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Inferior parietal lobule contributions to visual word recognition

Magdalena W. Sliwinska, Alyson James, and Joseph T. Devlin

Experimental Psychology, UCL, Gower Street, London WC1E 6BT, UK

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Corresponding author: Magdalena W. Sliwinska
Experimental Psychology, UCL
Gower Street, London WC1E 6BT
Email: magdalena.sliwinska.09@ucl.ac.uk
Phone: +44 (0)207 679 27551

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Abstract

This study investigated how the left inferior parietal lobule (IPL) contributes to visual word recognition. We used repetitive transcranial magnetic stimulation (TMS) to temporarily disrupt neural information processing in two anatomical fields of the IPL, namely the angular (ANG) and supramarginal (SMG) gyri, and observed the effects on reading tasks that focussed attention on either the meaning or sounds of written words. Relative to no TMS, stimulation of the left ANG selectively slowed responses in the meaning, but not sound, task whereas stimulation of the left SMG affected responses in the sound, but not meaning, task. These results demonstrate that ANG and SMG doubly dissociate in their contributions to visual word recognition. We suggest that this functional division-of-labor may be understood in terms of the distinct patterns of cortico-cortical connectivity resulting in separable functional circuits.

Introduction

Reading is one of the most important skills humans need to learn in order to function in modern society and understanding how this complex process is achieved by the brain is an important goal of cognitive neuroscience. On a neurological level, reading involves a set of brain regions that work together in order to recognize a visual input and link it to its corresponding sound and meaning. For example, extrastriate visual areas are critical for recognizing the visual form of a word while higher order association areas located in the frontal, parietal and temporal lobes are important for processing its sound and meaning (Price & Mechelli, 2005; Pugh et al., 2001; B. A. Shaywitz et al., 2002). Here we specifically focused on the functional contributions of the left inferior parietal lobule (IPL) to visual word recognition.

Joseph Jules Dejerine (1891) was the first to highlight the importance of the IPL in reading. He described the case of a 63 year old sailor who became unable to read or write due to a lesion of the left posterior IPL, more specifically the angular gyrus (ANG). Dejerine reasoned that the patient's inability to recognize visual words (alexia) coupled with his writing difficulty (agraphia) indicated a central loss of visual word forms, which he argued were stored in ANG. Subsequent studies of patients with acquired reading deficits have confirmed the importance of the IPL for reading, but have introduced uncertainty regarding the specific anatomical fields. For instance, Warrington and Shallice (1980) reported two patients with profound reading impairments subsequent to lesions predominantly affecting either the anterior (supramarginal gyrus (SMG)) or posterior (ANG) fields of the IPL. Similarly, Philipose and colleagues (2007) found that reading deficits were more commonly due to SMG, rather than ANG, lesions.

In contrast to Dejerine's hypothesis that the IPL stores visual word forms, others have claimed that this brain region performs the procedures necessary for converting spelling to sound during visual word recognition (Booth et al., 2004; Joubert et al., 2004; Law et al., 1991; Pugh et al., 2000; Roux et al., 2012; S. E. Shaywitz et al., 1998). For instance, Shaywitz and colleagues (1998) used functional MRI (fMRI) to measure brain activity during a set of silent reading tasks and observed that normal, skilled readers robustly engaged ANG when performing a nonword rhyming task (e.g., "Do jete and leat rhyme?"). Unlike words, pronounceable nonwords do not have a learned, associated phonology and thus require the reader to assemble the phonological code from the orthography (Marshall & Newcombe, 1973). As a result, the authors associated ANG activation with spelling-to-sound conversion rather than with storage of visual word forms. Consistent with this claim, they found that developmental dyslexics, who were by definition poor at phonological assembly, showed abnormally low ANG activation (see also Pugh et al., 2000). Using a similar task but a different methodology, Roux et al. (2012) found that SMG – not ANG – was the critical site for spelling-to-sound conversion. In this experiment, they used intracranial stimulation in awake neurosurgical patients to temporarily disrupt local processing in the stimulated region and measure its effect on behaviour. Stimulation of the left anterior SMG preferentially interfered with reading nonwords (e.g., "dasul") but did not affect real words, suggesting that the SMG was necessary for spelling-to-sound conversion. Therefore, although these studies agree that the IPL plays a critical role in spelling-to-sound conversion, there is no consensus regarding the specific anatomical locus of this function with some focusing on ANG (Horwitz, Rumsey, & Donohue, 1998; Pugh et al., 2000; S. E. Shaywitz et al., 1998), others on SMG (Jobard, Crivello, & Tzourio-Mazoyer, 2003; Law et al., 1991; Roux et al., 2012) and still others arguing that both fields are important for this process (Booth et al., 2002; Booth et al., 2004; Booth et al., 2003; Joubert et al., 2004).

A third hypothesis associates ANG and SMG with different functional properties during visual word recognition. By this account, ANG is involved when processing the meaning of words while SMG contributes to processing their sound (Demonet, Price, Wise, & Frackowiak, 1994; Graves, Desai, Humphries, Seidenberg, & Binder, 2010; Price & Mechelli, 2005; Price, Moore, Humphreys, & Wise, 1997). This hypothesis builds on the findings that ANG is considered a key node in the cortical semantic system (Binder, Desai, Graves, & Conant, 2009) and that SMG is important for phonological processes associated with verbal working memory (Buchsbaum & D'Esposito, 2008). Several neuroimaging studies have confirmed a double dissociation within IPL when processing the sound and meaning of written words (Devlin, Matthews, & Rushworth, 2003; Mummery, Patterson, Hodges, & Price, 1998; Price et al., 1997; Vigneau et al., 2006). It is unclear, however, whether the differential contribution of ANG and SMG to semantic and phonological processing is *necessary* because of the nature of the neuroimaging techniques which can only indicate correlations between brain and behaviour, but do not allow causal relations to be drawn. Moreover, in patients with IPL lesions this double dissociation is not readily apparent, in part because focal lesions selectively affecting either ANG or SMG are rare.

