Activation of the Posterior Cingulate by Semantic Priming: A Co-Registered ERP/fMRI Study

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Abstract

While the N400 is the best understood semantically sensitive component of the event-related potential (ERP), others have been observed as well. In an earlier lexical decision study, an N300 event-related potential (ERP) was found to be enhanced to unprimed targets, although the effect could also be characterized as a prolonged P2 to primed targets as described in other reports. Since its scalp topography suggested its neural source might be of interest, a source localization was conducted that suggested that this component emanated from the dorsal posterior cingulate cortex (dPCC). In order to confirm this word N300 localization, a functional magnetic resonance imaging (fMRI) study was conducted to replicate the ERP study with a separate sample of 17 participants in an event-related design, using a 3T scanner. A significant activation in the right dPCC was found corresponding to the N300 localization. The activation was greater on the related prime trials, supporting the characterization of the ERP component as being a P2 rather than an N300. A review is provided which suggests that a number of separate lines of ERP research regarding the word N300, the picture N300, the word P2, the phonological mismatch negativity, and the word midline frontal negativity may be most parsimoniously regarded as dealing with the same ERP component and that they all therefore emanate from the dPCC. It is suggested that this region plays a role in stimulus-response mapping in polymodal fashion. It is also suggested that the ERP component be termed a P2-dPCC.

Section: Cognitive and Behavioral Neuroscience

Keywords: Event-Related Potentials, Posterior Cingulate, Functional Magnetic Resonance Imaging, Semantic Priming, Source Localization

1. Introduction

1.1 Semantic ERP Components

One of the chief tools for investigating the neural basis of semantics has been the N400 response, a component of the event-related potential (ERP) that is sensitive to deviations from the current semantic context (Kutas & Federmeier, 2000; Kutas & Hillyard, 1980), as in semantic priming tasks. Semantic priming is said to have occurred when a stimulus is recognized more quickly or accurately because of prior exposure to another related stimulus. A common semantic priming paradigm is the lexical decision task in which the participant decides whether a letter string is a word (Meyer & Schvaneveldt, 1971). If the target is a word, it will be recognized more quickly if it is preceded by a related word than if it is preceded by an unrelated word. Even the simple lexical decision task can involve multiple semantic processes (McNamara, 2005; Neely, 1991), let alone the more complex case of sentence comprehension. Given the complexity of language processing, there has been increasing interest in whether other ERP components might provide additional insights into semantic processing.

It was therefore of interest when a recent study of semantic priming reported an additional semantic effect, dubbed an N300, in addition to the N400 (Franklin, Dien, Neely, Waterson, & Huber, 2007). An N300 component was first noted in a picture-matching task where it was larger for mismatches (Barrett & Rugg, 1990). It has been suggested it might reflect a system dedicated to processing semantics of pictures (Barrett & Rugg, 1990) or integrating pictorial-semantics into higher-level representations (McPherson & Holcomb, 1999). However, the finding that an apparently identical N300 can be observed in a word stimulus experiment (Franklin, Dien, Neely, Waterson, & Huber, 2007) with a scalp topography very similar to the picture N300 as seen in a report using the same recoding equipment (Hamm, Johnson, & Kirk, 2002) suggests that the picture N300 may not be specific to pictures. If it proves to be the case that the word N300 and the picture N300 component are the same, then the hypothesis that the picture N300 reflects a picture-specific semantic process (Barrett & Rugg, 1990; McPherson & Holcomb, 1999) would have to be revised.

Furthermore, there have also been reports in other visual word experiments of a similar-looking component which has variously been termed part of an N330 (Nobre & McCarthy, 1994), an N310 (Hill, Ott, & Weisbrod, 2005; Hill, Strube, Roesch-Ely, & Weisbrod, 2002), and a mid-frontal negativity or MFN (Frishkoff, Tucker, Davey, & Scherg, 2004; Frishkoff, 2007). These appear to be the only current reports of such an N300 to words, which is not surprising since in all three cases it required careful topographic analysis of high-density data to clearly distinguish from the N400; without such an examination it can appear to be simply an anterior portion of the N400 effect. Note that this midline N300 is different from an N300 that has a left anterior temporal scalp distribution and is larger for related, rather than unrelated, words (Dien, Frishkoff, Cerbone, & Tucker, 2003; Frishkoff, 2007; Nobre & McCarthy, 1994).

It is not known at this point exactly what the word N300 (and the picture N300) reflects, other than being sensitive to semantics under some circumstances. In the preceding ERP study (Franklin, Dien, Neely, Waterson, & Huber, 2007) there was a trend towards it being more significant for a 500 ms stimulus onset asynchrony or SOA (not significant for the short 150 ms SOA when tested separately), suggestive of it reflecting a controlled process rather than automatic spreading activation (ASA). Also, one of the MFN studies, which may or may not be the same as the word N300, reported finding it to be stronger for long versus short SOAs (Frishkoff, 2007). On the other hand, a different lexical decision study (Hill, Strube, Roesch-Ely, & Weisbrod, 2002) reported that the word N300 was only significant for a short SOA condition (without explicitly testing the priming effect for an interaction with SOA) and suggested it therefore reflected ASA (but see Hill, Ott, & Weisbrod, 2005).

Another putative component may provide more information. A number of studies (Barnea & Breznitz, 1998; Carreiras, Vergara, & Barber, 2005; Landi & Perfetti, 2007; Liu, Perfetti, & Hart, 2003) have reported a P2 effect that upon close inspection (as helpfully pointed out by a reviewer of this manuscript) has the same appearance as the N300 effect (see also Coulson, Federmeier, Van Petten, & Kutas, 2005). It is often difficult to determine whether an ERP effect is an enhanced negativity in one condition or an enhanced positivity in the other and this one seems to be particularly ambiguous. Furthermore, the long duration of this effect (starting close to the peak of the P2 but extending past the P2, on to the end of the N400) makes it hard to determine its peak latency. Although the original reports (Barnea & Breznitz, 1998; Carreiras, Vergara, & Barber, 2005; Liu, Perfetti, & Hart, 2003) implicated the P2 effect in phonological processing, the most recent report (Landi & Perfetti, 2007) found P2 effects in a semantic task as well, leaving its nature unclear. Given the close correspondence between the P2 and the word N300 effects in terms of scalp topography, time course, and semantic effects, this manuscript will make the parsimonious assumption that it is the same component, although one report (Landi & Perfetti, 2007) made the unsupported observation that the P2 effect was not as frontal as the MFN (Frishkoff, Tucker, Davey, & Scherg, 2004; Frishkoff, 2007).

A source analysis of the P2 effect using LORETA placed it in the right hemisphere prefrontal region in the vicinity of BA 6 and 8 (Liu, Perfetti, & Hart, 2003) whereas the MFN appeared to localize to the anterior cingulate (Frishkoff, Tucker, Davey, & Scherg, 2004; Frishkoff, 2007) using BESA. These contrasting effects could indicate that they are different components (Landi & Perfetti, 2007) or it could reflect differences in the source analysis procedure. The source of the effect or effects would be important both for helping determine whether these are the same component and for interpreting their nature. For example, the anterior cingulate is a region of great current interest in studies of executive function (Bush, Luu, & Posner, 2000; Holroyd & Coles, 2002; Isomura & Takada, 2004; Posner, & Rothbart, 1991; Rushworth, Walton, Kennerley, & Bannerman, 2004).

1.2 Experimental Design Issues

The present study was therefore conducted to perform source analysis on the N300 and to try to confirm results with an fMRI replication. In order to maximize comparability with the ERP dataset, the same experimental design in all respects was utilized. This was done with the recognition that the original N300 finding was a serendipitous observation made in a study (Franklin, Dien, Neely, Waterson, & Huber, 2007) designed to contrast backward and forward associative priming. The effect was observed primarily for symmetrically related filler pairs that were included to establish desired listwise parameters for the task. These symmetric pairs were conventional semantically related items (both associative and semantic features) and were not matched to the asymmetric items since they were not originally intended to be analyzed. Although it might be of interest to also be able to analyze the backward and forward pairs, existing datasets (e.g., Dien, Franklin, Michelson, Lemen, Adams, and Kiehl, in press) show that the N300 effect is not always present (an argument against it reflecting ASA) and thus appears to be controlled by as yet undetermined parameters. Thus, changing the stimulus list could potentially eliminate the subject of interest. There was also the concern that increasing the number of backward and forward priming trials would lengthen the experiment past the session time available. The decision was therefore made to proceed with the project using the current experimental design rather than let it be possibly derailed by this side interest.

The only comparison of *a priori* interest is that of the symmetrical v. unsymmetrical word pairs, based on the ERP results. The forward and backward pairs are not compared with the symmetric pairs because they are not of primary interest and are not properly matched either in terms of number of stimuli or psycholinguistic parameters. Furthermore, there are too few of them to provide sufficient statistical power for the present fMRI analyses (although they did yield some effects of interest for the ERP analyses, for which more subjects could be collected). The forward and backward priming pairs were included in the stimulus set solely to maximize correspondence with the ERP dataset due to concern that changing the stimulus set could possibly adversely affect the N300 effect and are treated as filler pairs for the purposes of the present analysis. To confirm that nothing of interest was being overlooked, however, the forward-related v. forward-unrelated and backward-related v. backward-unrelated contrasts were examined.

There is a need to first consider the co-registration strategy implemented in this study. The first issue is whether it is preferable to collect data concurrently or in separate samples. There are both advantages and drawbacks to each approach. The chief advantage of collecting the data concurrently is that it eliminates any concern that the data might not be comparable due to differences in the sample or in the context of the experimental sessions. On the other hand, effects that do not generalize out of the scanner setting or the sample would be of reduced interest to ERP researchers. Drawbacks to concurrent collection also include strong electroencephalographic (EEG) artifacts induced by the rapidly alternating magnetic fields, loss of expensive fMRI data when the corresponding ERP data prove to be unusable (especially likely due to the

EEG scanner artifacts and the weight of the prone head on the electrodes), and longer fMRI scanning sessions (that again increases the costs). Thus, concurrent collection risks both higher costs and reduced data quality compared to that obtained when separate recording sessions are used. This report therefore takes the approach of optimizing data quality via separate recording sessions, with the caveat that divergent results must be taken skeptically; conversely, results that converge point towards robust generality even under differing experimental contexts and samples.

