	3288	3267	3144	3391	2951
Std. Error	119	122	73	138	181	139	201	167	120
Std. Deviation	503	520	308	586	768	588	851	707	508
Descriptive Statistics Accuracy									
Mean	0.67	0.64	0.63	0.67	0.64	0.64	0.64	0.63	0.62
Std. Error	0.03	0.04	0.03	0.02	0.03	0.04	0.04	0.04	0.02
Std. Deviation	0.13	0.15	0.12	0.10	0.12	0.15	0.15	0.17	0.10

16 trials per condition (SD = 2.7, 2.1, and 2.7 for No TMS, AG TMS, and Vertex TMS, respectively). We conducted two separate 3 × 3 within-subject ANOVAs (one for RTs and one for accuracy measures) with the repeated-measures factors Condition (Cue Context, LC Cue Target, and HC Cue Target) and Session Type (No TMS, TMS to left AG, and TMS to vertex). Correction for multiple comparisons was applied on the planned pairwise comparisons, according to our hypotheses. In detail, (1) LC Cue Target conditions were expected to be slower than HC Target conditions in absence of AG TMS (i.e., during Vertex TMS and No TMS sessions only) and (2) for HC Cue Target conditions, we expected AG TMS to induce slower RTs than Vertex TMS and No TMS. Finally, correction for nonsphericity (Greenhouse–Geisser procedure) was applied to the degrees of freedom and p values associated with factors having more than two levels (i.e., Condition and Session Type).

RESULTS

Discomfort/Distractibility Scores and Reading Times

The scores obtained were moderate (AG distracting: average = 3.8, SD = 1.3; AG uncomfortable: average = 3.9, SD = 1.3; vertex distracting: average = 3.3, SD = 1.2; vertex uncomfortable: average = 3, SD = 1.4). TMS over AG or vertex showed similar distractibility scores, $t(17)$ = 1.22, p = .238. TMS over the AG, however, obtained higher scores on the discomfort scale as compared to TMS over the vertex, $t(17)$ = 2.12, p = .049. Interestingly, reading times for the target passage showed that there was no significant effect of Session Type, $F(1.919, 32.618)$ = 0.551, p = .574, η_p^2 = .031, or significant Condition × Session Type interaction, $F(1.893, 32.181)$ = 0.231, p = .783, η_p^2 = .013. Thus, despite TMS over the AG obtained higher scores of discomfort as compared to TMS over the vertex, applying TMS over the left AG did not disrupt reading performance more than TMS over the vertex (Figure 4).
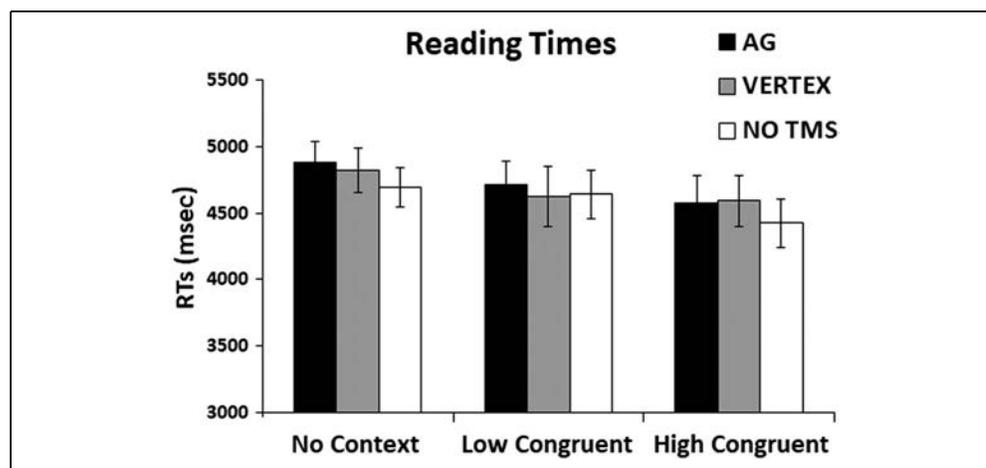
Memory Task

