Rapid Communication

Visual word recognition: the first half second

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We used magnetoencephalography (MEG) to map the spatiotemporal evolution of cortical activity for visual word recognition. We show that for five-letter words, activity in the left hemisphere (LH) fusiform gyrus expands systematically in both the posterior–anterior and medial–lateral directions over the course of the first 500 ms after stimulus presentation. Contrary to what would be expected from cognitive models and hemodynamic studies, the component of this activity that spatially coincides with the visual word form area (VWFA) is not active until around 200 ms post-stimulus, and critically, this activity is preceded by and co-active with activity in parts of the inferior frontal gyrus (IFG, BA44/6). The spread of activity in the VWFA for words does not appear in isolation but is co-active in parallel with spread of activity in anterior middle temporal gyrus (aMTG, BA 21 and 38), posterior middle temporal gyrus (pMTG, BA37/39), and IFG.
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Keywords: Reading; Visual word form; Visual analyzer; Inferior frontal gyrus

Introduction

In many cognitive models of reading, the first stage of printed word processing involves the operation of a "visual analysis system" (Coltheart, 1981; Ellis, 2004). This converts the symbols on a page to abstract letter representations that are invariant for font-type, font-size, and retinal position. In addition, the visual analysis system extracts information about where letters are positioned with respect to each other in the string. The task of identifying letter strings as familiar words is the responsibility of the "visual word form" processor. This is said to be a mental word-store that contains representations of the written forms of all familiar words, and is a "... stage in the reading process prior to phonological or semantic analysis" (Warrington and Shallice, 1980). Recently, Cohen et al. (2002) have suggested that visual

word form representations "... are subtended by a restricted patch of left-hemispheric fusiform cortex [average Talairach coordinates: $x = -43$, $y = -54$, $z = 12$], which is reproducibly activated during reading" (p. 1054). Accordingly, Cohen et al. showed that the visual word form area (VWFA) responds more strongly to alphabetic letter strings than checkerboard stimuli, more strongly to words than consonant strings and demonstrates invariance with respect to retinal position. In addition, VWFA shows font-type invariance (Dehaene et al., 2002).

Others contest the claim that the VWFA is uniquely involved in representing visual word forms. In a recent critical review, Price and Devlin (2003) point out that the same area is engaged: when subjects make manual "twist" or "pour" actions in response to pictures of familiar objects relative to perceptual judgments on the same stimuli; when they hear, repeat or think about the meaning of auditory words; and when congenitally blind subjects read tactile words with abstract meanings in Braille. None of these acts, so runs the counter claim, requires access to a visual word form.

We shed light on this controversy by applying synthetic aperture magnetometry (SAM) to magnetoencephalography (MEG) data to map the spatiotemporal evolution of cortical activity during performance in a visual lexical decision task.

Experimental procedures

Subjects and tasks

Ten adult right-handed skilled readers (six males, four females; mean age: 34 years, 4 months [range, 28–48 years] with no recorded history of dyslexia) were required to indicate whether a presented letter-string was a recognizable word, or an anagram of one of the words from the test battery. Anagrams were produced by switching the internal letter position of five-letter words in a counter-balanced fashion: 1/3 of the anagrams contained second and third letter position swaps (e.g., HOUSE to HUOSE), 1/3 contained third and fourth letter position swaps (e.g., HOUSE to HOSUE), and 1/3 contained second and fourth letter position swaps (e.g., HOUSE to HSUOE) (Cornelissen et al., 1998). The mean Kucera–Francis frequency of the words was 168.2 (SD = 240.8, range = 42–1815). Systematic bigram frequency differences

between the three classes of anagram were sought by extracting all the position-dependent token frequencies of bigrams from the CELEX psycholinguistic database (Centre for Lexical Information, Nijmegen, the Netherlands). We calculated a position-sensitive bigram frequency score for each anagram class and then compared scores across the three classes of anagram. A one-factor ANOVA of token frequency determined no statistically significant difference between the three bigram groups $F(2,213) = 0.65$, $P > 0.05$. This suggests that there was little information, other than the location of the position swap, which distinguished the three types of anagram.

