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Two brain pathways for attended and ignored words

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The dependency of word processing on spare attentional resources has been debated for several decades. Recent research in the study of selective attention has emphasized the role of task load in determining the fate of ignored information. In parallel to behavioral evidence, neuroimaging data show that the activation generated by unattended stimuli is eliminated in task-relevant brain regions during high attentional load tasks. We conducted an fMRI experiment to explore how word encoding proceeds in a high load situation. Participants saw a rapid series of stimuli consisting of overlapping drawings and letter strings (words or nonwords). In different blocks, task instructions directed attention to either the drawings or the letters, and subjects responded to immediate repetition of items in the attended dimension. To look at the effect of attention on word processing, we compared brain activations for words and nonwords under the two attentional conditions. As compared to nonwords, word stimuli drove responses in left frontal, left temporal and parietal areas when letters were attended. However, although the behavioral measures suggested that ignored words were not analyzed when drawings were attended, a comparison of ignored words to ignored nonwords indicated the involvement of several regions including left insula, right cerebellum and bilateral pulvinar. Interestingly, word-specific activations found when attended and ignored words were compared showed no anatomical overlap, suggesting a change in processing pathways for attended and ignored words presented in a high attentional load task.

Keywords: Brain; fMRI; Word processing; Attention; Perceptual load

The focus of attention has a fundamental impact on brain dynamics. When attention is focused on a spatial location, an object, or certain features of a stimulus, a set of frontal and parietal regions initially code for the appropriate attentional template (Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002). In many cases, this top–down focus generates an enhancement of pre-target activation in brain areas coding for task-relevant information (Luck et al., 1997; Kastner et al., 1999), preparing the system to respond when the relevant target stimulus arrives (Corbetta et al., 1991; see also Chawla et al., 1999). This set of neural processes helps the organism prioritize and respond to the specific dimensions of the environment selected as relevant from among the many distractions competing for the control of behavior. Accordingly, during any given act of perception, attentional focus may act to exclude many irrelevant items from the available set.

Considerable debate spanning several years has centered on the fate of ignored information and questions concerning whether ignored information might gain access to high-level processing (see Lavie and Tsal, 1994; Driver, 2001), with evidence supporting both early and late selection theories. One of the fields in which this question has been extensively investigated is word encoding, a classical example of automatic processing (see for example, Driver, 2001). Although several behavioral studies have suggested that attention is needed for some forms of word processing (e.g. Fuentes et al., 1994; Besner and Stolz, 1999; Naccache et al., 2002), many others indicate that unattended and/or unconscious words do access high-level lexical and semantic analyses (e.g. Fuentes and Ortells, 1993; Merikle et al., 2001; Catena et al., 2002; Ortells et al., 2003; Ruz et al., 2003). Investigations using ERP have shown that removing attention from words eliminates (McCarthy and Nobre, 1993; Bentin et al., 1995; Ruz et al., 2005) or attenuates (Holcomb, 1988; Bentin et al., 1993) components such as the N400, an index of semantic processing. For example, using a dichotic listening task, Bentin et al. (1995) reported that both the N400 and explicit memory were absent for ignored words, whereas implicit indexes such as false recognition of semantic associates and repetition priming remained for unattended items. This class of results can be taken to support the conclusion that although words only reach high-level controlled processing when they are attended to, evidence of more automatic processing can be observed by means of implicit measures.

In the more general literature on attention and automaticity, one currently prevailing view holds that perceptual task load is the main determinant of the fate of ignored stimuli (Lavie, 2000). The Perceptual Load theory by Lavie (1995) assumes that perceptual

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processing proceeds in an automatic, but limited, manner and this determines the resources available for task-irrelevant stimuli. When the task is easy, perceptual load is low and the spare resources spill over to irrelevant ignored items, which are then processed and able to affect the ongoing behavior. In contrast, when the perceptual load of the task is high enough, all resources are occupied and information not directly relevant to the task does not gain access to high-level processing.