The results for the memory task are summarized in Figure 5 and Table 2. RTs showed a main effect of Condition, $F(1.998, 33.968)$ = 9.443, p = .001, η_p^2 = .357, suggesting that speed for LC Cue Target condition was slower as compared to HC Cue Target (p = .003) and Cue Context conditions (p = .009). There was no significant difference in speed between the HC Cue Target and Cue Context conditions (p > .999). The main effect of Session Type was not significant, $F(1.966, 33.42)$ = 0.188, p = .826, η_p^2 = .011, suggesting that overall performance was not particularly affected by TMS. RT results revealed the expected significant Condition × Session Type interaction, $F(3.235, 54.996)$ = 3.446, p = .02, η_p^2 = .169. Importantly, to ensure that this significant interaction was not solely driven by the Cue Context conditions, we further conducted a 2 × 3 within-subject ANOVA for RTs with the repeated-measures factors Condition (LC Cue Target and HC Cue Target) and Session Type (no TMS, TMS to left AG, and TMS to vertex). Again, we found a significant Condition × Session Type interaction, $F(1.979, 33.646)$ = 4.037, p = .027, η_p^2 = .192. This was assessed via planned pairwise comparisons. For all pairwise comparisons, we provide an effect size (Cohen's d) and a Bayes factor (BF_{10} > 3 suggests substantial evidence for a difference between the pairs, and BF_{10} < 0.3 suggests substantial evidence for a null effect; see Jeffreys, 1961). Reporting BFs is useful for hypothesis testing because they provide a coherent approach to determining whether nonsignificant results support a null hypothesis over a theory, or whether the data are just insensitive.

As mentioned above, our planned t tests focused on a one-sided procedure for hypothesis testing because our hypotheses dictated a specific direction of the effects: We expected (1) LC Cue Target conditions to be slower than HC Target conditions in absence of AG TMS (i.e., during Vertex TMS and No TMS sessions only), and that (2) for HC Cue Target Conditions, AG TMS should induce slower RTs than in the other two sessions (Vertex TMS and No TMS).
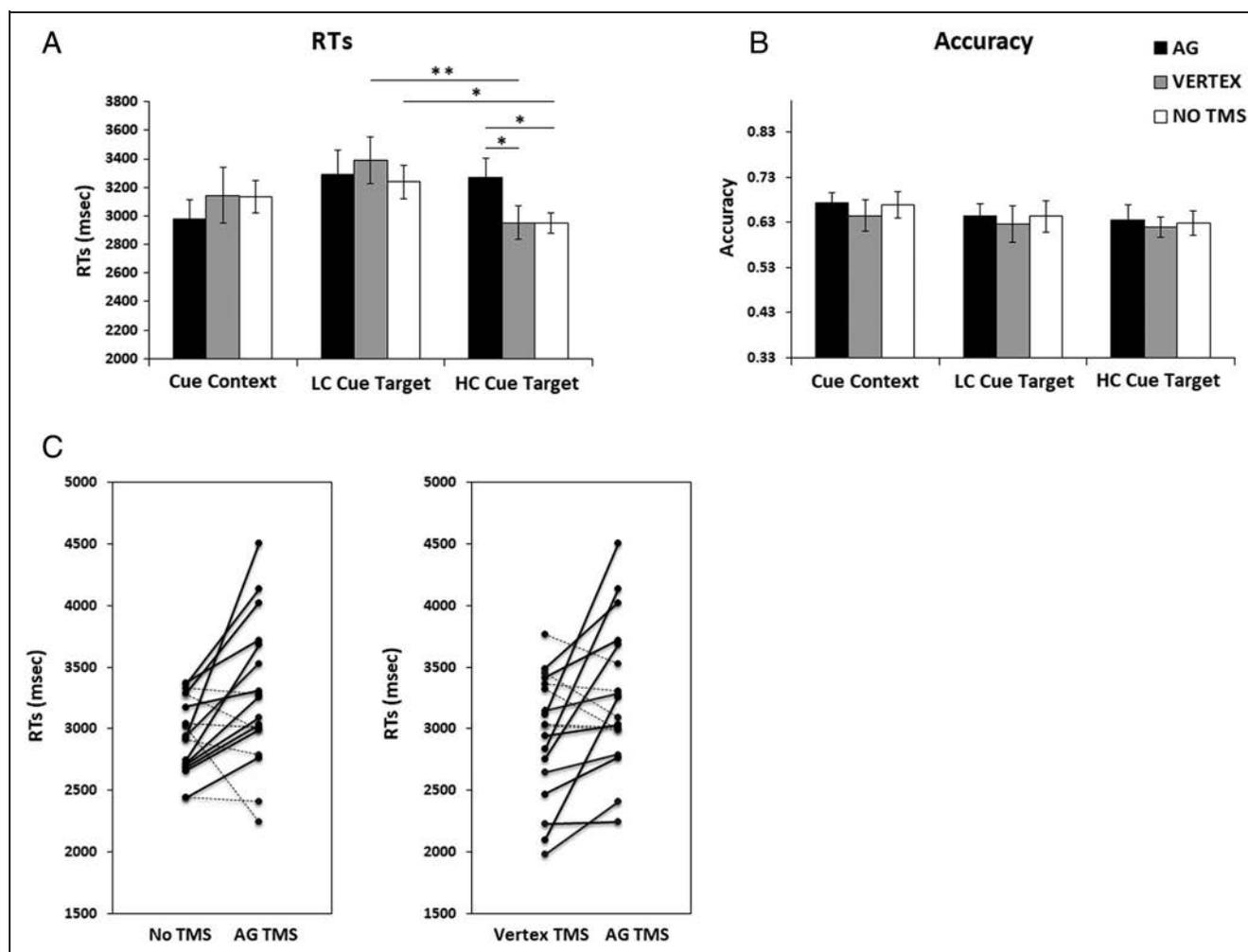
Figure 4. Reading task. Results for reading times for NC, LC, and HC conditions. Error bars correspond to SEs.