During the task, a fixation cross was presented for 500 ms. This was replaced by the stimulus letter-string for 100 ms, which in turn was masked for 100 ms. Subjects responded by a button press whether they saw a word or not. Their responses were delayed by 1400 ms and were prompted by a briefly flashed spot on the screen. Behaviorally, mean percentage correct responses for words and anagrams were 97% (SD, 2.7%) and 83% (SD, 9.4%), respectively.

Data acquisition

MEG data were collected using a 151-channel CTF Omega system (CTF Systems Inc., Port Coquitlam, Canada) at Aston University. Data were sampled at 625 Hz with an antialiasing cut-off filter of 200 Hz. Subjects viewed the stimuli on a computer monitor directly, such that word stimuli subtended a visual angle of approximately $4 \times 1°$. All subjects were also scanned with MRI to get a high resolution T1 volume with typically at least $1 \times 1 \times 1$ mm voxel dimensions. Immediately after finishing data acquisition, a 3-D digitizer (Polhemus Isotrak) was used to digitize the shape of the subject's head in the MEG laboratory and the relative position of the headcoils for the nasion, left and right ear on the headset, which is then matched to the subject's MRI.

Image analysis

The MEG data were analyzed using synthetic aperture magnetometry (SAM), which is an adaptive beam-forming technique for the analysis of EEG and MEG data (Robinson and Vrba, 1999; Van Veen et al., 1997; Vrba and Robinson, 2001). SAM has been previously used in a variety of studies on the functions of the motor cortex (Taniguchi et al., 2000), the human somatosensory cortex (Hirata et al., 2002), swallowing (Dziewas et al., 2003), Stroop task (Ukai et al., 2002), and midline theta rhythms (Ishii et al., 1999). In addition, SAM has been shown to be able to unveil changes in cortical synchronization that are spatially coincident with the hemodynamic response found with functional magnetic resonance imaging (Singh et al., 2002). This has also been shown to hold true for combining SAM statistics across individuals (Singh et al., 2003). Related techniques, such as distributed imaging of coherent sources (Gross et al., 2001) and source localization using minimum current estimates (Jensen and Vanni, 2002), have also been used to study inter-regional coherences within specific frequency bands. The statistical difference maps that are generated for the whole brain for an individual are based on the covariance of the data gathered from this individual, and can thus image changes in spectral power such as event-related synchronization (ERS) and event-related desynchronization (ERD) that are not necessarily phase-locked to a stimulus. There is some debate regarding the functional meaning of ERS versus ERD, but it has been demonstrated that ERD is a correlate of *increased* neural activation (Pfurtscheller and Lopes da Silva, 1999). Until proven otherwise from, for example, simultaneous recordings of MEG and local field potentials in experimental animals, and, in the light of existing data, in this paper, we assume that synchronization and desynchronization in SAM are equally meaningful correlates of neural activity.

Furthermore, using the appropriate anatomical information from an individual enables the statistical maps to be transformed to a standard MNI space and used to make group statistical inferences. The main limitation of adaptive beam-former techniques is dealing with sources that are perfectly temporally correlated. Perfect synchrony between two sources in the brain over the entire course of the experiment is very unlikely, and it has been shown that the two sources can be resolved even at relatively large temporal correlation levels (Sekihara et al., 2002; Van Veen et al., 1997).

The SAM analysis links each voxel in the brain to the detection array using an optimal spatial filter for that particular voxel (Robinson and Vrba, 1999). The data from the MEG sensors is then projected through this spatial filter to give a weighted measure of current density, as a function of time, in the target voxel, which means that the time series for each voxel has the same millisecond time resolution as the original MEG signals. Fourier analysis was used to calculate the total amount of power in each frequency band within each of the *active* and *passive* time epochs of the time series. The jack-knife statistical method is used to calculate the difference between the spectral power estimates for the *active* and *passive* states over all epochs to produce a true *t* statistic. A three-dimensional image of differential cortical activity is produced by repeating this procedure for each voxel in the whole brain.

In this experiment, the SAM analysis created a volume for covering the whole brain in each individual with a voxel size of $5 \times 5 \times 5$ mm. The *passive* state was defined at the time period between -700 and -500 ms before stimulus onset, and the *active* state was defined as a moving 200 ms window starting at -150 ms before stimulus onset to 300 ms after. Power changes between the *active* and *passive* states were calculated in the frequency band of $10–20$ Hz, which has previously been shown to produce changes in cortical synchronization that are spatially coincident with the hemodynamic response found with functional magnetic resonance imaging (Singh et al., 2002). Furthermore, in the data analysis, we took care to eliminate eyeblink artefacts.