In summary, then, there are three hypotheses concerning IPL contributions to visual word recognition. The first claims that the IPL is the site of stored visual forms of written words although it remains unclear precisely where within the IPL these are stored. The second hypothesis argues that the procedures for converting spelling-to-sound are a function of the IPL but it is unclear whether these are specifically located in ANG or SMG, or both. Finally, a third hypothesis suggests that the angular and supramarginal fields of the IPL preferentially contribute to semantic and phonological processing of written words, respectively. The aim of the current study was to evaluate these hypotheses using repetitive transcranial magnetic stimulation (rTMS) to temporarily and selectively disrupt processing in

left ANG and SMG during visual word recognition and measure the effect on reading behaviour.

MATERIALS & METHODS

Participants

Seventeen people volunteered for this study and 12 (7 women, 5 men; aged 18-42, mean = 26) participated in the main experiment. One of the five excluded participants experienced right hand twitching during SMG stimulation that interfered with making a button press response and therefore could not participate in the experiment. In the other four, functional localization failed to identify an appropriate ANG (2) or SMG (2) testing site. All of the remaining participants were right-handed, monolingual native English speakers with normal or corrected to normal vision. They reported having no neurological conditions and no form of dyslexia. Each person provided informed consent after the experimental procedures were explained and was paid for their participation. The experiment was approved by the University College London Research Ethics Committee.

Experimental procedures

The experiment consisted of three separate testing sessions for each participant. The first lasted approximately 30 minutes and involved acquisition of a T1-weighted magnetic resonance imaging (MRI) scan [FLASH sequence, repetition time (TR) = 12 ms, echotime (TE) = 5.6 ms, flip angle = 19°, resolution = 1 mm × 1 mm × 1 mm] at the Birkbeck-UCL Centre for Neuroimaging (BUCNI). The structural images were used for anatomical identification of left ANG and SMG in each participant. Scanning was followed by two TMS sessions in which either ANG or SMG were tested, with the order counterbalanced over

participants. The TMS sessions were separated by at least two days and lasted approximately one hour each. Each testing session consisted of a TMS-guided functional localization and then the main experiment. The aim of the localization procedure was to identify specific testing sites within ANG and SMG. In other words, the testing sites used in the main experiment were determined using a TMS-based functional localization procedure (Ellison, Lane, & Schenk, 2007; Pattamadilok, Knierim, Duncan, & Devlin, 2010; Taylor, Nobre, & Rushworth, 2007), similar to “functional localizer” scans commonly used in fMRI experiments (Kanwisher, McDermott, & Chun, 1997; Kraft et al., 2005). The aim of this functional localization procedure was to customize the stimulation site in each individual taking into account inter-subject functional-anatomical variability.

In order to identify appropriate testing sites we chose localization tasks that optimized the constraints placed by the three hypotheses under investigation. According to the first hypothesis, left IPL stores visual word forms and therefore the only constraint was that the task used real words (i.e., as opposed to pseudowords). The second hypothesis suggests that IPL is involved in orthography-to-phonology conversion. In this case localization required a task that involved letter-to-sound conversion, a procedure that is thought to occur automatically in virtually all reading tasks (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; R. Frost, 1998; Plaut, McClelland, Seidenberg, & Patterson, 1996). Finally, the third hypothesis claims that ANG and SMG are required in semantic and phonological processing of written words, respectively, and thus localization required separate tasks that were either semantically or phonologically demanding. As a result a visual semantic category judgement task was used to localize stimulation sites within ANG while a visual rhyme judgement task was used for SMG. Semantic category judgments focused the participant’s attention on the meaning of the words by forcing them to decide whether the two visually presented words came from the same semantic category (e.g., inch – mile) or not (e.g., eagle – mayor). Rhyme

judgments focused the participant's attention on the sounds of words by forcing them to decide whether two visually presented words rhymed (e.g., queen – green) or not (e.g., slug – muck). The stimuli were designed such that half of the words in rhyme trials had different spellings (e.g., razor – laser) while half of the non-rhyming pairs had similar spellings (e.g., farm – warm). This prevented participants adopting a purely orthographic strategy.

Note that we purposely did not localize both semantic and phonological processing within a single region because none of the three possible outcomes were relevant here. The neuroimaging evidence suggests that the most likely outcome would be an inability to localize semantic processing within SMG or phonological processing within ANG. That would be a null result, however, and therefore not informative due to the potential that we inaccurately delivered stimulation, incorrectly selected stimulation sites, inappropriately chose localization tasks, or any number of other experimental failures. In other words, it would needlessly expose participants to an extra 160 trials with rTMS to no purpose because a lack of evidence could not be used as evidence for a lack of semantic or phonological processing in SMG or ANG, respectively. A more interesting possibility would be if both types of processing were localized at different locations within an anatomical region (e.g., within SMG). Although informative, it would answer a different question than the one we investigated here. The final possibility would be that both the semantic and phonological localizer tasks would identify the same location within each anatomical region – a possibility we explicitly test in the main experiment (see below). As a result, it was only necessary to localize phonological processing in SMG and semantic processing in ANG. Critically, though, both localization tasks required recognizing visual word forms and converting spelling-to-sound so were equally appropriate for localizing stimulation sites relevant for all three hypotheses, thereby avoiding the potential for circularity in the results.

