


DOI: <https://doi.org/10.1007/s00429-022-02512-y>

Brain Structure and Function
<https://doi.org/10.1007/s00429-022-02512-y>

REVIEW



Multiple functions of the angular gyrus at high temporal resolution

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Received: 17 January 2022 / Accepted: 22 May 2022

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Multiple functions of the angular gyrus at high temporal resolution

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Acknowledgement: This work was funded by Khalifa University's HEIC.

Keywords: angular gyrus, electroencephalography (EEG), magnetoencephalography (MEG), transcranial magnetic stimulation (TMS), transcranial electrical stimulation (TES).

ABSTRACT:

Here, the functions of the angular gyrus (AG) are evaluated in the light of current evidence from transcranial magnetic/electric stimulation (TMS/TES) and EEG/MEG studies. 65 TMS/TES and 52 EEG/MEG studies were examined in this review. TMS/TES literature points to a causal role in semantic processing, word and number processing, attention and visual search, self-guided movement, memory, and self-processing. EEG/MEG studies reported AG effects at latencies varying between 32 ms and 800 ms in a wide range of domains, with a high probability to detect an effect at 300-350 ms post-stimulus onset. A three-phase unifying model revolving around the process of sensemaking is then suggested: (1) early AG involvement in defining the current context, within the first 200 ms, with a bias toward the right hemisphere; (2) attention re-orientation and retrieval of relevant information within 200-500 ms; and (3) cross-modal integration at late latencies with a bias toward the left hemisphere. This sensemaking process can favour accuracy (e.g. for word and number processing) or plausibility (e.g. for comprehension and social cognition). Such functions of the AG depend on the status of other connected regions. The much-debated semantic role is also discussed: (1) there is a strong TMS/TES evidence for a causal semantic role, (2) current EEG/MEG evidence is however weak, but (3) the existing arguments against a semantic role for the AG are not strong. Some outstanding questions for future research are proposed. This review recognizes that cracking the role(s) of the AG in cognition is possible only when its exact contributions within the default mode network are teased apart.

Introduction:

Located in the posterior region of the inferior parietal lobule, the angular gyrus (AG) is part of the heteromodal parietal association cortex. fMRI/PET studies have provided valuable insights about the roles of the AG at high spatial resolution, with roles that vary with stimulus, task, context and AG subregion. Thanks to its rich connectivity, these roles run across diverse domains such as semantic processing, reading and comprehension, memory retrieval, mathematical cognition, spatial cognition, reasoning and social cognition; for review see (Seghier, 2013). Such diverse roles engage complex dynamic interactions within and across many brain networks at variable spatio-temporal scales. From this fMRI/PET literature, the AG emerged as “a cross-modal integrative hub that gives sense and meaning to an event within a contextualized environment, based on prior expectations and knowledge, and toward an intended action” (Seghier, 2013). A recent review stressed the critical role played by the AG in episodic and semantic memory thanks to its capacity to dynamically combine distinct forms of information, such as multiple sensory modalities or different spatiotemporal frameworks (Humphreys et al., 2021). In a recent multi-method investigation across different domains, left and right AG emerged as key region for social cognition (Numssen et al., 2021), with a strong involvement of the left AG in lexical decision. Previous reviews dedicated to the AG (Humphreys et al., 2021; Ramnan et al., 2018; Seghier, 2013) have evaluated current evidence from fMRI/PET or lesion studies, but these methods do not offer high temporal resolution to depict these roles at the millisecond level. Indeed, there are no published systematic reviews that specifically examined the role(s) of the AG at high temporal resolution. Hence, this brief review aims to appraise current evidence from EEG/MEG studies, irrespective of task or domain, to ultimately map the function(s) of the AG at the millisecond level. Other studies that used brain stimulation techniques such as transcranial magnetic stimulation (TMS) and transcranial electrical stimulation (TES) are also included here when they offer evidence for a *causal* role for the AG in different domains.

Different time windows for the AG involvement have been reported in current literature across a wide range of domains, which might point to distinct processes sustained by the AG at different latencies after stimulus onset. To illustrate the diversity of existing opinions when it comes to the role(s) of the AG at high temporal resolution, one can look at how the AG was encompassed in some models within the same domain. The language domain was selected here for this purpose, but the same conclusions hold if a different domain was selected instead. It is beyond the scope of this review to provide a comprehensive list of all existing language models, compare them, or examine their assumptions and predictive power, so the emphasis here was mainly put on what roles (if any) were typically assigned to the AG in these language models and at what time windows.

Since early work in the language domain, questions were raised about the “when” of AG’s involvement in different processes, with some groups reporting early involvement (around 200 ms) in object naming (Salmelin et al., 1994)), while others reported later effects (around 600 ms) in word processing (Halgren et al., 1994)). In an early anatomical model about picture naming, Levelt and colleagues (1998) suggested a multi-stage model with the following processes: computing a visual percept, activating an appropriate lexical concept, selecting the target word from the mental lexicon, phonological encoding, phonetic encoding, and initiation of articulation. Early activation was assigned to the right parietal (including the AG) at 150-275 ms for lemma selection (or most likely to the shifting of attention to the location of an expected object part or property), and a later activation in Wernicke’s area and the left AG at 275-400 ms for phonological encoding (Levelt et al., 1998). In an anatomical model about word production, the AG was not assigned any reliable role (cf. Figure 3 of (Indefrey and Levelt, 2004)), though the authors did not rule out a potential role in semantic interference between 200 ms and 400 ms (Indefrey and Levelt, 2004). In a recent model about semantic processing that relies on meaning-making mechanisms, Hagoort (2020) defined the AG as a conceptual hub (Hagoort, 2020) that predominantly interacts with the rest of the language system in the beta range (15–30 Hz) (Hagoort, 2020; Schoffelen et al., 2017). In another recent model about meaning composition, that is the ability to compose complex meanings from simpler representations, the AG was defined as an important region for argument structure representations at 200-250 ms (Pylkkanen, 2020). This specific role was placed between early visual word form recognition in the fusiform gyrus and later lexical access in middle temporal cortex at around 400 ms (Pylkkanen, 2020). An important role for the left AG in semantic processing at 300-550 ms, with the anterior temporal lobe, was also suggested in another model about visual word recognition (Carreiras et al., 2014).

There are however other models that do not suggest a role to the AG within the language system (Friederici, 2002; Friederici, 2011; Lau et al., 2008; Strijkers and Costa, 2016). The AG was disregarded in some of these models because different alternative brain regions were judged to be more relevant to language processing than the AG (e.g. (Friederici, 2011)), while other models explicitly examined current evidence about the role of the AG but found it to be weak or unreliable (e.g. (Lau et al., 2008)). For example, in her 2011 model, Friederici described a three-phase model of auditory language comprehension, spanning a time window between 100 ms to 600 ms (Friederici, 2011). The AG was disregarded and not assigned any reliable role in this model. Other regions were shown to be more likely involved in lexical-semantic integration at 400 ms (the superior temporal gyrus) and in sentence-level integration processes of syntactic and semantic information at 600 ms (the posterior superior temporal gyrus and the basal ganglia). The absence of a strong evidence for a (semantic) role for the AG (Friederici, 2011) was previously emphasised by Lau and colleagues in their account of the N400 component (Lau et al., 2008). The N400 is a negative-going potential that peaks around 400 ms post-stimulus onset (its latency can

vary between 250 and 550ms). It responds to a wide range of meaningful and potentially meaningful stimuli in different modalities (Kutas and Federmeier, 2011), including both linguistic and non-linguistic stimuli. Using the N400 as an index of lexico-semantic processing, Lau and colleagues suggested an involvement of posterior temporal regions in lexical access, and an involvement of the anterior temporal cortex and inferior frontal gyrus in lexical integration. The involvement of the left AG in semantic processing was mentioned as 'possible' but the evidence was 'not reliable' (cf. Table 1 of (Lau et al., 2008)). Moreover, in their retrieval-integration account of language comprehension (Brouwer et al., 2012), Brouwer and colleagues suggested the posterior middle temporal gyrus as the main source for the N400 component involved in retrieval of word meaning and the inferior frontal gyrus as a source of the P600 component involved in semantic integration (Brouwer and Hoeks, 2013). The P600 component is a positive-going deflection that peaks at 600ms after stimulus onset and lasts several hundred milliseconds. It is elicited by grammatical and syntactic anomalies (Gouvea et al., 2010), in both visual and auditory modalities, and can also be seen during semantic processing and integration (Shen et al., 2016). The authors however did not rule out a possible role of the AG in retrieval of conceptual event representations with an activity reflected in the N400 component (Brouwer and Hoeks, 2013).

These language models highlight at least two issues: (1) major differences in the level of importance given to the role(s) played by the AG, varying from none to critical, and (2) the diversity in time windows at which these roles might involve the AG. One can reasonably expect even wider differences when other domains are also examined. In this context, it was not possible to make sense of current (massive) EEG/MEG literature without being selective; hence, this review only considers studies that included source-level analyses with effects explicitly localized in the AG, irrespective of domain. Given the wide range of domains covered in this review, it was not possible to do justice to each domain. Each domain requires a systematic review that examines the potential role(s) of the AG within the research tradition of that particular domain, in the light of the connectivity that the AG entertains with the core nodes of that domain, and given the type of stimuli/tasks typically manipulated in that domain. Such domain-specific reviews are extremely important, but this review is not one of them. Rather, this review's scope is to unravel the different processes assigned to the AG in current EEG/MEG and TMS/TES literature, irrespective of domain. The identified roles of the AG are an emerging depiction as I go through the current literature.

This brief review is divided into six main sections. To help readers appreciate what to expect in each section, the following succinct statements describe the adopted review type for each section:

- (1) Section 1 provides an overview of the methodological choices made during the analysis of current EEG/MEG and TMS/TES literature. This section also provides succinct definitions of some key concepts used in the next sections.

- (2) Section 2 offers a scoping review to identify the wide range of roles assigned to the AG with TMS/TES. It examines the following (conditional) statement “if the AG is stimulated, then a change to task performance follows”. From this section, the reader will get a sense of the different *causal* roles assigned to the AG, irrespective of domain.
- (3) Section 3 presents a mapping review that charts the time windows of the AG involvement. It looks at the main roles and their corresponding latencies when a brain source is localised within the AG. From this section, the reader will appreciate the many roles assigned to the AG at different time windows, irrespective of domain.
- (4) Section 4 proposes a unifying model to account for findings from diverse domains. When current evidence is unreliable, prior knowledge from previous models is used (Seghier, 2013).
- (5) Section 5 is a critical review that appraises current evidence for (or against) a role of the AG in semantic processing.
- (6) Section 6 discusses a set of outstanding questions that warrant further investigations.

Section 1: Methodological and conceptual considerations about current literature

Some methodological choices are discussed in this section so that readers can appreciate the type of inferences one can or cannot make from current EEG/MEG and TMS/TES literature. This is because the reliability/accuracy of current evidence examined in this review is bounded by the reliability/accuracy of the methods used to generate that evidence. Given the poor spatial resolution of electrophysiological measurements, writing a review about a specific single brain region based on EEG/MEG studies is not a typical task one might undertake. Previous EEG/MEG reviews typically addressed questions about the dynamics of a given function at the millisecond level (e.g. word reading (Salmelin et al., 2000) or number processing (Hinault and Lemaire, 2016)), the meaning of a specific component (e.g. the meaning of the N400 (Kutas and Federmeier, 2011) or the P600 component (Bornkessel-Schlesewsky and Schlewsky, 2008)), neural oscillations (Prystauka and Lewis, 2019; Vassileiou et al., 2018), or brain waves asymmetry (Metzen et al., 2021; Vallesi, 2021). Reading EEG/MEG findings at a specific brain location (here the AG) brings its own challenges and limitations as discussed below.

The 10 central messages of Section 1 are succinctly summarised as follows: (1) in the majority of EEG/MEG and TMS/TES studies, AG effects were anatomically labelled as posterior/inferior parietal effects, and thus studies that did not explicitly mention the AG as a source or a target region were excluded; (2) there is a bias in the frequency of the use of the AG as an anatomical label across domains, with the AG being more often used as an anatomical label in language and number processing domains; (3) only studies on neurotypical adults were included if observed effects were reported in the form of time-locked-evoked or event-related potentials or magnetic

fields; (4) precise source localization within the AG might be hindered by many methodological issues; (5) the AG is a core node of the default mode network, a consistent finding that has major implications on some of the AG's functional proprieties; (6) the AG is often portrayed as a hub or a convergence zone in many studies, which has implications on its involvement in a wide range of domains; (7) different issues related to focality and mechanisms of action can complicate the interpretation of TMS/TES findings; (8) to assess causal brain-behaviour associations, a wide range of online/offline stimulation protocols were used in current TMS/TES literature; (9) there is a huge diversity in tasks and stimuli previously used in EEG/MEG and TMS/TES studies across many domains, and such differences can inevitably influence the exact timing of the involvement of the AG; (10) effects reported in current EEG/MEG studies were mainly based on reverse inference with a bias toward reporting positive effects. Each central message is further elaborated in the next paragraphs of this section.

Parietal versus AG effects: The first methodological choice concerns the inclusion/exclusion criteria for relevant studies. There is clearly a huge EEG/MEG (and TMS/TES) literature that reported effects in posterior parietal regions across many domains. Yet, in the majority of these studies, gross anatomical labels such as “posterior parietal” or “inferior parietal” were used. It was not possible to assign these parietal effects to the AG with high confidence for the following two reasons. First, the cortical volume of the AG in MNI space is on average $12.7 \pm 3.5 \text{ cm}^3$ and $13.6 \pm 2.7 \text{ cm}^3$ in the left and right hemisphere respectively (Wild et al., 2017), and this volume estimate represents a relatively smaller size than the volume of the supramarginal gyrus, making previous effects in the inferior parietal lobule difficult to assign to the AG with high confidence. Neighbouring inferior parietal regions can show different or even opposite effects (see a recent illustration with quadripulse TMS (Kaneko et al., 2020)), and hence it was important to not conflate contributions of neighbouring inferior parietal areas in this review. For example, TMS to both the AG and the supramarginal gyrus revealed a causal effect of the AG but not the supramarginal gyrus during number line representation (Gobel et al., 2001), whereas the reverse pattern was observed when making judgments about the mid-point of a horizontal line (Oliveri and Vallar, 2009). Second, it was not possible to make a precise anatomical definition on behalf of the original authors as this can run the risk of introducing my own interpretation (bias) when analysing current evidence. For instance, even when MNI coordinates were provided after a source-level analysis or in some EEG-fMRI studies, these studies were still excluded if the AG was not used by the original authors as a relevant anatomical label. Hence, only studies that explicitly mentioned the AG as a source that generated the scalp potentials measured noninvasively with EEG/MEG were examined in this review. Nevertheless, the absence of an explicit mention of the AG in some EEG/MEG studies that identified parietal sources cannot be taken as evidence for the absence of a role for the AG in a given process. The selected studies represented roughly around 10% of all potentially relevant papers; i.e. a search on PUBMED with

the query [“angular gyrus” AND (eeg OR meg)] retrieved a number of studies that was around 10% of the total papers retrieved with the query [(“posterior parietal” OR “inferior parietal”) AND (eeg OR meg)]. The selected 52 EEG/MEG studies that met the inclusion criteria are discussed in Section 3 below. The same criteria were applied to TMS/TES literature and 65 studies were selected accordingly.