Group statistical maps were generated by first normalizing the SAM functional volumes to standard MNI space (Collins et al., 1994) and then combining these volumes across subjects for each time window and frequency band. The normalization parameters were obtained using FMRIB's Linear Image Registration Tool (FLIRT; Jenkinson and Smith, 2001) to reslice each individual's anatomical MRI to the same orientation and position as the SAM functional volume and finding the transformation matrix from this functional space into the standard MNI space. This transformation matrix was then applied to each of the functional SAM volumes, in each time window and frequency band, and for each subject. A simplified mixed-effects model was used to generate group statistical maps by combining volumes across individuals for each contrast by calculating the sum of individual statistical values divided by the square root of the number of subjects over each voxel in the standard brain. These group statistical maps were then

thresholded at $t > 2.3$, and superimposed on the MNI template brain with the cerebellum removed.

Results

The analysis revealed that the most salient activity in our dataset was to be found in the $10–20$ Hz frequency band. Accordingly, Fig. 1 shows a montage of the significant cortical activation in this frequency band for word and anagram presentations in four time windows. Event-related desynchronization (ERD) is represented in blue and event-related synchronization (ERS) in red. Note that because subjects' button responses were delayed by approximately 1.5 s, we did not find any differences in average reaction times to words versus anagrams.

The early cortical responses to words can be divided into at least two phases. In the time window between 0 and 200 ms, ERS activity is present in the lingual gyrus, cuneus, and also predominantly left hemisphere (LH) posterior fusiform gyrus (BA18/19) [X, Y, Z: $-14, -88, -6$, and X, Y, Z: 30, $-94, -6$]. At $100–300$ ms, an ERD appears in a more anterior part of fusiform gyrus [X, Y, Z: $-32, -64, -6$] close to the VWFA as defined by Cohen et al. (2002). This activity is temporally coincident with activity in the posterior superior IFG (BA44/6) [X, Y, Z: $-60, 8, 22$], which then spreads inferiorly. In the same time window from 100 to 300 ms, the presentation of anagrams elicited activation in the IFG but not in the VWFA. Activity related to anagrams did appear in the VWFA region, but this appeared later in the $150–350$ ms window (see Fig. 2) and was significantly time delayed with respect to responses to words. Moreover, the activity in the IFG appears

earlier for anagrams, in the $75–275$ ms window, compared to words. In both cases, the activity in the fusiform gyrus expands systematically in both the posterior–anterior and medial–lateral directions over the course of the first 500 ms after stimulus presentation.

The third row of Fig. 2 is a direct comparison between word and anagram responses for each of the 13 time points. Critically, this analysis shows that there is no difference between the activation for words and anagrams in the posterior fusiform (BA 18/19) during the $0–200$ ms time window. However, this analysis also reveals a greater degree of synchrony for words compared to anagrams in more anterior fusiform territory en route to the VWFA for the same time window.

Later stages of word processing in the $200–400$ and $300–500$ ms time windows included co-activation in the anterior middle temporal gyrus (aMTG, BA 21 and 38). Furthermore, from around 200 ms post-stimulus, we also see activity predominantly in left posterior middle temporal gyrus (pMTG, BA37/39) that peaks around $300–500$ ms. In its early stages, the pMTG activity is accompanied by co-activation in the angular and supramarginal gyri (BA 39/40), and subsequently in the superior temporal operculum.