Another issue is whether it is even reasonable to expect that results might correspond across two such very different recording modalities. An initial examination of this issue in an animal model (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001) reported that both electrophysiological and fMRI data reflect the same aspect of neuronal activity, the modulation of dendritic inputs. Although there was a subsequent report that they did not correspond linearly (Devor et al., 2003), it has been reported that linearity is a reasonable approximation for their relationship (Sheth et al., 2004); furthermore, it has been reported that these non-linearities are primarily observed when rats are anesthetized, not awake (Martin, Martindale, Berwick, & Mayhew, 2006), consistent with reports in awake humans (Arthurs & Boniface, 2003).

While findings overall support the feasibility of identifying corresponding effects in ERP and fMRI data, reports suggest that the relationship may have a number of subtleties. For example, it has been reported that attentional distraction can reduce the fMRI response to somatosensory stimuli without reducing the ERP response that is thought to originate in the same region (Arthurs, Johansen-Berg, Matthews, & Boniface, 2004), although it is possible that this observation is instead an indication that they do not in fact correspond. It has also been reported in humans that ERP and fMRI relationships may not be the same in different cortical regions (Huettel et al., 2004).

Overall, these reports suggest that it is reasonable to seek correspondences between the two data modalities but reinforces the normal hesitancy to interpret null effects.

A final issue is the strategy for localizing the ERP activity prior to the co-registration process. Two difficulties that are encountered when trying to perform source analysis (with point equivalent algorithms) is that specifying the wrong number of dipoles (Achim, Richer, & Saint-Hilaire, 1991) or the presence of overlapping ERP components (Zhang & Jewett, 1993) can lead to substantial localization errors. The strategy pursued here is to try to isolate the ERP component using principal components analysis (PCA), a procedure that addresses both these issues. Results with both simulation datasets (Dien, Khoe, & Mangun, 2007) and real data (Dien, Spencer, & Donchin, 2003) suggest that it can be an effective approach. Although it is also possible to use a combination of expert judgment and appropriate experimental manipulations to generate compelling source solutions (e.g., Scherg, Vajsar, & Picton, 1989), it is suggested that a procedure that can be more readily replicated by others is preferable.

It is the experience of the present experimenters that using PCA does not by any means guarantee success. A simple guideline for identifying a promising source solution is that the residual variance (the amount of the waveform not accounted for by the source solution) should be no more than 10%. Furthermore, another guideline is that even a good fit should be considered skeptically if the equivalent dipole is located at a deep level, such as the brain stem, since, in the experience of the present authors, the broadly distributed scalp topographies corresponding to such solutions allow for a very wide range of locations that still meet the 10% criterion. Finally, it should be recognized that point equivalent dipole solutions correspond to the location of the generator if it is a dimensionless point; the point solution therefore corresponds to a set of more superficial solutions with increasingly wider circumferences along the line determined by the orientation of the dipole (Scherg & Von Cramon, 1986). To be a plausible solution, a suitable cortical surface should be positioned along the line ranging from the point to the surface of the skull.

Because there is not a current consensus on how to evaluate confidence intervals for such point equivalent dipole solutions, the procedure was adopted of only evaluating the best fit location for the source solution and only judging the fit a success if it was located in relatively close proximity to an appropriate fMRI activation. The decision was therefore made to avoid the common practice of seeding the dipole locations according to fMRI activations out of concern that it might allow too much latitude for correspondence. Seeding also has the drawback that doing so ignores the point source nature of point equivalent dipoles; for anything other than an activation with zero radius (impossible of course), seeding the dipole within the fMRI activation area is likely to be inappropriate. Instead, we followed the procedure of deriving the best fit location and then tracing the line from the point location to the cortical surface along the line of the dipole orientation to determine if an fMRI activation lay along this line; such a procedure is more consistent with the nature of point equivalent dipole solutions.

Whereas the lack of a significant fMRI activation at the location of the source solution would not be interpretable for a number of reasons already considered, as well as due to the always present possibility of a Type II error due to insufficient statistical power, it is suggested that the presence of correspondence would provide strong support for the N300 source solution as well as the status of the word N300 as being a genuine ERP component separate from the N400. In doing so, it should be noted for the ERP readership that fMRI analyses (using SPM) incorporate strong multiple comparison controls.

1.3 Experimental Design Summary and Goals

To summarize, the same lexical decision task paradigm as the previous ERP study was used (Franklin, Dien, Neely, Waterson, & Huber, 2007), using only the long SOA (500 ms) condition. Thus, backward associative, forward associative, and symmetrical associative+categorical prime pairs were utilized. The focus of analysis is the symmetrical priming contrast that was significant for the ERP data. The intention is to leave the issues regarding ASA, SOA, and priming type for future ERP studies. The first chief question is whether a source analysis of the word N300 effect (and thus potentially of the MFN and/or the P2 effects) could be verified with an fMRI replication, given the uncertainties of ERP source analysis methods. Potential sites are the anterior cingulate (Frishkoff, Tucker, Davey, & Scherg, 2004; Frishkoff, 2007) and dorsal prefrontal cortex (Liu, Perfetti, & Hart, 2003). The second chief question is whether the fMRI data could provide guidance as to whether the word N300 effect is indeed an enhanced N300 for unrelated targets or an enhanced P2 for related targets by determining the direction of the corresponding BOLD response. If a plausible source is identified, then the corresponding functional neuroanatomical literature will be utilized to generate a preliminary hypothesis for this ERP effect(s) that thus far has no specific cognitive function associated with it (them).

2. Results

2.1 Behavioral Data

A one-way repeated measure ANOVA was conducted for only correct “word” responses for participants’ reaction times to forward-related, forward-unrelated, backward-related, backward-unrelated, and symmetrical primes. Arithmetic means of the individual participants’ median RTs are presented in Table 1. It was found that the median reaction times for the individual prime types significantly differed, $T_{WJt}/c(4, 12.8)=8.90$, $p=.013$. Additionally, further analysis showed that there were significant priming effects for all three main analyses: forward-related vs. forward-unrelated, backward-related vs. backward-unrelated, and symmetrical vs. unsymmetrical ($T_{WJt}/c[1,14]=8.05$, $p=.016$; $T_{WJt}/c[1,14]=4.71$, $p=.046$; and $T_{WJt}/c[1,14]=36.74$, $p=.001$, respectively).

Similar results were found for the accuracy data in Table 2. It was found that the median accuracies for the individual prime types significantly differed, $T_{WJt}/c(4, 11.2)=8.32$, $p=.016$. There was a trend for forward priming and significant priming effects for backward and symmetric priming: ($T_{WJt}/c[1,14]=3.53$, $p=.082$; $T_{WJt}/c[1,14]=8.96$, $p=.014$; and $T_{WJt}/c[1,14]=16.53$, $p=.0011$, respectively).

2.2 ERP Data

There were three semantically sensitive ERP components reported in the original ERP experiment (Franklin, Dien, Neely, Waterson, & Huber, 2007): N300, N400, and N400RP. In the long SOA condition that was replicated in the present report, the N300 factor had a significant symmetric priming effect; in addition, the N400 factor had significant symmetric priming and forward asymmetric priming effects (Figure 1). The factor for the N400RP did not provide a clean (low residual variance) solution and will not be further considered.

Source localization of the factor accounting for the N300 ERP component from the original ERP experiment (Franklin, Dien, Neely, Waterson, & Huber, 2007) yielded a PCC location [+/-21 -37 27] with a solution that accounted for 95.5% of the variance (see Figure 2). The source solution was not noticeably lateralized, an observation that is not likely to be meaningful given the proximity of the two hemispheric dipoles to each other.

Source localization of the N400 factor yielded a subcortical location [+/-19 1 20], accounting for 98.9% of the variance. It was therefore not necessary to introduce additional dipole pairs in either case; as noted earlier, solutions requiring multiple dipoles are suspect in any case. The attainment of such a clean solution was the goal of the PCA procedure, in order to avoid the localization errors that arise when multiple dipoles are necessary (Zhang & Jewett, 1993). The results in both cases were independent of the starting location of the dipoles during the iterative fitting procedure.

2.3 fMRI Data

For the fMRI results, cluster-level analysis (corrected for multiple comparisons) revealed two significant activations for symmetric priming (Table 3). A bilateral cluster in the posterior cingulate was significant in the symmetric related versus unrelated contrast. Inspection of the topography of the cluster (see Figure 2) suggests that it consists of two major foci, corresponding to the first two locally most significant voxels in the cluster. The latter voxel tested as significantly right-lateralized in the follow-up region of interest (ROI) analysis. The latter corresponded most closely to the right dipole of the N300 source localization result (Figures 2 and 3). Conversely, the unrelated versus symmetric related contrast implicated the left inferior frontal gyrus (with the ROI surrounding the most significant voxel testing as significantly left-lateralized).

For forward priming, three clusters were observed (Table 3). The clusters were centered on the right lateral sulcus, the left prefrontal region, and the cerebellum. Only the second locally most significant voxel of the cerebellum cluster was significantly lateralized (to the left).

For backward priming, three clusters were observed (Table 3). The first was bilateral and encompassed the extrastriate visual cortex. The second cluster was located in the middle frontal gyrus. Although it was only marginally significant (p=.055), when examined at a voxel threshold of p = .01 it was quite significant. The ROI surrounding the third locally most significant voxel was significantly right-lateralized. The third cluster was marginally significant (p=.060) and remained marginally significant even at a threshold of p = .01.

Parametric analysis for symmetric related priming pairs (Table 4) revealed two clusters for total frequency of the pair. The first was located in the anterior cingulate and the ROI surrounding the second most locally significant voxel was right-lateralized. The second, located on the left inferior frontal gyrus, was not significantly lateralized. Parametric analysis for trial order revealed a number of significant clusters located in the parietal and the frontal regions, including significant right-lateralization for the frontal region and left-lateralization for the inferior parietal region.

No significant effects were found for any of the other parameters.

Additionally, an ROI analysis for the source localization of the N400 yielded no significant activations. No other effects were obtained (including at different threshold settings).

3. Discussion

Using a lexical decision task, a significant change in activity in response to symmetrically related versus unrelated word pairs was found in the dPCC. A right-lateralized portion of this cluster corresponds closely to the source analysis location for the word N300 component reported earlier by this lab (Franklin, Dien, Neely, Waterson, & Huber, 2007). Thus, the fMRI study fully bore out the prediction by the ERP data that there would be a PCC semantic priming effect. This study therefore suggests a possible role for the dPCC in semantic tasks. It also provides clues as to the functional significance of the N300/P2 effect, both in terms of the direction of the effect as well as the functional neuroanatomy. In addition, left inferior prefrontal cortex (LIPC) was observed for unrelated vs. symmetric related trials. Forward unrelated vs. related trials yielded activations in the right lateral sulcus, left prefrontal ranging from inferior to dorsolateral, and bilateral cerebellum. Backward unrelated vs. related trials yielded activations in the bilateral inferior occipital regions and right middle frontal gyrus and a trend towards the right superior frontal gyrus. A parametric analysis of the symmetric related trials found a negative correlation between frequency and the anterior cingulate and the LIPC. Finally, a parametric analysis with trial number yielded positive correlations with the right superior parietal lobe, the left frontal region, bilateral mid-frontal gyrus, and left inferior parietal lobe. No effects of imageability/concreteness were found. The following discussion on the N300/P2/dPCC is admittedly both speculative and post-hoc and is proffered on the grounds that a theoretical consideration and review of the matter will at least provide a useful starting point for further discussion and study.