Anatomical labelling of AG effects across domains: Another issue concerns the prevalence use of the anatomical label “temporo-parietal junction” in many EEG/MEG studies, in particular in the domain of social cognition. This region extends beyond a specific lobe and includes parts of the inferior parietal lobule, posterior temporal and superior occipital regions (see atlas-based labelling of different subregions of the temporo-parietal junction in (Schurz et al., 2017)). Studies that reported effects in temporo-parietal junction without mentioning the AG were also excluded because many neighbouring regions within the temporo-parietal junction might also be critical for similar domains that involve the AG (e.g. social cognition, semantic processing, self-processing), and hence it was important to not conflate these effects with AG. Perhaps most importantly, it is worth noting that, unsurprisingly, EEG/MEG studies followed the anatomical naming tradition of their respective domains, and this might yield inherent bias in the selection of relevant studies. For instance, because language processing was influenced in its early days by the work of Dejerine and Geschwind, the label angular gyrus was more often used in EEG/MEG studies about language than other domains. This was also the case for number and arithmetic processing given the widely adopted anatomical models of number processing that included the AG. Other domains such as attention, spatial processing and memory were keeping with the tradition of considering parietal regions as key anatomical labels without being specific about the AG as a key region. Consequently, this might have introduced a selection bias in terms of relevant EEG/MEG studies in this review. A systematic bibliometric analysis of current EEG/MEG literature (e.g. (Ismail and Karwowski, 2020; Yeung et al., 2017)) can estimate the size of the existing bias in the frequency of the use of the anatomical label ‘AG’ across domains, but this issue is beyond the scope of this review.

Imprecise localization of AG effects: In the same way, parietal effects in some EEG studies were reported in terms of electrodes/channels in the international 10–20 system (e.g. effects at P3 or Pz electrodes) or by referring to them as centro-parietal waveforms. This however does not offer an accurate spatial definition for effects in the AG. The estimation of the cortical projections of the international 10–20 system in MNI or Talairach space has an average standard deviation of 8 mm (Okamoto et al., 2004). This point has also implications for transcranial brain stimulation studies, given the variability in the exact definition of the AG across different atlases (Xiao et al., 2018) and its high inter-individual variability (Horvath et al., 2014). For example, according to a widely used definition, the AG with the supramarginal gyrus were localized at electrode TP3 (a location

between P3 and T3 electrodes) (Herwig et al., 2003) as P3 electrode was mainly assigned to other parietal areas not including the AG (Herwig et al., 2003). Incidentally, TP3 has the highest range of inter-individual variations of around 23 mm as compared to other locations (Herwig et al., 2003), which again shows the difficulty of assigning effects to the AG with high accuracy in previous EEG/MEG and TMS/TES studies.

Even when the AG was used as an anatomical label, the robustness of source localization in EEG/MEG can be hindered by many methodological issues, including the existing large variability between subjects in brain structure and function. For example, a source localization of the N400 component showed wide differences in cortical sources localization that vary with subject, task and model for sources reconstruction (Haan et al., 2000). Furthermore, there is a lack of consensus on how source localization should optimally be conducted (see discussion in (He et al., 2018a; Westner et al., 2022)). Source localization using current source density algorithms (e.g. sLORETA) may not accurately identify patterns that include multiple sources (Bradely 2016), thus high false positives and negatives are a big concern when multiple sources are expected as the case for many domains that implicate multi-region systems. Although source localization can be improved by using systems with a higher number of channels (e.g. high-density EEG) in combination with precise information of the head anatomy (Michel and Brunet, 2019; Song et al., 2015), high-density EEG devices (e.g. 256-channel systems) were not often used in the EEG literature about the AG.

A focus on time-locked evoked AG responses: This review mainly discussed effects reported in the form of time-locked-evoked or event-related potentials (ERPs) or magnetic fields. It does not appraise current findings about the synchronous neural oscillations (frequency bands or brain waves) measured with EEG/MEG (Lopes da Silva, 2013; Ward, 2003). There are many ERP components associated with different processes (for a comprehensive description of the different ERP components see (Luck and Kappenman, 2011)). The meaning of each component and the most likely processes that might give rise to each component can vary with domain (e.g. language (Beres, 2017; Dikker et al., 2020; Swaab et al., 2011) including key ERP components for semantics (Morgan et al., 2020), episodic memory (Wilding and Ranganath, 2011), attention (Hillyard and Anllo-Vento, 1998; Woodman, 2010), number processing (Hinault and Lemaire, 2016)). An illustration of relevant ERP components for each domain can be found elsewhere (cf. Table 1 in (Nelson and McCleery, 2008)). ERP components can show age-related differences (Mueller et al., 2008), hence studies that investigated developmental changes are excluded. This selective review only includes studies on neurotypical adults. Studies were also excluded if they were designed as intervention protocols; e.g. EEG studies that showed changes in the AG activation after mindfulness/zen sessions or with neurofeedback protocols were excluded.

The AG within the DMN: The AG is an important region of many networks, including language, number processing, semantic memory, social cognition, self-processing and attention. But there is one network that is frequently and consistently associated with the AG that is the default mode network (DMN), a fact that has major implications on some of the AG's functional proprieties. The DMN is a set of brain regions that are interconnected during rest and deactivated in attention-demanding tasks (Raichle et al., 2001). The AG is one of the posterior nodes of the DMN, displaying a rich functional connectivity with regions within and outside the DMN (Uddin et al., 2010; Yeo et al., 2011). Its core location within the DMN has probably facilitated its involvement in many domains, as the DMN is associated with a wide range of cognitive functions (Buckner et al., 2008; Spreng et al., 2009). Current fMRI literature has demonstrated a significant spatial heterogeneity of the DMN, with a reliable spatial fractionation of its nodes, including the AG. The existence of different AG subregions and their specific roles are not particularly emphasized in this review given the low spatial resolution of EEG/MEG and TMS/TES. Moreover, this review does not discuss current EEG/MEG findings about the DMN. There is indeed a large EEG/MEG literature about the DMN, but this literature is primarily concerned with DMN nodes' interactions within and across different frequency bands (Brookes et al., 2011; Knyazev et al., 2011) and with the association between spontaneous fMRI fluctuations and the power of EEG/MEG frequency bands (Neuner et al., 2014; Yuan et al., 2012). Furthermore, this DMN literature does not allow the roles of the AG to be straightforwardly identified in isolation from other DMN nodes. Here, the DMN is particularly discussed in Section 5 that examines the potential role of the AG in semantic processing.

Hubs and convergence zones. The roles of the AG cannot be identified in isolation but need to be understood in parallel with its interactions with other regions (Seghier, 2013). The structural/functional connectivity of the AG is not discussed here at length as this literature is mainly based on diffusion and functional MRI; for more details see (Bullock et al., 2019; Burks et al., 2017; Seghier, 2013; Uddin et al., 2010). The major white matter tracts that are relevant for explaining the involvement of the AG in diverse domains are mentioned in Section 4. The terms 'hub' and 'convergence zone' are also defined below, both have been linked to the AG. The concept of 'hub' is derived from graph theory analysis of brain networks and it refers to a brain region with a dense connection pattern, which is important for cross-modal integration (van den Heuvel and Sporns, 2013). Although different types of hubs exist in the brain (Gordon et al., 2018; Sporns et al., 2007; van den Heuvel and Sporns, 2013), here the term 'hub' is used in its broader sense to describe a brain region with high connectivity degree. Likewise, the term 'convergence zone' (Damasio, 1989; Damasio and Damasio, 1994) refers to a brain region that receives a disproportionately high level of information flow (Misic et al., 2014) to support multi-modal integration, a process that stores and binds together separate features (Binder and Desai, 2011;

Coutanche and Thompson-Schill, 2015). This concept of convergence zone was originally introduced in models about concepts creation and representation in the brain (Damasio, 1989).

Causality with TMS/TES: TMS/TES can address questions about causality beyond correlational brain-behaviour associations (Bergmann and Hartwigsen, 2021; Valero-Cabre et al., 2017). The induced electrical field strength in the target area can be directly related to behavioural effects, which provides particularly strong evidence for a causal role (Kuhnke et al., 2020a; Weise et al., 2020). TMS/TES studies were included in this review irrespective of their exact mechanism of action (excitation, facilitation, suppression, disinhibition...etc) (Hallett, 2007; Siebner et al., 2009; Yamada and Sumiyoshi, 2021). Both techniques are based on different neural mechanisms, with TMS can elicit action potentials (Sandrini et al., 2011), and anodal (cathodal) TES is typically assumed to modify membrane polarization to increase (decrease) cortical excitability (Nitsche and Paulus, 2000). A detailed comparison between TMS and TES across 22 different stimulation features can be found elsewhere (cf. Table 1 of (Valero-Cabre et al., 2017)). The induced effects might depend on the stimulation protocol, using either online (during the task) or offline (before the task) protocols. Online TMS can directly interfere with processing, whereas offline TMS can induce longer-lasting after-effects modulation of cortical excitability (Hartwigsen, 2016; Klomjai et al., 2015) and can yield large-scale network reorganization (Hartwigsen et al., 2017), rendering it difficult to assign a specific causal role to the stimulated area alone (Bergmann and Hartwigsen, 2021). Online single-pulse TMS can evoke a transient excitation followed by reduced activity (Romero et al., 2019), and can be delivered at different time intervals to elucidate the time course of a given process (Amassian et al., 1989; Pascual-Leone et al., 1999). Likewise, online repetitive TMS (rTMS) typically applies short bursts of high-frequency (5–20 Hz) or ultra-high frequency TMS (50Hz as in theta-burst stimulation protocols) delivered during specific time windows at which the stimulated brain region contributes to task execution (Valero-Cabre et al., 2017). TMS-induced effects can vary across individuals (Maeda et al., 2000) and they might depend on the targeted region's neurochemical state (Jung et al., 2022). Furthermore, TMS-induced effects on behaviour might depend on stimulation frequency as shown in a recent quantitative meta-analysis (Beynel et al., 2019).

The same issue applies to online and offline TES (Thair et al., 2017), with different behavioural effects might result from online versus offline stimulation (Pozdniakov et al., 2021; Zivanovic et al., 2021). Both TES variants are considered in this review, including transcranial alternating current stimulation (tACS) and transcranial direct current stimulation (tDCS), see review in (Thair et al., 2017; Woods et al., 2016). As the case for EEG/MEG, previous parietal TMS/TES studies did not always mention the AG as the exact targeted region; for an illustration of this issue, see Table 1 about TES-induced effects in (Klink et al., 2020). Beyond the issues of focality and mechanisms of action, the relevant empirical evidence sought here is that a significant change

in behaviour should follow stimulations over the AG, though the reliability of such stimulation-induced effects might be unclear, e.g. for TES see (Horvath et al., 2015). Indeed, inferences about stimulation-related causal effects are not always unequivocal because such causal effects can result from indirect network-induced (remote) effects (Herbscher and Voss, 2020; Hobot et al., 2020).

Low spatial resolution of TMS/TES: The induced field distribution by transcranial stimulation might depend on multiple stimulation parameters such as time, intensity and duration of stimulation (Lerner et al., 2021; Sandrini et al., 2011; Westwood and Romani, 2017; Yeh and Rose, 2019), which makes the location and size of the stimulated cortical areas difficult to define accurately (Karabanov et al., 2019; Laakso et al., 2018; Weise et al., 2020). TES has a low spatial resolution, rendering selective stimulation of the AG without concomitant stimulation of nearby areas extremely difficult, as evidenced by simulations and *in vivo* measurements (Saturnino et al., 2019; Wang et al., 2022). The spatial resolution of TMS (Deng et al., 2013) is generally higher than that of TES, but TMS over the AG can also often induce relatively high stimulation intensities in other nearby areas (Kuhnke et al., 2020a), as mentioned above. To elucidate the precise location, extent and magnitude of the TES/TMS-induced electrical field, computational simulations are particularly helpful in this context (Opitz et al., 2011; Thielscher et al., 2015). This issue of spatial resolution has many implications on the spatial sampling of the stimulation-induced effects on behaviour, see discussion about TMS in (Cattaneo, 2018). In this context, it was not possible to rule out that previous brain stimulation studies that targeted the AG, in particular with TES, might have induced electrical fields in neighbouring regions, including regions in the supramarginal gyrus, the posterior temporal cortex and the intraparietal sulcus.