Neuroimaging results have added to the wealth of research supporting this view. In the first such study, Rees et al. (1997) reported that blood–oxygen level dependent (BOLD) response in V5 generated by irrelevant moving stimuli was modulated by the degree of perceptual load on an unrelated task. When task demands were low (e.g. case decision on a letter string), irrelevant background motion generated a large BOLD response in area V5. However, in blocks where task demands were high (e.g. a challenging syllabic decision on a letter string), motion related activation in this area was absent. This attenuation of neural response to irrelevant stimuli during high attentional load has also been shown in brain regions early in the processing stream, including Lateral Geniculate Nucleus (O'Connor et al., 2002) and V1 (Schwartz et al., 2005). Similarly, Yi et al. (2004) showed that BOLD response to task-irrelevant places measured in the Parahippocampal Place Area was obliterated when perceptual demands of a task performed on faces presented at fixation increased (see also Pinsk et al., 2004).

Given the potential impact of these developments for studies of automaticity in word recognition, few investigations have devised high attentional load paradigms to examine word responses in attended vs. unattended conditions. Rees et al. (1999) used fMRI to measure the BOLD response in a high attentional load task manipulating attention either to letters or drawings presented in overlapping spatial positions. Results showed that those regions differentially activating for words and nonwords when attention was focused on letter stimuli were silent to this same contrast when attention was 'fully withdrawn' from the letter domain (Rees et al., 1999). Therefore, the authors suggested that within a high perceptual load task, attention to other stimuli eliminates irrelevant processing of even highly practiced words.

Most fMRI studies investigating stimulus processing in high load situations employ the strategy of identifying specific brain regions typically associated with processes of interest and demonstrating a lack of responsiveness under high attentional load conditions when attention is otherwise engaged (Rees et al., 1997; O'Connor et al., 2002; Yi et al., 2004; although see Schwartz et al., 2005). However, whereas this 'selective region-of-interest (ROI) strategy' has the advantage of higher statistical power and is consistent with some a priori predictions, it carries the risk of missing effects that might arise in regions not expected to be relevant for a given task. This drawback is particularly relevant in the field of selective attention, because unattended information may not be processed in the same fashion or through the same pathways as attended items. For example, previous work (e.g. Raichle et al., 1994) has reported that when the same task and stimuli are presented in situations that pose either high or low attentional demands on processing, different brain pathways are recruited to perform the task. Thus, it could be the case that in situations of high load, different sets of structures are sensitive to information when ignored, as opposed to when attended, due to compensatory strategies. In this case, an approach covering the whole brain might be more useful in revealing regions important for the analysis of task-irrelevant information. Several lines of evidence suggest this alternate-pathway option to be plausible.

Recent electrophysiological research in our lab (Ruz et al., 2005) indicates that irrelevant ignored words are indeed processed in the high attentional load task devised by Rees et al. (1999) to investigate inattentional blindness. Results of this electrophysiological study showed that both late anterior and posterior electrophysiological components differentiated between ignored words and ignored nonwords when attention was fully focused on overlapping drawings. This outcome resonates with previous studies suggesting that participants' own names are able to capture attention when presented in this same inattentional blindness paradigm (Mack et al., 2001; see also Mack and Rock, 1998; Wolfe, 1999) and is in agreement with a large literature establishing, in many aspects, an automaticity of visual word encoding (i.e. Posner, 1978; Dehaene et al., 2001).

The goal of the present study was to investigate potential brain regions sensitive to unattended word processing in the high attentional load paradigm originally devised by Rees et al. (1999; see Lavie, 2005). This paradigm demonstrated a form of inattentional blindness for ignored words by manipulating whether attention was directed to words vs. superimposed drawings. We used fMRI to obtain whole-brain images while participants were engaged in these two contrasting high attentional load conditions. Guided by results in the original study (Rees et al., 1999) and later research extensions (Ruz et al., 2005), we expected that withdrawing attention from the letter dimension would reduce or even eliminate activation in brain regions responding to attended words. At the same time, we hypothesized that other brain areas would support some level of word encoding in inattention situations (e.g. Raichle et al., 1994), a result which would be in agreement with previous reports (Mack et al., 2001; Ruz et al., 2005). In this way, we expected to extend the knowledge on the effect of attention on brain dynamics related to word encoding in high attentional load situations.

Materials and methods

Subjects

Twelve paid subjects gave written consent to participate in the study. All reported right-handedness, normal or corrected to normal vision, and were monolingual English speakers. The Institutional Review Board of the Weill Medical College of Cornell University approved the protocol of the study.

