Attentional shifting and the role of the dorsal pathway in visual word recognition

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Abstract

A substantial amount of evidence has been collected to propose an exclusive role for the dorsal visual pathway in the control of guided visual search mechanisms, specifically in the preattentive direction of spatial selection [Vidyasagar, T. R. (1999). A neuronal model of attentional spotlight: Parietal guiding the temporal. Brain Research and Reviews, 30, 66–76; Vidyasagar, T. R. (2001). From attentional gating in macaque primary visual cortex to dyslexia in humans. Progress in Brain Research, 134, 297–312]. Moreover, it has been suggested recently that the dorsal visual pathway is specifically involved in the spatial selection and sequencing required for orthographic processing in visual word recognition. In this experiment we manipulate the demands for spatial processing in a word recognition, lexical decision task by presenting target words in a normal spatial configuration, or where the constituent letters of each word are spatially shifted relative to each other. Accurate word recognition in the Shifted-words condition should demand higher spatial encoding requirements, thereby making greater demands on the dorsal visual stream. Magnetoencephalographic (MEG) neuroimaging revealed a high frequency (35–40 Hz) right posterior parietal activation consistent with dorsal stream involvement occurring between 100 and 300 ms post-stimulus onset, and then again at 200–400 ms. Moreover, this signal was stronger in the shifted word condition, compared to the normal word condition. This result provides neurophysiological evidence that the dorsal visual stream may play an important role in visual word recognition and reading. These results further provide a plausible link between early stage theories of reading, and the magnocellular-deficit theory of dyslexia, which characterises many types of reading difficulty.

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1. Introduction

There are numerous models of reading and word recognition (Caramazza & Hillis, 1990; Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Whitney, 2001) but one commonality between them is the assumption of a stage requiring the early visual analysis of words as visual patterns. Pelli, Farell, and Moore (2003) have demonstrated that an ability to recognise individual letters provides initial limits on word recognition, and we have demonstrated that readers are sensitive to the internal configuration of word-like symbol strings that require no lexical analysis. This sensitivity predicted reading ability in children (Pammer, Lavis, Hansen, & Cornelissen, 2004) and word recognition in adults (Pammer, Lavis, Hansen, & Cornelissen, 2005). Such evidence implies that word recognition not only requires the complex synthesis of orthographic and phonological information, but is also dependent upon accurate visual analysis very early in the processing sequence. Indeed early visual analysis in word recognition must involve accurate selection and binding of features so that we recognise “T” and not “L”, and the difference between “paternal” and “parental”.

Vidyasagar (1999, 2001) has provided a neural model of early attentional selection that may provide a neurological mechanism for early spatial selection in visual word recognition and reading. This model relies on the physiological and anatomical distinction between the dorsal and ventral visual pathways. Despite a certain amount of interaction (Merigan & Maunsell, 1993) the two pathways are relatively distinct, with the dorsal
pathway responsible for the processing of spatial information such as motion, depth and object location, receiving much of its input from magnocellular cells, while the ventral pathway is sensitive to featural qualities of a stimulus, such as colour, and detail (Livingstone & Hubel, 1988; Logothetis & Sheinberg, 1996; Merigan & Maunsell, 1993). The two pathways have distinct anatomical projections, with the ventral pathway extending through into the left inferiortemporal cortex, and the dorsal pathway through V5 to the right parietal cortex. Neural signaling through into the left inferiortemporal cortex, and the dor-

100 ms (Martinez et al., 1999).

sional evidence (Cheng, Eysel, & Vidyasagar, 1998) supports the suggestion that the dorsal pathway may provide a mechanism for the early, preattentive selection of features in space. In this model, the dorsal path-