Large variability in tasks and stimuli: Despite many existing guidelines on improving consistency and reproducibility in terms of conducting and reporting EEG/MEG experiments (e.g. (Gross et al., 2013; Keil et al., 2014; Pernet et al., 2020; Picton et al., 2000)), there is a huge variability (discrepancies) in current EEG/MEG literature. One example is the huge diversity in tasks previously used to implicate the AG, varying in terms of stimulus material, domain, modality, control condition, response type, and paradigm design. In the same way, differences in data acquisition and analysis procedures (Darvas et al., 2004; Puce and Hamalainen, 2017) are also present. A recent review identified more than 70 properties about design, data pre-processing, measurement, and statistics that can explain the lack of consistency across previous studies (Soskic et al., 2021). Such differences will inevitably yield differences in the exact timing and amplitude of ERP components and in the exact number and locations of brain sources. For instance, the spatiotemporal overlap between N400 and P600 components may change with baseline (Delogu et al., 2021), and the exact latency of the N400 component can vary with task and stimulus (Khateb et al., 2010). Here, emphasis was particularly put on consistent findings

and thus such inevitable methodological differences were ignored. Furthermore, some EEG/MEG studies might have used suboptimal (or invalid) inferences when examining the role of the AG; a recent critical evaluation of EEG/MEG studies listed some common ‘fallacies’ such as hasty generalization, inferring from group to individual, or inferring causality from correlation (Sinnott-Armstrong and Simmons, 2022). Such invalid inferences are likely present in current literature, and it was important to minimise their impact by focusing on the most frequently observed effects in the AG with the assumption that robustness and reliability would increase with repeatability across studies.

Reverse inference about AG effects: Numerous cognitive processes associated with the AG were reported in previous studies, mainly based on reverse inference. For instance, the AG has been shown to be involved in self-processing (Dor-Ziderman et al., 2016), action observation and execution (Sebastiani et al., 2014), attention modulation (Walz et al., 2014), perception of illusory movements (Casini et al., 2006), numerosity (Ishii et al., 2014; Salillas et al., 2019), faces and body parts perception (Meeren et al., 2013), and in bodily self-consciousness (Brechet et al., 2018). The logic of this type of reverse inference has been extensively discussed in fMRI literature, regarding its limitations (D’Esposito et al., 1998; Poldrack, 2006), its validity that depends on region and task setting (Hutzler, 2014), and its potential for answering questions about functional selectivity (e.g. (Costa et al., 2021)). The suboptimal use of reverse inference is considered as a major concern in existing EEG/MEG (Sinnott-Armstrong and Simmons, 2022), and it has implications on how to read current evidence for a given AG role. A typical example of this reverse inference can take this form: based on prior knowledge, if cognitive process X (or mental event) occurs, then a given brain event (ERP) Y occurs; in this study, the (ERP) event Y was observed with a source localised in the AG, therefore the cognitive process X has occurred and it is sustained by the AG. This type of inferences, though still widely used in current EEG/MEG studies, is logically invalid (i.e. a conditional statement and its converse are not equivalent). This concern motivates the inclusion of brain stimulation techniques TMS/TEM as well in this review in order to combine evidence from different techniques and to ultimately derive a reliable unifying model about the role(s) of the AG.

Bias toward positive AG effects: There are obviously many EEG/MEG and TMS/TES studies that did not find any significant effects in the AG when such effects were hypothesized or predicted a priori. For example, no significant role for the AG was identified for semantic memory (Martin and Chao, 2001), verb-argument combinations (Kim and Pyllkanen, 2021), color and form binding (Esterman et al., 2007), lexical integration (Lopopolo et al., 2021), idiomatic processing (Boulenger et al., 2012), semantic integration of gesture and speech (He et al., 2018b), thematic processing (Teige et al., 2019), semantic processing at the level of N400 (Kielar et al., 2015), syntactic manipulation (Matar et al., 2021), combinatorial processing (Pyllkanen et al., 2014),

associative memory encoding (Koen et al., 2018), visual tactile multisensory integration (Pasalar et al., 2010), and in adaptive behaviour in post-perturbation movement bias (Savoie et al., 2020). Studies that reported null/negative effects are not extensively discussed in this review as the main question addressed here concerns the most likely role(s) played by the AG when a significant positive effect was observed. This might skew evidence toward positive effects. Ideally, one could include all papers that tested a null hypothesis about a possible role for the AG. However, not all studies reported their findings as confirming or rejecting a formulated null hypothesis about the AG, with some effects in the AG were (or were not) observed in the absence of a clear theoretical background or prediction.

In sum, the methodological points highlighted above do not mean that current EEG/MEG literature cannot answer important questions about the role(s) of the AG. To the contrary, this literature brings another dimension about time, a dimension so often neglected in current literature about the role(s) of the AG in cognition that is dominated by fMRI/PET. As discussed previously (Hauk, 2016), there are many arguments that strongly favour or support the study of the brain at high temporal definition to unravel the different cognitive processes that occur very rapidly in the brain. One major advantage is the high sensitivity of EEG/MEG to subtle or early short-lived processes compared to fMRI; see examples in (Chen et al., 2013; Geukes et al., 2013). Another motivation concerns the possibility to assign different role(s) to the AG at different time windows. This possibility is extremely important because it can shed light on early versus late cognitive processes, with the possibility to elucidate how so many diverse cognitive domains rely on the AG.

Section 2: Causal role(s) evidenced by transcranial brain stimulation

This section offers a scoping review to examine current evidence for *causal* role(s) for the AG using brain stimulation techniques TMS and TES. The roles identified in current literature span a wide range of domains, including semantic processing, reading, episodic memory, number processing, attention in visual search, movement precision, and self-processing. The main findings of the selected sixty-five TMS/TES studies are succinctly summarised below according to their respective domains of interest. The main conclusions of the selected TMS/TES studies are briefly summarised in Table 1.

Table 1: TMS/TES studies that identified an effect after stimulation over the AG (listed alphabetically). rTMS: repetitive TMS; tACS: transcranial alternating current stimulation; tDCS: transcranial direct current stimulation.

Study	Stimulation modality	Stimulation site	Timing of stimulation [ms]	Main finding/role
(Baarbe et al., 2021)	Single-pulse TMS (conditioning stimulation)	Left and right AG	At 5ms/15ms for left/right AG before test stimulus	Righ AG is essential for goal-directed hand movements through interactions with left primary motor cortex.
(Bjoertomt et al., 2009)	Online rTMS (5 pulses at 20Hz)	Righ AG	At stimulus onset	TMS over the right AG caused subjects to report lines as being longer ipsilateral to the stimulation site, but only in near space.
(Block et al., 2013)	Offline rTMS	Right AG	---	AG stimulation affects the computation of the magnitude of visual and proprioceptive realignment based on visuoproprioceptive weight. The AG is critical for proprioceptive realignment.
(Bocca et al., 2015)	Online rTMS	Right AG	During the intertrial interval	AG stimulation increased the amplitude of the visual component evoked by the upcoming stimuli. The AG plays a causal role in the formation of combined expectancies to optimize visual search performance.
(Bonnici et al., 2018)	Offline rTMS	Left AG	---	AG stimulation resulted in a selective reduction in the free recall, but not cued recall, of autobiographical memories. The AG is critical for producing the subjective experience of remembering.
(Branzi et al., 2021)	Online TMS (5 pulses at 10Hz)	Left AG	500ms before 'target'	AG stimulation disrupted context-dependent integration during reading.

(Capotosto et al., 2014)	Offline rTMS	Left and right AG	---	The AG plays a causal role in the modulation of resting state alpha rhythms in the posterior cortical regions.
(Cattaneo et al., 2009)	Online TMS (3 pulses)	Left and right AG	Between the presentation of the prime and the target stimulus.	The AG plays plays a critical role in the allocation of visuospatial attention modulated by the mental number line.
(Chambers et al., 2007)	Single-pulse TMS (10Hz)	Right AG	At cue onset	The right AG is involved in reflexive spatial attention, which is critical for controlling perception and action.
(Coldea et al., 2021)	tACS	Left AG	---	Null effectst were reported, with no significant tACS modulation during an endogenous attention task.
(Costanzo et al., 2012)	Offline rTMS	Left AG	---	AG stimulation improved non-word reading accuracy. The AG has a prevalent role in grapheme-to-phoneme conversion.
(Croce et al., 2018)	Online rTMS (3 pulses)	Left AG	At cue onset	A causal involvement in the period that precedes a predictable event in semantic memory tasks.
(Croce et al., 2021)	Online rTMS (for 150ms duration)	Left AG	At cue onset	rTMS over left AG selectively suppressed a phonological-related microstate during semantic decision. The AG has a crucial role in semantic memory.
(Cummine et al., 2019)	Anodal and cathodal tDCS	Left AG	---	AG stimulation modulated reading aloud performance of words that varied in degree of mageability.
(Davey et al., 2015)	Offline TMS	Left AG	---	TMS to AG disrupted thematic judgments. The AG is critical for the efficient automatic

				retrieval of specific semantic information.
(de Boer et al., 2020)	tDCS	Right AG	---	There is causal relation between right AG and alterations in spatiotemporal self-location (perspective-taking). Self-identification can be decoupled from the bodily self.
(Douglas et al., 2015)	Anodal tDCS	Left AG	---	AG stimulation (plus primary motor cortex) altered the reported time of conscious movement intention during a self-generated movement task.
(Gallace et al., 2014)	Offline rTMS	Left and right AG	---	The AG plays an important role in sustaining and/or modulating lower level physiological functions such as thermoregulatory control.
(Gobel et al., 2001)	Online rTMS (5 pulses)	Left and right AG	Before stimulus onset	AG stimulation disrupted performance of a visuospatial search task, and also disrupted organization of the putative 'number line'.
(Gutierrez-Herrera et al., 2017)	Offline rTMS	Right AG	---	AG stimulation significantly increased reaction times for leftward internally-guided movements.
(Hamilton et al., 2013)	Offline rTMS	Right AG	---	AG stimulation induced more veridical visual perception on the sound-induced flash illusion task. The AG is important for audiovisual integration.
(Hartwigsen et al., 2015)	Online rTMS (5 pulses at 10Hz)	Left AG	At keyword onset	The left AG is causally relevant for the comprehension of degraded speech.
(Hartwigsen et al., 2016)	Offline rTMS	Left AG	---	Semantic decisions were impaired when (offline) rTMS to AG was combined with

				(online) rTMS to anterior inferior fontal gyrus.
{Heinen, 2011 #682	Online rTMS (3 pulses)	Right AG	90ms after target onset	AG stimulation selectively affected perceptual discrimination of right but not left visual targets.
(Hirayama et al., 2021)	Cathodal and anodal tDCS	Left and right AG	---	Anodal right AG and cathodal left AG significantly increased the probability of left-hand choice. The AG plays an important and asymmetrical role in hand-choice control.
(Hirnstein et al., 2011)	Offline rTMS	Left AG	---	The left AG is critical for left-right discrimination. It integrates spatial information with the meaning of the words 'left' and 'right'.
(Hopfinger et al., 2017)	tACS	Right AG	---	The right AG is important for the disengagement of attention, with endogenous and exogenous attention affected at gamma (40Hz) and alpha (10Hz) stimulation respectively.
(Jargow et al., 2021)	Offline rTMS	Right AG	---	AG stimulation led to increased activity in bilateral AG after stimulation, which was more pronounced in an on-task condition requiring active task performance.
(Kamke et al., 2012)	Offline rTMS	Right AG	---	AG stimulation selectively improved veridical perception of visual events under conditions that produce a robust flash illusion. The AG is involved in modulating the binding of visual and auditory stimuli in the sound-induced flash illusion.

(Khalighinejad and Haggard, 2015)	Anodal tDCS	Left and right AG	---	The left AG contributes to the sense of agency by monitoring the linkage of actions to outcomes. It plays a key role in the perceptual experience of agency.
(Koch et al., 2010)	Offline rTMS	Left and right AG	---	TMS revealed that left connectivity between the primary motor cortex and the AG is critical during early preparation of reaching and grasping movements only when the movement was made with a whole hand grasp towards contralateral objects.
(Koen et al., 2018)	Online rTMS (5 pulses)	Left AG	500ms after stimulus onset	AG stimulation during encoding did not reduce subsequent memory performance. AG stimulation however interfered with confidence judgments.
(Kuhnke et al., 2020a)	Online rTMS (4 pulses at 10Hz)	Left AG	100ms after word onset	AG stimulation selectively increased errors for action judgments on low sound–low action words. The AG is causally relevant for processing action but not sound knowledge.
(Kwon et al., 2022)	Offline rTMS	Left AG	---	AG stimulation selectively reduced the association between memory precision and self-referential reality monitoring decisions.
(Lifshitz-Ben-Basat and Mashal, 2021)	Anodal and cathodal tDCS	Left AG	---	Cathodal tDCS over the left AG had a beneficial effect for the generation of novel metaphors through restraining the control network.
(Longo et al., 2022)	Anodal and cathodal tDCS	Left and right AG	---	Both anodal and cathodal stimulation over left and right AG yielded slower reaction

				times during semantic categorization.
(Maurer et al., 2016)	Online rTMS (10 pulses)	Left and right AG	At stimulus onset	Right AG and the left AG are important for subtraction and multiplication tasks, respectively
(Montefinese et al., 2017)	Online rTMS (4 pulses)	Left and right AG	100ms after stimulus onset	Left and right AG are important for addition tasks, needed in verbal processing of numbers and in visuospatial attention processes, respectively.
(Muggleton et al., 2008)	Single-pulse TMS	Left and right AG	At target onset	TMS over right, but not left AG, decreased subjects' sensitivity during a conjunction visual search task.
(Nakano, 2017)	Offline TMS	Right AG	---	TMS to the right AG decreased the spontaneous eyeblink rate.
(Oliveira et al., 2010)	Single-pulse TMS	Left and right AG	100ms after the onset of the reach target	The AG has a causal role in decisions of hand choice.
(Oyachi and Ohtsuka, 1995)	Single-pulse TMS	Left and right AG	100ms after the offset of the central target	Right AG stimulation degraded accuracy of rightward and leftward memory-guided saccades in all subjects.
(Pergolizzi and Chua, 2015)	Anodal and cathodal tDCS	Left and right AG	---	The AG plays a causal role in episodic memory retrieval and can enhance subjective aspects of memory.
(Petitet et al., 2015)	Offline TMS	Right AG	---	The AG has a causal role in distributing visual attention across space.
(Pick and Lavidor, 2019)	Anodal and cathodal tDCS	Right AG		AG stimulation interrupted creative abilities and enhanced automatic abilities.
(Price et al., 2016)	Anodal tDCS	Left AG	---	Anodal stimulation to the left AG resulted in faster comprehension of semantically