Stimuli and apparatus

Sixty five-letter words were selected from the Kucera and Francis (1967) database (60 mean frequency), 70 strings of five consonants were created and 100 drawings were selected from the Snodgrass and Vanderwart (1980) set. Words were divided in four lists matched in mean frequency that were used as attended words, ignored words and foils for the recognition memory test. The same stimuli (drawings, words and nonwords) were presented 11.5 times on average across the repetition detection task. All material was counterbalanced across subjects and conditions.

Participants saw a rapid stream of sequentially presented stimuli (each lasting 250 ms presented every 500 ms with a jitter of ±100 ms between presentations),[1] consisting of green drawings and overlapping red letters of approximately 5° of visual angle (see Fig. 1). Stimulus presentation was done using a PC running E-Prime v1.0 (PST, Pittsburgh, PA) with a screen refresh rate of 60 Hz.

Procedure

During four separate runs, lasting 4 min 48 s, participants were instructed to attend either to the drawings or to the letters and to press a button every time a stimulus was repeated in the attended dimension. Each run was composed of eight 36-s interleaved task and rest blocks. Half of the blocks contained only nonwords whereas the other half had 60% words and 40% nonwords in the letter dimension. In all cases, the first eight trials always contained nonwords. Immediately after the repetition detection task, participants performed a surprise memory test. Sixty words (attended and unattended words together with 30 foils) were presented in the center of the computer screen after a 1000 ms fixation point. Participants were asked to respond by a button press as to whether they thought they had seen that word during the repetition detection task or not. The response of the participant erased the word from the screen and initiated the next trial.

fMRI acquisition

We used a 3 T whole body fMRI system for the acquisition of a T2*-weighted gradient echo planar imaging (EPI) sequence sensitive to the BOLD contrast [TR = 4000, TE = 35 ms, flip angle 90°, with a matrix of 64 × 64 and field of view (FOV) of 200 mm (voxel size of 3.125 × 3.125 mm)]. We acquired 42 3.5 mm thick contiguous axial slices along the AC-PC plane as determined by the mid-saggital section. T1-weighted anatomical high-resolution structural images were acquired (TR = 2300, TE = min full, flip angle 20°, matrix of 256 × 160 matrix and FOV of 240 mm; 124 contiguous axial slices of 1.5 mm thickness) for each participant. Also, T2-weighted anatomical images in the same orientation as the functional images (TR = 3.3 sec, TE = 68 ms, data matrix 256 × 192) were obtained for individual coregistration of functional scans with high-resolution structural data.

Image preprocessing and statistical analyses

Image processing was performed with SPM2 (Welcome Department of Imaging Neuroscience, University of London, London, UK). Functional images were realigned using a least squares approach and a six parameter (rigid body) spatial transformation to correct motion artifacts. EPI images were registered to each participant's T1-weighted structural images and then transitively to the high-resolution images. For group analysis purposes, the high-resolution structural images were normalized to MNI space and the resultant transformation parameters were then applied to the functional images. Voxels were resampled to a 2 mm^3 size for normalization, and a 8 mm^3 full width at half maximum Gaussian kernel was used to smooth the EPI images.

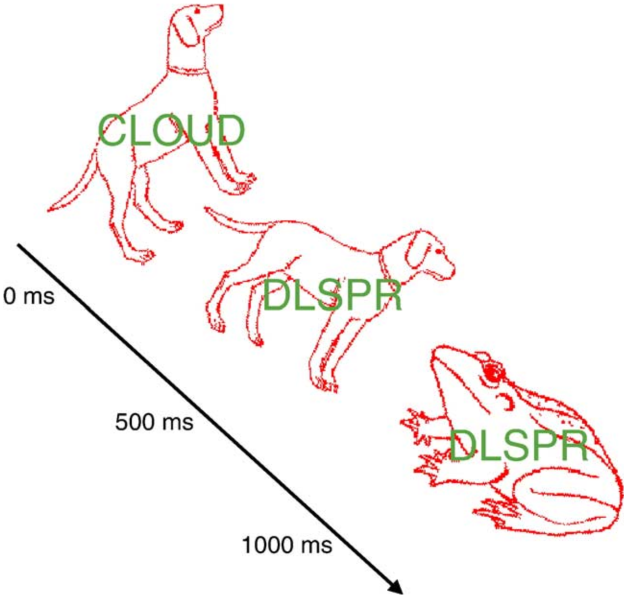

Fig. 1. The experimental procedure for the repetition detection task. Stimuli were presented foveally for 250 ms as subjects monitored for a repetition in the attended dimension (letters or pictures).