Prior to the TMS sessions, three potential stimulation targets were anatomically identified and marked within each region on an individual's MRI scan using theBrainsight frameless stereotaxy system (Rogue Research, Montreal, Canada). For ANG, three potential stimulation sites were marked using standard space coordinates based on a study by Seghier et al. (2010) who identified three functionally distinct sub-regions within ANG. These were located within dorsal ANG at $[-30 -66 42]$, middle ANG at $[-48 -68 28]$, and ventral ANG at $[-48 -68 20]$ (see Figure 1A). For SMG, a different method of marking potential stimulation sites was applied. Instead of using standard space coordinates, sites were marked anatomically within the anterior part of the left SMG since this area has been shown to be most consistently involved in visual word recognition across a number of neuroimaging studies (Devlin et al., 2003; Petersen, Fox, Posner, Mintun, & Raichle, 1988; Price, 2000; Price et al., 1997; Roux et al., 2012; Seghier et al., 2004). The three sites were located: (i) just superior to the termination of the posterior ascending ramus of the Sylvian fissure; (ii) at the ventral end of the anterior SMG, superior to the Sylvian fissure, posterior to the postcentral sulcus, and anterior to the posterior ascending ramus of the Sylvian fissure; and (iii) approximately halfway between these sites and approximately 10-15 mm from the other two (see Figure 1A). This resulted in different standard space coordinates for each potential stimulation site across individuals (see online Supplemental Materials). Each site within ANG and SMG was then tested to functionally localize the specific target site where stimulation interfered with a semantic category or a visual rhyme judgement task, respectively.

Insert Figure 1 here

Functional localization

A TMS session began with functional localization. For localization in ANG, participants performed a visual semantic categorization task that focused their attention on the meaning of the words. They were asked, “Do these two words belong to the same semantic category?” For localization in SMG, participants performed a visual rhyme judgement task designed to focus their attention on the sounds of the words. Subjects were asked, “Do these two words rhyme?” Participants were seated approximately 60 cm in front of computer display and responded using the keyboard. At the beginning of each trial, a white fixation cross was centrally presented on the black screen for 1000 ms immediately followed by two words presented in 32pt white Helvetica font that appeared simultaneously above and below the cross and remained there for 500 ms. Participants had to make their response during a 2500 ms inter-trial interval by pressing the appropriate button using their left and right index fingers. The pairing of yes/no responses with fingers was counter-balanced across participants. All stimuli presentation and response recording was performed using MATLAB 2010 (Mathworks Inc.) and the COGENT 2000 toolbox (www.vislab.ucl.ac.uk/cogent/index.html).

Each run consisted of 34 trials and lasted 1 min 35 sec. There were five different stimuli lists for each localization task. In both tasks, word stimuli (n = 160 plus 10 dummy trials in each task) ranged in length from three to eight letters and were divided into five separate lists, matched for concreteness, familiarity, written word frequency, number of letters, and number of syllables [one-way ANOVA, all $F(1, 158) < 1.7$, $p > 0.14$ for both tasks]. Concreteness and familiarity ratings were taken from the MRC Psycholinguistic database (Coltheart, 1981) while British English word frequencies came from the Celex database (Baayen & Pipenbrook, 1995). In addition, within each list trials were divided into TMS and no-TMS items equally distributed between yes and no trials and also matched

across these five factors [all $t(30) < 1.8$, $p > 0.1$ for both tasks]. Repetitive TMS (10Hz, 500 ms) was delivered on half of the trials with trial order pseudorandomized within each run. Stimulation involved five pulses starting from the onset of the stimulus and separated by 100 ms. The data from the first two trials in each run were discarded to allow participants to get past anticipating the first stimulation trials.

At the beginning of the localization procedure, the participant performed a practice run without stimulation to get familiarized with the task and ensure that it was understood correctly. The next step was to introduce the participant to the sensation of rTMS at the first testing site by placing the coil on the scalp such that the line of maximum magnetic flux intersected the target site. Once familiarized with the sensation, each subject went through one more practice run with concurrent rTMS. Localization then began at the first testing site using one of the five matched stimulus sets. When rTMS facilitated (i.e., shortened) RTs relative to non-TMS trials, the next site was tested. When rTMS increased RTs, the site was re-tested in order to determine whether stimulation produced consistent slow-downs at this site. All three sites were tested but only a site that produced two or more RT slowdowns during the localizer task was used as a stimulation site in the main experiment. Any numeric increase in RTs, including a few milliseconds, was qualitatively distinct from the facilitation effects typically observed at incorrect sites and therefore considered a slowdown. The important criterion here was reproducibility of the direction of the effect, rather than its magnitude. The order of testing the target sites was counter-balanced across participants. If after 10 runs, no site resulted in consistent TMS-induced slowdowns, then the experiment terminated and the participant was not tested in the main experiment.

In order to identify testing sites in terms of standard space coordinates, each participant's structural scan was registered to the Montreal Neurological Institute-152 template using an affine registration (Jenkinson & Smith, 2001). Note that all stimulation was

done in native anatomical space – the standard space coordinates were computed solely for reporting purposes. In addition, for illustrative purposes a group mean structural scan was created in standard space and used as a background image when presenting the stimulation sites in order to accurately reflect the anatomical variability across subjects (Devlin & Poldrack, 2007).