				meaningful combinations relative to non-meaningful combinations. The AG has a causal role in the integration of lexical-semantic information.
(Rochas et al., 2014)	Online rTMS (3 pulses)	Left and right AG	50ms after stimulus onset	Early right AG stimulation affected emotional word processing.
(Rosenthal et al., 2009)	Offline rTMS	Right AG	---	AG stimulation abolished perceptual sequence learning. Training of covert attention to spatial locations led to probabilistic sequence learning, which was dependent on the right AG.
(Rusconi et al., 2005)	Offline rTMS	Left and right AG	---	Left AG stimulation disrupted tasks requiring access to the finger schema and number magnitude processing.
(Salatino et al., 2019)	Offline rTMS	Left and right AG	---	Right AG stimulation induced neglect-like bias during line length estimation.
(Schuhmann et al., 2019)	tACS	Left AG	---	10Hz tACS over the AG resulted in a greater leftward bias in reaction times during the endogenous attention task.
(Sestieri et al., 2013)	Online rTMS (150ms duration)	Left AG	At picture presentation onset	AG stimulation affects subjective aspects of source monitoring associated with the weighing of relevant retrieved information for source attribution. The AG is involved in episodic memory retrieval.
(Silvanto et al., 2009)	Online rTMS (3 pulses)	Left and right AG	---	The AG plays a critical role in exerting top-down modulation on occipital visual areas
(Sliwiska et al., 2015)	rTMS (5 pulses at 10Hz)	Left AG	First pulse at stimulus presentation; 4 pulses post-	Slow responses in reading tasks that focused attention on the meaning but not sounds of written words. AG stimulation

			stimulus presentation	slowed semantic, but not phonological judgements.
(Spitoni et al., 2013)	tDCS	Left and right AG	---	Right AG tDCS improved performance for tactile stimuli on the contralateral limbs. Right AG has a crucial role in the metric component of the body representation.
(Spitoni et al., 2021)	Anodal tDCS	Right AG	---	Right AG stimulation affected the discrimination of visual distances on the body. The right AG plays an important role in the processing of on-body and off-body distances in both visual and tactile modalities.
(Studer et al., 2014)	Offline rTMS	Left and right AG	---	The AG is involved in decision making when encoding of visuospatial representations of decision information is required.
(Taylor et al., 2011)	Online rTMS (5 pulses at 10Hz)	Right AG	2000ms after end of stimulus presentation	The right AG is critical in attentional reorienting mechanism, and this effect is modulated by the implicit memory of the previous trial.
(Thakral et al., 2017)	Offline rTMS	Left AG	---	AG stimulation reduced the number of internal (i.e., episodic) details produced. The AG is critical for both episodic simulation and episodic memory.
(Thakral et al., 2020)	Offline rTMS	Left AG	---	AG stimulation reduced the number of episodic details produced for the simulation task and reduced idea production on divergent thinking.
(Vesia et al., 2010)	Online rTMS (3 pulses)	Left and right AG	300-700 ms after target offset.	The AG is involved in the motor planning of both saccades and reach.

(Wynn et al., 2018)	Offline rTMS	Left AG	---	The AG is involved in familiarity and subjectively perceived memory confidence, but not in recollection.
(Yazar et al., 2014)	rTMS (3 pulses at 50Hz)	Left AG	After study phase	AG stimulation yielded recollection confidence reduction. There is a causal relationship between the AG and source recollection confidence.
(Yazar et al., 2017)	rTMS (3 pulses at 50Hz)	Left AG	After phase trials	AG stimulation reduced participants' ability to perform memory judgments that required the integration of auditory and visual information.
(Zou and Kwok, 2022)	Offline rTMS	Left AG	---	The AG is causally involved in gauging the vividness, but not the confidence, of memory.

Semantic and word processing. Using high-definition tDCS to a functionally defined left AG, anodal stimulation resulted in faster comprehension of semantically meaningful combinations relative to non-meaningful combinations (i.e. combinatorial semantic processing), suggesting a causal role of the left AG in the integration of lexical-semantic information (Price et al., 2016). In a recent study on 72 subjects, both anodal and cathodal tDCS yielded slow reaction times when left and right AG were stimulated during a semantic categorization task (Longo et al., 2022). Another TMS study with a semantic decision task revealed a causal role of the AG in semantic processing (Hartwigsen et al., 2016) but the functional significance of this role within the semantic system depended on the functional integrity of the anterior inferior frontal gyrus (Hartwigsen et al., 2016). TMS over the left AG interfered with performance during a semantic decision task (Croce et al., 2021) and during the automatic retrieval of specific concepts from the semantic store (Davey et al., 2015), suggesting a causal role of the AG in semantic processing and in automatic semantic retrieval (Croce et al., 2021; Davey et al., 2015). Overall, brain stimulation studies seem to support a critical role of the AG in semantic processing (see also review in (Joyal and Fecteau, 2016)).

TMS over the left AG disrupted context-dependent integration during reading, suggesting a causal role in on-line context-dependent integration during language processing (Branzi et al.,

2021). TMS to the left AG, during reading tasks that focused attention on either the meaning or sounds of written words, selectively slowed responses in the meaning but not sound task (Sliwinska et al., 2015). The left AG showed causal role in grapheme-to-phoneme conversion, in particular in non-word reading (Costanzo et al., 2012), and tDCS over the same region modulated reading performance in subjects who read aloud words that varied in the degree of imageability (Cummine et al., 2019). Current TMS/TES literature points to a causal role of left AG in word reading (see recent review in (Arrington et al., 2022; Turker and Hartwigsen, 2021)). Although a critical role of the left AG for speech comprehension was not identified as reliable in a previous review of brain stimulation studies (Zoefel and Davis, 2017), the AG might have a critical role in facilitating speech comprehension in challenging listening conditions (Hartwigsen et al., 2015). Regarding the right AG, a previous TMS study reported a critical role in emotional word processing (Rochas et al., 2014).

Memory and information retrieval. TMS over the left AG demonstrated a critical role in both episodic simulation and episodic memory (Thakral et al., 2017), with a significant effect on the predictability of events in semantic memory tasks (Croce et al., 2018), though such effects observed could have emerged from other network-wide TMS effects (Herbscher and Voss, 2020). A causal role in episodic memory retrieval and in enhancing subjective aspects of memory was shown with both tDCS (Pergolizzi and Chua, 2015) and TMS (Sestieri et al., 2013). In a study that tested free and cued recall of autobiographical memories and word-pair memories, TMS over the AG resulted in a selective reduction in the free recall, but not cued recall, of autobiographical memories (Bonnici et al., 2018). The authors suggested that the AG has a causal role in the integration of memory features in a way that enables the subjective experience of remembering events from personal pasts (Bonnici et al., 2018). The ability to retrieve context features across multiple modalities (Yazar et al., 2017) and recollection confidence (Yazar et al., 2014) were significantly reduced during TMS over the left AG, suggesting that the left AG is necessary for the multimodal integration of episodic features into a unified conscious representation that enables the experience of remembering (Yazar et al., 2017). During tasks that tap into processing action and sound features of concepts, TMS over the left dorsal AG decreased performance on action but not sound judgments, suggesting a causal role of the left AG for the retrieval of action knowledge but not sound knowledge (Kuhnke et al., 2020a), a finding that might challenge the position of the left AG as a multimodal conceptual hub.

There are however other TMS studies that did not identify a causal role for the left AG in memory and information retrieval. For instance, TMS over the left AG did not interfere with episodic retrieval (Koen et al., 2018), affect recollection (Wynn et al., 2018), and with assessment of memory confidence (Zou and Kwok, 2022). These three studies suggested alternative roles for the left AG in encoding processes in subjective mnemonic experience (Koen et al., 2018), in improving both

familiarity and the subjectively perceived confidence in participants with low baseline memory recognition (Wynn et al., 2018), and in gauging the vividness of memory (Zou and Kwok, 2022). Indeed, there is still a debate about the exact causal role of the left AG in the successful execution of memory-based tasks in previous TMS/TES studies. I also note that almost all previous studies were concerned with the role of the AG in the left hemisphere, but this cannot rule out a possible role of the right AG as this region was not often stimulated in previous TMS/TES memory studies.

Attention and visual search. There is a large body of research that investigated the involvement of the AG in attention. TMS studies suggested a causal role of the right AG in attentional control (Heinen et al., 2011; Silvanto et al., 2009), in visual attention across space (Petitet et al., 2015), in attentional reorienting mechanisms (Taylor et al., 2011), and in mediating reflexive shifts of attention within and between sensory modalities (Chambers et al., 2007). Using tACS, the right AG was shown to be critically important for the disengagement of endogenous attention (Hopfinger et al., 2017), though this effect might not be significant in exogenous (stimulus-driven) attention (Schuhmann et al., 2019) (but see (Coldea et al., 2021)). In tasks that involve conflict resolution (e.g. the Simon, the Flanker and the Stroop task), there is evidence from previous TMS studies for a causal role of the right AG in mediating the allocation of spatial attention and orienting during the control of attention (see also review in (Olk et al., 2015)). TMS over the right AG revealed a causal role in visual search, in particular in the formation of combined expectancies binding together stimulus- and response-characteristics that can optimize visual search performance (Bocca et al., 2015). TMS over the right AG disrupted the ability to search for a target defined by a conjunction of features (Muggleton et al., 2008), and also affected decision-making when visuospatial attention is required (Studer et al., 2014), suggesting that the AG might contribute to perceptual decision-making by guiding attention to relevant information in the visual environment (Studer et al., 2014). What emerges from these studies is a causal role of the AG, in particular in the right hemisphere, in attention control to guide search for relevant information irrespective of the type of the latter.

Agency and self-processing. A causal association between right AG and alterations in spatiotemporal self-location (i.e. perspective-taking) was identified (de Boer et al., 2020) in a tDCS experiment with a full-body illusion paradigm, a paradigm used to disentangle between endogenous versus exogenous attention in self-identification processes. In body-space representation, tDCS revealed a crucial role of the right AG in the metric component of the body representation (Spitoni et al., 2013), in the perceptual experience of agency (Khalighinejad and Haggard, 2015), and in 'near-space' visuospatial processing (Bjoertomt et al., 2009). TMS over the left AG showed a critical involvement of the left AG in left-right discrimination (Hirnstein et al., 2011). Stimulation of the AG selectively reduced the association between memory precision and self-referential reality monitoring decisions, suggesting a causal role in filling remembered

experiences with a sense of self-agency (Kwon et al., 2022). In this domain, many studies showed a particular role of the inferior parietal lobule, including the AG, in the definition of the boundaries of our bodies and in the integration and comparison of sensorimotor information flows to correctly attribute movements agency (for review see (Crivelli and Balconi, 2017)).

Self-guided movement. One of the first TMS studies reported a causal role for the right AG in the control of memory-guided saccades, and showed that the superior part of the right AG is causally involved in maintaining spatial accuracy of remembered target locations of memory-guided saccades (Oyachi and Ohtsuka, 1995). The right AG is crucial for controlling the generation of spontaneous eyeblinks in humans (Nakano, 2017), and during the execution of internally-guided movements (Gutierrez-Herrera et al., 2017). The right AG is critical in planning the reach vector for a specific hand (Vesia et al., 2010), in the early preparation of reaching and grasping movements (Koch et al., 2010), in perceptual (motor) sequence learning (Rosenthal et al., 2009) and in goal-directed hand movements (Baarbe et al., 2021). The AG might also play a critical role in movement precision, in particular to mediate the interaction between visuo-proprioceptive weighting (i.e. contribution of each modality in sensory integration) and realignment (i.e. recalibrating the estimates given by mono-sensory inputs) (Block et al., 2013). The right AG is critical for processing tactile metricity on the body, suggesting the AG as a supramodal comparator of quantities (Spitoni et al., 2021). The left AG has been shown to have a causal role in selecting which hand to use when making a unimanual reach (Hirayama et al., 2021; Oliveira et al., 2010) and in modulating conscious movement intention in the context of self-generated movement (Douglas et al., 2015).

Number processing. Early TMS work reported a causal role of the right AG in spatial representation of numbers (Gobel et al., 2001). Bilateral AG has a casual role in shifting visuospatial attention, for instance when mentally organizing numbers along a left-to-right oriented horizontal mental number line (Cattaneo et al., 2009). TMS over the left AG disrupted tasks requiring access to the finger schema (e.g. during counting with fingers) and number magnitude processing (Rusconi et al., 2005), with greater role for the left AG in verbal processing of numbers and a greater role of the right AG in visuospatial attention processes during arithmetic addition (Montefinese et al., 2017). A high error rate was induced by TMS over the right AG and the left AG during subtraction and multiplication tasks respectively (Maurer et al., 2016); for a recent review about the AG's involvement in numerical cognition with TMS see (Garcia-Sanz et al., 2022).

Other domains. There are other causal roles assigned to the AG beyond the domains mentioned above, though the effects of stimulation revealed complex dynamics (e.g. see (Jargow et al., 2021)). For example, brain stimulation over the left AG disrupted the ability to generate metaphors (Lifshitz-Ben-Basat and Mashal, 2021), and severely affected idea production during divergent

thinking (Thakral et al., 2020) and automatic thinking (Pick and Lavidor, 2019). Given the role of the AG in the default mode network, it has been suggested that the AG plays a causal role in the modulation of dominant low-frequency alpha rhythms during rest (Capotosto et al., 2014). Thanks to its role in multimodal integration, the AG has shown to play a causal role in the emergence of many illusory effects including illusory depth perception (Salatino et al., 2019) and other illusory phenomena that depend on the integration of auditory and visual information (Hamilton et al., 2013; Kamke et al., 2012). Last but not least, TMS over the AG disrupted homeostatic control (Gallace et al., 2014), suggesting a potential role beyond classic cognitive processes.

Discussion of Section 2: Previous TMS/TES studies have demonstrated a significant change in task performance in many domains after stimulation over the AG, providing strong evidence for multiple and apparently distinct roles played by the AG. The current TMS/TES evidence has some potential biases, considering the methodological limitations discussed in Section 1. In particular, the stimulation-induced change to task performance can alternatively result from other unspecific remote effects in regions beyond the exact targeted stimulation site within the AG, as stimulation-induced effects can propagate to neighbouring and distant connected regions (Clemens et al., 2014; Hebscher and Voss, 2020). This begs the question of how confident can one be that the AG is causally involved in all these domains? If we take the example of the causal role of the AG in self-guided movement, some of the reported effects can be explained to some extent by the spread or leakage of the TMS/TES-induced electrical field to nearby action-related areas in the supramarginal gyrus and the intraparietal sulcus (Culham and Valyear, 2006; Johnson-Frey, 2004; Turella and Lingnau, 2014). The same issue applies to the AG's role in attention and visual search, with stimulation-induced effects in neighbouring parietal regions might explain the observed behavioural changes (Rushworth et al., 2001; Wojciulik and Kanwisher, 1999). Furthermore, other TMS studies have stressed the importance of looking at causal role(s) for the AG in combination with the contribution of other critical regions, for instance frontal regions in visual search (Ellison et al., 2014) and semantic processing (Hartwigsen et al., 2016), and primary motor cortices in goal-directed hand movement intention and preparation (Baarbe et al., 2021; Douglas et al., 2015; Koch et al., 2010).