The proposal that the visual dorsal pathway provides a mech-

anism for the early spatial selection and binding of features in visual word recognition also has intriguing implications for the description of the underlying neural code. Oscillatory synchroni-

sation has been implicated in the mediation of bottom-up visual feature binding, for example, high frequency gamma oscillations have been demonstrated (e.g., Eckhorn et al., 1988; Engle, Roelfsema, Fries, Brecht, & Singer, 1997; Gray, König, Engle, & Singer, 1989; Gray & Singer, 1987) that are unique to specific configurations and combinations of visual stimuli. This work led to the suggestion that cellular synchronisation of oscillatory responses in different parts of the cortex, might provide a mechanism for the sensory integration of visual signals (e.g., Gray et al., 1989). These findings sparked a large amount of research exploring the functional significance of high frequency cortical oscillations, particularly in the role of cortical binding, and it has been suggested that high frequency gamma activity may mediate the cognitive integration of coherent stimuli (refer to Hermann, Munk, & Engel, 2004; Pulvermüller, Birbaumer, Lutzenberger, & Mohr, 1997; Ward, 2003 for reviews). For example, high frequency cortical oscillations around 30 Hz have been observed in Kanizsa triangles, but only when the pac-men formed the illusionary triangle, not when the pac-men were oriented away from each other (Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996). Similar high frequency activity has been associated with the ‘pop-out’ of a coherent picture from a noisy background (Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1997), and stereoscopic fusion of a 3D picture (Revonsuo, Wilenius-Emet, Kuusela, & Lehto, 1997), as well as; passive viewing of coherently moving stimuli (Muller et al., 1996), upright but not inverted Mooney faces (Rodriguez et al., 1999), and words but not pseudowords (Lutzenberger, Pulvermüller, & Birbaumer, 1994). If high fre-

quency cortical activity plays a role in the selection and binding
of stimulus features (Treisman, 1999), then it is not unreasonable to suggest that any role that the dorsal system may play in early visual-spatial selection and binding, may be mediated by a high frequency cortical code, which should be demonstrable in a neuroimaging technique sensitive to both the temporal and frequency dynamics of the underlying neural signal.

The current study used MEG to investigate the role of the dorsal pathway in visual word recognition. High frequency cortical activity is much less pronounced than activity in other frequencies i.e., there is an inverse relationship between frequency and the number of cells that generate the response (Pulvermüller et al., 1997). To accommodate this, Pulvermüller et al. (1997) have suggested that stimuli should be optimised to cause maximum cortical responses. Therefore, here participants were presented with a lexical decision task in which the constituent letters of the word stimuli are presented in a conventional configuration (‘Words’ condition), or with the letters shifted randomly above or below a central axis ('Shifted-words’ condition). If the dorsal pathway is involved in the early attentional selection of visual features in word recognition, and perceptual binding, then we should see right PPC activity less than 200 ms after stimulus presentation, and possibly represented by gamma frequency oscillations. This activity is likely to be most pronounced in the Shifted-word recognition condition where the dorsal pathway has to work harder to select and configure the constituent letters, compared to the word recognition condition where the letters are in their normal configuration. If no early activation is apparent in the Words, or Shifted-words conditions within the right PPC, then this would suggest no specific role for the dorsal stream in visual word recognition. Alternatively, if there is simply a prolonged activation in the PPC, particularly at lower frequencies, then this would suggest that disrupting the spatial configuration of text merely increases general attentional demands in the observer (Cooper, Croft, Dominey, the spatial configuration of text merely increases general attentional demands in the observer (Cooper, Croft, Dominey, Suffczynski, Kalitzin, Pfurtscheller, & Lopez da Silva, 2001) with a lexical decision task in which the constituent letters of the target were vertically displaced randomly above or below the midline, relative to each other (e.g., P-L-A-N-T). The target stimulus was displayed for 100 ms, and was followed immediately by a pattern mask for a further 100 ms. Non-words were produced by switching the internal letter position of five-letter words in a counter-balanced fashion: 1/3 of the anagrams contained 2nd and 3rd letter position swaps (e.g., PLANT to PLANT), 1/3 contained 3rd and 4th letter position swaps (e.g., PLANT to PLAT), and 1/3 contained 2nd and 4th letter position swaps (e.g., PLANT to PNALT). The mean Kucera–Francis frequency of the words was 168.2 (S.D. = 240.8, range = 42–1815). Presentation of the conditions was randomised throughout the experiment.

Subjects were asked to respond by button press whether they had seen a recognisable word or not. A response was required for each trial with one button indicating the stimulus was a word and a different button indicating the stimulus was a non-word. Their responses were delayed by 1.5 s and cued by a briefly flashed white dot. The next trial followed immediately after the response. A response delay was used as the experiment was also designed to be compatible with fMRI recording. The fMRI results formed the basis of a larger project, and will not be discussed here. This sequence was repeated 80 times per condition with a unique word or non-word for each trial, such that there were 40 presentations of each word and Shifted-word stimuli, and a matched number of non-words stimuli.