3.1 Theoretical Interpretation of N300/P2 Effect

An important consequence of the fMRI co-registration result is that it strongly suggests that the effect in the present study is an enhancement of a P2 to related stimuli rather than an enhancement of an N300 to unrelated stimuli. Although the correspondence between ERPs and fMRI data is not absolute, the fMRI data are very suggestive and provide some guidance to an ERP component of otherwise ambiguous polarity. The remainder of this discussion will therefore characterize it as a P2. Using this observation as a starting point, one can therefore start developing a hypothesis as to its nature based on the ERP data and then the functional neuroanatomy results can be consulted for further insights.

Initial reports of the P2 effect seemed to suggest that it was phonological in nature. For example, the initial report (Barnea & Breznitz, 1998) found that the P2 was enhanced during a phonology (rhyming) judgment of Hebrew characters (by native speakers) but not in an orthography (same-different) task. A following study (Liu, Perfetti, & Hart, 2003) with Chinese speakers reported also finding P2 effects only in a phonology task (and not in a semantic task), but also an orthographic aspect in that the P2 was smaller when the characters were graphically similar. A further phonology study (Carreiras, Vergara, & Barber, 2005) reported a larger P2 for words presented in two differently colored halves when the division line did not coincide with a syllabic boundary versus when it did. It has also been reported that a P2 difference can be observed for orthographically regular vs. irregular exception words (Sereno, Rayner, & Posner, 1998), which could also reflect a phonological effect.

A recent study (Landi & Perfetti, 2007) indicates that the P2 effect can be observed in semantic studies as well. It presented word pairs with a 400 ms SOA and had participants perform a phonological task (rhyming) and a semantic relatedness task. There was a bigger P2 for related pairs for both the semantic and phonology tasks. Furthermore, it provided a useful contrast with the ERP data (Franklin, Dien, Neely, Waterson, & Huber, 2007) for the present study in that it used categorical (e.g., lemon-pear) and associative+categorical (e.g., cat-dog) pairs (as opposed to associative and associative+categorical pairs) and also found a larger effect for the associative+categorical pairs. This observation suggests that the effect reflects the associative relationship more than the categorical relationship, although a measure to ensure equivalent category relatedness is not available. The study also included a picture priming condition. Although it labeled the resulting effect an N400, the topography of the effect appeared to be similar to that found in the other conditions as well as to that found in picture N300 studies (more frontal than the typical N400).

In contrast, two picture priming ERP studies report that the picture N300 (likely the same as the P2 effect) is especially responsive to categorical relationships. A word-prime/picture-target study (Hamm, Johnson, & Kirk, 2002) in which the task was to silently name the picture reported that the picture N300, unlike the N400, only responded to between-category mismatches (e.g., "robin" - picture of collie) as opposed to within-category mismatches (e.g., "poodle" - picture of collie). This observation could be interpreted as phonological mismatches with the silently named picture (e.g., "poodle", expect a dog, see a collie, name "dog" to self). However, another study (Federmeier & Kutas, 2002) of picture priming, using sentence primes (e.g., "The firefighters wanted to have a mascot to live with them at the firehouse. Naturally, they decided it would have to be a dalmatian/poodle/zebra.") also reported an N300 that responded significantly more to between-category mismatches than within-category mismatches (it tested the difference between the two difference waves so it is unknown whether the within-category effect *per se* was likewise non-significant). This design is less consistent with a phonological account in that the mismatch types should be equally unlikely to be covertly voiced in advance. Although posed in terms of category effects, these findings could also be interpreted in terms of responsiveness to associative relatedness insofar as the within-category mismatches are likely to be more highly associated than the between-category mismatches.

Another line of research concerns an ERP component with striking similarities to the P2, the Phonological Mismatch Negativity or PMN. Although usually observed in studies using auditory stimuli (Connolly, Stewart, & Phillips, 1990; Connolly, Phillips, Stewart, & Brake, 1992; Connolly & Phillips, 1994; Connolly, Service, D'Arcy, Kujala, &

Alho, 2001; Phillips, Klein, Mercier, & de Boysson, 2006; Revonsuo, Portin, Juottonen, & Rinne, 1998), it has been shown to be evoked by visual stimuli as well (Connolly, Phillips, & Forbes, 1995). In the key studies using both auditory (Connolly & Phillips, 1994) and visual sentences (Connolly, Phillips, & Forbes, 1995), it was demonstrated that the PMN to the terminal word was responsive to the distinction between an incongruent ending with the same phoneme as the expected word and an incongruent ending with a different phoneme as the expected word whereas the N400 responded only to semantic congruency. It was therefore suggested that the PMN reflected expectations for the stimulus identity maintained at the phonological level.

Further studies have pointed towards a prelexical basis for the PMN effects. One such study (Connolly, Service, D'Arcy, Kujala, & Alho, 2001) demonstrated that the PMN effect was produced when participants were presented with a visual word, given a letter with which to modify it, and then told to anticipate an auditory word form that would begin with the letter and would rhyme with the visual word (e.g., house, m: mouse or telk, w: welk). The observation that the PMN was produced even for auditory non-words was further evidence that the effect was reflecting prelexical phonological level processes, contrary to competing accounts (Hagoort & Brown, 2000; van den Brink, Brown, & Hagoort, 2001; van den Brink & Hagoort, 2004) involving top-down semantic influences on lexical or semantic selection. A further study (Newman, Connolly, Service, & McIvor, 2003) reported a consonant deletion task in which participants were presented auditorally with two words in succession and asked to judge whether the second word was the same as the first word, minus the initial consonant (e.g., "clap" and "lap"). It was found that all incorrect stimuli, both word and non-word, elicited equivalent PMN responses regardless of whether they rhymed with the initial word, suggesting that the PMN reflects an all-or-none matching process.

There has been some contention over whether the PMN is a separate component from the N400. One study (Van Petten, Coulson, Rubin, Plante, & Parks, 1999) using auditory stimuli reported not finding a statistically separable PMN effect although a rebuttal (Newman, Connolly, Service, & McIvor, 2003) argued that even this dataset showed evidence of a separate PMN. Likewise, another study (Diaz & Swaab, 2007) reported not finding a separable PMN effect for sentences (although a possible effect in alliterative word lists). Such null effects, of course, may just reflect difficulty in separating the overlapping N400 from the PMN. The componentry analyses in these two studies were largely limited to visual inspections of the interpolated scalp topographies and ANOVAs of the windowed measures. Alternatively, it is possible that some aspect of their experimental designs differed in some critical manner that has not yet been identified. Given the clear evidence for frontal effects in repeated other studies, it seems more likely that the effect does exist and to proceed with efforts to characterize it.

In any case, the PMN appears to have the same scalp topography, time course, and pattern of experimental effects as the P2 and is therefore likely to be the same thing. Although there has been a tendency for visual studies to term frontal phonological effects a P2 and auditory studies to term frontal phonological effects a PMN, there has been a visual study in which such an effect has been termed a PMN (Connolly, Phillips, & Forbes, 1995). Although it is certainly possible that visual and auditory studies produce different phonological effects with apparently identical scalp topographies and time courses, the most parsimonious interpretation is that they are one and the same. The primary apparent difference between the two putative components, their polarities, is highly ambiguous in both sets of literatures and they could both be positive or both be negative. For example, it is difficult to determine if a modulation in the P2 range reflects a change in that P2 (and thus a positivity) or the superposition of a positivity or a negativity on top of the P2. Given that the "P2" effect continues long after the definitive P2 peak has finished, superposition of a positivity or a negativity seems more likely.

Some possible evidence on the componentry issues regarding the P2, the PMN, the word N300, the picture N300, and the MFN are localization results. MEG studies of the PMN have reported either no PMN (Helenius et al., 2002) or a PMN anterior to that of the N400 (Kujala, Alho, Service, Ilmoniemi, & Connolly, 2004). The latter suggested a LH anterior temporal source but the inconsistent findings underscore the ambiguities of source localization results, even with MEG. A current source density study (Connolly, Service, D'Arcy, Kujala, & Alho, 2001) of the PMN also suggested a left anterior source but visual inspection of the published figure suggests considerable ambiguity in the results with other conclusions possible as well. Another PMN source analysis study (D'Arcy, Connolly, Service, Hawco, & Houlihan, 2004) suggested both left inferior frontal and inferior parietal sources. However, any time there are simultaneous sources it can be difficult to properly separate them and hence the source analyses may be inaccurate (Zhang & Jewett, 1993). The P2 has been localized to RH BA 6 and 8 using LORETA (Liu, Perfetti, & Hart, 2003). The picture N300 has been localized to bilateral frontal areas and bilateral occipital/parietal areas (Hamm, Johnson, & Kirk, 2002). The MFN has been localized to a number of sources of which the anterior cingulate seems to be a prominent contributor (Frishkoff, Tucker, Davey, & Scherg, 2004; Frishkoff, 2007).

However, without converging support from a method with strong spatial resolution, all of these results must be considered tentative and subject to confirmation. It is quite possible that they are all the same effect and that the differences reflect variations in the source analysis methods and inaccuracies in the algorithms. Furthermore, they have not used signal separation methods that can be critical for accurate localization efforts.

For example, BESA source localization of the P300 yielded very implausible, but replicable, results (Dien, Spencer, & Donchin, 2003; Mecklinger & Ullsperger, 1995) that changed dramatically when PCA was applied, resulting in a new solution that converged quite strongly with fMRI results (Dien, Spencer, & Donchin, 2003). We therefore turn next to the fMRI results of the present report and how they converged with the PCA-enhanced ERP source localization solution.