Overall, there is a strong evidence in current TMS/TES literature for diverse *causal* role(s) of the AG in cognition: the left AG is most likely involved in semantic processing, word processing, and information retrieval, whereas the right AG is most likely involved in attentional control and reorientation, self-processing, and during the processing of internally-guided movements. What is missing in this literature is a systematic investigation of the timing of the AG's involvement, using for instance chronometric TMS protocols. By varying the timing of stimulation in online TMS protocols, one can reveal the critical time windows at which stimulation over the AG might

produce a measurable behavioural effect. As detailed in Table 1, for single-pulse TMS studies, mainly with motor and visual search tasks, stimulation was typically delivered 50-100 ms after stimulus onset. With repetitive TMS, 3-10 pulses were delivered at different time windows that depended on the specific design of the task of interest (e.g. varying with the presentation onset of cues, inter-trial intervals or target stimuli). In these online rTMS studies, the stimulation over the AG typically continued for a duration of 500 ms, which does not allow an attribution of specific processes to the AG at high temporal definition. Therefore, the next Section 3 aims to look specifically at this critical issue of timing in current EEG/MEG literature.

Section 3: AG activations at different time windows with EEG/MEG

This section describes current evidence about the most likely time windows at which an activation in the AG might be observed. Fifty-two EEG/MEG studies, published between 1994 and 2022, were included (as detailed in Table 2). Those selected 52 studies satisfied the different criteria as discussed above (i.e. an effect explicitly localized in the AG, identified with source localization in neurotypical adults). Around 70% of EEG/MEG studies reported an effect in the left AG, 20% in the right AG, and 10% reported bilateral effects, though this bias toward the left hemisphere can be explained by the fact that more than half of EEG/MEG studies of Table 2 used language tasks. MEG studies were more likely to report an early effect in the AG than EEG studies. Figure 1 summarizes the likelihood, across EEG/MEG studies, for an effect in the AG to be observed at a given time window. This was done by estimating a histogram of all latencies (Table 2) at which a source was identified in the AG, irrespective of domain. The histogram indicated a probability of 20% of observing an effect in the AG within the first 200 ms after stimulus onset, irrespective of domain. This probability increased to 65% to detect an effect in the interval 200-500 ms. Late effects in the AG after 500 ms were not frequently observed (with a small relative frequency of 15%). Interestingly, the highest likelihood to observe an effect in the left AG was within the time interval 300-350 ms (Figure 1). Ideally, a more accurate comparison of latencies should be generated for each domain separately, following a detailed analysis of the individual tasks/stimuli and a proper definition of the zero line. However, for some domains (e.g. self-processing, social cognition), only very few EEG/MEG studies are available, which makes domain-specific comparison of latencies not meaningful.

Figure 1: A histogram of all latencies reported in previous EEG/MEG of Table 1 with a source localized in the AG. Latencies are calculated across studies for the left (top plot) and right (bottom plot) AG (bin width = 10 ms).

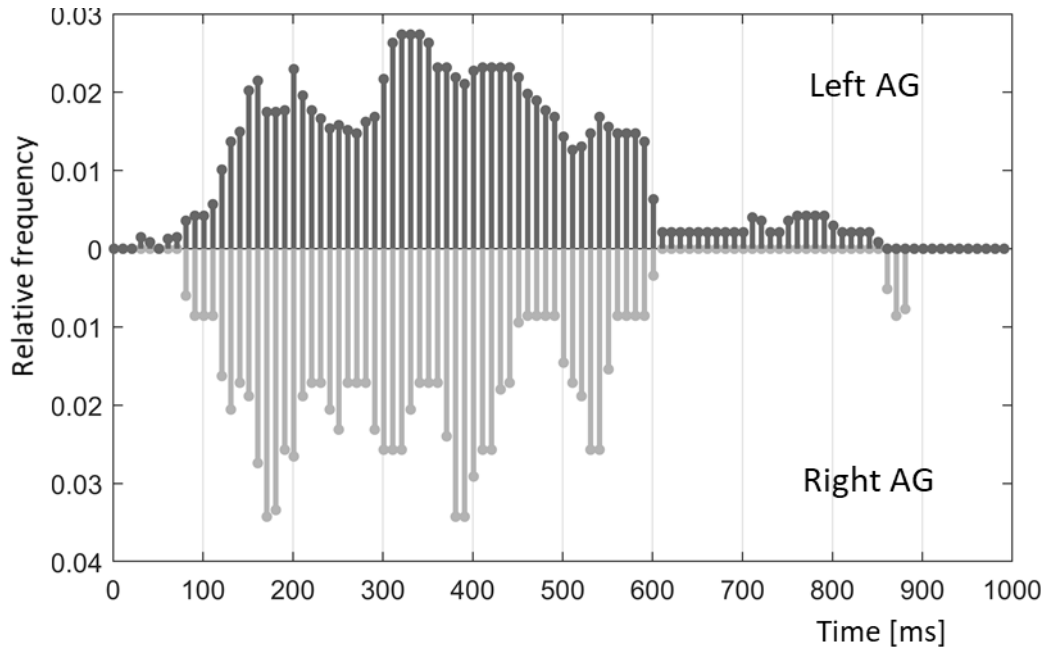


Table 2: EEG/MEG studies that identified an effect in the AG (listed alphabetically).

Study	Imaging modality	Hemisphere	Latency [ms]	Main effect/role
(Ala-Salomäki et al., 2021)	MEG	Left AG	200-600	identification and semantic processing of an object
(Arcara et al., 2021)	MEG	Left AG	300	higher activations for fast than slow responses during a simple single-digit multiplication production task
(Arcara et al., 2021)	MEG	Right AG	500-600	high responses for fast than slow responses in the delta band during multiplication tasks
(Astesano et al., 2004)	EEG	Left AG	800	comparing prosodically congruous versus incongruous sentences in French
(Bayer et al., 2018)	EEG	Left AG	150-220	affective categorization of faces during congruent trials (word matched the facial expression)

(Bemis and Pylkkanen, 2012)	MEG	Left AG	110-460	linguistic coding of numeric stimuli with no dissociation between combinatorial tasks
(Bemis and Pylkkanen, 2013)	MEG	Left AG	537-591	significant combinatorial activity in the auditory modality (with a marginal effect in the visual modality)
(Bendixen et al., 2014)	EEG	Left AG	125-165	implication in predictive mechanisms that support spoken word recognition
(Bermudez-Margaretto et al., 2020a)	EEG	Left AG	300-500	higher activations for novel than known written words
(Bermudez-Margaretto et al., 2020b)	EEG	Right AG	373-550	strong effects during the processing of novel written word-forms
(Bernstein et al., 2008)	EEG	Left AG	160	audiovisual speech integration
(Boulenger et al., 2012)	MEG	Left AG	180	silent reading of sentences
(Bowyer et al., 2004)	MEG	Left AG	239	verb generation
(Carreiras et al., 2015)	MEG	Right AG	120-130	higher evoked responses for numbers than symbols
(Carreiras et al., 2015)	MEG	Left AG	120-130	significant effect for words and pseudowords compared to symbols
(Casini et al., 2006)	MEG	Left AG	400	perception of illusory hand movements elicited by tendon vibration
(Casini et al., 2008)	MEG	Left AG	400-800	similar responses to both fast and slow of illusory hand movement
(Cebolla et al., 2014)	EEG	Bilateral AG	32	proprioceptive processing and more complex body-action representations, by enhancing in a top-down fashion the N30 component of the somatosensory evoked potential
(Dirani and Pylkkanen, 2020)	MEG	Left AG	310-380	semantic facilitation in object naming tasks

(Egorova et al., 2014)	MEG	Left AG	<200	access to referential semantic knowledge during naming
(Farahibozorg et al., 2022)	EEG-MEG	Left AG	0-450	The AG supports semantic connectivity at later stages of word processing.
(Flick et al., 2021)	MEG	Left AG	300-600	significant contribution to adjective-noun composition
(Gow et al., 2008)	MEG/EEG	Left AG	280-480	involved in sublexical phonological representation during the categorization of perceptually ambiguous speech sounds
(Granda et al., 2021)	EEG	Right AG	290-330	manipulation of rotated hands; significant role in the spatial transformation of mental images
(Jost et al., 2011)	EEG	Left AG	-	fact retrieval during simple arithmetic calculations
(Kocagoncu et al., 2017)	MEG	Left AG	-	semantic competition in speech comprehension
(Kropotov and Ponomarev, 2009)	EEG	Left AG	200	involvement in GO/NOGO tasks
(Lewis et al., 2015)	MEG	Left AG	309-355	thematic processing, but also involvement in taxonomic processing.
(Lyu et al., 2019)	MEG	Left AG	120	support integration of the meanings of successive spoken words in an utterance
(Matar et al., 2021)	MEG	Left AG	188-207 708-723	sensitivity to noun definiteness (early window) sensitivity to syntax complexity (late window)
(Matar et al., 2021)	MEG	Right AG	861-885	sensitivity to adjective form typicality and definiteness
(Meeren et al., 2013)	MEG	Left AG	120-180 200-300	sensitivity to faces (early window) sensitivity to body parts (later window)

(Paoletti et al., 2019)	MEG	Bilateral	-500-0	pre-stimulus AG activity predicted oculomotor accuracy for trials with fast saccadic reaction times
(Proverbio and Adorni, 2008)	EEG	Left AG	300-350	grapheme to phoneme conversion
(Proverbio and Carminati, 2019)	EEG	Left AG	300	significant differences between correct and incorrect solutions when combined finger/number processing
(Proverbio et al., 2020)	EEG	Right AG	155-185	significant effect during the comparison between multidigit numbers presented in digits or verbal format; spatial processing to support early numerosity processing
(Rahimi et al., 2022)	EEG/MEG	Left AG	60-65	task differences between lexical and semantic decision tasks
(Robinson et al., 2020)	MEG	Left AG	146–237	greater activation to violated expectations relating to head orientation than to face identity
(Robinson et al., 2020)	MEG	Right AG	166–447	greater activation to violated expectations about face identity than to violated expectations about head orientation
(Rochas et al., 2014)	EEG	Right AG	132-156	Greater activation for emotional words than for neutral words, for words presented in the left visual field.
(Roll et al., 2017)	EEG	Left AG	136–204	pre-activation of morphemes and words in speech perception
(Salillas et al., 2019)	MEG	Right AG	80-160	part of a magnitude system for the estimation of duration during the processing of time.
(Salillas et al., 2019)	MEG	Left AG	80-160	numerical magnitudes processing
(Salmelin et al., 1994)	MEG	Bilateral	200-400	significant effects during picture naming
(Sebastiani et al., 2014)	MEG	Bilateral	125-208	action observation and execution

(Sekiguchi et al., 2001)	MEG	Left AG	300-500	repetition-induced reduction of activations for words but not nonwords
(Sel et al., 2015)	EEG	Right AG	160-200	integration of multimodal information, showing how one's facial expression of happiness significantly modulated the cortical responses to other's facial expressions
(Tomasello et al., 2019)	EEG	Left AG	192–232	pragmatic processing of hand gestures and their interaction with spoken language
(Vandewouw et al., 2021)	MEG	Left AG	259-300	implicated in emotion regulation and attention, as it was activated more during inhibition compared to vigilance when viewing angry faces
(Walz et al., 2014)	EEG	Bilateral	525-550	modulation of focused attention during visual oddball tasks
(Williams et al., 2017)	MEG	Left AG	170-260	sensitive to relationality in the linguistic domain, with no significant effect in event representation or combinatorial context
(Xiang et al., 2004)	MEG	Bilateral	248	significant effect when comparing between reversed words and normally oriented words
(Yamanoi et al., 2006)	EEG	Left AG	350-600	phonological processing during the recognition of Hiragana characters
(Yamanoi et al., 2014)	EEG	Right AG	373-427	recalling the names of body parts (line drawings)
(Zhang et al., 2020a)	EEG	Left AG	300-600	source of P300 component during visual search and attention control
(Ziegler and Pykkänen, 2016)	MEG	Left AG	400-600	semantic composition, showing an increased activation for intersective modification of low-specificity nouns over their non-compositional one-word controls

AG involvement in the first 200ms. One surprising observation is the involvement of the AG at very early latencies (cf. Table 2 and Figure 1) within the first 200 ms post-stimulus presentation. For example, during duration (time) processing, MEG effects were observed in the right AG as early as 80-160 ms (Salillas et al., 2019), and a difference between lexical and semantic decision tasks was observed in the left AG as early as 60 ms (Rahimi et al., 2022). These early activations were observed for different stimulus types including words, faces, and numbers (Bayer et al., 2018; Bemis and Pylkkanen, 2012; Boulenger et al., 2012; Carreiras et al., 2015; Meeren et al., 2013; Proverbio et al., 2020; Rochas et al., 2014; Sel et al., 2015). Some of the features that induced early activations included sensitivity to number magnitude (Salillas et al., 2019), time duration (Salillas et al., 2019), word form (Carreiras et al., 2015), morphemes (Roll et al., 2017), and face identity (Meeren et al., 2013; Robinson et al., 2020). The main cognitive processes reported at early latencies included multimodal integration (Bernstein et al., 2008; Sel et al., 2015), action observation (Sebastiani et al., 2014), emotional content processing (Rochas et al., 2014), proprioceptive processing in body-action representations (Cebolla et al., 2014), integration of meaning (Lyu et al., 2019), spatial processing in numerosity (Proverbio et al., 2020), pragmatic processing of hand gestures (Tomasello et al., 2019), and access to referential semantic knowledge (Egorova et al., 2014).