Main experiment

The main experiment included three different visual tasks: (i) a synonym judgement task where participants were asked, “Do the two words mean the same thing?” (e.g., student – pupil or soap – cream); (ii) a homophone judgement task where participants were asked “Do the two words sound the same?” (e.g., brake – break or circle – circus); and (iii) a control task where participants were asked, “Are the two letter strings identical?” (e.g., wrdmb – wrdmb or bxgwf – bnpvf). The first two tasks were conceptually similar to the localisation tasks and shared all aspects of visual word recognition in order to provide an unbiased test of the three hypotheses. Critically, these tasks were not identical to those used in the localization procedure to avoid circularity. Rhyme and homophone judgements both focused attention on phonological aspects of written words but in different ways. The former required matching the final syllables while the latter involved matching the phonological forms of the whole words. In addition, both tasks required processing of visual word forms (hypothesis I) and spelling-to-sound conversion (hypothesis II), therefore the task tested all three hypotheses. Similarly, category and synonym judgements draw participants’ attention to semantic aspects of written words but required searching for either semantically related or identical pairs of words, respectively. Once again, these tasks required visual word form processing and by many accounts, also involve spelling-to-sound conversion (Coltheart et al., 2001; R. Frost, 1998; Plaut et al., 1996; Van Orden, Johnston, & Hale, 1988), thereby testing all three hypotheses. In other words, both the localization and main experimental tasks were designed

to be unbiased with respect to the three hypotheses. The third task served as a control condition that included orthographic processing but none of the hypothesized processes expected to engage IPL. Consonant letter strings are often used as a low level control in reading studies because they convey orthographic information but are immediately recognized as non-lexical items (Howard et al., 1992; Joubert et al., 2004; Mayall, Humphreys, Mechelli, Olson, & Price, 2001; Petersen, Fox, Snyder, & Raichle, 1990; Price et al., 1994; Pugh et al., 1996). We chose a visual matching task because it was intuitively similar to phonological matching (homophone decisions) and semantic matching (synonym decisions) and it controlled for processes unrelated to reading including sustained attention, decision making and response selection. Across tasks, the number of “yes” and “no” responses was equal in all cases.

There were four versions of the experiment. The stimuli from each task were first divided in half creating two sets of different items to avoid repetition across the two testing sessions. Then within each set, items were divided in half again and TMS was assigned to one half of the items for one version and other half in the other version, ensuring that any effects of TMS were not simply due to item differences. The word stimuli used in the main task (96 trials plus 6 dummy trials in each task) ranged in length from 3 to 10 letters and were fully matched between TMS and no-TMS items for concreteness [$F(3, 178) = .71, p = .55$], familiarity [$F(3,180) = 1, p = .37$], imageability [$F(3,179) = 1.4, p = .24$], written word frequency [$F(3,186) = .54, p = .66$], number of letters [$F(3,188) = .29, p = .83$], and number of syllables [$F(3,188) = 1.6, p = .18$]. In other words, items in the phonological and semantic tasks were matched across the four versions as well as within the two versions of each task. In addition, consonant strings were matched in length to the lexical stimuli. These consisted of five letter strings that were either identical (e.g., msxqr – msxqr) or differed only in the middle letters (e.g., bztgj – bwrcj) so that matching could not rely solely on the initial or final

letter. The order of the tasks within each version was counterbalanced across subjects. The order of the testing sites was counter-balanced across participants.

The experiment was presented in 12 blocks (6 per session) of 24 trials each to minimize task-switching costs. Each session was divided into two runs of three blocks with each run lasting approximately 3 min 40 sec. In between runs, subjects took a self-paced break. Each block started with a short instruction screen to remind the participant of the task. An extra “dummy” item was used for the first trial in each block and discarded from the analysis to avoid the RT cost of switching tasks. The remaining 24 items in the block constituted the data used for further analysis. A trial began with a fixation cross displayed for 500 ms and then stimuli presentation for another 500 ms. A blank screen was then presented for a random interval between 1300 and 2300 ms, giving an average duration of 2500 ms per trial. The stimulus presentation characteristics and button press responses were identical to those used during localization. Testing started with a practise run without TMS to familiarize participants with the task requirements. It included all three tasks and provided practice in switching between them. Each word was only used once in the experiment. Response times were recorded from the onset of the stimuli and only correct responses were analysed. In all statistical analysis, median RTs were used to minimize the effects of outliers (Ulrich & Miller, 1994).

The three hypotheses associated with IPL contributions to visual word recognition make different predictions regarding the effects of TMS. If one or both fields of the IPL store orthographic word forms then TMS to that region(s) should affect both lexical tasks equally because both use highly familiar words. Similarly, if stimulation affects both tasks but the effect is exaggerated in the phonological task, it would indicate that the IPL plays an important role in converting orthographic into phonological information. In contrast, if ANG and SMG contribute to semantic and phonological processing, respectively, we expected to

observe a three-way interaction where rTMS to ANG affects semantic but not phonological judgements and rTMS to SMG affects phonological but not semantic judgements.

Transcranial Magnetic Stimulation

Stimulation was performed using a Magstim Rapid² stimulator (Magstim, Carmarthenshire, UK) and 70-mm diameter figure-of-eight coil. The stimulation intensity was set to 55% of the maximum stimulator output and held constant for all subjects. During the localizer and main tasks, trains of five pulses (i.e., 10 Hz for 500 ms) were delivered with the first pulse administered at the onset of the stimulus presentation and the additional pulses occurring at 100, 200, 300, and 400 ms post-stimulus onset in half of all trials. TMS and non-TMS trials were pseudorandomly ordered. The TMS frequency, intensity, and duration were well within established international safety limits (Rossi, Hallett, Rossini, & Pascual-Leone, 2009; Wassermann, 1998). During testing, a Polaris Vicra infrared camera (Northern Digital, Waterloo, ON, Canada) was used in conjunction with the Brainsight frameless stereotaxy system (Rogue Research, Montreal, Canada) to register the participant's head to their own MRI scan in order to accurately target stimulation throughout the experiment. All participants used an earplug in their left ear to attenuate the sound of the coil discharge and avoid damage to their hearing (Counter, Borg, & Lofqvist, 1991).