3.2 Theoretical Interpretation of the Posterior Cingulate Cortex Effect

Whereas the anterior cingulate has become well-established as a central region in executive functions, the cognitive functions of the posterior cingulate cortex (PCC) remain much less well understood. The PCC is not generally considered to be involved in language processing, which raises the possibility that it may reflect a more general cognitive process that is acting upon phonological information in the present studies but can also act upon other types of information

To begin with, a strong case (Vogt, Vogt, & Laureys, 2006) has been made that the PCC is structurally and functionally divided into a ventral (vPCC) and a dorsal (dPCC) region. These authors then go on to speculate that the vPCC and dPCC correspond to the ventral pathway of the visual system which mediates object recognition and the dorsal pathway which mediates spatial processing (Haxby et al., 1991; Ungerleider, & Mishkin, 1982) and/or action control (Goodale & Milner, 1992; Goodale & Westwood, 2004) respectively. Additionally, the retrosplenial cortex (RSC) is implicated as a third functional region in this analysis (Vogt, Vogt, & Laureys, 2006).

By this account (Vogt, Vogt, & Laureys, 2006), the vPCC has the role of mediating the evaluation of self-relevant information. Thus, it tends to be active in situations of self-monitoring (Vogt & Laureys, 2005), self-reflection (Johnson et al., 2002), and awareness (Vogt & Laureys, 2005). Such a role could also account for its tendency to be activated by painful stimuli (Nielsen, Balslev, & Hansen, 2005; Vogt, 2005) and emotions (Vogt, 2005). This role in evaluating self-relevance could also explain its activation, along with the RSC, during episodic retrieval (Nielsen, Balslev, & Hansen, 2005; Vogt, 2005) and threatening stimuli (Maddock, 1999; Maddock, Garrett, & Buonocore, 2003; Maddock & Buonocore, 1997). The RSC itself has been suggested to be more specifically concerned with the interaction between emotion and episodic memory (Maddock, 1999; Maddock, Garrett, & Buonocore, 2003).

In contrast, the dPCC is suggested to mediate self-orientation in visual space (Vogt, Vogt, & Laureys, 2006). In making this suggestion, the authors cited just four reports, that the dPCC is active for making predictions about the results of actions (Blakemore, Rees, & Frith, 1998), eye-hand coordination (Inoue et al., 1998), and spatial navigation (Maguire, Frackowiak, & Frith, 1997; Maguire, Frith, Burgess, Donnett, & O'Keefe, 1998). This view raises concerns for the present report because it does not accommodate the semantic priming effect.

Rather than the model raising questions about the current findings, it is suggested that the current findings raise questions about the model. In doing so, it is very important to understand that this is not a case of questioning a consensus in the field. There is no current consensus on the dPCC. The review in question (Vogt, Vogt, & Laureys, 2006) is just providing a tentative interpretation based on just four studies, and it is argued that even those do not support it well. What the review does well and convincingly is to argue for a functional division of the PCC, primarily based on their work with animal models. The current report just argues that a broader review of the human cognitive neuroimaging literature, combined with the present data, favors a different interpretation for the functional significance of one of the regions that they identified, the dPCC, at least in humans.

A closer inspection of the four citations suggests that they do not support the dPCC self-orientation position (Vogt, Vogt, & Laureys, 2006). The two spatial navigation studies cited by these authors (Maguire, Frackowiak, & Frith, 1997; Maguire, Frith, Burgess, Donnett, & O'Keefe, 1998) have activations located in the precuneus, [-14 -60 26] and [-10 -48 44], rather than in the dPCC, strictly speaking (see Figure 3). The remaining two studies (Blakemore, Rees, & Frith, 1998; Inoue et al., 1998) have activations clearly in the dPCC, [6 -24 30] and [-6 -33 36] respectively, but differ in that the first is concerned with perceiving the consequences of self-generated actions (hearing tones in response to irregular self-paced button presses versus unpredictable tones and/or no movement) and the second with eye-hand coordination (reaching for a target with visual feedback versus without visual feedback); thus, neither are clearly concerned with self-orientation in space, in that the first does not involve spatial representations and the second should involve spatial orientation even in the absence of visual feedback. Furthermore, spatial orienting tasks (Miller, Valsangkar-Smyth, Newman, Dumont, & Wolford, 2005; Small et al., 2003; Small et al., 2005) implicate the vPCC, not the dPCC.

A broader review of dPCC findings suggests an alternative view that can help account for the current findings. To begin with, evidence suggests that the dPCC is involved with response control. Reports (Booth et al., 2003; Brown, Goltz, Vilis, Ford, & Everling, 2006) indicate that this same region, [9 -27 24] and [4 -26 33] respectively, is activated by nogo stimuli in go-nogo tasks. Significantly, a frontal positivity termed the nogo P3 is also seen in go-nogo ERP experiments (Pfefferbaum & Ford, 1988; Pfefferbaum, Ford, Weller, & Kopell, 1985) and could very well be the same as the present P2 effect. This task involves responding steadily to a stream of stimuli and inhibiting response to an occasional nogo stimulus that indicates not to respond. Such a response control account, broadly stated, would be consistent with the two other studies just described (Blakemore, Rees, & Frith, 1998; Inoue et al., 1998).

The apparent correspondence between the ERP and the fMRI data provide some additional insights into the nature of this response control process. Although the dPCC activation to nogo stimuli would seem to implicate it in inhibitory processes, in the ERP studies it (via the P2 effect) has apparently been associated with faster response cells, not slower (as in related vs. unrelated trials).

At this point, it is not possible to provide a strongly grounded hypothesis that accounts for all these observations. In order to provide a sense of possible lines of future enquiry and to help move the topic forward, one possibility is that this dPCC region mediates a mapping between a stimulus category and a response program. In tasks it is often necessary to map a range of stimuli into one or another response category. Many of the tasks reviewed herein clearly have this nature. The increased activity to symmetrically related vs. unrelated stimuli in the present experiment could therefore reflect a stimulus-response mapping to the "word" response that is more unequivocal and more consistently time-locked to the event. Likewise, the PMN experiments could be understood as tasks in which the response is the covert generation of a specific vocalization response. While such an account would not be very consistent with the dorsal spatial processing pathway model (Haxby et al., 1991; Ungerleider, & Mishkin, 1982), it is quite compatible with the alternative dorsal action control pathway model (Goodale & Milner, 1992; Goodale & Westwood, 2004).

By this reasoning, the phonological effects would therefore represent only one possible type of information processed by this region. For example, the dPCC [4 -27 34] was also activated when consciously categorizing dot patterns according to a learned set of dot pattern prototypes (Reber, Gitelman, Parrish, & Mesulam, 2003). Another study (de Zubicaray, Zelaya, Andrew, Williams, & Bullmore, 2000) presented participants with a series of exemplars and then either tasked them with generating the appropriate superordinate category label or with suppressing this response by generating any label other than the appropriate one; the dPCC [3 -28 42] was activated by the category generation task, not by the suppression task (thus also demonstrating that the dPCC is not dedicated to inhibition per se). One would still need to account for two categorization studies that did not report dPCC activations, including a dot pattern categorization task (Reber, Wong, & Buxton, 2002) and a task judging whether two successive objects are in the same category (Saneyoshi, Kaminaga, & Michimata, 2006). One possible explanation is the finding (Koenig et al., 2005) that categorization based on similarity recognition produces dPCC [-8 -36 20] activation but not based on formal rules. Thus, a response based on lower-level processes seems to involve the dPCC more than one based on more deliberative processes.

An ERP study (Szucs, Soltesz, Czigler, & Csepe, 2007) that is also consistent with this reasoning presented participants with a series of colored letters and numbers. The task was to judge either whether consecutive colors were the same or whether consecutive stimuli were in the same category (numbers vs. letters). Both tasks produced a fronto-central negativity that was termed an N2b to mismatches. The topography of the effect is very similar to that of the P2 *et al* and the polarity is again somewhat ambiguous (although one figure does appear to favor interpreting it as a negativity). The expectancy-based stimulus-response mapping interpretation of the P2-dPCC effect would be consistent with observing it in this task.

Likewise, a series of studies have reported a frontal N270 component in a number of situations, such as observing an incorrect answer to an arithmetic problem (Wang, Kong, Tang, Zhuang, & Li, 2000) or mismatches in consecutive presentations of colored numbers in terms of the color or in terms of the magnitude of the number (Wang, Wang, Kong, Cui, & Tian, 2001). These observations were interpreted as reflecting a conflict resolution mechanism (presumably based in the anterior cingulate) but could also be understood as the effect of violating expectancies in a stimulus-response mapping process.

The greatest current challenge is to determine why most semantic priming studies have not yielded a dPCC effect (Cardillo, Aydelott, Matthews, & Devlin, 2004; Copland et al., 2003; Copland, de Zubicaray, McMahon, & Eastburn, 2007; Giesbrecht, Camblin, & Swaab, 2004; Gold et al., 2006; Kotz, Cappa, Von Cramon, & Friederici, 2002; Matsumoto, Iidaka, Haneda, Okada, & Sadato, 2005; Mummery, Shallice, & Price, 1999; Price et al., 1994; Raposo, Moss, Stamatakis, & Tyler, 2006; Rissman, Eliassen, & Blumstein, 2003; Rossell, Price, & Nobre, 2003; Wheatley, Weisberg, Beauchamp, & Martin, 2005; Wible et al., 2006). One possibility is that in the present dataset there were more non-words than words, perhaps rendering the task more like the go-nogo task where the nogo stimuli are also in the minority.

There has been one other semantic priming study that has reported activations in the dPCC, at both short and long SOAs, in a lexical decision task (Rossell, Bullmore, Williams, & David, 2001). However, the task in this study was to indicate which of two stimuli presented on either side of a fixation point was a word, possibly introducing a spatial aspect to the task. Indeed, a follow up study (Rossell, Price, & Nobre, 2003) with a more conventional design of lexical decision on a single stimulus at fixation did not report a posterior cingulate effect. The activations were posterior to that of the present study, veering into that of the precuneus (see Figure 3). On the other hand, as noted earlier, spatial orienting tasks (Miller, Valsangkar-Smyth, Newman, Dumont, & Wolford, 2005; Small et al., 2003; Small et al., 2005) have implicated the vPCC, not the dPCC. The present report lends support to this latter view as the N300 was source localized to the dPCC, as was the corresponding fMRI activation; unlike the prior study (Rossell, Bullmore, Williams, & David, 2001), a central presentation was utilized, ruling out a spatial orienting component to the task. It may be that the two semantic priming studies with dPCC effects have unique characteristics that allow this effect to be observed. The designs varied widely with regards to the stimuli, the task, the proportion of different types of stimuli, and so forth. Information is insufficient at this point to formulate a hypothesis. All that can be said at this point is that one, arguably two, semantic priming studies have reported dPCC effects and a number of semantic ERP studies have reported effects that appear to be linked to the dPCC.