Figure 5. Memory task. Results for (A) RTs and (B) Accuracy (proportion of correct responses) for Cue Context, LC Cue Target, and HC Cue Target conditions. Error bars correspond to *SE*s. (C) Individual stimulation RT effects during the HC Cue Target condition in the memory task. Continuous black lines indicate slower performance for AG TMS as compared to No TMS or Vertex TMS, whereas dashed black lines reflect faster performance for AG TMS as compared to No TMS or Vertex TMS.

In keeping with (1), we found that LC Cue Target conditions were significantly slower than HC Cue Target conditions when TMS was applied to the vertex (control site), $t(17) = 3.779$, $p = .0015$, Cohen's $d = 0.89$, $BF_{10} = 52.687$, or when it was not applied at all, $t(17) = 2.613$, $p = .027$, Cohen's $d = 0.61$, $BF_{10} = 6.380$. Interestingly, the same effect was not observed when TMS was applied to the left AG, $t(17) = 0.227$, $p > .999$, Cohen's $d = 0.053$,

$BF_{10} = 0.29$, suggesting that AG TMS may have affected HC Cue Target conditions specifically. Accordingly and in line with (2), HC Cue Target conditions became slower when TMS was applied to the left AG as compared to when it was delivered to the vertex, $t(17) = 2.463$, $p = .024$, Cohen's $d = 0.58$, $BF_{10} = 4.958$, or when it was not delivered at all, $t(17) = 2.576$, $p = .02$, Cohen's $d = 0.607$, $BF_{10} = 5.991$.

Table 2. Memory Task: RT Results Relative to the Planned Comparisons

Planned Comparisons	Mean and Std. Error	t Test Statistics	Effect Size (d)	BF_{10}
No TMS: LC Cue Target > HC Cue Target	289 (111)	$t(17) = 2.613$, $p = .027$	0.610	6.380
Vertex TMS: LC Cue Target > HC Cue Target	440 (116)	$t(17) = 3.779$, $p = .0015$	0.890	52.687
AG TMS: LC Cue Target > HC Cue Target	21 (91)	$t(17) = 0.227$, $p > .999$	0.053	0.290
HC Cue Target: AG TMS > Vertex TMS	316 (128)	$t(17) = 2.463$, $p = .024$	0.580	4.958
HC Cue Target: AG TMS > No TMS	317 (123)	$t(17) = 2.576$, $p = .02$	0.607	5.991

In light of the results observed for the discomfort scale, we conducted a regression analysis to ensure that the observed TMS effect (AG TMS > Vertex TMS) for the HC Cue Target condition was not driven by differences in discomfort scores (see Holmes & Meteyard, 2018). Our results showed that AG TMS > Vertex TMS differences in discomfort measures were not predictive of AG TMS > Vertex TMS differences in RTs for the HC Cue Target condition (Beta = 0.042, $p = .868$; the overall model fit was $R^2 = .002$), leading to the conclusion that perceived discomfort did not play any influence on the observed TMS effect (AG TMS > Vertex TMS) for the HC Cue Target condition. This conclusion was further corroborated by a further linear mixed-effects models analysis (Baayen, Davidson, & Bates, 2008). The model was fitted using RT in the memory task as the dependent variable, and Session Type (AG TMS and Vertex TMS) and Condition (LC Cue Target and HC Cue Target) as two fixed effect factors at the level of individual trials. Importantly, we included the discomfort scores as a covariate of the fixed effect terms. Furthermore, by-item and by-subject random intercepts were included in the model to account for variability in the RT responses at the level of individual participants and individual items, in addition to the variability of individual trials already modeled by the fixed effect terms (Type of Session and Condition). The model parameters were estimated using the restricted maximum likelihood approach. In line with the regression analysis outcome, results showed that, whereas the Type of Session × Condition interaction was significant ($F = 3.659, p = .026$), the Type of Session × Discomfort Scores ($F = 1.915, p = .167$) and Condition × Discomfort Scores interactions ($F = 1.122, p = .326$) were not significant.