RESULTS

Functional localization

For each localizer task, median RTs to TMS and no-TMS conditions were compared between the main testing site and non-localized sites. In 12 out of 16 participants, TMS led to successful identification of the main testing site within both ANG and SMG. There was no

single ANG or SMG site where stimulation consistently interfered with semantic or phonological processing, respectively. Instead, it varied across individuals as illustrated in Figure 1. Within ANG, the most common stimulation site was Seghier et al.'s (2010) dorsal ANG [7 participants], followed by ventral ANG [3 participants], and then medial ANG [2 participants]. These three locations are marked with white circles and labelled with the number of subjects slowed by TMS at each site. The right panel shows the spread of SMG stimulation sites – individual testing sites are shown as white filled circles. The mean coordinate in standard space was $[-52 -34 30]$ and is shown as a black filled circle.

Stimulation at each individual's ANG testing site produced a significant mean inhibitory effect of 47 ms relative to no-TMS trials [paired t-test; $t(11) = 6.4, p < .001$]. This represented a 7% slowdown after normalizing for between-subject variance in RTs (Loftus & Mason, 1994). In contrast, stimulation of the other ANG sites resulted in a non-significant 7 ms facilitation effect [paired t-test; $t(11) = .65; p = .53$]. To test whether this apparent difference was statistically reliable, we conducted a 2×2 repeated-measures ANOVA with TMS (TMS vs. no TMS) and Site (main testing site vs. the non-testing sites) as within-subject factors. A significant TMS \times Site interaction ($F(1,11) = 21.6, p < .001$) indicated that the effect of TMS on the non-localized sites was reliably different from the main testing site (see online Supplemental Materials). A similar pattern of localization was observed in SMG, where stimulation led to a significant 35 ms increase of RTs in the localized site [paired t-test; $t(11) = 6.5, p < .001$] and represented a 5% slowdown in RTs. In the remaining sites, stimulation produced a non-significant 4 ms decrease of RTs [paired t-test; $t(11) = .37, p = .72$], that was reliably different from the main testing site [TMS \times Site interaction, $F(1,11)=8.9, p = .01$]. In other words, in these 12 participants, the inhibitory effects of rTMS were highly localized with clearly different effects on the final testing site than on adjacent stimulated regions located as little as 1 cm away.

In the remaining 4 participants, functional localization only succeeded in one of the two regions (2 in ANG, 2 in SMG). Without a testing site in both regions, however, we were unable to continue testing these participants in the main experiment.

Main experiment

The mean accuracy across the tasks was relatively high (89%) suggesting that participants did not encounter any difficulties performing the tasks. Accuracy data were analyzed with a $2 \times 3 \times 2$ repeated measures ANOVA with Site (ANG and SMG), Task (Semantic, Phonological, and Visual), and Stimulation (TMS and no-TMS) as independent factors. There was a significant main effect of Task [$F(2, 22) = 13.02$; $p < .01$], indicating that the semantic task (85%) was significantly more difficult than either phonological (92%; paired t-test, $t(47) = 4.7$, $p < .001$) or visual (89%; paired t-test, $t(47) = 2.7$, $p < .01$) tasks. However, there was no evidence that accuracy in any of the three tasks was affected by TMS since neither the main effect of TMS [$F(1,11) = .04$, $p = .85$] nor its interaction with Task [$F(2,22) = .2$, $p = .82$] was significant. No other main effects or interactions were significant (all $F < 1$).

To investigate the effects of TMS on RTs, the median RTs of each participant were also analysed with a $2 \times 3 \times 2$ repeated measures ANOVA and the results are presented in Figure 2. The analysis revealed a main effect of Task [$F(2,22) = 29.3$, $p < .001$], indicating that responses on the semantic task (777 ms) were significantly slower than on the phonological task (723 ms; $t(47) = 5.3$, $p < .001$) and the visual task (636 ms; $t(47) = 10.7$, $p < .001$). The main effect of TMS also reached significance [$F(1,11) = 5.6$, $p = .04$] indicating that RTs in TMS condition (745 ms) were significantly slower than response times in no-TMS condition (734 ms). This was, however, qualified by a highly significant three way

interaction [$F(2,22) = 15.8, p < .001$], indicating that TMS affected the semantic, phonological, and visual tasks differently depending on the stimulation site.

Insert Figure 2 here

To characterize the interaction further, a 2×2 repeated measures ANOVA was conducted for each task with Site (ANG and SMG) and Stimulation (TMS and no-TMS) as independent factors. For the semantic task, the main effects of Site and TMS were not significant (both $F(1,11) < 1$). There was, however, a reliable interaction ($F(1,11) = 18.0, p < 0.001$) indicating that TMS had differential effects depending on the stimulation site (Figure 2). Specifically, stimulation to ANG slowed responses by 48 ms (paired t-test, $t(11) = 3.1, p = 0.01$) whereas SMG stimulation speeded responses by 24 ms (paired t-test, $t(11) = -1.8, p = 0.096$). The opposite pattern was observed in the phonological task where stimulation of SMG selectively slowed responses by 47ms ($t(11) = 2.7, p < .05$) while ANG stimulation speeded responses by an average of 5 ms ($t(11) = 0.5, n.s.$). This difference was confirmed statistically by a significant Site \times TMS interaction ($F(1,11) = 7.8, p = 0.017$) in the absence of a significant main effect for either Site ($F(1,11) = 0.8, n.s.$) or TMS ($F(1,11) = 3.9, p = 0.073$). Finally, TMS had no significant effects on the visual task; neither the main effects nor interaction (all $F(1,11) < 1.8, p > 0.2$) were significant.