An alternative view has been provided by the other semantic priming study that reported activation in the dPCC (Rossell, Bullmore, Williams, & David, 2001). It was noted by these authors that the stimulus set had high imageability ratings and speculated that the dPCC effects reflected a "mind's eye" function (Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1996) in which the words were translated into a visual format. The authors (Rossell, Bullmore, Williams, & David, 2001) suggested that the unrelated pairs gave rise to more bizarre, complex images. By this reasoning, an activation in the RSC to unrelated pairs reflected high imageability whereas activations in the dPCC to related pairs in two conditions [-6 -53 26] and [-3 -47 31] reflected low imageability. Since the present study had an imageability confound, it is possible that the dPCC effect reflected the lower imageability of the stimulus pairs. When put to the test, however, no parametric effect of imageability/concreteness was found in the present study. Furthermore, a recent study of imageability effects (Sabsevitz, Medler, Seidenberg, & Binder, 2005) reported effects only in the RSC, not the dPCC while another imageability study (Giesbrecht, Camblin, & Swaab, 2004) did not find medial parietal effects at all.

On the other hand, a memory retrieval study of paired associates did report an effect of association strength in the dPCC for imageable pairs only (Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1996) and the effect was of greater activation for more highly related pairs, consistent with the present symmetrical priming main effect (although the parametric analysis of association strength did not yield a significant effect). It is possible that the proposed stimulus-response mapping process was mediated, in that case, by visual representations and thus required a minimum level of imageability. The stimuli in the present study nearly all fell into the imageable range (greater than 300) as defined by the study (Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1996) so the issue cannot be evaluated with the present dataset. Further research will be needed to examine this issue more directly.

A final question raised by the present report is how to name the ERP component if, in fact, the word N300, the picture N300, the word P2, the phonological mismatch negativity, and the word midline frontal negativity are all different names for the same ERP effect. Although in principle there is no reason for these not to be the same component (for example, even if the PMN is evoked by mismatches with phonological expectations, it would seem to follow that it should appear in all semantic priming tasks since they should in turn activate phonological expectancies), direct comparisons are needed to be certain. For now, it is suggested that reports on these components make sure to note the possible connection with the other putative components. Given the findings in the present report, this lab at least will start terming the effect a "P2-dPCC" rather than a "word N300".

3.3 Areas Other Than the Posterior Cingulate Cortex

Although not the primary focus of interest for this study, the N400 factor was examined but did not co-localize with an fMRI activation. One possibility is that its source was in the nearby anterior medial temporal lobe (AMTL), which may contribute to the N400 (Nobre, Allison, & McCarthy, 1994; Nobre & McCarthy, 1995). The absence of recording electrodes on the underside of the head could introduce sufficient imprecision to make this scenario quite possible for an apparently vertically oriented field like the N400, even with the partial correction provided by the PARE procedure. If the N400 source was in the AMTL, then the susceptibility artifact that is known to affect this region (Devlin et al., 2000) could have prevented the corresponding fMRI activity from being detected. Alternatively, ERP and fMRI effects do not necessarily need to correspond, although data indicate that they do both reflect the same dendritic activity (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). Finally, it is possible that this lack of co-localization simply results from a Type II error in the fMRI data.

The LIPC activation is commonly seen in semantic experiments and was an expected effect. It was not of interest to the present study because no ERP effects have thus far been convincingly linked to it, although there have been some attempts to relate the PMN to this region (Connolly, Service, D'Arcy, Kujala, & Alho, 2001; D'Arcy, Connolly, Service, Hawco, & Houlihan, 2004). To the extent that the present word N300 can be identified with the PMN, the source localization results indicate that it is associated with the dPCC rather than the LIPC. The present LIPC effects correspond to the anterior LIPC (Gold et al., 2006; Vigneau et al., 2006; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001) implicated in controlled retrieval (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001) and facilitative priming (Gold et al., 2006). It may be that this activation reflects the additional effort required to retrieve the unprimed words.

Although it was not appropriate to formally contrast the backward and forward priming trials with the symmetrical trials due to lack of proper matching (as explained in the methods section), an informal examination of them was made to avoid missing any effects of potential interest. These effects should be considered exploratory and reflect a low statistical power due to the limited number of trials of these types.

The results of the forward priming comparison are less interpretable. Effects were only found for the unrelated vs. related comparison. The first effect was found in the RH BA40 temporo-parietal junction area that tends to be implicated in the P300 seen in oddball paradigms (see Dien, Spencer, & Donchin, 2003). The amplitude for the ERP measure was more positive in related condition, rather than the unrelated condition, of the ERP study (Franklin, Dien, Neely, Waterson, & Huber, 2007) but since the measure was expected to be a combination of the P300 and the N400 it could not be directly interpreted in this respect. It is unclear why this effect was not seen for the other priming contrasts. The left (not statistically asymmetrical) dorsolateral activation was intriguing in that this region is implicated in verbal working memory processes (Fiez et al., 1996; Jonides et al., 1997; Petrides, Alivisatos, Meyer, & Evans, 1993; Smith & Jonides, 1997). It is possible that it reflected a working memory role in detecting forward associations. The bilateral cerebellar activations are consistent with a variety of studies reporting cerebellar involvement in language, both in functional imaging and lesion studies

(Gordon, 1996; Leiner, Leiner, & Dow, 1995; Marien, Engelborghs, Fabbro, & De Deyn, 2001; Schmahmann, & Pandya, 1997). It is not clear why it would be specific to the forward priming contrast.

The results for backward priming were intriguing but inconclusive. There were effects only for the unrelated vs. related contrast. First of all, there were bilateral effects in the inferior occipital regions. It is not clear why they were specific to backward priming since these are basic visual areas rather than being specifically involved with language or even orthography. It is possible that during the process of evaluating the existence of a backward association, the participants were visually rearranging the two stimuli to determine if they formed a compound stimulus but this suggestion is highly speculative. The right middle frontal region (which was of marginal significance at a voxelwise threshold of .005 but highly significant at a threshold of .01) is not well understood. It is of interest that in the ERP data (Franklin, Dien, Neely, Waterson, & Huber, 2007) there was a right-lateralized ERP component selectively associated with the backward priming trials, the N400RP, although it could not be source localized with a satisfactory residual variance (i.e., less than 10%) in the present dataset. Likewise, there was a right-lateralized (not significantly) superior frontal effect (.06 marginal effect) as well, again suggestive of a right hemisphere role in processing backward primes. Such a hemispheric role is consistent with behavioral data using the visual half-field technique (Koivisto, 1998; Koivisto, 1999).

The only stimulus parameter to yield significant effects was word frequency. Anterior cingulate effects were found to negatively correlate with word frequency (for symmetric related trials). This pattern is consistent with prior reports that the anterior cingulate and the LIPC were more activated to lower frequency words was consistent with previous reports (Carreiras, Mechelli, & Price, 2006; Chee, Westphal, Goh, Graham, & Song, 2003; Nakic, Smith, Busis, Vythilingam, & Blair, 2006). It may be of interest that although an ERP study of word frequency effects reported a posterior N1 effect (Sereno, Rayner, & Posner, 1998), examination of the published figure suggests that a corresponding frontal positivity was even more significant; it is possible that this frontal positivity emanates from either the LIPC or the anterior cingulate region. For the purposes of the present report, the only significance of this observation is that it confirms that the reported dPCC effects are not due to residual confounds with word frequency.

Likewise, the findings of a positive correlation between trial order and the right (not significantly lateralized) superior parietal lobe, left (not significantly lateralized) prefrontal cortex, right middle frontal gyrus, and left inferior parietal lobe is again to confirm that an unrecognized confound is not the source of the effects of interest. It seems likely that these effects are due to changes in alertness over the course of the recording session.

Conclusion

The significant activity in the dPCC found in this study mirrors the word N300 ERP activity seen in a previous study (Franklin, Dien, Neely, Waterson, & Huber, 2007), with both having a stronger response to symmetric priming word pairs in a lexical-decision task and co-registering to the same region. This finding is important as it provides additional clues regarding the nature of this poorly understood region. This review also shows how a number of apparently independent lines of electrophysiological studies (regarding the P2, the PMN, the MFN, the word N300, and the picture N300) may actually reflect the same cognitive process. Furthermore, the localization to the dPCC suggests that the process may not be restricted to phonological information, as is thought for the PMN and possibly the P2, but is rather involved in a more general cognitive function, regarding which some suggestions have been made. Finally, based on the reviewed literature, it is suggested to term the ERP effect a "P2-dPCC".

4. Experimental Procedure

Participants

Seventeen participants (F= 13, M= 4) aged 20-41 years were recruited for monetary compensation. All participants were right-handed, native-English speaking, had no history of neurological damage or disorders, and were not taking psychotropic medications.

Stimuli

The experiment consisted of 360 prime-target pairs, divided into four blocks of 90 trials each, in an event-related design. The stimuli included asymmetrically associated word pairs consisting of 40 compound items (i.e., compound words such as “fruit-fly”) and 40 non-compound items (e.g., “stork-baby”), taken from published sources (Kahan, Neely, & Forsythe, 1999; Thompson-Schill, Kurtz, & Gabrieli, 1998). As determined from the Nelson norms (Nelson, McEvoy, & Schreiber, 1999), the mean prime-to-target and mean target-to-prime associative strengths for these pairs were .144 (*SD* = .16) and .02 (*SD* = .05), respectively, $t(79) = 6.492$, $p < .05$. Twenty pairs for each of the four different priming conditions: backward related (e.g., “hop-bell”), backward unrelated (e.g., “baby-cane”), forward related (e.g., “bell-hop”), and forward unrelated (e.g., “sugar-nip”) were formed from both the sets of compound (10 pairs) and non-compound (10 pairs) words. To form the forward unrelated pairs, the primes and targets from half of the forward related word pairs were re-paired. Which half of the pairs served as forward related and forward unrelated pairs was counterbalanced across participants.

Additionally, 70 symmetrically related ("mad-angry") and 210 prime words paired with non-words ("red-bler") were included in each list.

Four stimulus lists were constructed, such that across the four lists each asymmetrically associated pair was presented once in each of the four priming conditions. Thus, "bell-hop" might appear in one list as a forward related pair: "bell-hop", in the second list as a backward related pair: "hop-bell", in the third list as a forward unrelated pair: "red-hop", and in the fourth list as a backward unrelated pair: "red-bell". A given list contained twenty pairs in each of these four conditions. The overall relatedness proportion, how predictable the targets are from the primes, was kept at .60 to encourage expectancy and the nonword ratio was kept at .78 to encourage semantic matching. The order of the stimuli was the same in each of the four lists, other than the counterbalancing changes in the asymmetric pairs.