Statistical analysis was performed with a General Linear Model for each participant with regressors for each of the four conditions (attended words, attended nonwords, unattended words, and unattended nonwords) convolved with the standard hemodynamic response function, and covariates for the six motion realignment parameters. High-pass filtering (128 s) for low frequency variation was applied and global changes in signal intensity were removed by proportional scaling. The weighted sums of the beta weights for the four conditions for each subject (resulting from the combination of the factors of Attention and Lexical category of strings) were used as inputs to a random-effects ANOVA. Thresholds of $P < 0.001$ (uncorrected) were imposed except where specified. To avoid false-positives, only clusters with more than 20 contiguous voxels were considered.

Results

Behavioral

Participants responded to 69.3% immediate letter string repetitions while under attend letter instructions, and to 72.9% of picture repetitions while under attend drawings instructions. A within-subjects ANOVA performed on these data including factors for Attention (Attended Letters vs. Attended Drawings) and Lexical Status (Words vs. Nonwords), showed no effect of Attention, $F(1,11) = 1.099$, $P > 0.316$ or Lexical Status, $F(1,11) = 1.883$, $P > 0.19$, and demonstrated no interaction between the two factors, $F < 1$. Although the interaction was not significant for d prime ($F(1,11) = 2.533$, $P > 0.13$), based on our a-priori predictions, we conducted simple comparisons that revealed higher sensitivity in word blocks (3.5) than in nonword blocks (2.7) when letters were attended, $F(1,11) = 6.87$, $P < 0.05$, whereas this was not true when letters were

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[1] This jitter was used to make the paradigm compatible with an electrophysiological study using the same task (Ruz et al., 2005) and not for event-related fMRI purposes.

Fig. 2. Results of the unexpected recognition memory test following the experiment, displayed as percentage of endorsements for recognized words (‘yes’ responses) for stimuli previously presented attended words (AW), unattended words (UW) and foils. Words previously encountered in the AW condition were correctly recognized in a high proportion of trials, whereas words presented under unattended conditions produced no measurable memory trace above the false alarm rate of the foils.

ignored (4.3 vs. 4.6, $F < 1$). To ensure that all participants were accurate in following the attention instructions in every block, we conducted an ‘inverse d prime’ analysis for each participant in which hits were defined as responses to repetitions in the unattended domain and false alarms as responses in all trials in which there was no repetition in the unattended stream. The average of this measure across blocks was −0.13 (range −0.73 to 0.6), showing that in no block did any participant respond to the unattended modality. Reaction time (RT) was 531 ms for letter strings and 509 ms for drawings. The same ANOVA as before revealed that neither Attention ($F(1,11) = 1.97$, $P < 0.19$) nor Lexicallity ($F(1,11) = 3.32$, $P > 0.09$) were significant, although the interaction between the two variables was, $F(1,11) = 6.66$, $P < 0.05$. This was so because whereas words and nonwords differed in RT when they were attended, 548 ms. vs. 513 ms, $F(1,11) = 5.67$, $P < 0.05$, they did not differ when they were ignored (506 vs. 511, $F < 1$). Finally, in the surprise memory test, word recognition accuracy was high for attended words (81% of ‘yes’ responses, MSE: 0.11) and significantly different from that of ignored words (20%; MSE: 0.11; $F(1,11) = 152.5$, $P < 0.001$) or foils (18%; MSE: 0.13; $F(1,11) = 135.4$, $P < 0.001$). Responses to ignored words and foils were statistically equivalent, $F < 1$ (see Fig. 2).