Discussion

The current findings show that stimulation to the left ANG slowed semantic, but not phonological, judgements whereas stimulation to the left SMG showed the opposite pattern, selectively affecting responses in the phonological, but not semantic task. Moreover, the visual task was not significantly affected by stimulation, confirming that the effects of TMS

were specific to these semantic and phonological processes. These results demonstrate a functional double dissociation within the left IPL and additionally provide evidence for a causal link between ANG and semantic processing, on the one hand, and between SMG and phonological processing, on the other. These findings are consistent with previous studies that found TMS of SMG increased response times across a range of phonological tasks including initial sound similarity, stress assignment in multi-syllable words, and digit span (Romero, Walsh, & Papagno, 2006), syllable counting (Hartwigsen et al., 2010), and auditory lexical decisions (Pattamadilok et al., 2010). In contrast, evidence that TMS to ANG influences semantic processing is less common. For instance, Hartwigsten et al. (2010) asked participant to judge the animacy of auditory and written words (e.g., “zebra”) and did not observe any significant effects of ANG stimulation. Other studies have used TMS to map eloquent cortex in preparation for neurosurgical intervention and reported small effects of ANG stimulation on picture naming abilities (Krieg et al., 2014; Lioumis et al., 2012; Picht et al., 2013) that may be due to semantic disruption, although other explanations exist. Thus the current findings are the first to demonstrate a clear effect of ANG stimulation on semantic processing. More generally, this double dissociation between different cortical fields of the inferior parietal lobule is largely inconsistent with claims that the IPL stores the visual forms of words or that the region is responsible for converting orthographic information into phonological codes, but was predicted by the third hypothesis.

According to the original Dejerine (1891) hypothesis, stimulation of ANG should interfere with both the semantic and phonological tasks by temporarily disrupting the ability to match visual input with the stored images of words. Instead, ANG stimulation selectively affected the semantic task without significantly affecting the phonological task. Clearly, these results are not compatible with this hypothesis even if SMG, rather than ANG, was the site of stored visual word forms.

The relation between the data and the second hypothesis is less clear, in part because the interpretation is theory-dependent. Many theories of visual word recognition assume that access to a word's meaning is only possible by first accessing its phonology (R. Frost, 1998; Van Orden et al., 1988). If correct, then the current results are incompatible with this hypothesis because both tasks required orthographic-to-phonological conversion. Alternately, some theories suggest that semantic information is available directly from the written word without accessing phonology (Seidenberg & McClelland, 1989; Ziegler, Benraïss, & Besson, 1999), although they acknowledge that in normal, healthy adults semantic and phonological information would be accessed in parallel and moreover, that these processes interact. According to these accounts, the phonological task would *require* orthographic-to-phonological conversion but even the semantic task would involve converting spelling-to-sound and consequently disruption of this process should still have an impact on reaction times. If these procedures were associated with the SMG (Jobard et al., 2003; Law et al., 1991; Roux et al., 2012), this would be consistent with the fact that TMS to SMG significantly slowed responses in the phonological task but inconsistent with the finding that TMS actually facilitated responses in the semantic task, albeit non-significantly. It is also worth noting that this hypothesis would only explain one half of the double dissociation seen here.

A wide range of neuroimaging studies implicate SMG in phonological processing (Booth et al., 2004; Petersen et al., 1988; Raizada & Poldrack, 2007; Seghier et al., 2004; Yoncheva, Zevin, Maurer, & McCandliss, 2010; Zevin & McCandliss, 2005), consistent with the current TMS findings. By this account, reading tasks that engage SMG do so because they require phonological processing, not because spelling-to-sound conversion procedures are stored here. More specifically the SMG may be important for covertly articulating and monitoring inner speech (Pattamadilok et al., 2010; Price, 2012). This ability is a core

component of verbal working memory (Baddeley, 2003) and strongly associated with SMG, as well as the ventral premotor cortex (Buchsbaum & D'Esposito, 2008; Paulesu, Frith, & Frackowiak, 1993). Given its proximity to the caudal parabelt fields of the auditory cortex (Hackett, Preuss, & Kaas, 2001; Sweet, Dorph-Petersen, & Lewis, 2005), SMG is likely to encode some form of higher order auditory information. In contrast, neurons in ventral premotor cortex control oro-facial movements of the lips, tongue and larynx, playing an important role in articulation (Petrides, Cadoret, & Mackey, 2005; Sereno & Dick, 2008). Reciprocal connections between these regions via the third branch of the superior longitudinal fasciculus (Catani, Howard, Pajevic, & Jones, 2002; Makris et al., 2005; Martino et al., 2013) implement a reverberating sensory-motor circuit or, in other words, a verbal working memory. Indeed, TMS to either region has a disruptive effect on phonological judgements that require some form of monitoring internal speech (Gough, Nobre, & Devlin, 2005; Hartwigsen et al., 2010; Nixon, Lazarova, Hodinott-Hill, Gough, & Passingham, 2004; Pattamadilok et al., 2010; Sliwinska, Khadilkar, Campbell-Ratcliffe, Quevenco, & Devlin, 2012). Consequently, we suggest the most likely explanation for the current SMG findings is that stimulation interfered with participants' ability to covertly articulate and monitor their inner speech, which was critical for the phonological tasks and irrelevant to the semantic tasks.

A different explanation is necessary to account for the fact that ANG stimulation selectively affected synonym judgements presumably by interfering with some aspect of semantic processing. Functional neuroimaging studies consistently demonstrate ANG involvement in semantic processing (Binder et al., 2009; Bonner, Peelle, Cook, & Grossman, 2013; S. J. Frost et al., 2005; Mummery et al., 1998; Noonan, Jefferies, Visser, & Ralph, 2013; Seghier et al., 2010; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996), although there is a debate regarding its specific contribution. One claim is that the region

represents conceptual information as part of a larger, anatomically distributed system (Binder et al., 2009) while another suggests that ANG's role in the distributed semantic system is to guide the selection of relevant semantic information (Whitney, Kirk, O'Sullivan, Ralph, & Jefferies, 2011). Both of these processes contribute to our synonym task and thus the current findings cannot distinguish between them. All we can say is that ANG has a causal role in semantic processing and that further work will be necessary to elucidate the specific processes involved.