Discussion

We have presented novel MEG data mapping the spatio-temporal evolution of cortical activity for visual word recognition in the first half second. Ideally, data like these should help us to untangle the sequence of events in the reading network, and
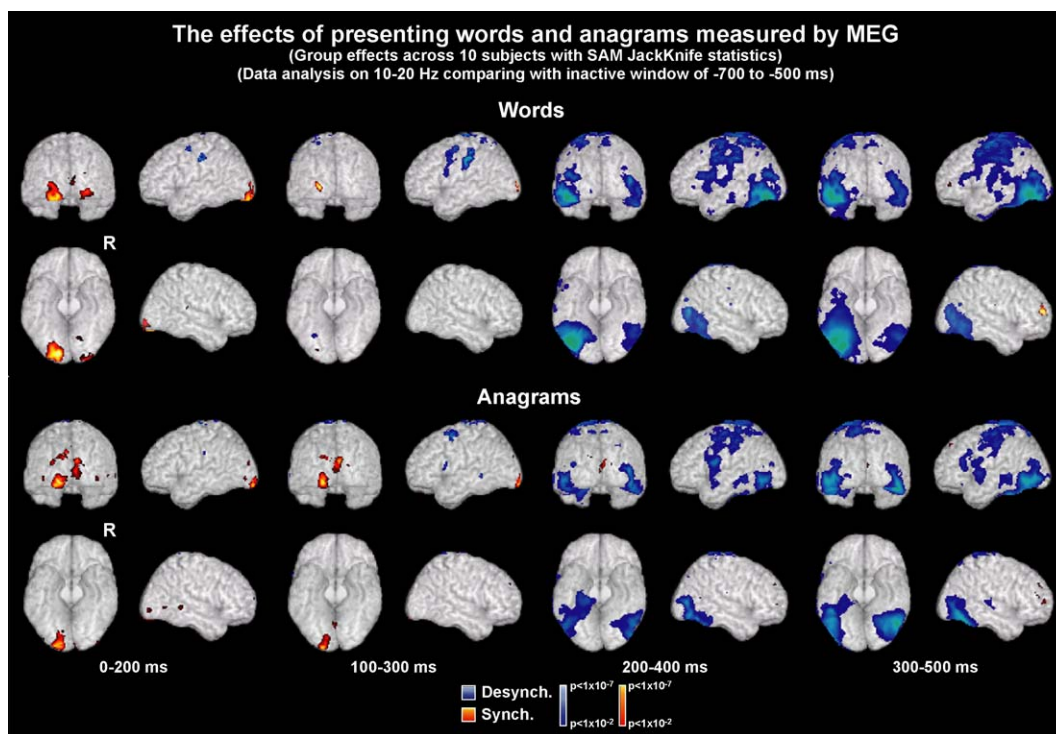

Fig. 1. The brain activity elicited by presenting words and anagrams measured by MEG. At the top of the figure is the SAM group analysis of brain activity in the $10–20$ Hz band to words in four time windows ($0–200$, $100–300$, $200–400$, $300–500$ ms) superimposed on a canonical brain with the cerebellum removed. At the bottom of the figure is the brain activity elicited by anagrams in the same time windows.
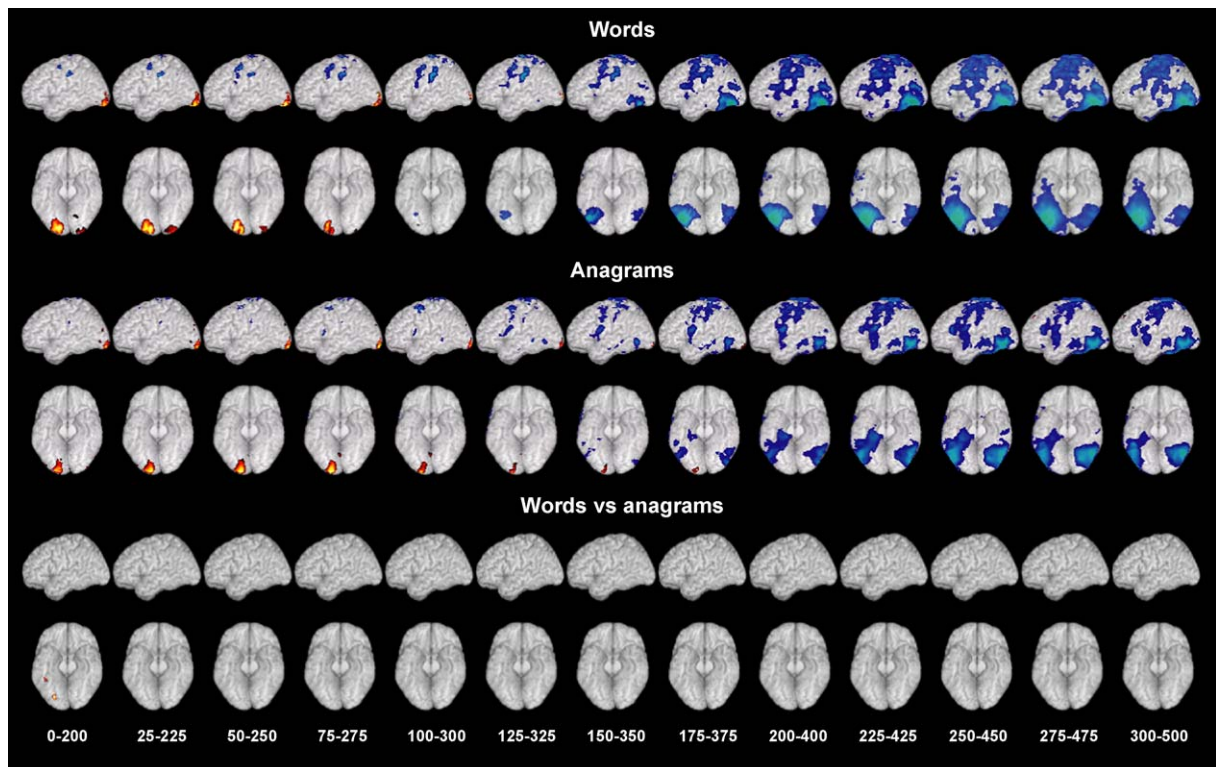
Fig. 2. Temporal evolution of left hemisphere and ventral brain activity elicited by visual word and anagram presentation. The figure shows the SAM group analysis of brain activity measured every 25 ms with MEG (in the 10–20 Hz band) and superimposed on a canonical brain with the cerebellum removed. Rows 1 and 2 show the activity for words; rows 3 and 4 for anagrams; rows 5 and 6 a direct comparison between words and anagrams.