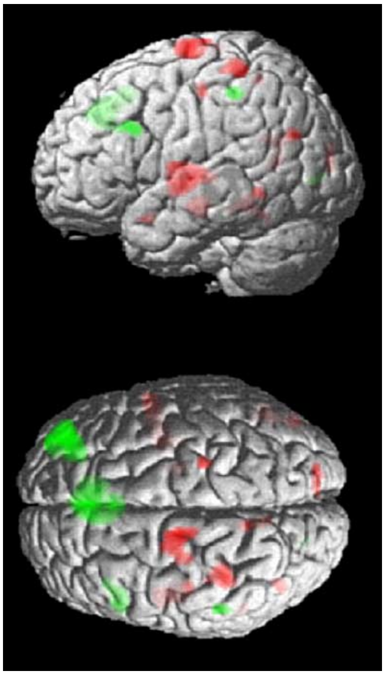

Fig. 3. Left hemisphere and superior surface projections of the main effect of attention to letters vs. drawings. Regions more active during blocks in which attention was directed to letters are depicted in green and those more active for attention to the drawings are shown in red. Anatomical labels and statistical values of each activation cluster are depicted in Tables 1 and 2.

fMRI results

The top–down focus of attention, as manipulated by the letter vs. picture instructions, had a profound impact on BOLD response. When attention was focused on letters, bilateral frontal regions and the left inferior parietal lobule recorded greater activity than when participants attended to drawings (see Table 1, Fig. 3). Alternatively, when pictures were task-relevant, more posterior and sub-cortical regions were recruited, including the fusiform gyrus, insula, and superior temoral gyrus bilaterally (see Table 2, Fig. 3). Table 3 shows the regions sensitive to the attention by lexicality interactions.

Attending to blocks containing words, in contrast to nonwords, resulted in greater activity in left inferior frontal and superior/middle temporal regions, as well as the right precuneus extending to the right posterior cingulate (see Table

Table 1
Main effect of attention letters > drawings

Anatomical area	Cluster peak (*xyz*)			*z*	*k*
Cingulate gyrus	10	29	28	4.15	194
R medial frontal gyrus	6	35	33	3.86	
L medial frontal gyrus	−6	33	30	3.59	
R superior frontal gyrus	42	48	22	3.57	23
	32	42	27*	3.28	
L inferior parietal lobule	−55	−35	46*	2.65	22
L middle frontal gyrus	−53	19	27*	2.53	82

$P < 0.001$ uncorrected.
Talairach coordinates. L = left; R = right.
* Denotes $P < 0.01$.

Table 2
Main effect of attention drawings > letters

Anatomical area	Cluster peak (*xyz*)			*z*	*k*
R cuneus	20	−86	21	4.40	60
L postcentral gyrus	−40	−36	59	3.43	35
L hippocampus	−22	−18	−9	3.39	84
L precentral gyrus	−16	−8	69	3.36	77
R middle occipital gyrus	50	−57	−4	3.22	45
R fusiform gyrus	44	−65	10	2.76	
L superior temporal gyrus/insula	−46	−14	1	3.10	126
L precuneus	−8	−59	23	3.10	28
R superior temporal gyrus	51	0	2	3.05	382
R insula	38	−17	3	3.04	
R hippocampus	30	−20	−9	2.87	

$P < 0.005$ uncorrected.
Talairach coordinates. L = left; R = right.

Table 3
Attention by lexicality interactions

Anatomical area	Cluster peak (*xyz*)			*z*	*k*
R globus pallidus	24	−8	−1	4.38	245
	20	−14	−4	3.74	
R hippocampus	30	−14	−8	3.38	
L thalamus	−24	−19	8	4.03	311
L pulvinar	−10	−27	9	3.87	
L claustrum	−36	−18	−4	3.63	130
L lentiform nucleus	−30	−8	0	3.40	
R superior parietal lobule	26	−49	60	3.35	20
R insula	28	−25	9	3.34	24
R precuneus	6	−68	38	3.75	184
R supramarginal gyrus	59	−49	23	3.63	197
L superior parietal lobule	−38	−54	49	3.45	138
L inferior parietal lobule	−38	−51	38	3.43	

$P < 0.001$ uncorrected.
Talairach coordinates. L = left; R = right.

Table 4
AW < AS sensitivity regions

Anatomical area	Cluster peak (*xyz*)			*z*	*k*
L inferior frontal gyrus	−42	21	27	3.75	239
L superior/middle temporal gyrus	−57	−46	−13	3.06	61
	−53	−62	12	2.96	
R precuneus	14	−51	32	3.03	129

$P < 0.005$ uncorrected.
Talairach coordinates. AW = attended words; AS = attended strings; L = left; R = right.