To record the data, we used a whole head, 151 channel CTF Omega MEG scanner with the SQUID sensors arranged in a helmet-shaped array. Data was acquired at 625 samples/s in a magnetically shielded room. The MEG data was then mapped onto the subjects structural MRI, so individual head models were taken from each subjects’ MRI. This was achieved by positioning three coils on three anatomical landmarks and determining the shape of the subjects head as well as the locations of the coils using a Polhemus 3D-digitiser (Polhemus Isotrack, Kaiser Aerospace Inc., Vermont, USA). Before recording, a small electrical current was sent through the coils inducing a small magnetic field. The known location of the coils and therefore of the head, allows the mapping of the individual MEG signals onto the individual MRI brains.

2.3. Analysis

The data were analysed using Synthetic Aperture Magnetometry (SAM) to generate statistical parametric maps of significant cortical activity. SAM is a spatial beamforming technique in which a weighted spatial filter is calculated for every voxel, and signal strength at any given location is computed as the weighted sum of all the MEG sensors. The ‘spatial beamforming’ occurs because each sensor closest to each brain region (voxel) maximises the signal strength from that location, while attenuating the signal from surrounding locations. Each filter is based on the input from the signals at the surrounding locations (Baillet, Mosher, & Leahy, 2001; Hillebrand & Barnes, 2001; Singh, Barnes, & Hillebrand, 2003; Vaar, 2002). The resulting time series is analysed by dividing it into “active” and “control” windows, upon which a statistical comparison of the difference activity can be made for each voxel and a volumetric statistical map of activity generated (Barnes & Hillebrand, 2003; Barnes, Hillebrand, Fawcett, & Singh, 2004; Fawcett, Barnes, Hillebrand, & Singh, 2004; Robinson & Vaar, 1999, 2002; Singh et al., 2002; Singh, Barnes, Hillebrand, Forde, & Williams, 2002; Van Veen, van Drongelen, Yuchtman, & Suzuki, 1997; Vaar & Robinson, 2001). The primary limitation of a spatial beamforming technique such as SAM is the possibility that spatially disparate sources may cancel out or attenuate if their activity is perfectly correlated (Van Veen et al., 1997). However, perfectly correlated sources are highly unlikely to be maintained over the 200 ms time windows used here, and SAM source reconstruction has been demonstrated to be robust even over transient source correlations (Hadjipapas, Hillebrand, Holliday, Singh, & Barnes, 2005).

SAM maps of cortical activity are specified in terms of time by frequency windows. In the current study, the ‘active’ and ‘control’ windows were both 200 ms, with the ‘control’ window constituting −700 to −500 ms pre-stimulus onset. The ‘active’ period constituted a moving window, 200 ms wide; 0–600 ms post-stimulus onset. The entire recording epoch for each trial was 3.7 s, including a 700 ms pre-stimulus recording period. The relevant analysis windows were taken from this recording epoch. In the frequency domain, each analysis was a 5 Hz window, ranging from 5 to 50 Hz. Each of the time-by-frequency combinations constituted a separate analysis, and this was done for each stimulus presentation condition.

2.3.1. ERD/ERD analysis

SAM produces information regarding changes in cortical activity in terms of event-related decrease in activation in the active period compared to the
control period, as well as event-related increases in oscillatory activity in the active compared to the control period. The phenomenon referred to as Event Related Synchronisation (ERS) and Event Related Desynchronisation (ERD) refers to the localized increase or decrease, respectively, in recorded brain activity compared to a specified condition or baseline, measured using either EEG or MEG that is frequency specific (refer to Pfurtscheller and Lopez da Silva, 1999 for a review). In the current study, ERS is represented as a positive value (red/yellow colour scale) and ERD is represented as a negative value (blue/pink colour scale). The comparison epoch was the −700 to −500 pre-stimulus control period. Unlike evoked event related potentials, ERD/ERS are not phase-locked to a stimulus event which means that they are generally unlikely to be detected by analysis techniques that involve averaging over epochs. However, SAM is particularly useful for the analysis of induced as well as evoked oscillatory activity because the calculation of statistical maps of cortical activity does not depend upon initial averaging of epochs over time.