thereby set limits on the likely functional roles for each of its components. However, to achieve this, it is fundamentally important to know whether the activity we see is related to feedforward or feedback effects, or some combination of the two.

Feedback versus feedforward

Human electrophysiological studies assume that ERP components from 50 to 150 ms post-stimulus represent measures of signaling through a hierarchical visual organization (Sereno and Rayner, 2003). That anatomical hierarchies exist in the visual system is well established (VanEssen et al., 1990). Confirmation that a sequential progression can be also defined functionally in humans has come from combined ERP and fMRI studies (Martinex et al., 1999). In addition, there is a developing argument that the speed of processing and information flow through the visual system is more rapid than has traditionally been assumed (Thorpe et al., 1996). For example, there is evidence that the first afferent volley reaches frontal cortex 80 ms post-stimulus and continues through the top-down feedback loops that modulate further processing in sensory areas (Foxe and Simpson, 2002). Findings like these have led to models (e.g., Lamme, 2003) in which stimulus activation of the visual system produces a rapid fast-forward sweep followed by a slower set of recurrent interactions operating both within an activated area and backwards to lower levels of the system. This may mean that the later an ERP/MEG component is in time, the more likely it is to be indicative of recurrent feedback-driven processes rather than the first information sweep through the system (Buchner et al., 1997).

Two phases of occipitotemporal activation

On the basis of our findings, we suggest that the early stages of visual word processing can be decomposed into two distinct phases. The first phase of activity, between 0 and 200 ms, has the form of an ERS localized to lingual gyrus, cuneus, and also predominantly left hemisphere (LH) posterior fusiform gyrus (BA18/19). The posterior fusiform component of this response is spatially and temporally coincident with the so-called LH Type II response in fusiform gyrus revealed in previous MEG studies of reading (Cornelissen et al., 2003; Salmelin et al., 1996; Tarkiainen et al., 1999, 2002). Critically, this Type II response is in fact posterior to the VWFA location of Cohen et al. (2002) and it has a latency of approximately 150 ms (when modeled with equivalent current dipoles), thereby falling into the 0–200 ms window of the current SAM analysis. Functionally, Type II responses to written words in the fusiform gyrus are clearly distinguished from those to geometrical forms, faces, and other objects. But they *cannot* be distinguished from either nonwords (e.g., POLMEX) or random consonant strings; hence, they are letter sensitive but nevertheless prelexical. This pattern of responses is consistent with one of two possibilities. The first is the operation of the "visual analysis system" in which letter-forms are explicitly encoded in posterior LH fusiform gyrus, as suggested by many cognitive models. The alternative is that the Type II response in posterior fusiform gyrus reflects the activity of a general system for correlation-based learning whose spatial organization in the cortex of a skilled reader reflects the temporal and spatial clustering of letters with letters in the environment (cf. Polk and Farah, 1998), that is, part of a general