4, Fig. 4). A smaller cluster than the specified threshold (19 voxels) was also observed in the right inferior frontal gyrus. To investigate the possibility of the involvement of any of these regions in the ignored word vs. the ignored nonword blocks, we created a mask including those areas above $P = 0.01$ (uncorrected) for the attended words greater than attended nonword contrast and used this to look for voxels showing greater response to unattended words over unattended nonwords. Not a single voxel was activated in these masked areas, even when the threshold was lowered to $P < 0.05$ (uncorrected). To account for individual variability, we repeated the procedure but masked the data on an individual subject level, with the same lack of overlap for attended and ignored word-related activation.

In the critical contrast of the study, when a whole brain volume search was conducted, unattended words yielded clusters of activation in many other regions, mainly subcortical, when compared to unattended nonword blocks (see Table 5, Fig. 4). The left insula, bilateral pulvinar and superior temporal gyri, together with the right cerebellum and putamen were more active during the presentation of unattended words. None of these regions were present in the contrast showing voxels greater for attended words than attended strings. Furthermore, an additional conjunction analysis was run to examine voxels that conjointly activated in this contrast as well as the contrast between UW and fixation. Two sets of activations, the left insula and bilateral pulvinar, passed this additional test,[2] providing further evidence that not only do such regions demonstrate sensitivity to the lexicality of ignored strings but also reflect increased responsiveness to ignored words.

Discussion

The present study shows the dramatic effect of the focus of attention on patterns of BOLD response during high attentional load tasks. Despite identical stimulus presentations, attention to letters generated activations in frontal and parietal regions whereas attention to drawings uniquely restricted activation to occipital and temporal regions (see Fig. 4). The interaction between the attended dimension and the lexical status of letter strings involved many areas that responded differentially to words and nonwords, depending on the focus of attention. When letters were attended to, a set of language-relevant areas including left inferior prefrontal, left superior temporal and right precuneus differentiated words from nonwords. When the same items were ignored, these areas were no longer activated by this stimulus contrast and instead a completely different set of brain structures, including left insula, right cerebellum, thalamus and putamen, differentiated words from consonant strings. These results suggest that fully removing attention from letters may lead to some form of suppression of word-specific responses in typically activated areas and the involvement of supplementary brain regions influential in modulation of information processing and sensitive to word stimuli.[3]

Behavioral results support the successful manipulation of attention and the high load nature of this task. On-line indices of performance show that word–nonword differences were evident when attending to letters, in the sense that participants were more sensitive to repetitions of words than nonwords (d prime 3.5 vs. 2.7). However, when participants were attending to drawings, the presence of words or nonwords in the unattended letter dimension had no effect in performance, as assessed by either response latency or d prime. This lack of interference from unattended items is a common pattern for ignored information in high perceptual load situations (Lavie, 1995) and has previously been used as evidence for absence of irrelevant item processing in this kind of tasks (e.g. Rees and Lavie, 2001; Lavie, 2005). Similarly, results point to the important role of attention in memory formation, in the sense that recognition of attended words was high (80% of 'yes' responses) whereas ignored words were no different from foils (20 vs. 18% of 'yes' responses). Thus, both behavioral and brain activation indices suggest that the instructional manipulation was effective in directing participants' attention to the two different stimulus dimensions and that this had the effect of fully withdrawing attention from the ignored domain.

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[2] Activations found for UW > US could be a result of increases in UW activation relative to baseline, or deactivations of US relative to baseline. To identify the regions specifically tied to UW-related increases, an implicit mask generated from UW > baseline, $P < 0.01$ (uncorrected) was used to query UW > US, $P < 0.001$.

[3] Eye movements are not a likely source of differences between conditions given the anatomy of the results. Furthermore, although they were not monitored during the fMRI session, a previous ERP study using the same paradigm (Ruz et al., 2005) showed that eye movements were minimal in all conditions (less than 3% of trials for every participant). In addition, the short stimulus presentation time (250 ms) and short ISI were selected in part to discourage eye movement during each presentation, and to reduce the likelihood that such eye movements could provide a strategic benefit for the repetition detection task.