AG involvement within 200-500ms. Perhaps the most frequent effects in the AG were observed between 200-500ms (reported in two thirds of previous EEG/MEG studies, Figure 1). This intermediate time window includes some important ERP components that have been associated with the AG in some studies, in particular the N400 component. The most common stimuli that yield strong effects in this window are written words, pictures of objects, numbers and speech sounds (Ala-Salomäki et al., 2021; Arcara et al., 2021; Bermudez-Margaretto et al., 2020b; Dirani and Pylkkanen, 2020; Gow et al., 2008; Lewis et al., 2015; Salmelin et al., 1994; Sekiguchi et al., 2001). Other stimuli such as body parts, including hands, fingers and faces, have also been shown to involve the AG within this time window (e.g. (Granda et al., 2021; Meeren et al., 2013; Proverbio and Carminati, 2019; Vandewouw et al., 2021; Yamanoi et al., 2014)). The processes that might occur within this window are object identification, thematic processing, semantic facilitation and composition, phonological processing, novel word acquisition, spatial transformation of mental images, and attention control (Table 2). The most frequent process within this window is semantic processing (Ala-Salomäki et al., 2021; Dirani and Pylkkanen, 2020; Lewis et al., 2015; Ziegler and Pylkkanen, 2016), and this might support the idea of the AG being one of the sources that generate the N400 component when semantic information is manipulated (Kutas and Federmeier, 2011).

AG involvement after 500ms. Sources in the AG at late time windows (>500 ms after stimulus onset) were also observed for processes that include attention modulation, combinatorial processing and sentence-level processing (Astesano et al., 2004; Bemis and Pylkkanen, 2013;

Matar et al., 2021; Walz et al., 2014). Not many studies reported effect in the AG after 500ms but this does not constitute an evidence for an absent role of the AG at later latencies. Late time windows (600-1000 ms) for instance were not always submitted to source-level analyses. Parietal regions were identified in some EEG/MEG studies with source localization at such late latencies, but the AG was not explicitly mentioned as a source for these effects.

Discussion of Section 3: The current EEG/MEG literature revealed an involvement of the AG in diverse domains, in both left and right hemisphere, but at variable time windows varying from 32ms to 800ms (Table 2), though onsets and offsets of such effects need to be interpreted with caution (Sassenhagen and Draschkow, 2019). The meaning of a given latency might vary with task and stimulus. For example, an effect at 200 ms might be classified as early for a complex integration process or as late for the detection of a salient low-level visual feature. The question of the involvement of the AG at either early or late latencies in some domains is still an ongoing debate. Regarding early involvement, evidence for modulation of early ERP components within the first 200ms is generally considered weak (see systematic review in (Nieuwland, 2019)), because such early effects are typically small or highly variable across studies as they tend to strongly vary with task and stimulus (Pulvermüller et al., 2009). For instance, an early involvement of the right AG at 140ms during a visuomotor adaptation task (Savoie et al., 2018) was not replicated in a follow-up experiment that used a single-pulse TMS delivered at around 150ms over the same region (Savoie et al., 2020). Nevertheless, such early effects might reflect the exertion of different rapid parallel processes (Strijkers et al., 2017). If we consider the visual modality for instance, object recognition and categorization can be achieved in just 80–100 ms after stimulus onset (see review in (Crouzet et al., 2010; Fabre-Thorpe, 2011)), involving early interactions between object and context (Fabre-Thorpe, 2011). Given the location of the AG along the dorsal pathway of visual information processing, it is likely that rapid magnocellular pathways connect to this region. Although feedforward processing might be sufficient (Masquelier et al., 2011), feedback processes, including top-down effects that can modulate neuronal responses by context or attention (Lamme et al., 1998), are key to sustain processes as complex as making meaning of a sentence or completing a calculation task. With its rich connectivity with frontal regions (cf. Figure 2 of (Seghier, 2013)), top-down effects are expected to modulate AG effects in this early time window, in particular to define the current context in which a task is being executed (e.g. (Cebolla et al., 2014; Rahimi et al., 2022)). Regardless of the exact underlying feedforward or feedback mechanisms, the definition of the current context during task execution seems to involve the AG at early latencies.

The importance of the N400 component to semantics and meaning processing is well documented (Alday, 2019; Kutas and Federmeier, 2011), hence the lack of a strong evidence for a role of the

AG in the emergence of this component is an important observation that has many ramifications for understanding the exact role(s) played by the AG in cognition. The N400 component usually reaches its maximum amplitude between 380 and 440 ms after stimulus onset (Swaab et al., 2011). In a recent large-scale EEG study, N400 was found to be involved in semantic facilitation when composing sentence meaning for predictable words (Nieuwland et al., 2020), a semantic role that was also observed during naturalistic language processing (Alday, 2019). The N400 has been identified with many paradigms beyond the classic semantic violation or incongruities in presented sentences (Beres, 2017), for instance during incongruent arithmetic processing (Jost et al., 2004; Niedeggen and Rosler, 1999). The N400 might reflect the update of semantic information in working memory (Jacob and Huber, 2020), with strong impact of expectations and predictions on its amplitude (Bornkessel-Schlesewsky and Schlesewsky, 2019; Kotchoubey, 2006). Current evidence points to the N400 as a component indexing retrieval processes rather than integration (Aurnhammer et al., 2021; Brouwer et al., 2012; Delogu et al., 2021; Huang et al., 2018). Accordingly, this might suggest that processes involving the AG at mid time windows, in particular at around the N400 latency, are dominated by information retrieval processes rather than semantic integration. However, I note that even when the same N400 component was measured, the spatial topographies of the EEG maps were not identical across studies, suggesting multiple brain sources for the N400 component. The N400 component might have sources in parietal regions (Domalski et al., 1991), but sources in temporal regions were deemed more plausible than the AG (Brouwer and Hoeks, 2013; Grisoni et al., 2021; Lau et al., 2008; Maess et al., 2006; Swaab et al., 2011). Therefore, the current EEG/MEG evidence for an N400 source in the AG is weak, making any transfer of the roles indexed by the N400 to the AG unreliable.

Likewise, current evidence for a role of the AG at late time windows is also weak. As mentioned in Section 1, late time windows were not always submitted to source analysis in previous EEG/MEG studies. Future work needs to look at the most likely processes that involve the AG at late latencies. In particular, there is still the unanswered question about whether the important P600 component might have a source in the AG, given the associations between the P600 component and integration processes (Bornkessel-Schlesewsky and Schlesewsky, 2008; Brouwer et al., 2012). Last but not least, in this discussion of EEG/MEG findings over the last two decades, a clear relationship between ERP components and specific functions/processes was assumed reliable, but this assumption might be debatable. Future EEG/MEG work needs to examine how AG latencies, for each specific domain, varies with task, stimulus and context.

Section 4: A unifying model about the AG in sensemaking:

A unifying model that integrates different roles is proposed in this section, accounting for the causal roles identified with TMS/TES at different time windows measured with EEG/MEG. In contrast to previous models that limited the AG involvement to semantic and episodic memory (Deldar et al., 2021; Humphreys et al., 2021; Irish and Vatansever, 2020), the proposed unifying model aims to encompass other domains as well including attention and self-processing. It was thus important to devise a model that can give justice to current evidence for a wide range of processes supported by the AG. This model involves both left and right AG (Gray et al., 2020), with a relative left-right difference expected to vary with time and domain (Bemis and Pylkkanen, 2012). According to the ‘neural context’ hypothesis (McIntosh, 2004), the functional roles of the AG depend on the status of other connected regions. Given AG’s rich connectivity along a heteromodal axis (Gonzalez Alam et al., 2021; Kernbach et al., 2018), providing a comprehensive catalogue of such complex connectivity at the millisecond level is not achievable. Therefore, the focus here was made on the most likely major connections and pathways that can sustain, or might have predetermined, the different roles played by the AG. In this unifying model, the AG role(s) are described in terms of the most plausible processes rather than specific task/stimulus responses that tend to be domain-dependent. This is because the same process can arise during different tasks or stimuli. For instance, the same process of fact retrieval occurs whether the task is to add two digits or to complete a sentence. Likewise, the same task and stimulus can yield different processes. For instance, regular familiar words can be read by direct translation of orthography to phonology or via lexico-semantic associations of previously learnt words. Furthermore, when a process is assigned to the AG in the proposed model, this does not necessarily mean that the AG is critical (e.g. a central hub) for that particular process; thus, an involvement of the AG is essentially assumed beyond the notion of causality/centrality, specificity/selectivity or whether the AG is sufficient/necessary for that particular process.

At the core of the unifying model is the process of sensemaking when the brain is giving meaning to external sensory information or internal thoughts. Sensemaking is dynamically constructed. It is flexible and plastic, allowing the brain to make sense of a rapidly-changing environment to enable reasonable actions and decisions. Sensemaking is an ongoing multimodal process, involving different aspects (cf. (Weick, 1995)) that intertwine as the brain interpret events. Some of these aspects include agency, defining the current context, allocating attentional resources, extracting relevant information, supporting social cognition, and converging toward plausible accounts of events and contexts. Making sense underpins many vital tasks, for example reading a text, understanding a mathematical equation, interacting with people, making an appropriate gesture or body movement, or pointing to the right direction in space or to the right body part. This sensemaking process can combine a wide range of information not restricted to linguistic

materials but also expands to other types of nonverbal information like gestures, facial expressions and body movements. These types of information can all convey a *meaning*, and perhaps this can explain why many EEG/MEG studies reported effects in the AG during the presentation of such diverse stimulus types irrespective of task and modality.

According to the free energy principle (Friston, 2009; Friston, 2010), sensemaking can be implemented by the brain as an active optimization process that combines bottom-up information (i.e. type, size and quality of sensory information) with top-down predictions (i.e. prior experiences, context, and purpose) with the ultimate goal to minimise surprise; for a similar rationale, see Figure 3 in (Seghier, 2013). In this model, sensemaking process aims to make sense of an information in a way that optimally considers current context, prior knowledge and goal. Interestingly, the different tasks and conditions that involved the AG in previous TMS/TES and EEG/MEG studies seem to suggest the existence of two optimization objectives of this sensemaking process, one that favours accuracy in tasks that rely on the retrieval and manipulation of facts and learned rules (e.g. number processing, phonological and semantic word processing), and another optimization objective that favours plausibility in tasks that reply on contextualization and selection between competing possibilities (e.g. comprehension under adverse conditions, reasoning and social cognition). This concept of optimization objective is introduced here to stress the importance of defining the current context to understand the roles of the AG, a step that is explicitly included in the model below.

The proposed unifying model includes three phases. The first phase involves defining and outlining current context in the first 200ms, with a lateralization bias toward the right hemisphere. Figuring out the current context is important so that relevant information can subsequently be retrieved and updated. This phase involves setting the boundaries between self and external environment, thereby relying on self-referential processing and agency in the AG (Brechet et al., 2018; Khalighinejad and Haggard, 2015). This can be mediated by interactions with frontal and insular regions, most likely supported by connections along the superior longitudinal fasciculus (Barbeau et al., 2020) and other connections (Ghaziri et al., 2017). This phase might rely on fast proprioceptive processes that are supported by quick efferent sensory information transfer (Proske and Gandevia, 2012), with the AG probably receiving this rapid sensory information through an intraparietal tract that was recently identified as linking the AG to the postcentral gyrus (Catani et al., 2017). This role is also facilitated by the location of the AG along a dorsal stream important for exploration for salient and relevant information (see discussion in (Sheth and Young, 2016)), a stream dominated by magnocellular pathways that enable rapid activations in parietal regions (Bullier, 2001). This possibility of fast magnocellular inputs to the AG is borrowed from previous magnocellular models of dyslexia (cf. (Stein and Walsh, 1997)). These rapid processes are important to enable an active interaction between self and external

environment (Gapenne, 2014; Gonzalez-Grandon et al., 2020). Indeed, this early process involving the AG, and other brain regions, is vital to ensure apposite exchanges between self and external environment when making sense of a given stimulus, condition, thought or action.

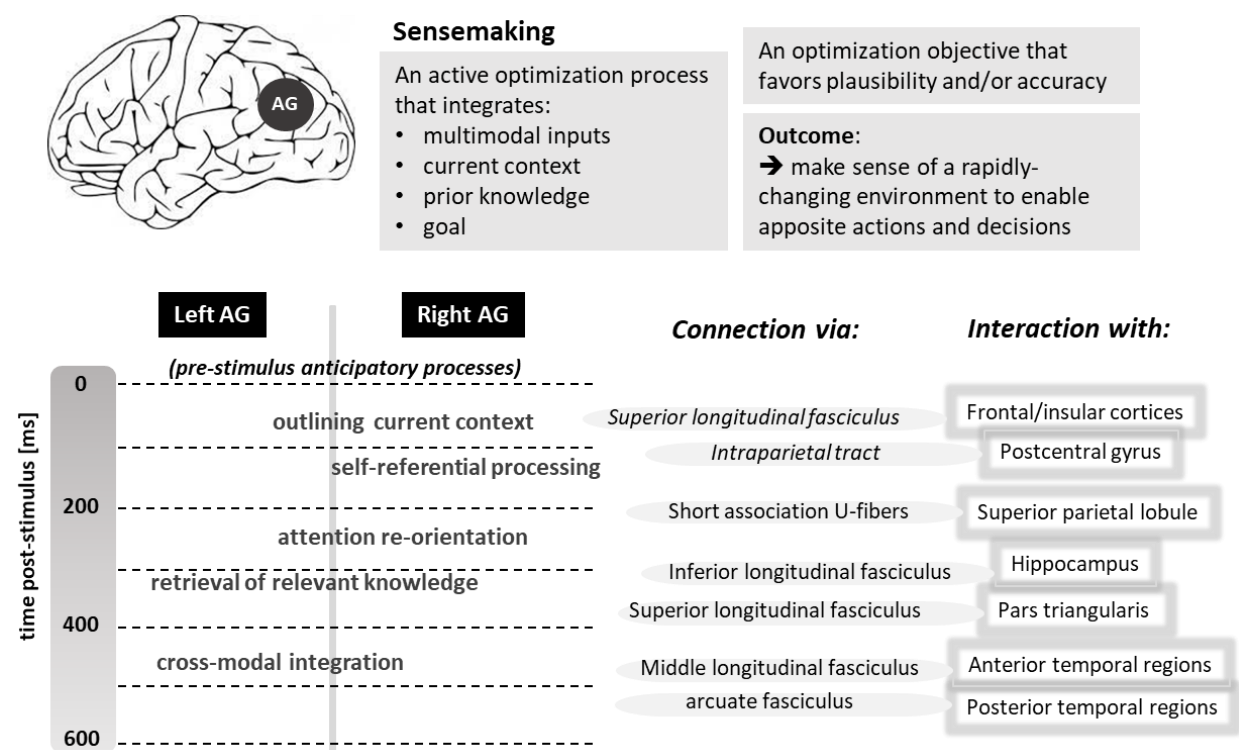
In the second phase, in the time window 200-500ms, the AG enables attention re-orientation to relevant information and retrieval of relevant knowledge and facts (Bloechle et al., 2016) (or inhibition of irrelevant information (Lewis et al., 2019)), given the task at hand and current context. This role is supported by bottom-up mechanisms (Cabeza et al., 2012) that can direct retrieval processes toward relevant information, a relevance that is flexible (Solomon et al., 2019) and shaped by context and goal. This process starts with a slight dominance in attention reorientation toward the right hemisphere that diminishes and flips toward the left hemisphere at later latencies during retrieval processes. This time-dependent relative left-right difference is based on previous studies that reported right lateralization for attentional mechanisms (Shulman et al., 2010) and left lateralization for retrieval processes (Sohn et al., 2003) in inferior parietal regions. This phase involves interactions with superior parietal regions (Burks et al., 2017; Catani et al., 2017; Makris et al., 2017), hippocampal regions via the inferior longitudinal fasciculus (Maller et al., 2019), inferior frontal regions via branch II of the superior longitudinal fasciculus (in particular with pars triangularis (Barbeau et al., 2020)), and other middle frontal regions (Wang et al., 2016).