The primes and targets for the symmetric pairs had median raw Kucera-Francis (Kucera, & Francis, 1967) frequencies of 28.0 and 36.5, which for log freq scores yielded, $T_{WJt}/c(1,55) = 0.56$, n.s. The median raw frequency of 36.5 for the symmetric-pair targets is comparable to the average, 29.3, of the medians for the forward and backward asymmetrical unrelated targets when tested on the log freq scores, $T_{WJt}/c(1,96.21) = 1.21$, $p = .28$. As determined from the Nelson, McEvoy and Schreiber (1999) norms, the median prime-to-target and median target-to-prime associative strengths for these symmetric pairs were .38 (sd = .23) and .18 (sd = .22), respectively, $T_{WJt}/c(1,53) = 8.38$, $p = .006$.

Whereas the frequency ratings were equated, the concreteness and imagery ratings were not equated according to the MRC Psycholinguistic Database (Wilson, 1988). The median concreteness ratings of the symmetric related targets was 460 (57 ratings available out of 70), which was significantly less than the symmetric unrelated targets, which was the 581.8 (123 ratings available out of 160) average of the medians for the forward and backward asymmetrical targets: $T_{WJt}/c(1,66.43) = 19.48$, $p < .00001$. The median imagery ratings of the symmetric related targets was 505 (59 ratings available out of 70), which was significantly less than the symmetric unrelated targets, which was the 575.5 (125 ratings available out of 160) average of the medians for the forward and backward asymmetrical targets: $T_{WJt}/c(1,61.34) = 14.32$, $p = .0005$.

The stimulus pairs were also not equated with respect to semantic similarity. The asymmetric primes and targets had a mean semantic similarity of 0.27 as determined from the latent semantic analysis website at the University of Colorado (Landauer & Dumais, 1997). The symmetric primes and targets had a mean semantic similarity (Landauer & Dumais, 1997) of 0.44, which was significantly higher than that for the asymmetrically related pairs, $T_{WJt}/c(1,106.99) = 25.02$, $p < .0001$.

Priming in the symmetric condition was evaluated relative to the mean of the forward unrelated and backward unrelated conditions. Ideally, one would want to assess symmetric priming relative to an unrelated condition that contained the same targets re-paired with primes from other symmetric prime-target pairs. However, this would have required adding more unrelated trials, which would have lowered the relatedness proportion. Although adding even more symmetric buffer trials could have counteracted this, this would have made the test list too long to be administered in one sitting without fatigue becoming a factor. This comparison was justified on the grounds that the frequency of the symmetric targets was statistically comparable to the mean of the forward and backward unrelated targets. A more detailed description of the stimuli is provided in Franklin and colleagues (2007).

Procedure

Data were acquired using a gradient echoplanar imaging sequence (EPI) on a 3T Siemens Allegra scanner at the Hoglund Brain Imaging Center at the University of Kansas Medical Center. Functional data were scanned using single-shot gradient EPI imaging fMRI scans consisting of 29 contiguous axial slices (TR/TE = 2100/30, flip angle equal to 90 degrees, field of view equal to 192 mm, matrix equal to 64x100, slice thickness equal to 4 mm with a .5 mm interslice gap, in plane resolution equal to 3x3 mm). Four 7.53 min blocks were recorded from each participant. The scans were begun two TRs (4.2 s) before the trials began. These two scans plus three more (10.5 seconds total) were dropped to allow for scanner stabilization, leaving 215 scans for analysis (and thus discarding the first trial of each session). Stimuli were presented to participants via goggles that binocularly displayed the information from the presentation PC in the control room, using E-Prime. The anatomical scan consisted of T1-weighted images using a 3D MP-RAGE sequence (TR/TE = 2300/4.4, flip angle of 8 degrees, field of view equal to 256 mm, matrix equal to 256x256, and 208 slices with slice thickness equal to 1 mm, in plane resolution equal to 3x3 mm). A vitamin E capsule was used to confirm L/R orientation of the image.

The experimental run consisted of a 30-trial practice block and then four, 90-trial experimental sessions. Each trial consisted of a 3500 ms intertrial interval, then a 150 ms prime presentation, then a 350 ms interstimulus interval or ISI (500 ms stimulus onset asynchrony or SOA), and then a 150 ms target duration. Finally there was a fixed 850 ms response window that followed the offset of the target. The stimuli were presented using 18-point CourierNew font in black on a white screen. The prime was in upper-case and the target was in lower-case. A plus-sign (18-point CourierNew) was present at all times other than during stimulus presentation in order to help participants maintain fixation. It is not possible to provide visual angle information as the nature of the stimulus presentation equipment precluded measurement of both the screen size of the stimuli and the distance from the viewer. Participants were asked to respond with one button if the target was a word and with another button if the target was not a word and to do so both quickly and accurately. Which hand was used to make which response was counterbalanced across participants.

The trials were presented in an event-related design identical in parameters to the original ERP experiment, except with an intertrial period of 3500 ms instead of 1000 ms. In order to optimize the characterization of the hemodynamic response, a staggered timing design (Josephs, Turner, & Friston, 1997) was utilized in which the TR (2100 ms) is not an even multiple of the trial length (5000 ms); such a design results in the scans corresponding to a different point of the hemodynamic response on each trial, in a manner psychologically transparent to the participant.

Statistical Analysis

For the inferential tests, SAS/IML code (Keselman, Wilcox, & Lix, 2003) for conducting robust statistical tests (generally made available at http://www.umanitoba.ca/faculties/arts/psychology/) was ported to Matlab (available for download at http://wwwpeople.ku.edu/~jdien/downloads. html). A 5% symmetric trim rule was used (1 observation dropped at either extreme within each cell). The seed for the number generation was set at 1000. The number of simulations used for the bootstrapping routine was set at 50,000 to ensure stable *p*-values. The robust statistic is meant to improve (more closely comply with the nominal alpha rate) on the conventional ANOVA by: 1) not assuming a normal distribution, 2) being more resistant to outliers, and 3) not assuming between-subject cells have the same error variance. Further description of the inferential issues, as they apply to ERP data, is available elsewhere (Dien, Franklin, & May, 2006). P-values are rounded to the second significant digit.

For the ERP source analysis, the N300 ERP component, as characterized by factor analysis, was obtained from a prior study (Franklin, Dien, Neely, Waterson, & Huber, 2007). It was not necessary to set a time window (the scalp topography for a temporo-spatial factor is invariant across the full epoch due to the nature of the PCA process). Likewise, choice of the high-pass filter setting is irrelevant (no high-pass used). The dipole analysis was conducted with BESA (5.1.2) using a four-shell elliptical head model. The dipole pair was constrained to have symmetrical mirror locations but free orientations. A mirror dipole pair was used since it is common for neural activations to occur in both hemispheres, even when asymmetric. The seven periocular channels were dropped to minimize the effect of ocular artifacts. An iterative algorithm was utilized in which the program automatically shifted the position of the dipoles until it found a position of maximum fit. The analysis was conducted with three starting locations to confirm that the results were not dependent on starting location.

Imaging analysis was conducted using SPM5 version 826 (Wellcome Department of Imaging Neuroscience, http://www.fil.ion.ucl.ac.uk) under Matlab 7.4 on OS X. The data were imported directly from DICOM into Nifti format. Slice timing correction was conducted before realignment due to the use of interleaved slice order acquisition, with the middle slice as the reference slice. This step was followed by realignment and unwarping. Spatial normalization was performed by matching mean EPI (echoplanar imaging) images to the SPM EPI template and the data were resliced into 2mm isotropic voxels. The images were spatially smoothed with a 12x12x12 mm kernal. In addition to the two TRs dropped from the beginning of each block, 3 more TRs of experiment recording were removed (for a total of 10.5 s of data removed) to reduce stabilization artifact. Data were analyzed using event-related random effects analysis with a temporal derivative. Stimuli were presented with timing that was not an even multiple of the image acquisition time (TR), resulting in staggered timing that enhances characterization of the hemodynamic response in event-related analyses (Josephs, Turner, & Friston, 1997). AR(1) correction was made for temporal autocorrelation (see Smith, Singh, & Balsters, 2007). The default 128 sec high-pass filter was employed and no proportional scaling was performed to avoid artifacts (see Desjardins, Kiehl, & Liddle, 2001). The realignment parameters were included as covariates in order to control for residual movement artifacts (Friston, Williams, Howard, Frackowiak, & Turner, 1996). The height threshold was set at .005.

The SPM analysis was conducted with all five types of events (forward-related, backward-related, symmetric-related, forward-unrelated, backward-unrelated) simultaneously entered as variables of interest. Comparisons made were: forward-related v. forward-unrelated, backward-related v. backward-unrelated, and symmetrical v. unrelated word pairs. Parametric analyses were conducted in the same fashion, with the addition of a parametric term to the symmetric related events (one parameter in a given analysis since inter-parameter correlations would interfere with the analysis if they were all entered simultaneously). For parametric analyses, only the parameter was entered into the contrasts. For each cluster, the most significant voxel and secondary voxels that are at least 8 mm apart are given. Laterality tests were computed for all such voxels by defining a spherical 4 mm radius region of interest (ROI) centered on the most significant voxel and the corresponding voxel in the other hemisphere. To keep the test comparable to the SPM statistics, a conventional repeated measures ANOVA was conducted on these ROIs rather than the robust statistic.

Both word and word pair measures were examined. For the word parameters the values of the prime and the target were averaged together since the SOA was too short to expect that the hemodynamic response would distinguish between them. The word parameters were the average of the imageability and concreteness measures(Wilson, 1988), word frequency (Kucera, & Francis, 1967), and word length. The imageability and concreteness measures were averaged together because they are theoretically related and have generally been reported to correlate highly (r=.80 in this stimulus set, with 47 missing values out of the 300). The relation measures were latent semantic similarity (Landauer & Dumais, 1997) and prime-target and target-prime association strengths (Nelson, McEvoy, & Schreiber, 1999). Finally, experiment-wise sentence order was entered in as a parameter.

For figures, activations have been rendered onto the Colin27 head (obtained from the Montreal Neurological Institute). For presentation purposes, the extent threshold was set at 400 voxels to exclude non-significant clusters (no significant effects were excluded). Brodmann areas were identified using the Talairach Space Utility (http://www.ihb.spb.ru/~pet_lab/TSU/TSUMain.html). Anatomical landmarks were identified using the Brainvoyager Brain Tutor (http://www.brainvoyager.com/BrainTutor.html).