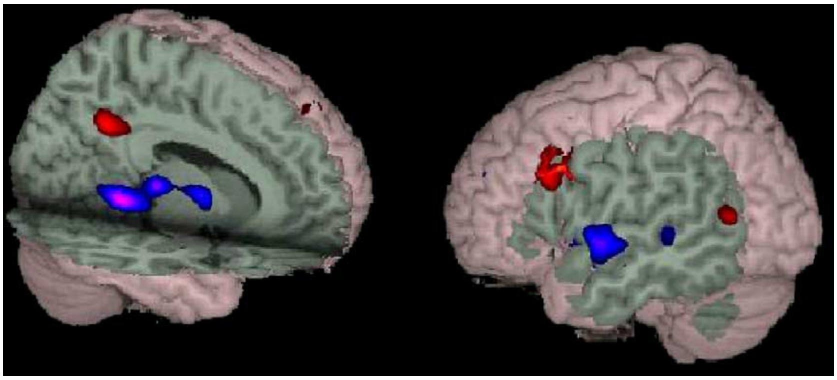

Fig. 4. Cutaway image depicts the right and left hemisphere activations in cortical and subcortical regions for the words vs. nonwords contrast within the attend letters condition (displayed in red) and words vs. nonwords contrast within the attend drawings condition (displayed in blue). Anatomical labels and statistical values of each activation cluster are depicted in Tables 4 and 5. The coloring of regions is due to contours and not a representation of significance.

Results of the present study are consistent with previous effects showing that attention has a large impact on brain dynamics in high attentional load situations. Previous neuroimaging results have shown that brain regions sensitive to the presence of irrelevant information during low-demand conditions cease to respond when perceptual demands are high (Rees et al., 1997, 1999; O'Connor et al., 2002; Pinsk et al., 2004; Yi et al., 2004). Among investigations suggesting that high load prevents processing of ignored information, one particular study (i.e. Rees et al., 1999) is especially relevant to the present investigation. Although a large subset of the current findings replicate the results of this previous study, the partial volume approach used by Rees et al. (1999, see note 18) may have restricted their analysis of ignored word vs. ignored nonword activations to only those regions first demonstrating sensitivity to attended words vs. attended nonwords. However, such a restriction rests on the implicit assumption that any word-specific activity under the attended pictures condition should belong to the set of areas involved in word processing when letters are attended.

In our study, attending to letters generated more activation for words than nonwords in a set of brain areas previously shown to be related to language processing (for reviews, see Price, 2000; Martin, 2003). The role of left inferior frontal areas in semantic retrieval has been shown several times (i.e. Cabeza and Nyberg, 2000) and there is some consensus on the association of this area with effortful semantic processing (Price, 2000; Pugh et al., 2000). Phonological processes have been linked to the responsivity in the superior temporal regions (Pugh et al., 2000). The precuneus is activated in many situations requiring attention to phonology (e.g. McDermott et al., 2003), phonological working memory (Zurowski et al., 2002), detection of accents (Berman et al., 2003) or auditory word priming (Kotz et al., 2002) and imagery of letters (Raij, 1999).

Table 5
UW > US sensitive regions

Anatomical area	Cluster peak (*xyz*)			*z*	*k*
L insula	−42	4	−2	4.36	207
	−38	−10	0	3.39	
L superior temporal gyrus	−52	−2	−2	3.40	
R cerebellum (Culmen)	14	−45	−3	3.78	241
L pulvinar	−8	−25	5	3.53	
R lingual gyrus	4	−33	−2	3.37	
R putamen	30	0	−8	4.21	47
R superior temporal gyrus	48	9	−7	3.43	35
R thalamus	10	−4	0	3.50	23

$P < 0.001$ uncorrected.
Talairach coordinates. UW = unattended words; US = unattended strings; L = left; R = right.

From previous literature, it would be expected to obtain basal temporal activations for this contrast. The Visual Word Form area (VWFA) is a fusiform region that is tuned to respond to the regularities of written words in a bottom-up manner (McCandliss et al., 2003) and has been shown to be responsive even to unconscious words (Dehaene et al., 2001).[4] However, the present task was not designed to study word encoding per se and thus it is not suited to draw strong inferences about bottom-up word related activation in normal reading conditions. For example, letters appeared in light green and overlapped with red drawings to prevent automatic capture by salient items. This spatial overlap could have led to competition for resources between letters and drawings, given the closeness of the representation of these items in fusiform regions (e.g. Joseph et al., 2003). Moreover, higher saliency of red colored drawings could have given advantage in the competition with the green letters and result in a lack of availability of resources for letters in these regions. Additionally, previous research has shown that the rate of item presentation modifies the pattern of language-related activations (Price et al., 1996; Mechelli et al., 2000), and the fast rate in our study was not optimized to activate all word encoding areas. Indeed, unpublished results from our laboratory show that participants performing the same one-back task but with items presented at a slower pace and without the distracting drawings do show VWFA activation as expected, in agreement with published results (e.g. Pugh et al., 2000).