This functional double dissociation of phonological and semantic processing within IPL is in accordance with anatomy of this region. For instance, a recent parcellation study subdivided IPL into two functionally distinct regions using a new scheme combining resting-state functional connectivity MRI with fMRI data related to memory-retrieval (Nelson et al., 2010). The anterior and posterior parts of IPL, corresponding to SMG and ANG respectively, displayed distinct retrieval success effects demonstrating a clear functional dissociation between these regions. In addition, SMG and ANG differ in both their cytoarchitectonic structure and connectivity profiles, consistent with separate functional properties. The two areas essentially correspond to Brodman's (1909) areas 40 and 39, von Economo and Koskinas's (1925) areas PF and PG, or to von Bonin & Bailey's (1947) PF and PG areas (Caspers et al., 2008; Caspers et al., 2006), respectively. Critically, the two regions have distinct patterns of connectivity and thus participate in separable functional circuits (Caspers et al., 2011; Göbel, Rushworth, & Walsh, 2006). Specifically, SMG has strong reciprocal connections with pars opercularis and ventral premotor cortex via the third branch of the superior longitudinal fasciculus (Makris et al., 2005; Martino et al., 2013). This fronto-parietal circuit plays a key role in verbal working memory (Buchsbaum & D'Esposito, 2008; Romero et al., 2006) and in phonological processing more generally (Demonet et al., 1994; Devlin et al., 2003; Mummery et al., 1998; Price et al., 1997). In contrast, ANG sits at the

posterior end of the middle longitudinal fasciculus, linking it with middle and anterior temporal lobe regions involved in semantic memory (Binder et al., 2009; Makris et al., 2009; Price, 2010). These cortico-cortico connectivity patterns presumably explain the observed double dissociation between phonological processing in SMG and semantic processing in ANG.

It is worth introducing a word of caution here regarding the anatomical specificity of the current findings. Although we have discussed them in terms of the two major subdivisions of the inferior parietal lobule, namely SMG and ANG, our results are actually more focal than that. A great advantage of using TMS as an investigative tool is its spatial precision, which is approximately 5-10mm (Brasil-Neto et al., 1992; Ravazzani, Ruohonen, Grandori, & Tognola, 1996; Thielscher & Kammer, 2002; Toschi, Welt, Guerrisi, & Keck, 2008). In other words, although the basic pattern of SMG stimulation slowing phonological, but not semantic, processing while ANG stimulation slowed semantic, but not phonological, processing the specific stimulation sites varied between participants. Moreover, within a participant, different sites within a region responded differently during localization (see the online supplemental materials at http://www.neurolang.com/wp-content/uploads/2014/08/Sliwinska_2014_Supplemental.pdf). As a result, we cannot rule out the prospect that within a region it may be possible to find two different sites that show this same pattern. Instead, all we can conclude is that the current findings are consistent with functional and structural neuroimaging studies that suggest these two regions broadly serve different functions (Göbel, Walsh, & Rushworth, 2001; Nelson et al., 2010; Rushworth, Johansen-Berg, Göbel, & Devlin, 2003) by virtue of participating in separable neuronal circuits (Caspers et al., 2011; Rushworth, Behrens, & Johansen-Berg, 2006).

Finally, our results show considerable variability in the exact localization of testing sites within ANG and SMG across participants. Although Seghier et al. (2010) identified

three separable regions within ANG involved in distinguishable semantic processes (i.e., semantic associations, search for semantics, and conceptual identification), these appear to be trends present in groups of participants rather than predictive of individuals. We observed considerable inter-subject variability in the precise location within ANG where TMS disrupted semantic processing and also within SMG where it affected phonological processing, similar to variability in the localization of language functions described by Ojemann et al. (1989) in neurosurgical patients. In both the neurosurgical work and the current study, the disruptive effects of stimulation were very focal ($\leq 1\text{cm}$) and certainly did not extend to cover a significant portion of a macroanatomical region (e.g., SMG), suggesting that large activations in functional neuroimaging studies can be somewhat misleading. Clearly they demonstrate a reliable overall pattern of activation at a fairly large scale (cms) but these hide considerable inter-subject variability in terms of the precise anatomical fields. In other words, it is important to recognize that the results of group imaging studies represent a spatial averaging that may not be predictive in individuals. This, presumably, is why using published “peak coordinates” to guide TMS studies can be problematic and require larger numbers of participants than using an individualized functional localization method (Sack et al., 2009). More generally, it means that descriptions linking function to macro-anatomical labels may be broadly correct on aggregate, but not in detail.

To conclude, this study showed that the two main subdivisions of the left IPL make distinct functional contributions to visual word recognition. On average, ANG plays crucial role in semantic processing while SMG is necessary for phonological processing during reading. It is worth stressing, however, that our results apply to only specific parts of these large anatomical regions and moreover, that the precise location varies somewhat from person to person. Nevertheless, the findings are consistent with pattern seen in functional neuroimaging

studies and help to demonstrate that these activations appear to be causally linked to semantic and phonological processing in ANG and SMG, respectively.