During the third phase at later time windows after 500ms, the AG is involved in the integration of multiple modal representations (Lyu et al., 2019; Ramnan et al., 2018; Rugg and King, 2018). This integration also involves online monitoring (van Kemenade et al., 2019) and re-evaluation mechanisms, and it is most likely biased toward the left hemisphere. This multimodal integration can deal with asynchronous inputs (Spence and Squire, 2003) to ensure insensitivity to small differences in the arrival time of different converging modality-specific signals to the AG. This phase is mediated by interactions with different posterior temporal regions, inferior and anterior temporal regions through the posterior segment of the arcuate fasciculus (Bernard et al., 2019), the posterior segment of the superior longitudinal fasciculus (Wu et al., 2016), and the middle longitudinal fasciculus (Bullock et al., 2019; Jung et al., 2017; Makris et al., 2017) (but see (Latini et al., 2020; Maldonado et al., 2013)).

This three-phase model is similar to my previous unified model (Seghier, 2013) with some updates that reflect the following observations: (1) current TMS/TES and EEG/MEG literatures are relatively in line with fMRI/PET literature (Seghier, 2013) in terms of the diversity of domains that involve the AG, (2) compared to my previous unified model, the new model about sensemaking puts more emphasis on the importance of self-referential and context setting as early processes in the AG than my previous model in order to be consistent with existing TMS/TES evidence, (3) the new model offers a time map that can help pinpoint different processes at a

given time window, (4) the new model implicitly takes into account the relative difference in lateralization between left and right AG contributions, and (5) although semantic processing is integral to sensemaking, compared to my previous model, the new model however is deliberately not very explicit about when the bulk of semantic processing is exactly taking place in the AG, as this process can emerge during retrieval processes (Phase 2) and/or during multimodal integration processes (Phase 3). The difficulty to take a side in this debate about semantic processing in the AG is discussed in the next section.

Figure 2: A schematic illustration of the role(s) of the AG in sensemaking. (top) Sensemaking is an active optimization process that culminates in the integration of different sources of information (converging multimodal inputs, current context, prior experiences, and goal/purpose). The converging inputs to the AG convey information not limited to linguistic materials but might also include for instance gestures, facial expressions, or body movements. The outcome of this process is to give meaning to external sensory information or internal thoughts so that apposite actions and decisions are made within a rapidly-changing environment. See Section 4 for a detailed rationale. (bottom, left) the main processes involved in the three-phase unifying model are illustrated along two dimensions: by time of occurrence on the vertical axis (in [ms] after stimulus presentation) and by hemisphere on the horizontal axis (with a bias toward the left or right AG). For example, outlining current context is defined at early latencies with a relative dominance/bias toward the right AG. Likewise, retrieval of relevant knowledge is defined at later latencies with a relative dominance/bias toward the left AG. (bottom, right) the most likely white matter connections and cortical regions that interact with the AG at different time windows (roughly ranked from top to bottom for early versus late interactions). This list of connection and regions is not exhaustive. This is also a crude approximation as some interactions may start early but last longer than other interactions, and some regions might be activated much earlier but only interact with the AG at later stages. For a detailed discussion see Section 4.



Section 5: Is there a semantic role for the AG?

Current TMS/TES literature reviewed above strongly supports a causal role of the AG in semantic processing. However, current EEG/MEG evidence for the same role is not reliable; e.g. the AG still described as “a region with a debated role in semantic cognition” in very recent work (Rahimi et al., 2022). This is intriguing as the evidence for a semantic role is supported by a substantial number of fMRI/PET and TMS/TES studies (for review, see (Binder et al., 2009; Joyal and Fecteau, 2016; Price, 2000; Price, 2012; Seghier, 2013)). I note that the semantic tasks used in the majority of EEG/MEG studies under controlled conditions were too ‘simplistic’ to reflect the rich and dynamic nature of semantic processes involved in sensemaking, a process more complex than the meaning of single words used in typical EEG/MEG experiments (see similar discussion in (Hagoort, 2020)). The lack of naturalistic EEG/MEG protocols to study sensemaking in an ecological way might be one of the reasons for a lack of AG activations, but this still cannot explain the discrepancy between TMS/TES and EEG/MEG studies. Below, some conceptual issues are discussed in an attempt to take a different look at current EEG/MEG literature.

Semantic processing: the when question. The AG’s role in semantic processing is typically tied to the behaviour of the N400 and/or P600 components in semantic processing, even though both components might sustain different processes (e.g. retrieval and integration respectively). The failure to identify the AG as a reliable source at these two components does not necessarily mean that the AG is not involved in semantics. One possibility is that sensitivity to semantic manipulation also occurred outside typical latencies of the N400 and P600, as other earlier (<300 ms) and later (>700 ms) semantic-related effects were reported in some EEG/MEG studies (e.g. (Costa et al., 2009; Hauk et al., 2006; Honari-Jahromi et al., 2021; Jouen et al., 2021; Strijkers and Costa, 2011)). For example, sensitivity to word frequency as early as 50-80 ms (Fairs et al., 2021; Sereno et al., 2020) and 120-180ms (Penolazzi et al., 2007) was reported. Early semantic access (Davis et al., 2019) and early lexico-semantic processes were also detected in many studies (Miozzo et al., 2015; Munding et al., 2016; Pytkanen et al., 2014). Previous language models also incorporated the possibility of a reliable early semantic processing in the first 200ms (for example, a form-related lexical process at 100 ms and a lexico-semantic process at 150–200 ms (Pulvermuller et al., 2009)). It might be possible that the AG is involved in some of these early lexico-semantic effects, most likely through ultra-rapid parallel activation dynamics (Fairs et al., 2021) at different frequency bands (Sato et al., 2021).

However, a re-evaluation of current EEG/MEG literature suggests that an early semantic processing in the AG is highly unlikely. This is based on how AG’s latencies compare to latencies observed in other semantic regions. Previous studies that explicitly compared the latencies of semantic effects in the AG against other language regions in the anterior temporal lobe and the inferior frontal gyrus seem to agree on a later rather than an earlier semantic effect in the AG.

More specifically, many EEG/MEG studies for instance reported later semantic effects in the AG than in the anterior temporal lobe during the comprehension of simple adjective-noun phrases in both visual and auditory modalities (Bemis and Pykkänen, 2013), semantic composition (Ziegler and Pykkänen, 2016), object categorization (Mollo et al., 2017), semantic processing of written words (Farahibozorg et al., 2022), and during sentence-level conceptual-semantic processing (Matchin et al., 2019). Using effective connectivity analysis on MEG data, the AG showed higher evidence to explain effects at later latencies (within 450 ms), whereas the left anterior temporal lobe activity better explained earlier semantic effects (within 250 ms) (Farahibozorg et al., 2022). Likewise, the AG showed later latencies than the inferior frontal gyrus during recognition of familiar words (Cornelissen et al., 2009; Pammer et al., 2004; Wheat et al., 2010) and later effects than the posterior temporal cortex during semantic processing (Lyu et al., 2019). Therefore, reliable semantic effects in the AG might most likely occur at later latencies, with earlier semantic effects most likely taking place in the anterior temporal lobe (Bemis and Pykkänen, 2011) and the posterior temporal cortex (Lyu et al., 2019). This implies that if a semantic role for the AG is plausible, then semantic effects should be expected in the AG after temporal regions at late latencies, most likely after 400ms post-stimulus onset. This is based on a previous chronometric TMS study that reported a semantic effect in the anterior temporal lobe at around 400ms (Jackson et al., 2015), though earlier semantic effects at around 150ms were also observed (Teige et al., 2018). However, as reviewed in Section 3, current EEG/MEG studies failed to identify robust semantic effects in the AG at later latencies, for example at the level of the N400 and P600 components.

Semantic processing: the what question. Perhaps one reason about the difficulty to predict exactly when a semantic effect can occur concerns the multiplicity of semantic processes reported in current EEG/MEG literature. Semantic processes were reported under different names, including semantic access, semantic retrieval, semantic decision, semantic association, semantic matching, semantic control, semantic competition, semantic coherence, semantic facilitation, semantic composition, semantic integration, and semantic combination (see examples in (Graessner et al., 2021; Jefferies et al., 2020; Kocagoncu et al., 2017; Li and Pykkänen, 2021; Lyu et al., 2019; Price et al., 2015)). It is not clear whether these processes meant completely distinct processes sustained by different semantic systems, and whether they can emerge at different latencies or involve different AG subregions. The existence of different semantic systems, based on behavioural and lesion studies, for the representation of conceptual knowledge (Riddoch et al., 1988; Shallice, 1988) and meaning (Hart and Gordon, 1992), and for the acquisition of different categories of knowledge (Warrington and McCarthy, 1987) has been discussed extensively in previous literature. While this assumption of multiple semantic systems might help to understand inter-patient variability in category-specific semantic deficits (Thompson et al., 2015), it can add confusion about what each system does and how such presumably different systems share labour in a coherent way (it is tempting here to borrow Caramazza's critic of multiple semantic systems

as ‘multiple confusions’ (Caramazza et al., 1990)). Differences across studies exist regarding the number, the function and the anatomy of each semantic system. For instance, a distinction between semantic knowledge (i.e. stored semantic representations) and semantic access (i.e. the mechanisms used to access and manipulate semantic representations) (Lambon Ralph et al., 2017), both being sustained by two systems, has not been replicated in recent work (Chapman et al., 2020).

In the same way, the existence of two systems for semantic cognition, one for semantic control and another for semantic representation, has been put forward within the controlled semantic cognition framework (Chiou et al., 2018; Lambon Ralph et al., 2017). The AG seems to have neither a role in the semantic control system, as shown in a recent meta-analysis (Jackson, 2021), nor in semantic representation (Lambon Ralph et al., 2017). Another popular account considers two main types of semantics in the form of taxonomic and thematic associations. Taxonomic categories code feature-based relations and thematic associations code function-based relations when manipulating conceptual knowledge. According to the dual-hub theory (Coslett and Schwartz, 2018; Schwartz et al., 2011), taxonomic categories are supported by the anterior temporal lobes, whereas thematic associations are supported by the AG (or the left temporoparietal junction), for review see (Jefferies et al., 2020; Mirman et al., 2017). The AG is likely to process thematic relations thanks to its connections with hippocampal regions (Davis and Yee, 2017). Noticeable differences between the two types of association can appear at the level of the N400 component (Chen et al., 2014), with possible earlier activation of thematic relations than taxonomic relations (Savic et al., 2017; Wamain et al., 2015). Other MEG studies identified an involvement of the AG for both thematic and taxonomic processing (Lewis et al., 2015). What follows from these different models is that the exact role played by the AG in semantics depends on what theoretical (or anatomical) model is used to explain empirical data.

An alternative perspective is to depict the role of the AG beyond the fractionation of the semantic system into multiple systems. The AG, being furthest away from regions contributing to sensory and motor systems as demonstrated with network-level topographical analyses (see review in (Smallwood et al., 2021)), can act as a convergence zone (Damasio, 1989) where different systems might overlap. In line with this view is the suggestion by Xu and colleagues (2017), with the AG acting as the central connector hub that links three semantic subsystems that support multimodal experiential representation, language-supported representation, and semantic control (Xu et al., 2017). A possible role for the AG as a cross-system connector is also supported by its core location within the default mode network (DMN); however, it is precisely because of its location within the DMN that the AG is denied a specific role in semantic processing.

The consequence of being part of the DMN. Being part of the DMN is, surprisingly, a frequent argument used against a specific role for the AG in semantics. Even when semantic effects were

observed in the AG, these effects were referred to as non-semantic effects. Put another way, the current debate is not about a lack of empirical evidence for an activation of the AG during semantic tasks, but rather concerns how activations were interpreted in the light of the role of the AG in the DMN. The argument against a specific role of the AG in semantics typically takes the following form: an effect is observed in the AG during the processing of conceptual knowledge, but due to differences in difficulty and demands across tasks or conditions, effects in the AG might be due to difficulty-dependent deactivation differences, and therefore the AG is not involved in semantic processing. This argument, though mainly derived from fMRI studies, is frequently mentioned in current EEG/MEG literature. Indeed, many authors have argued that current evidence about the role of the AG in semantic processing has many caveats, with AG involvement in semantic processing attributed to difficulty-related deactivations (in particular its ventral subregion) (Humphreys et al., 2021). Being part of the DMN and with a (de)activation level strongly dependent on task difficulty, the current neuroimaging evidence for an AG role in semantic processing has been evaluated as not reliable (see detailed discussion in (Jackson, 2021; Lambon Ralph et al., 2017)). In this view, the AG does not have a role in semantic processing, and previous observed effects in the AG can alternatively be attributed to its 'disinterest' in non-semantic tasks (Humphreys et al., 2015).