system for extracting the features required for object recognition, including those for letter identification. Either way, both accounts lead us to predict that activity in the posterior fusiform (BA 18/19) should be the same for words and anagrams, because both stimulus sets contain exactly the same population of letters. The absence of a significant difference in synchrony between words and anagrams in BA 18/19 (shown in the third row of Fig. 2) supports this. But the same comparison also reveals greater synchrony for words relative to anagrams more anteriorly in fusiform gyrus, en route to the VWFA. We speculate that this might reflect a faster initial forward sweep through occipitotemporal cortex for words than anagrams before the initiation of recurrent feedback activity.

The second phase of occipitotemporal activity we found is in the region of the VWFA and has the form of an ERD. It does not appear until the time window 100–300 ms after word presentation. This fits the temporal profile seen in field potential recordings in humans (Nobre et al., 1994), as well as the ERP recordings of Cohen et al. (2000). Both show that nonwords can be distinguished from real words at around 250 ms post stimulus, but this is almost 100 ms later in time, and is at a site anatomically more anterior than the prelexical Type II response. However, these findings are not consistent with other reports in the literature about when lexical access for visually presented words first occurs. For example, the word frequency effect represents the difference in responses to high-frequency (HF) words that are most commonly used and low-frequency (LF) words that occur much less often. Word frequency effects are thought to indicate that lexical access has occurred and have been reported for the N100 response to both reading and lexical decision tasks (Sereno et al., 1998). Pulvermuller et al. (2001) also reported that the magnitude of the parieto-occipital N100 was significantly correlated with a measure of semantic association (i.e., a score related to the differences between function words, visual nouns, action verbs, and multimodal nouns). One way to resolve these apparent discrepancies in the timing of lexical access is to suggest that the early estimates (i.e., those based on the N100) might reflect the first sweep of activity through the system. The later estimates, including the current results, might be based on signals reflecting recurrent feedback activity. Clearly, further research is required to disambiguate these possibilities.

Finally, one striking result is the delay we found in VWFA activation for anagrams relative to words. Recently, Dehaene et al. (2003) used an unconscious masking paradigm to show that masked words activated left extrastriate, fusiform, and precentral areas. Furthermore, masked words reduced the amount of activation evoked by a subsequent conscious presentation of the same word in the territory of the VWFA. This repetition suppression effect was independent of whether the prime and target shared the same case, indicating that neurons in this region may be tuned for case-independent information about letter strings. If so, it is also plausible that letter-string tuning in VWFA territory may reflect the frequencies with which particular letter combinations are encountered in the real world, with familiar groupings eliciting a faster response. Accordingly, the fact the average token bigram frequency counts for the words in our stimulus set (mean = 18,670, SE = 50,134) was significantly higher ($t = 7.99$, $P < 0.0001$) than that for anagrams (mean = 394,313, SE = 17,503) might explain this delay.

Early IFG activity

The present results show that the response in the VWFA region is temporally preceded by activity in the posterior superior IFG (BA44/6), and that this occurs earlier for anagram stimuli (75–275 ms window) than it does for words (100–300 ms window). Since subjects had to respond by button press, the early IFG activation could, in principle, be related to motor preparation or the readiness potential (Kornhuber and Deecke, 1965). We think this is unlikely for two reasons. First, there was an approximately 1.5-s delay before subjects were prompted to press a button. Secondly, there is no reason to assume that motor preparation alone should be different for button presses in response to words versus anagrams, and yet we do see differences in latency.

Another possibility is that the IFG activity might relate to the dynamic control of task switching (Monsell, 2003). When an anagram is presented, the initial sweep of activity through the system should fail to elicit a lexical response. As a result, feedback processes might then initiate a switch from an automated mode of letter-string processing (i.e., the usual situation for skilled readers viewing familiar words), to a slower, more analytic processing mode appropriate to unpacking anagrams. Perianez et al. (2004) used MEG to map the spatiotemporal sequence of events during task-switching in an analogue of the Wisconsin card-sorting test (WCST). They found that IFG was active in the time period 100–300 ms after a shift cue. However, not only was this activity bilateral, unlike the left lateralized responses in our data, but also it localized to a more anterior, inferior region of IFG (BA45/47).