Figures and figure legends:

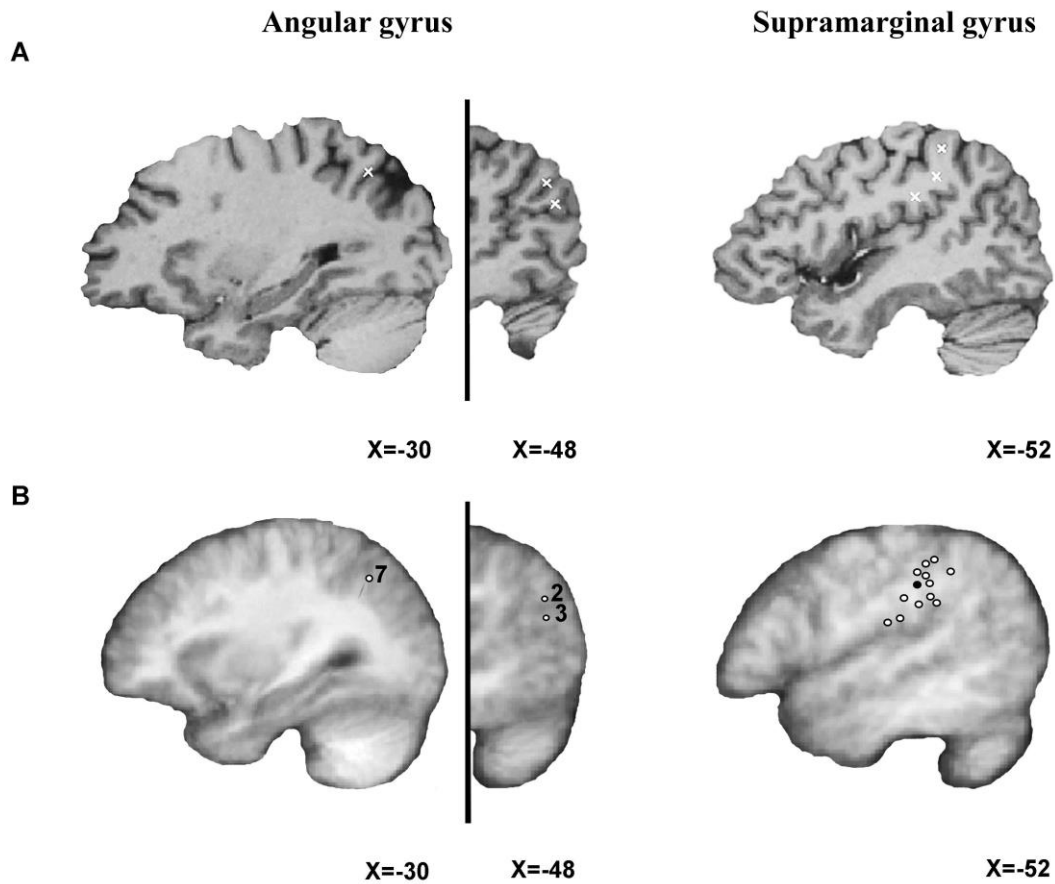


Figure 1: Stimulation sites in ANG and SMG. (A) Three possible stimulation targets marked within each participant's left ANG (left panel) and left SMG (right panel) using a frameless stereotaxy system. (B) The three ANG testing sites (left panel) on the same averaged brain. 7 participants had stimulation to dorsal, 3 to ventral, and 2 to medial ANG. The final SMG testing sites for all 12 participants (right panel) in white filled circles and the mean group location in black filled circle on the averaged brain of all participants shown on a parasagittal plane. Note that three ANG testing sites had exactly the same coordinates in each participant so they are represented only by three circles.

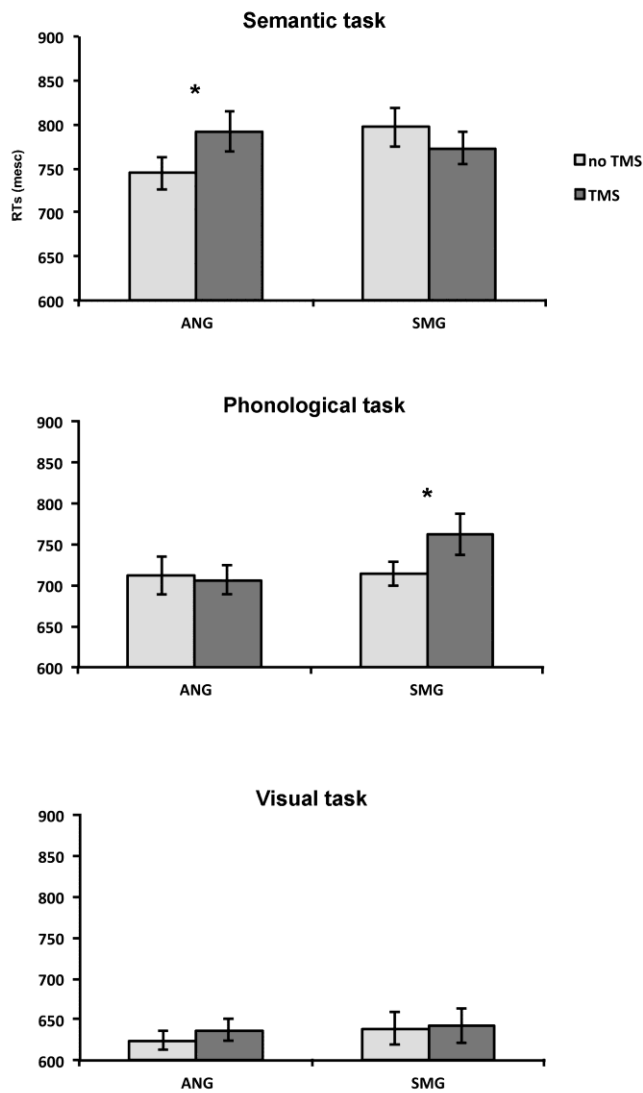


Figure 2: Group mean reaction times (RTs) for each of the three tasks in the main experiment. Error bars indicate SEM adjusted to reflect the within-subject design (Loftus & Masson, 1994). * $p < 0.05$.

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