Finally, TMS to the left AG did not impair RT performance for LC Cue Target conditions [AG TMS vs. Vertex TMS: $t(17) = -0.549, p > .999$, Cohen's $d = -0.129$, $BF_{10} = 0.17$; AG TMS vs. No TMS: $t(17) = 0.281, p = .782$, Cohen's $d = 0.066$, $BF_{10} = 0.30$] or Cue Context conditions [AG TMS vs. Vertex TMS: $t(17) = -1.109, p > .999$, Cohen's $d = -0.261$, $BF_{10} = 0.128$; AG TMS vs. No TMS: $t(17) = -1.303, p > .999$, Cohen's $d = -0.307$, $BF_{10} = 0.118$].

Note that RTs for error responses were not included in the main analyses because the hypothesis of AG TMS impairing the integration and encoding of a context-target representation can be assessed only by examining RTs for correct trials (and/or accuracy measures). In fact, one possibility is that AG TMS prevents the formation of an association between the information presented in context and target paragraphs, leading to a decrease in accuracy measures. Another possibility is that AG TMS does not prevent the formation of context-target associations, but it makes them weaker and therefore harder to retrieve. This should result in slower RTs for correct trials only. Consistent with this latter alternative, RT results for error responses did not show any significant TMS effect or interaction (main effect of Session Type: $F(1.665, 28.310) =$

$1.803, p = .187, \eta_p^2 = .096$; main effect of Condition: $F(1.919, 32.626) = 1.351, p = .273, \eta_p^2 = .074$; Condition × Session Type interaction: $F(2.417, 41.088) = 1.282, p = .292, \eta_p^2 = .07$).

Like previous studies assessing associative memory performance with three or more response choices (Cooper, Greve, & Henson, 2019; Wang, Clouter, Chen, Shapiro, & Hanslmayr, 2018; Clouter, Shapiro, & Hanslmayr, 2017; Yazar et al., 2017), accuracy was not high (on average 64%). Nevertheless, participants were engaged in the task (chance level is 33%). The accuracy data did not reveal any significant effect (main effect of Condition: $F(1.894, 32.2) = 2.087, p = .143, \eta_p^2 = .109$; main effect of Session Type: $F(1.946, 33.084) = 0.515, p = .598, \eta_p^2 = .029$; Condition × Session Type interaction: $F(3.166, 53.83) = 0.030, p = .994, \eta_p^2 = .002$).

In summary, we found substantial evidence ($BF_{10} > 3$; Cohen's $d \geq 0.58$) that TMS over the left AG selectively impaired encoding of context-target integrated representation for highly coherent narratives (HC Cue Target conditions), but not for the other conditions ($BF_{10} < 0.3$). The medium–large effect sizes reported here for AG TMS accord with the evidence that a small number of trials per condition does not necessarily represent an issue when it comes to power (Rouder & Haaf, 2018). Note that it is unlikely that the TMS effects observed in this study reflect disruption of retrieval processes (i.e., long-lasting after effects of TMS) rather than encoding processes during the reading task. In fact, EEG-TMS combined studies show that the type of stimulation used in this study induces on-line and short-lasting effects only (e.g., Thut et al., 2011). Thus, the short trains of stimulation delivered in this study, interleaved with long intervals (> 16 sec), probably caused direct and measurable condition-specific interference with patterns of ongoing neuronal discharge at the time of stimulation (Valero-Cabré, Amengual, Stengel, Pascual-Leone, & Coubard, 2017). Furthermore, if the AG TMS had induced general disruption of retrieval processes, this effect should also have been observed for the other conditions and especially for the Cue Target condition that showed similar RTs in the baseline conditions (No TMS: Cue Context vs. HC Cue Target: $t(17) = 1.738, p = .1$; Vertex TMS: Cue Context vs. HC Cue Target: $t(17) = 1.417, p = .175$). However, no such effect was observed.