Individual SAM maps were generated for each participant for each of the time × frequency combinations (0–600 ms in 200 ms time windows by 5–50 Hz in 5 Hz frequency bands, refer Fig. 1). This resulted in 81 individual maps of statistical activity, for each participant. Group maps over the 10 participants were then produced for each of the 81 analyses, spatially normalised, constructed from random effects models in SPM99 (http://www.fil.ion.ucl.ac.uk/) (Friston et al., 1995) and rendered onto the MNI template brain (http://www.aston.ac.uk/1hs/staff/singhkd/mri3Dx).

3. Results

A region of interest (ROI) in the right PPC was identified in the right inferior parietal lobule, bordering on the superior aspect of the angular gyrus (top of Fig. 1) spanning Talairach coordinates of; superiorly 44, medially 35, inferiorly 31, anteriorly −57 and posterior −72. This ROI was chosen based on the culmination of a number of factors; First of all it has been well documented from at least the time of Mishkin, Ungerleider, and Macko (1983) that the right PPC is the site for the primary projections for the dorsal pathway. After visual examination of all right hemisphere parietal activation over the critical time and frequency windows, this area demonstrated the most consistent and stable activation over multiple time × frequency windows. No other criteria were applied. Moreover, this region is dominated by the angular gyrus, which has been demonstrated to be intrinsically involved in spatial selection (Chambers, Payne, Stokes, & Mattingley, 2004), and the primary site of impairment in spatial neglect (Mort et al., 2003).

Average activation over all subjects was calculated for this ROI from the group SAM maps for each of the 81 time × frequency combinations, for both the Words condition, and the Shifted-words condition (Fig. 1). Therefore, the graphs in Fig. 1 represent the average activation in the right PPC, for each of the time × frequency windows in the Shifted-words and Words conditions. Only activation significant at $p < .001$ are represented. Significant ERD in the Shifted-words condition in the right PPC was found at 50–250 ms, 25–30 Hz (activation A1 in Fig. 1, peak activation $= −4.98$), followed at 100–300 ms by strong ERD at 35–40 Hz (activation B1 in Fig. 1, peak activa-

![Fig. 1. The region of interest identified by the SAM analysis for group data is represented in the whole-head and coronal sections; the left is the ROI in the right PPC for the Shifted-words condition. The right image is the same ROI for the comparison between the Shifted-words vs. Words conditions. The graphs represent the activation at the ROI identified in the sections for different time × frequency combinations. The scale represents significant activity (pseudo $t$, at $p < .001$ corrected) relative to the pre-stimulus control period, and this is the case for all the figures reported here. The left graph is the Shifted-words condition and the right graph is the Words condition. Activations at different time × frequency intervals are labelled. The star indicates activation that is significantly stronger in the Words-shifted compared to the Words conditions. All figures follow radiological convention such that ‘Left’ is on the left side.](image-url)
This was followed by significant ERD in the alpha frequency range, 10–15 Hz (activation C1 in Fig. 1, peak activation = −6.96), and then significant ERD resumed at 35–40 Hz, 200–400 ms (activation D1 in Fig. 1, peak activation = −6.5), which extended until the 300–500 ms time window (peak activation = −4.7). Activation in the alpha band resumed later in the time sequence (activation E1, peak activation = −6). A similar pattern of activation can be seen in the Words condition, labelled B–E to reflect the similar pattern of activity apparent in the Shifted-words condition. Early high frequency ERD was apparent for the Words condition, at 35–40 Hz, 50–250 ms (activation B2 in Fig. 1, peak activation = −3.7) and then again at 150–350 ms (activation D2 in Fig. 1, peak activation = −4) but activity was much reduced compared to the Shifted-words condition. Like the Shifted-words condition, this high frequency activation was interrupted by lower frequency ERS at 15–20 Hz (activation C2 in Fig. 1, peak activation = −3.6), and then followed later in the sequence by strong sustained activation in the alpha frequency range, 10–15 Hz (activation E2 in Fig. 1, peak activation = −6.6). A direct comparison between the Shifted-words and Words conditions demonstrated significantly (p < 0.01) increased activation in the Shifted-words compared to the Words condition, only in activations indicated by a star in Fig. 1—namely B, C and the later tail of D. No other activation was significantly different in the Shifted-words compared to the Words condition, and although activation A1 is significant in the Shifted-words condition, no correlate was apparent in the Words condition.