Tables

	Forward	Backward	Symmetrical
Related	467 (59.84)	491 (53.29	453 (64.22)
Unrelated	479 (58.43)	513 (57.48)	496 (57.96)@
Priming	+12*	+22*	+43*

Table 1. Mean Reaction Times for the Lexical Decision Task with Standard Deviations in Parentheses. @ Symmetrical unrelated is the average of the backward and forward unrelated cells. *denotes statistically significant effect at p < .05.

	Forward	Backward	Symmetrical
Related	.85 (.10)	.90 (.08)	.94 (.05)
Unrelated	.89 (.07)	.84 (.12)	.87 (.07)@
Priming	+.04	-.06*	-.07*

Table 2. Mean Accuracy for the Lexical Decision Task with Standard Deviations in Parentheses. @ Symmetrical unrelated is the average of the backward and forward unrelated cells. *denotes statistically significant effect at p < .05.

Cluster p	k_E	Voxel p	Voxel T	Coords	Hem F	Hem p	BA	Anatomical Landmark
Symmetric vs. Unrelated								
0.001	728	0.966	4.48	0 -14 38	n/a	n/a	24	Posterior Cingulate Gyrus
		0.990	4.26	16 -36 48	5.82	0.028	31	R Posterior Cingulate Sulcus
		1.000	3.77	-8 -18 40			31	L Posterior Cingulate Sulcus
Unrelated vs. Symmetric								
0.000	798	0.177	6.48	-48 38 14	7.40	0.015	46	L Inferior Frontal Gyrus
		0.182	6.46	-54 30 24			46	L Inferior Frontal Gyrus
		0.230	6.27	-48 30 18			46	L Inferior Frontal Gyrus
Forward Unrelated vs. Forward Related								
0.001	871	0.477	5.49	46 -34 24			40	R Lateral Sulcus
		0.835	4.78	46 -18 32			1	R Postcentral Sulcus
		0.993	4.08	36 -26 22			41	R Lateral Sulcus
0.023	448	0.610	5.23	-40 42 18			46	L Inferior Frontal Gyrus
		0.953	4.42	-36 56 16			10	L Middle Frontal Gyrus
		1.000	3.47	-30 46 14			46	L Middle Frontal Gyrus
0.031	419	0.899	4.62	-4 -58 -8			-	L Cerebellum
		0.937	4.49	-10 -62 -4	4.54	0.049	-	L Cerebellum

		1.000	3.14	10 -56 -12			-	R Cerebellum
Backward Unrelated vs. Backward Related								
0.003	561	0.982	4.37	8 -70 0			18	R Medial Occipital Gyrus
		0.997	4.10	-26 -68 -6			18	L Collateral Sulcus
		0.998	4.06	16 -74 -6			18	R Collateral Sulcus
0.055*	309	0.848	4.89	48 22 40			8	R Middle Frontal Gyrus
		1.000	3.86	48 16 48			8	R Middle Frontal Gyrus
		1.000	3.56	40 12 56	5.24	0.036	8	R Middle Frontal Gyrus
0.060	302	0.978	4.40	16 62 20			10	R Superior Frontal Gyrus
		0.992	4.24	30 54 26			10	R Middle Frontal Gyrus
		0.999	3.95	24 60 28			10	R Superior Frontal Gyrus

Table 3. Results of Main Effects Analyses. Cluster p-values are corrected. BA is Brodmann Area. Voxel p-values are FWE-corrected. Coordinates are MNI coordinates. *=significant at a threshold of .01 (p=0.005, k_E = 801).

Cluster p	k_E	Voxel p	Voxel T	Coords			BA	Anatomical Landmark
Total Frequency (negative correlation)								
0.000	1157	0.379	5.89	16 8 34			24	R Anterior Cingulate Sulcus
		0.550	5.53	16 18 32	4.91	0.042	24	R Anterior Cingulate Sulcus
		0.783	5.08	-2 26 38			32	L Medial Superior Frontal Gyrus
0.007	449	0.032	7.88	-50 32			46	L Inferior Frontal Gyrus

				20				
		0.767	5.11	-52 28 30			46	L Inferior Frontal Gyrus
		1.000	3.95	-46 26 14			45	L Inferior Frontal Gyrus
Order (positive correlation)								
0.000	1190	0.167	6.65	42 -42 54			7	R Superior Parietal Lobe
		0.458	5.78	40 -56 52			40	R Inferior Parietal Lobe
		0.999	4.13	38 -40 44			7	R Superior Parietal Lobe
0.000	785	0.950	4.68	-56 8 28			44	L Precentral Gyrus
		0.975	4.53	-48 20 36			9	L Middle Frontal Gyrus
		0.996	4.25	-46 36 20			46	L Inferior Frontal Gyrus
0.000	731	0.952	4.67	44 34 30			9	R Middle Frontal Gyrus
		0.988	4.41	40 28 46	4.95	0.041	9	R Middle Frontal Gyrus
		0.989	4.39	42 36 40	7.07	0.017	8	R Middle Frontal Gyrus
0.000	700	0.932	4.75	-42 -30 40			2	L Postcentral Sulcus
		0.991	4.36	-40 -42 36			40	L Inferior Parietal Lobe
		0.993	4.33	-52 -18 26	5.19	0.037	40	L Inferior Parietal Lobe

Table 4. Results of Parametric Analyses. Cluster p-values are corrected. BA is Brodmann Area. Voxel p-values are FWE-corrected. Coordinates are MNI coordinates.

Figure Legends

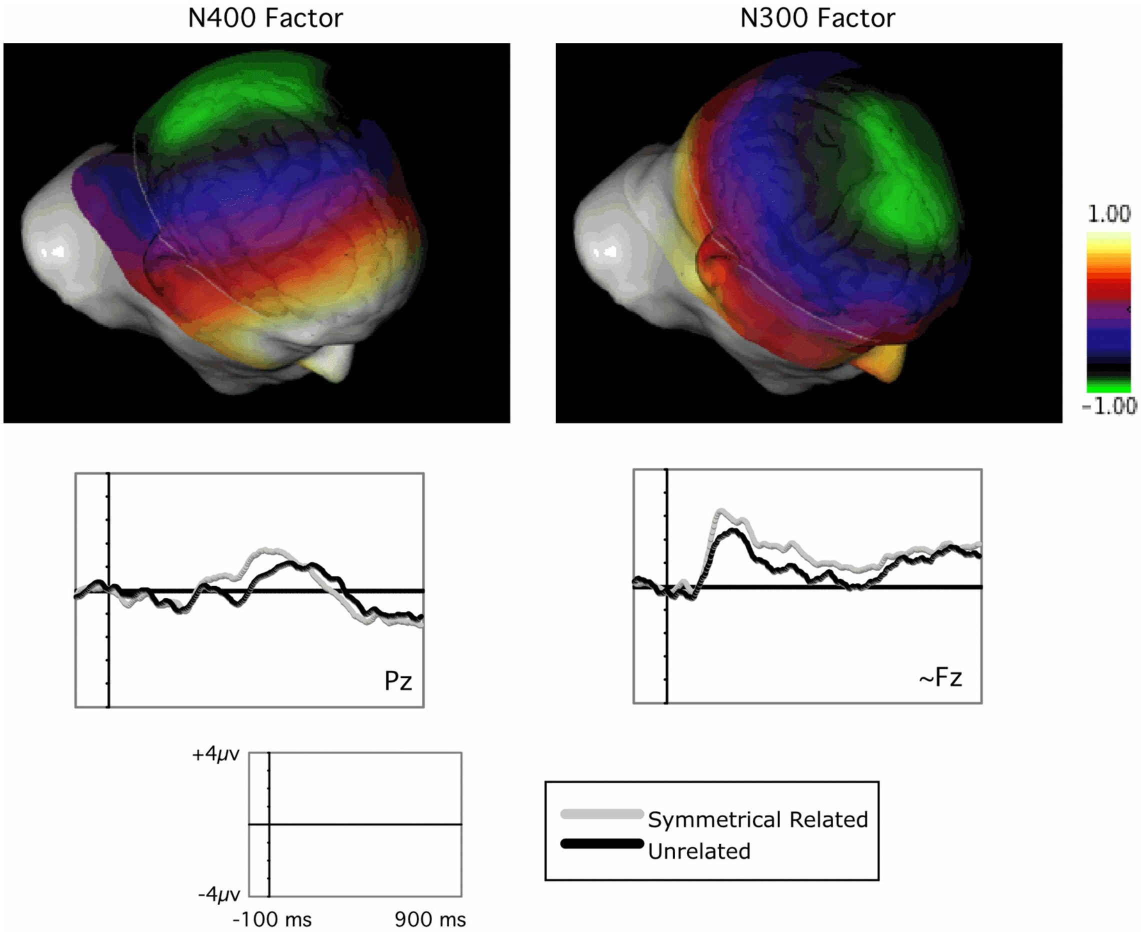

Figure 1. N300 and N400. The scalp topographies present the N300 and the N400, as characterized by the prior PCA report (Franklin, Dien, Neely, Waterson, & Huber, 2007). The amplitudes correspond to the symmetric priming effect. The waveforms are the grand averages from representative channels for each component.