It is important to review first the types of associations in the DMN between deactivations and task difficulty, putting aside the ambiguous inference one can make with the subtractive logic in fMRI/PET. Task-related deactivations and their dependency with task demands are not homogenous in the DMN (e.g. (Mayer et al., 2010; Tomasi et al., 2006; Zeng et al., 2017)) and in the parietal lobe (Cusack et al., 2010), though it is not clear what metrics can better measure task difficulty when it comes to DMN regions (Gilbert et al., 2012) given the complex deactivation dynamics of the DMN (Farooqui and Manly, 2018). Task difficulty can strongly modulate AG activations (Humphreys and Lambon Ralph, 2017; Vatansever et al., 2017), but not in all contexts and tasks (Fuentes-Claramonte et al., 2019; Lanzoni et al., 2020). If activations in the AG were merely the result of a comparison between easy and hard conditions, then this argument assumed that non-semantic tasks were much harder than semantic tasks in previous neuroimaging studies (by definition, demanding conditions must yield stronger deactivations in the AG). However, there are many studies that showed positive activations in the AG when contrasting difficult conditions versus easy control/baseline conditions (e.g. (Chou et al., 2009; Fuentes-Claramonte et al., 2019; Jost et al., 2011; Lewis et al., 2019; Seghier et al., 2010; Xu et al., 2018)).

Furthermore, the task difficulty argument does not explain why other DMN regions that showed difficulty-dependent deactivations (Arsalidou et al., 2013; Seghier and Price, 2012; Singh and Fawcett, 2008) are not activated like the AG in semantic tasks, even though these regions are also critical in encoding semantic categories and relations (Zhang et al., 2020b). In other words, it is

not clear why such ‘disinterest’ in non-semantic tasks (Humphreys et al., 2015) is not shared by other DMN regions. Besides, this argument was never retained against the involvement of the AG in other domains: for instance, the AG plays a major role in the sense of agency (Haggard, 2017), though such role also involves the DMN. It is worth noting that this argument was put forward without a systematic analysis of all control/baseline conditions used in previous studies that showed semantic effects in the AG. A meta-analysis of 1031 studies with the platform neurosynth (Yarkoni et al., 2011) for the term ‘semantic’ revealed a significant effect (z -score = 10.5, MNI-coordinates = [-48 -64 +22]) in the left ventral AG, an effect that is unlikely to be due to differences in difficulty-dependent deactivations alone across so many studies. In line with this observation is a recent analysis of semantic effects within the DMN (Zhang et al., 2022), showing a noticeable dissociation between difficulty-induced deactivation and task-induced deactivation, with significant difficulty-independent semantic activations located in bilateral AG (Zhang et al., 2022).

A competition with the anterior temporal lobe. Behind this argument against a specific role for the AG in semantic processing is an attempt to reconcile two points: (1) there must be one central semantic hub in the brain, and (2) this unique semantic hub cannot be the AG as other regions showed more reliable semantic effects than the AG. Indeed, the proponents of this argument aim to anchor the anterior temporal lobe in the semantic system as the central semantic hub (Lambon Ralph et al., 2017; Visser et al., 2010). This framework is shaped by the hub-and-spoke model (Rogers et al., 2004) that posits that concepts are formed by the interactions of modality-specific sources of information (the “spokes”) with a central representational hub located in the anterior temporal lobe that provides additional modality-invariant representational resource (Patterson et al., 2007; Patterson and Lambon Ralph, 2016). Perhaps this competition between the two regions for the central semantic hub role resulted manifestly in excluding the AG from the semantic system. There is however no computational or empirical evidence for a unique semantic hub against the alternative hypothesis of multiple hubs, taking into consideration the possibility that different hubs might emerge at different processing stages (Farahibozorg et al., 2022). There are at least five perspectives or criteria on what makes a brain region a semantic hub: (1) must be equally necessary for processing all types of meaning (Pulvermuller, 2013), (2) must have a high degree of hubness as defined with graph theory (Cole et al., 2010; Xu et al., 2016), (3) is the site of convergence of different inputs to form amodal or heteromodal conceptual representations (Bonner et al., 2013; Pobric et al., 2010), (4) must show consistent early activation (Hauk, 2016), and/or (5) must cause semantic deficits after damage (Chen et al., 2020; Schwartz et al., 2009). Some of these criteria are in fact met by the AG: the AG has a high degree of hubness (Buckner et al., 2009; Sato et al., 2016; van den Heuvel and Sporns, 2013), is a convergence site of different multimodal inputs (Binder and Desai, 2011; Bonnici et al., 2016; Seghier, 2013; Tibon et al., 2019),

and is implicated in many tasks that involve access to and processing of meaning (Binder et al., 2009).

In this debate, there is room for other alternative models that tend to move away from this emphasis on a unique central semantic hub in the anterior temporal lobe in order to encompass other regions that are also critical for the coding of perceptual information into conceptual representations (Binder and Desai, 2011; Duffau et al., 2014; Gainotti, 2011; Pulvermüller, 2013). Specifically, the AG is considered a cross-modal convergence zone or hub by alternative ‘hybrid’ models that posit that conceptual knowledge processing relies on a hierarchical neural architecture from modality-specific perceptual-motor regions to higher-level integrative cross-modal regions (Binder and Desai, 2011; Fernandino et al., 2016; Kiefer and Harpantner, 2020; Kuhnke et al., 2020b; Kuhnke et al., 2021; Reilly et al., 2016). In addition to the anterior temporal lobe and the AG, other critical regions for semantic processing can be considered as semantic hubs in the brain, including the inferior frontal gyrus (Devlin et al., 2003; Poldrack et al., 1999), the anterior cingulate cortex (Zhao et al., 2017), the middle fusiform gyrus (Forseth et al., 2018), and the posterior middle temporal gyrus (Turken and Dronkers, 2011). Such multiple hubs can emerge at different time windows (Farahibozorg et al., 2022), might be sensitive to different semantic features, and can show different connectivity profiles depending on context and goal. In summary, current arguments against a role of the AG in semantic processing on the basis of its difficulty-dependent responses are not strong. The lack of a consensus in current EEG/MEG literature about a reliable semantic role for the AG raises some important questions for future research.

Section 6: Outstanding questions for future research

There is a large body of research with EEG/MEG about the DMN (Chen et al., 2008; Hlinka et al., 2010; Neuner et al., 2014; Tang et al., 2017). One key question concerns the exact roles played by the AG within the DMN. Teasing apart the different contributions of the AG in the DMN would help fine-tune current models about the functions of the AG. This concerns many functions that are also supported by other DMN nodes in the domains of self-referential, memory, semantic processing, and social cognition. For instance, could a semantic role for a DMN node have resulted from a left-lateralized connectivity between control and heteromodal regions (Gonzalez Alam et al., 2021)? Furthermore, future work needs to investigate why left and right AG, both being part of the DMN, are displaying many dissimilar functional properties (e.g. (Bellana et al., 2016; Seghier and Price, 2012)).

Given the significant semantic effects reported in TMS/TES studies, it would be interesting to see how the AG interact with other regions that have also been shown to have a causal role with

TMS/TES in semantic processing, including the anterior temporal lobe (Pobric et al., 2007), the left inferior prefrontal cortex (Devlin et al., 2003), the posterior middle temporal gyrus (Teige et al., 2018), the left ventral premotor cortex (Cattaneo et al., 2010), and the right cerebellum (Gatti et al., 2020). Stimulation of the AG in combination with other regions would help address questions about single versus multiple processing pathways and sufficient versus necessary regions. For example, behavioural changes can be compared between conditions when TMS is applied to the AG alone, to a region X alone, or to both the AG and region X. This can help to identify key sites for semantic processing (Lorca-Puls et al., 2017), in the light of current theoretical frameworks about brain-behaviour relationships (Godefroy et al., 1998; Toba et al., 2020).

Mechanistic accounts with effective connectivity analyses are needed to describe how the AG interact with different regions at different time windows (Farahibozorg et al., 2022). One exciting possibility is to combine TMS with EEG/MEG (Farzan et al., 2016; Ilmoniemi and Kicic, 2010) to measure TMS-induced effective connectivity changes while varying the time at which the AG is stimulated to target specific time-locked processes as in chronometric TMS protocols. For example, future studies can investigate EEG/MEG states after TMS over the AG at early versus late stimulation times. The question about what regions come before or after the AG can shed light on the mechanisms that explain a particular brain function. The AG being activated at later latencies than other core regions during semantic processing is an interesting observation in previous EEG/MEG studies as discussed above. However, there are other domains where the AG showed earlier effects; for example, the AG activated earlier than the anterior cingulate cortex during simple arithmetic calculations (Jost et al., 2011), or the AG driving activations in the supramarginal gyrus between 80-280 ms and the inferior frontal gyrus between 480-750 ms during speech sound processing (Gow et al., 2008).

Examining brain oscillations with EEG/MEG can provide additional information about the roles of the AG and its functional dynamic connectivity at different frequency bands (Doesburg et al., 2016). Synchronous oscillations for instance can reveal how communication and information transfer across different regions can sustain a particular task (Fries, 2005; Uhlhaas et al., 2009). Such oscillations can be quantified at different frequency bands, i.e. delta (<4 Hz), theta (4–7 Hz), alpha (8–12 Hz), beta (13–30 Hz), and gamma (>30 Hz), and each band might map to different cortical topographies (Herrmann et al., 2016). The extent of the functional connectivity of the AG is expected to vary with frequency band (e.g. (de Pasquale et al., 2010; Rahimi et al., 2022; Taberna et al., 2021)), and future work needs to look at how AG's frequency-dependent connectivity varies with task and stimulus.

In the same way, EEG/MEG effects can be examined with TMS to identify the timing of the AG involvement that contributes to behaviour. One exciting possibility is to vary the timing of the

TMS stimulation as in chronometric TMS studies. Chronometric TMS involves single pulses or brief TMS bursts delivered during specific time windows in which one hypothesizes a given region might sustain a particular process (Valero-Cabre et al., 2017). Chronometric TMS was previously used over parietal regions such as the supramarginal gyrus (Pattamadilok et al., 2015; Sliwinska et al., 2012; Stoeckel et al., 2009) but there is a lack of similar studies on the AG. Future studies can use chronometric TMS to chart the time windows at which left or right AG functionally contributes to different tasks and domains. TMS over the AG can target different time windows that match the three phases of the unifying model of Section 4, which can ultimately test the explanatory power of the unifying model.

Studies that mapped brain dynamics in subjects with damage to the AG are scarce. Given the diversity of deficits following damage to the AG (Ardila et al., 2000; Roux et al., 2003), EEG/MEG can map the dynamics of functional reorganization at different time post-damage. For instance, the AG was previously defined as a multimodal integration centre within a core set of non-resectable brain areas (Ius et al., 2011), thus mapping the changes in brain networks after damage to the AG can provide valuable insights on how the brain can compensate for so many domains when the AG is no longer functional.

One topic not addressed in current EEG/MEG concerns the role of the AG in social interactions as part of a mentalizing system, given recent evidence for its reliable involvement in social cognition (Numssen et al., 2021). For example, EEG-based hyperscanning approaches can reveal the time-resolved processes sustained by the AG during social interactions (for review see (Wang et al., 2018)).

There is also an interest in how the AG is involved in task and event anticipation (Capotosto et al., 2017; Lee et al., 2021), and in detecting and replacing missing information in speech comprehension (Bendixen et al., 2014). Such anticipatory and predictive mechanisms are crucial for realistic and continuous events processing (Baldassano et al., 2017). The study of such mechanisms with EEG/MEG can provide insights on how predictions are built at the level of the AG at high temporal resolution, in particular to assess how prior knowledge shape the subjective experience of events (Lee et al., 2021).

There is a need for mechanistic accounts that offer an algorithmic-level understating of semantics (Barsalou, 2017). Specifically, future work can look at the type of semantic manipulations that can impact upon the activation level in the AG at different time windows. In the same way, future EEG/MEG studies can investigate another important dimension in semantics that is related to the individualization of meaning (personal semantics) at the millisecond level (Renoult et al., 2012; Saalasti et al., 2019). Another interesting aspect of the AG in the process of sensemaking is the ability to integrate multimodal information. One can draw parallels with a similar AG role in the

subjective nature of pain perception (Alhajri et al., 2021), as pain processing also depends on the integration of complex sensory, cognitive and emotional aspects in a personalized and context-dependent manner.

From a developmental perspective, one fundamental question relates to the different age periods at which these functions emerge in the AG, in the light of late maturation (myelination) of the AG (Glasser and Van Essen, 2011). Future work can also explore the multifaceted influence of learning and education on these functions, in particular how different ERP components that have a source in the AG would vary with age and learning.

Conclusion:

This review of TMS/TES and EEG/MEG studies complement previous reviews of fMRI/PET studies about the roles of the AG in a wide range of domains. This review identified many consistent findings in this literature, but also highlighted huge differences in terms of the exact roles assigned to the AG and the latencies at which these roles might emerge. Future work needs to systematically examine, for each specific domain, how the timing of the involvement of the AG varies with task and stimulus. The proposed unifying model can help make sense of the different roles at different time windows. Future work with TMS/TES and EEG/MEG can test the explanatory potential and predictive power of this model. This review also discussed the involvement of the AG in semantic processing, and it invites the community to contribute additional computational and empirical evidence to this debate. Future EEG/MEG work needs to apply, if source localization allows, accurate anatomical labels when reporting effects in the AG. This review recognizes the importance of understanding the roles of the AG in giving meaning and sense to the external world in parallel with the influence from other connected regions. It also recognizes the complexity of this endeavour due to the fact that the AG is a core node of the DMN, and hence all its contributions within the DMN have to be teased apart to ultimately fully understand the functions of the AG in such wide range of domains.

Compliance with Ethical Standards: This review article does not contain any data from human participants or animals.

Ethical approval: For this work, formal consent is not required.

Conflict of Interest: The author declares that he has no conflict of interest.

Data availability: Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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