DISCUSSION

In this study, we sought evidence for the hypothesis that the left AG is critical for integration of context-dependent information during language processing (Branzi et al., 2020; Humphreys & Lambon Ralph, 2015, 2017). This hypothesis was tested by asking participants to read short narratives consisting of two sequential paragraphs (context and target) and by delivering TMS pulses over the left AG between the context and target paragraphs, to disrupt on-line integration and therefore encoding of the narrative content (context and target integrated representation).

In a memory task, we measured RTs and proportion of correct responses to test the hypothesis that TMS-induced temporary disruption of AG activity during reading would have had an effect on encoding and, therefore, recall of integrated memory representation (context-target). We hypothesized that this effect would have been observed for HC conditions specifically, that is, when incoming information (target) matches the current knowledge-based schema (Humphreys & Lambon Ralph, 2015, 2017; Swallow et al., 2009; Speer & Zacks, 2005). In line with this hypothesis, we found that TMS delivered over the left AG made participants slower in retrieving context-related information during the memory task, only for coherent narratives (HC Cue Target conditions). This result also accords with the left AG profile of activation found in our previous fMRI study where, during reading, neural responses for HC conditions were the most enhanced as compared to the rest baseline (see Figure 3B). Importantly, this AG TMS effect (observed only for the HC Cue Target condition) cannot be explained by nonspecific stimulation side effects (e.g., auditory noise or discomfort). Discomfort measures were not predictive of the observed AG TMS effect nor were reading times affected by AG TMS.

Our results align with previous TMS evidence establishing the causal role of the left AG for the retrieval of HC thematic associations (Davey et al., 2015). In this study, the authors tested the contribution of the left AG in semantic retrieval using a thematic matching task. As with our study, this type of task involves some context-dependent processing of information. In fact, matching the picture-probe with the target word requires linking conceptual representations of objects from different semantic categories that are nevertheless found or used together in similar contexts. Our findings also accord with previous work showing that TMS over the AG can influence the encoding of novel associations into memory (Hermiller, VanHaerents, Raij, & Voss, 2019; Tambini, Nee, & D'Esposito, 2018). Nevertheless, the results from this study are distinct from previous works, as they establish a critical role of the left AG in continuous on-line integration of linguistic information.

In contrast to our findings, a recent TMS study failed to reveal a link between left AG functioning during encoding and subsequent associative memory performance (Koen et al., 2018). Differences in the type of task and stimuli might explain contrasting outcomes. In Koen et al. (2018), participants were presented with word pairs and were required to perform a size judgment task on them. Therefore, unlike our and other studies (van der Linden et al., 2017; Davey et al., 2015), integration was unlikely to be loading on automatic and context-dependent integration of information: The comparative size judgment task requires comparative working memory for two study items, rather than integration of rich and detailed contextual information. The importance of the left AG for the latter process has been demonstrated in a recent study, where activity of the left AG (1) increased as the presentation of coherent items

(pictures of thematically related objects) unfolded over encoding, and (2) predicted later memory performance (van der Linden et al., 2017). In accordance with our findings, these results suggest that the left AG activity is crucial for encoding and re-activation of long-term schema-consistent associative memories. In short, if the left AG supports context-dependent integration of rich and highly relational content, we should not necessarily expect its disruption to impair memory for arbitrary word pairs (see also Bonnici et al., 2016, for results consistent with this view).

Despite some TMS and patient studies indicating a role of the AG for language comprehension (Hartwigsen et al., 2015; Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004), our results did not reveal any AG TMS effect in reading times. Rather, our findings align with previous evidence showing that TMS effects in speech comprehension are more likely to be observed under perceptually challenging conditions (Hartwigsen et al., 2015).

Taken together, our results are consistent with the proposal that the AG supports context-dependent processing of information (Branzi et al., 2020; Humphreys & Lambon Ralph, 2015, 2017). However, what is the nature of the processes reflected by AG activity during language tasks? Some researchers have proposed that the left AG (more specifically the core, posterior AG area associated with the default mode network and targeted in this study) might play a key role in semantic representation or, more specifically, event semantics (Binder & Desai, 2011; Binder, Desai, Graves, & Conant, 2009; Humphries et al., 2007). Others have argued that left AG may support on-line, automatic information buffering processes on content that is perceived or represented elsewhere in the brain (Humphreys & Lambon Ralph, 2015, 2017; Vilberg & Rugg, 2012). According to both proposals, this portion of the AG is positively engaged in semantic tasks, but only when these require some context-dependent processing (Branzi et al., 2020; Baldassano et al., 2017; Lerner, Honey, Silbert, & Hasson, 2011). However, the very same parietal region is commonly deactivated during semantic tasks that do not require such processes (Humphreys et al., 2015; Visser & Lambon Ralph, 2011), which is inconsistent with proposals that the AG underpins semantic representation or a more general role in semantic processing.