Of interest was the presence of activation in other cortical areas in addition to the right PPC. However descriptions over all 81 time × frequency windows would result in a prodigious amount of information, therefore Figs. 2 and 3 are an attempt to summarise and represent this information. The aim of the current study is to explore whether the dorsal visual stream as represented by the right PPC is involved in early spatial selection when reading text. Therefore, of particular interest is the relationship between activation in the right PPC and other cortical areas associated with the early, posterior reading network including the visual cortex (Pammer et al., 2004a; Tarkiainen et al., 1999, 2002), the fusiform gyrus (Cohen et al., 2000, 2002; Dehaene, LeClec’H, Poline, LeBiha, & Cohen, 2002), and posterior temporal gyrus areas (Booth et al., 2003; Shaywitz et al., 2004; Simos et al., 2000, 2002). Fig. 2 is the same graph from Fig. 1, however now we have included the significant activations from elsewhere in the cortex for the time frames up to 150–350 ms. All brain sections in Fig. 2 represent significant (p < 0.001) ERS or ERD in the Shifted-words condition compared to the Words condition (i.e., Shifted-words versus Words contrast). In Fig. 2 we can see that the early high frequency activity in the right PPC was preceded by lower frequency (10–25 Hz) ERS in the visual cortex at the mid cuneus and pre cuneus (sections 2A, 2B, 2C of Fig. 2). This was followed by ERD in the cuneus at both 10–15 Hz (section 2E of Fig. 2) and 25–30 Hz (section 2D of Fig. 2). The low frequency ERD in the PPC, shared significant activation in the left inferior parietal lobule at 20–25 Hz (section 2F in Fig. 2), the cuneus again at 25–30 Hz (section 2G in Fig. 2), the left fusiform gyrus (section 2H in Fig. 2) and a strong ERD in the posterior cingulate (section 2I in Fig. 2). From the 150 to 350 ms time window, there was little significant difference between the Shifted-words and Words conditions at other cortical sites. Fig. 3 shows the activation in the Words condition (in yellow), with activation apparent in the left fusiform, mid temporal gyrus, inferior frontal gyrus and inferior temporal gyrus, consistent with other neuroimaging studies of reading and
word recognition. The graded activation (blue ERD to orange ERS) is once again the contrast between the Shifted-words and Words conditions. Therefore Fig. 3 represents the cortical activation associated with reading a word (yellow) together with the cortical activations that are unique to the Shifted-words condition (blue/orange) when a direct contrast is made between the two conditions.

To summarise the findings from Figs. 1–3: activity in the PPC appeared to involve an early high frequency signal, followed by a later, prolonged high frequency signal, separated by low frequency activity in the alpha range. Within the first 200 ms, only the first high frequency, and then the alpha signals are significantly different in the Shifted-words condition. The activity that was stronger in the Shifted-words condition also seemed to be associated with significantly stronger activation in visual areas as well as the posterior cingulate and left inferior parietal lobule. However, after 200 ms, there was little difference between the Shifted-words and Words conditions, with both conditions activating areas typically associated with the word recognition network.

Fig. 4 represents the magnetic evoked activation for one participant for all the sensors over time. The black line here represents the Words condition, and the red line, the Shifted-words. The ROI as described above is best captured by the sensors within the boxed area. These sensors recorded stronger activation in the Shifted-words condition than the Words condition, with a peak at approximately 185 ms post-stimulus onset.

Behaviourally, accuracy for each conditions over the 10 subjects was mean = 97.3%, S.D. = 2.4 for the Words condition, and 82.3%, S.D. = 2.7, for the Shifted-words condition. This difference was significant, $t(9) = 6.19, p < .05$.

4. Discussion

This study was designed to evaluate the proposal that the dorsal visual stream is involved in the early coding of spatial information when reading single words. The results demonstrate that the right PPC was active very early in the visual word recognition network. This activation occurred very close in time to the time frame identified elsewhere (Eulitz et al., 2000; Pammer et al., 2004a) for lexical access. This pattern of activity was apparent both when identifying single words, and was significantly stronger when the spatial configuration of the words had been manipulated to maximise spatial selection and thus dorsal stream involvement.