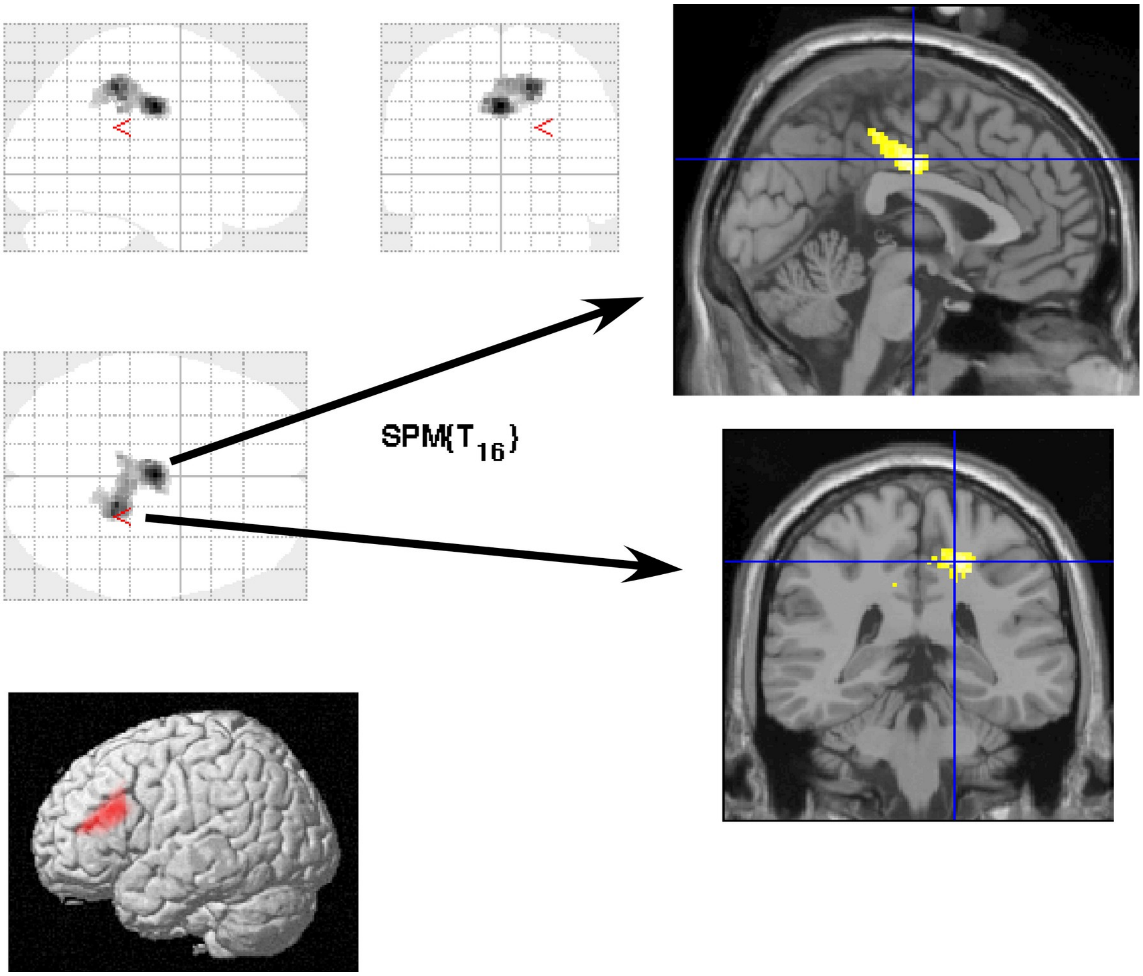

Figure 2. N300 Source Localization. The glass head shows the posterior cingulate activation for the symmetric related vs. unrelated contrast. The upper brain section corresponds to the most active voxel of the cluster. The lower brain section corresponds to the right-lateralized portion of the cluster that best matches the source localization. The red arrow indicates the right hemisphere side of the source localization solution dipole pair [+/-21 -37 27] for the N300 ERP component (Franklin, Dien, Neely, Waterson, & Huber, 2007). The arrow indicates the location but not the orientation. The source solution is overlaid on the fMRI results of the symmetrically related versus unrelated contrast. The rendered brain in the lower left-hand corner presents the significant cluster for the unrelated vs. symmetrically related contrast.

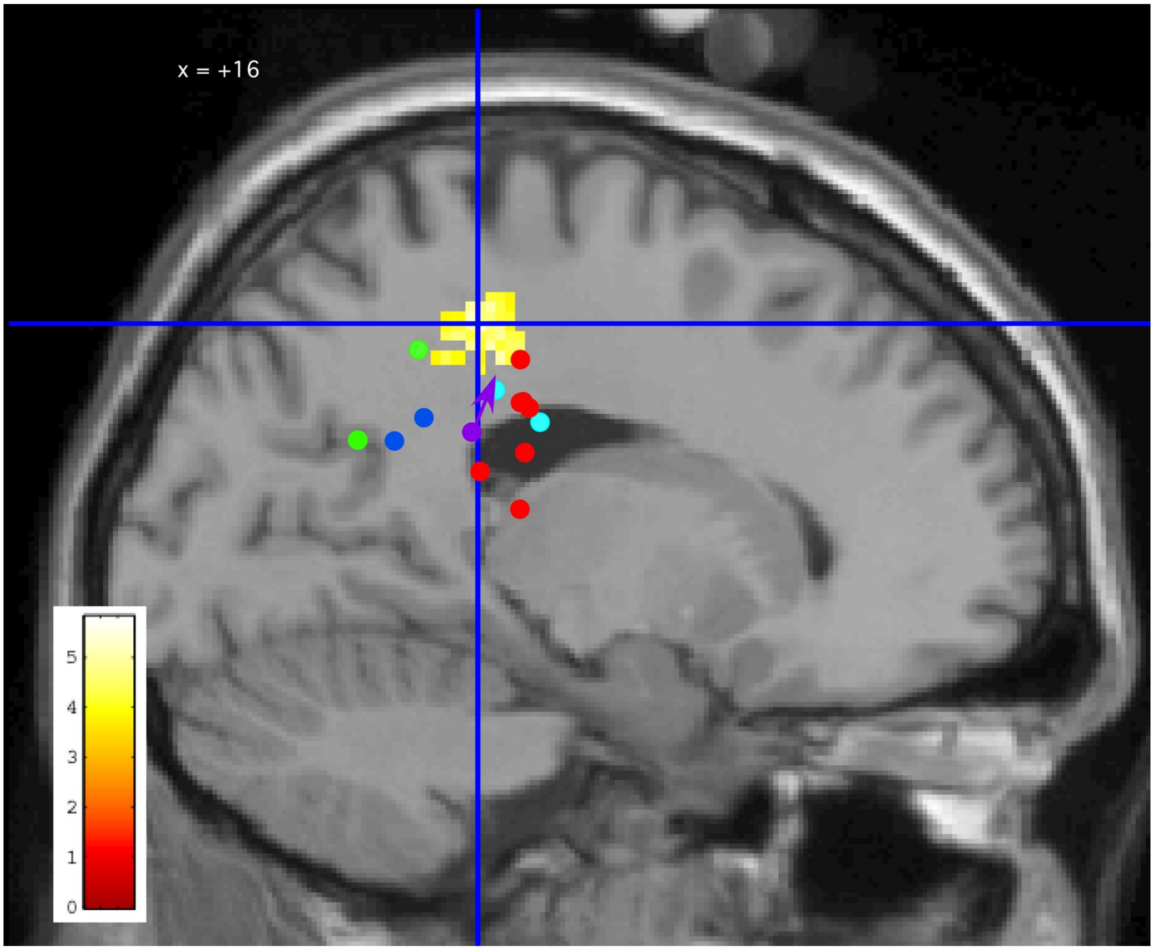

Figure 3. Posterior Cingulate Activations. The anatomical brain is the Colin head used for illustrative purposes. The yellow activations indicate the two significant clusters for the unrelated versus symmetrically related contrast. The blue cross-hairs are located at the second local maximum voxel of the dPCC cluster [16 -36 48]. The succeeding points are projected onto the x=+16 plane. The purple arrow indicates the site and orientation of the N300 source localization. The remaining dots represent the voxel of maximum significance for the PCC studies cited in the text. The two spatial navigation activations referenced in the text are located at the green dots (Maguire, Frackowiak, & Frith, 1997; Maguire, Frith, Burgess, Donnett, & O'Keefe, 1998). The two other studies cited as support for the self-orientation account are in light blue (Blakemore, Rees, & Frith, 1998; Inoue et al., 1998). The two semantic priming activations referenced in the

text are located at the blue dots (Rossell, Bullmore, Williams, & David, 2001). The remaining red dots are the other studies cited in the text of this paper (Booth et al., 2003; Brown, Goltz, Vilis, Ford, & Everling, 2006; de Zubicaray, Zelaya, Andrew, Williams, & Bullmore, 2000; Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1996; Koenig et al., 2005; Reber, Gitelman, Parrish, & Mesulam, 2003). It is notable that a number of the reported activations appear to fall into the corpus callosum, presumably due to inter-study differences in the coordinate system and individual differences in brain morphology.

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Appendix

Asymmetric Pairs

Bus-Stop
Flea-Market
Sugar-Cane
Cat-Nip
Dump-Truck
Tomato-Paste
Sling-Shot
Security-Blanket
Bare-Foot
Kingdom-Come
Star-Wars
First-Aid
Bulletin-Board
Barn-Yard
Eye-Shadow
Birth-Control
Crab-Legs
Cloak-Dagger
Swim-Suit
Table-Cloth
Seat-Belt
Cheese-Cake
Beet-Red
Spray-Paint
Peanut-Butter
Stomach-Ache
Check-Book
Stage-Fright
Pin-Cushion
Camp-Fire
Harvest-Moon
Roof-Top
Mirror-Image
Sleeping-Bag
Club-Soda
Jump-Rope
Belly-Button
Brick-Wall
Hatch-Back
Bell-Hop
Puppet-String
Stork-Baby
Proud-Lion
Deliver-Mail
Fan-Air
Chip-Shoulder
Piano-Key
Alibi-Crime
Beaver-Dam
Denim-Blue
Canary-Yellow
Ankle-Body
Afraid-Run
Garlic-Smell
Path-Road
Onion-Cry
Termite-Wood
Canyon-Deep
Viper-Snake
Mango-Fruit
Lamp-Light
Towel-Dry
Interest-Money
Pigeon-Statue
Zebra-Stripes
Maze-Lost
Swan-Bird
Turnip-Vegetable
Penguin-Tuxedo
Pain-Dentist
Picnic-Ant
Factory-Smoke
Duck-Water
Stove-Hot
Mortar-Weapon
Locust-Insect
Indian-Feather
Sheet-Paper
Mirage-Desert
Brittle-Candy

Symmetric Pairs

Lose-Find
Mad-Anger
Sickness-Health
Tire-Rubber
Gun-Shoot
Crowd-People
Open-Dilate
Clown-Circus
Why-Because
Over-Under
Tub-Bath
Walnut-Almond
Judge-Jury
Needle-Thread
Aunt-Niece
Web-Spider
Law-Justice
Nurse-Doctor

Sweet-Sour
Food-Eat
Sell-Buy
Shoe-Boot
Grass-Green
Die-Live
Man-Woman
Now-Then
Church-Priest
Spice-Herb
Tan-Beige
Leaf-Rake
Pound-Ounce
Long-Short
Robber-Thief
Leg-Arm
Nail-Hammer
Mars-Jupiter

Vacation-Trip
Roach-Bug
Construct-Build
Guilty-Innocent
Teach-Learn
Marsh-Swamp
Donkey-Mule
Scare-Spook
Stocks-Bonds
Mare-Horse
Debate-Argue
Rob-Steal
Here-There
Estate-Mansion
Acquire-Get
Hen-Chicken
Warmth-Heat
Itch-Scratch

Effort-Try
Loaf-Bread
Mutton-Lamb
Gift-Present
Kid-Toddler
Concept-Idea
Explain-Tell
Halo-Angel
Squid-Octopus
Sharp-Dull
Clothes-Wear
Fame-Fortune
Gown-Dress
Mystery-Fiction
Ask-Question
Hike-Walk

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