In considering the AG's function beyond semantic cognition alone, it is important to note that the left AG is positively activated by tasks requiring episodic processing (Tibon, Fuhrmann, Levy, Simons, & Henson, 2019; Ramanan et al., 2018; Rugg & King, 2018; Bonnici et al., 2016). One common aspect shared by the semantic context integration tasks (such as that probed in this study) and episodic memory tasks is that they both require on-line manipulation, retrieval, and integration of information (e.g., episodic details such as the contextual who, what, when, where, and why knowledge). Thus, it is possible to relate the left AG's core function to at least two mnemonic

mechanisms. One possibility is that the left AG is directly involved in the formation and representations of episodes (Ramanan et al., 2018; Bonnici et al., 2016; Shimamura, 2011). This hypothesis fits with findings showing that the left AG's activity is prominently observed at the end of an event, that is, when all the information has been already presented (e.g., Humphries et al., 2007). Alternatively, the left AG may buffer the combination of past information (episodically retrieved) with newly presented information to update the growing contextual meaning, as time unfolds. This hypothesis is consistent with both previous neuroimaging evidence (Branzi et al., 2020; Ramanan et al., 2018; Humphreys & Lambon Ralph, 2015, 2017; van der Linden et al., 2017; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005), and various neuropsychological findings (for a review, see Ramanan et al., 2018). In fact, patients with left AG lesions are not amnesic like patients with hippocampal lesions on standard source and associative memory paradigms. Rather, damage to the left AG seems mainly to diminish the confidence in recollection and the efficient on-line control of information (Simons, Peers, Mazuz, Berryhill, & Olson, 2010; Simons et al., 2008). This neuropsychological observation mirrors our finding that TMS on the left AG affects RTs, but not accuracy measures. Together, these results may suggest that disrupting the normal functioning of the left AG does not cause the key information to be lost (as per classical amnesia), but rather the formation of a less vivid and rich representation of a given episode, therefore making it less easy to retrieve (see also Yazar et al., 2014). Thus, our results seem to be more in line with the on-line buffering hypothesis, rather than with the possibility that AG reflects the coding and integration of this information per se (i.e., episodic and semantic representations might be coded in other regions, e.g., hippocampal regions and anterior temporal lobe, respectively). Of course, the left AG's role in on-line buffering of internal and external information sources would be a necessary precursor to the generation and the updating of context meaning, processing of the information in an episode, and so on.

Finally, in the memory task, we also observed slower RTs for LC Cue Target conditions as compared to HC Cue Target conditions. This result is consistent with previous studies showing that memory performance is affected by "event boundaries" (Swallow et al., 2009). In these studies, event boundaries were identified as changes in temporal, spatial, and personal dimensions in the course of information processing. To our knowledge, this is the first study to demonstrate that the same is true for "semantic boundaries" (i.e., a change of semantic context).

To conclude, our findings provide the first evidence of a causal role of the left AG in context-dependent integration of information and associative encoding during on-line naturalistic language processing. This result suggests that the AG role observed in previous studies (e.g., Branzi et al., 2020; Baldassano et al., 2017; Humphries et al., 2007) may be causally related to such processes. Future studies can

investigate whether the context-dependent processes supported by left AG during language tasks reflect domain-general buffering processes (Humphreys & Lambon Ralph, 2015, 2017) or formation of (semantic or/and episodic) representations per se.

Author Contributions

Francesca M. Branzi: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Validation; Visualization; Writing—Original draft; Writing—Review & editing. Gorana Pobric: Methodology; Resources; Supervision; Validation; Writing—Review & editing. JeYoung Jung: Investigation; Methodology; Validation; Writing—Review & editing. Matthew A. Lambon Ralph: Conceptualization; Funding acquisition; Project administration; Resources; Supervision; Writing—Original draft; Writing—Review & editing.

Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were M(an)/M = .408, W(oman)/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076

(Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

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