It was suggested in the introduction that should right PPC activation be apparent, consistent with a role in the early spatial selection and binding of stimulus features, then this activation may be demonstrated at the gamma frequency band which has been implicated in higher-order cortical binding. This was
clearly the case in this study, where right PPC activation was characterised by both high frequency (>20 Hz) and low frequency (<15 Hz) activity, with ERD particularly in the 35–40 Hz range less than 250 ms after seeing the word, and then returning with a more sustained pattern of activation up to approximately 500 ms. Could these two patterns of gamma activation reflect different types of neural oscillation? One difference between the high frequency oscillatory activity evoked by simple visual stimuli such as moving lines or bars, is that it occurs less than 200 ms after stimulus onset, whereas high frequency oscillatory activity that occurs in response to higher cognitive binding generally occurs more than 350 ms after stimulus presentation (e.g., Tallon-Baudry & Bertrand, 1999; Tallon-Baudry et al., 1996). This has led to the distinction between evoked gamma activity which is phased-locked to stimulus onset, and appears to occur early after stimulus onset, and induced gamma activity occurring later after stimulus presentation, has a longer time course, and not phase locked to stimulus onset (e.g., refer to the following for reviews; Başar-Eroğlu, Struber, Schürmann, Stadler, & Başar, 1996; Tallon-Baudry & Bertrand, 1999). Evoked activity is evident in raw waveforms because of the temporal consistency of the signal over recorded epochs, while induced activity will be lost in any analysis technique that averages epochs over trials because of the temporal jitter in the signal from trial to trial. In the SAM analysis technique, data is not averaged over epochs, and as a result, both evoked and induced gamma activity should be observable. Moreover the earlier transient and later sustained nature of this activation is consistent with the suggestion that the first gamma activation reflects evoked activity, while the later activation reflects induced activity (we use the terms transient and sustained here as purely descriptive, referring to activation that occurs either at a single time window or extends over two or more windows, respectively).

It is clear from Fig. 2 that multiple cortical areas are activated at a similar time course, but at different frequencies. Pfurtscheller, Neuper, Pichler-Zalaudek, Edlinger, and Lopez da Silva (2000) demonstrated a similar phenomenon for voluntary movement, showing oscillatory activity at different frequencies for both the hand and foot areas of the motor cortex. They argued that different cortical activation for the same cortical event may reflect differences in the sizes of associated neural populations. However in the current study we used a cognitively more complex word recognition task, rather than the simple finger movement task used by Pfurtscheller and colleagues. As such, it is not unreasonable to suggest that the activity demonstrated in different cortical areas at different frequencies are likely to underlie different aspects of cortical engagement, particularly as they appear to follow independent time courses. It is not surprising that the first high frequency signal (B1 in Fig. 1) was associated with activity in the visual cortex (signals 2A, 2B, 2C, 2D and 2E in Fig. 2). Not only does the right PPC receive input from the visual cortex, but there is increasing evidence to suggest that the visual cortex receives modulatory feedback as a result of focussed visual attention (Moran & Desimone, 1985; Motter, 1993; Vidyasagar, 1998) mediated by the dorsal pathway (Corbetta, Shulman, Miezin, & Peterson, 1995; Vidyasagar, 2001). Therefore, this pattern of activity is exactly what you would expect if the early, high frequency signal in the right PPC is involved in early spatial selection, supported by cortical networks in the visual cortex.