Our preferred interpretation for the left-hemisphere IFG response is also the most challenging. The cortical territory in and around Broca's Area in the inferior frontal gyrus (IFG) appears to be associated with fine-grained, speech-gestural, phonological recoding. This system has been found to function in silent reading and naming (see Fiez and Petersen, 1998 for review; Pugh et al., 1996, 1997) and is thought to be more strongly engaged by low-frequency words and pseudowords than by high-frequency words (Fiez and Petersen, 1998; Fiebach et al., 2002). Moreover, the particular region we see in the current data, that is, posterior superior IFG (BA44/6), fits remarkably well with the territory associated with phonological processing as revealed in a recent meta-analysis by Bookheimer (2002). We suggest that the combination of brief presentation times in combination with backward masking may well tax the reading network. Consequently, our lexical decision task may enhance the requirement for early phonological processing, perhaps to facilitate grapheme–phoneme mapping. Clearly, we need further SAM data to test whether contextual reading evokes similar, early left-hemisphere activity in IFG, and to exclude alternative hypotheses-like task switching. But if this finding is repeatable, and our interpretation correct, it would pose a strong challenge to the proposed role of the VWFA—which is supposed to be a "stage . . . prior to phonological and semantic analysis".

Other considerations

In the current data, later stages of word processing in the 200–500 ms windows included co-activation of cortical areas that have been associated in previous hemodynamic studies of semantic processing in the aMTG (BA 21 and 38) (Rossell et al., 2003). In addition, from around 200 ms post-stimulus, we also see activity predominantly in left pMTG (BA37/39) which peaks around 300–500 ms but which in its early stages is accompanied by co-activation in the angular and supramarginal gyri (BA 39/40) and subsequently in the superior temporal operculum (Mummery et al., 1999).

Traditionally, nonwords or pseudo-words have been used for comparison with words. We chose to use anagrams in the lexical decision task, as we wanted a minimalist intervention which allowed us to disturb the structure of a letter-string so as to break any automatic contact between graphemic, phonological, and semantic representations as early as possible in the chain of events that underlie visual word recognition. We know from behavioral evidence that abstract letter identity, independent of font type and case, represents the basic perceptual unit of visual word recognition (Besner and McCann, 1987; Grainger and Jacobs, 1996; Pelli et al., 2003). Thereafter, in order that letter identities can be mapped onto whole-word representations in memory, evidence suggests that we also compute letter position (Humphreys et al., 1990; Mason, 1981, 1982; Peressotti and Grainger, 1999). Therefore, we argue that anagrams of words, in which internal letter positions are swapped, provide us with such a minimalist tool. Only changes in letter position, rather than letter identity, determine whether or not the subject immediately perceives a word.

Overall, the pattern of responses to briefly presented, masked words suggests that current models of visual word recognition may need constraining. First, our data show activity in parts of IFG temporally preceding or at the same time as activity in the VWFA. While we cannot draw firm conclusions from the current data, we speculate that this may be due to phonological processing rather than task-switching, for example. If so, this would question the idea of a functional role of VWFA in word processing solely in the visual domain, as originally proposed by Warrington and Shallice (1980). Secondly, the spatiotemporal pattern of widespread activation in the fusiform gyrus over the course of 500 ms after stimulus presentation suggests that there could be multiple foci for cortical integration of, for example, either multimodal information and/or the influence of top-down processing, but this awaits further investigation. Thirdly, the widely distributed pattern of responses between 200 and 500 ms fits better with parallel distributed models of reading (Plaut et al., 1996) than it does with the (implicitly) hierarchical structures described by many cognitive models. The key idea here is that words need not be explicitly represented in a discrete system of localized units, and access to them does not depend on an orderly sequence of transformations of the visual input into the spoken output. Instead, words can be represented in a parallel distributed way, determined by the weightings of the connections between, for example, visual, phonological, and semantic representations. If so, the neurons in the VWFA may be more tuned to the fast temporal processing of words and not to anagrams, which provide a fast route for reading. This encoding appears, however, to rely on co-activations with other brain regions such as the IFG and thus the implication of the results presented in this paper is that current models of visual word recognition may need revision concerning the functional role of the VWFA.

Acknowledgment

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