During the low frequency PPC signal (signal C1 in Fig. 1) a number of different areas were activated, including the left fusiform gyrus, the posterior cingulate, and the left inferior parietal lobule (IPL). The left fusiform gyrus has been frequently implicated in early letter string analysis (e.g., refer to Price & Devlin, 2003 for a recent discussion), and it has been suggested that the IPL, specifically areas such as the left posterior superior
temporal gyrus, left superior temporal gyrus and supramarginal gyrus are involved in graphemic-phonological conversion when reading (refer to Jobard, Crivello, & Tzourio-Mazoyer, 2003 for a review). However, the posterior cingulate is an area not traditionally associated with the reading or language network. As this activity occurred in close temporal proximity to the PPC signals that were significantly stronger in the Shifted-word condition (i.e., signals 1B and 1C in Fig. 1), it is not unreasonable to suggest that the cingulate signal may be in some way involved in the requirement for spatial shifting inherent in the Shifted-words condition. There is some evidence to implicate the posterior cingulate in the larger attentional network (Hopfinger, Buonocore, & Mangun, 2000; Mesulam, Nobre, Kim, Parrish, & Gitelman, 2001; Mort et al., 2003; Olson, Musil, & Goldberg, 1993; Small et al., 2003; Tanabe, Tregellas, Miller, Ross, & Freedman, 2002). Kim et al. (1999) demonstrated posterior cingulate activation to both endogenous and exogenous spatial shifting. However, the explicit contribution the posterior cingulate makes to attentional shifting is remains unclear and may involve anticipatory mechanisms (Small et al., 2003), particularly if stimuli are emotionally salient (Mesulam et al., 2001), post-saccadic monitoring (Olson et al., 1993), or reflexive saccades (Mort et al., 2003).

The differential time course between alpha and gamma signal in the ROI is also intriguing. The co-occurrence of alpha and gamma signals is not new (e.g., Ihara & Kakigi, 2006; Muller et al., 1996), and the separation in the time course between the signals suggest different cortical networks and functional-ity. Klimesch and colleagues have demonstrated a distinction between lower (8–10 Hz) and upper (10–12 Hz) alpha activity which may mediate general alertness or attention, and memory retrieval respectively (Klimesch, 1997; Klimesch, Schmike, & Schwaiger, 1994). We have demonstrated elsewhere a right PPC signal in recognising words for both the 8–10 and 10–12 Hz frequency bands (Pammer, Hansen, Holliday & Cornelissen, in preparation). Thus it is possible that the early and late alpha signals here may similarly reflect general attentional engagement which is stronger in the more difficult Shifted condition, and then memory retrieval and rehearsal in both conditions.

The later time windows incorporating 200–600 ms, demonstrated little difference between the Shifted-words and Words conditions (Fig. 3). Both tasks engaged the later stages of the posterior letter string areas such as the fusiform gyrus, inferior temporal gyrus and mid temporal gyrus, as well as the language processing and consolidation areas such as the left inferior frontal gyrus, superior temporal gyrus and angular gyrus. Once again this is the pattern of activity that one would expect if the primary difference between processing words in the Shifted-words condition compared to the Words condition is in the initial visual encoding of the stimuli, after which both conditions demonstrate a typical spatio-temporal flow through the cortical reading network.

We suggest that the results here demonstrate neurophysiological evidence for the direct involvement of the visual dorsal stream in visual word recognition. However, in this experiment the ‘spatial’ stimuli was more difficult to read, thus resulting in a possible confound between task difficulty and reading condi-tion. The question of task difficulty is not easy to answer and intimately related to the meaning we attribute to increases and decreases in recorded cortical activity. Some studies have found decreases in activity in associated cortical areas with increases in task difficulty (e.g., Grady et al., 1996), with the assumption that the stimulus becomes harder to process as the underlying neural substrate becomes more disengaged. Conversely, other studies have demonstrated increases in activation in associated cortical areas with increases in task difficulty (e.g., Price et al., 1994), the assumption here is that the underlying cortical substrate is working harder to process the information. One possible explanation may be that the former inverse relationship between cortical activation and task difficulty may be more likely in early sensory coding, while the latter may be more likely in cognitive tasks requiring higher amounts of neural recruitment or synchronisation (Price, Moor, & Frackowiak, 1996). In regards to the current experiment, the stimuli were optimally designed to push the dorsal pathway to work harder in order to maximise the likelihood of getting a response (Pulvermüller et al., 1997). Are the results here however due to a general increase in cognitive effort? Price et al. (1996) demonstrated an inverse relationship between the duration of word stimuli and activity in the inferior parietal cortex, but no stimulus-dependent activation when stimulus rate was varied. Assuming that fast presentation rate and short stimulus duration should both reflect task difficulty, then in the Price et al. study at least, increasing task difficulty did not in general increase activation in the right PPC. Moreover, Senkowski and Herrmann (2002) explicitly investigated the relationship between task difficulty and the gamma response. They found that only the evoked gamma response increased with task difficulty. Thus a confound between an increase in task difficulty and reading conditions cannot be entirely ruled out in the current study and additional control conditions need to be included to fully address this possibility. The differential roles of the early evoked and later induced activity also need to be explored. Induced gamma signals have frequently been demonstrated in the construction of coherent representations (e.g., Revonsuo et al., 1997; Tallon-Baudry et al., 1996, 1997). If the role of the dorsal stream is to provide feedback to the visual cortex and ventral stream regarding spatial localisation (Vidyasagar, 1999), then a latency of greater than 250—demonstrated here in the second gamma response and elsewhere (e.g., Tallon-Baudry et al., 1996) seems too late to guide attentional spotlighting by the ventral stream. Indeed, responses to word recognition in the ventral stream are already strong by 125–325 ms (Pammer et al., 2005; Tarkiainen et al., 1999, 2002). One possibility is that the dorsal stream has two roles: a dorsally mediated preattentive mechanism which occurs early and insensitive to the perceived coherence of a stimulus, and a second mechanism which is involved with the coherence or identifiability of a stimulus. This suggestion is highly speculative at this stage and requires further research. Similarly, the implications of the delayed response need to be considered. However response organisation and memory maintenance characteristic of a delayed response generally engage the left and right dorso-lateral pre-frontal cortex (Croizé et al., 2004; Volle et al., 2005). Such activations were not apparent in the current study. At the very least this study dovetails nicely with the hypothesis that
the dorsal pathway may be involved in reading by virtue of its role in preattentive spatial selection. When we increased the spatial demands of reading, we obtained stronger activation in the right PPC potentially reflecting dorsal activity. Moreover, activation in the same ROI examined here has been demonstrated in reading music (Schön, Anton, Roth, Besson, & 2002). It could be argued that reading music is a more ecologically valid test of spatial engagement when reading, such that synthesising the visual representation with the auditory code first requires explicit attention to the diverse spatial properties of the component notes, and thus an integration of visual signals over space. These results therefore provide a possible correlate to the results we present here and provide yet another intriguing avenue for further research.

There are few theories in the literature that explicitly describe the nature of the contribution of dorsal stream processing to reading. As such, the link between a deficit in the dorsal stream (sometimes known as the magnocellular deficit theory of dyslexia), and reading ability remains controversial. If there is a deficit in processing early in the dorsal stream, then it is likely to make it more difficult to synthesise word features and positional information (Pammer & Vidyasagar, 2005; Vidyasagar, 1999, 2001). This is likely to have serious consequences for reading ability, particularly orthographic processing. Indeed it has been demonstrated psychophysically that dorsally mediated visual sensitivity specifically underlies orthographic processing in reading (Pammer & Kevan, in press; Talcott et al., 2000). The results here support this proposal by suggesting that any contribution the dorsal stream may have in reading ability is likely to be in the role of early visual coding, and synthesis of visual information.

The results demonstrated in this study are important for a number of reasons. We have for the first time demonstrated that the right PPC appears to be involved in the early stages of visual word recognition, possibly in the role of early spatial selection. The use of SAM as an analysis technique allowed us to explore this PPC activity in terms of the underlying neural code, such that it would appear that the PPC may in fact assume multiple roles in visual word recognition that is reflected in the temporal specificity of the high frequency and low frequency activation that appeared to reflect early evoked cortical activity followed by later, sustained induced neural oscillations. Finally, that different areas of the cortex appeared to be engaged at similar time frames, but at different frequencies is of particular interest. The spatio-temporal pattern of activity represented here at different frequencies is likely to underlie different functional components of the network, but the fact that putatively different functional areas are associated with different frequencies rather than the same frequencies (correlated) is intriguing as it suggests that different functional components of the network are engaged at the same time, but not ‘talking’ to each other in terms of coherent frequency oscillations. This distinction then between correlated and uncorrelated sources within the same cognitive network, and their functional consequences is of enormous interest and ripe for more focussed research.

These results allow us to develop current neurophysiological models of reading, and provide an intrinsic missing-link between models of reading, and dorsal stream deficits observed in poor readers. The current research allows us to only make judgements about single word recognition; therefore, the role of the dorsal stream in contextual reading now provides an area for fruitful exploration.

References