Regions found in the current experiment more active for words as compared to nonwords when attention was focused on drawings have been implicated in many language studies, although their specific roles remain less clear. For example, left insular activations have been reported in practiced verb generation (Raichle et al., 1994), second language learning (Raboyeau et al., 2004) and proficiency in a second language (Chee et al., 2004), low frequency word processing (Fiebach et al., 2002), verbal working

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[4] Indeed, we do find liberal threshold activation in fusiform regions for the attended word-nonword contrast. At $P < 0.03$, uncorrected, we find activation peaking at the −40, −54, −8 Talairach coordinates encompassing 48 voxels.

memory (Derrfuss et al., 2004), and Chinese character reading (e.g. Lee et al., 2004; Zhang et al., 2004). The right hemisphere of the cerebellum, connected to left cerebrum hemisphere, is also found in many studies related to language learning (Raboyeau et al., 2004), word generation (Raichle et al., 1994), memory retrieval (Andreasen et al., 1995; Buckner et al., 1996), lexical-semantic tasks (Roskies et al., 2001) and verbal fluency/lexical retrieval (see Justus and Ivry, 2001). The activation of the thalamus in language paradigms is not uncommon (i.e. Fiebach et al., 2002) and has been linked to acquisition of semantic information (Maguire and Frith, 2004) and language learning (Jarvis, 2004). The putamen, on the other hand, has been activated in word generation tasks (Crosson et al., 2003), language-based counting (Hinton et al., 2004), and is sensitive to semantic priming (Rossell et al., 2001) and syntactic violations (Friederici et al., 2003). Note, however, that these regions may subserve different roles outside language that could be relevant to explaining our results. For example, the insula has been found activated in several tasks involving cognitive control (Wager and Felman-Barret, unpublished manuscript) and also when the expected trial type changes (Casey et al., 2000). The pulvinar nucleus, on the other hand, is a key structure in attentional deployment and it seems to be especially relevant in situations in which attended and ignored information overlaps or competes (e.g. Danziger et al., 2004; and for full discussion, see Michael and Desmedt, 2004).

The present study directly tested the possibility of an alternative pathway involved in word processing when letters are ignored. Our experiment, which represents a close implementation of the Rees et al. (1999) inattentional blindness paradigm, shows a similar outcome when a partial search volume is conducted, in the sense that none of the regions activated by the attended word–nonword contrast is influenced by lexicality in the attention to pictures condition. However, when a whole brain search strategy is employed instead, a set of regions is found to be involved in differentiating between unattended words and nonwords. Therefore, our results do not support the conclusion derived from the original study that visual word recognition is fully dependent on attentional resources. Instead, results suggest that word-related information modulates different pathways according to attention allocation and generates differential effects on performance depending on task context.

While the critical contrast between unattended words vs. nonwords provides compelling evidence of some sensitivity to lexical status under these high attentional load conditions, deriving precise links between the specific brain regions implicated and the particular cognitive processes engaged by these two different conditions is limited however by a number of considerations. The current paradigm does not allow us to resolve whether the activations observed in response to ignored words reflect lexical processes triggered by these items or rather the impact that lexical activation might have on picture matching, such as a general effect of processing in the face of irrelevantly activated information, or even more specific competition between semantic entries activated by the simultaneous presence of words and pictures. For example, the activation of an attention-related nucleus such as the pulvinar specifically related to the presentation of unattended words could be indicating a higher need to resolve competition, semantic or otherwise, due to the presence of ignored words.

Some aspects of the current results, however, are not consistent with the notion that ignored lexical information led to increased competition or increased task difficulty for the matching condition. First, if responding to drawings requires that the representations of words are inhibited, the areas that need to be suppressed are those that differentially process words and nonwords when these are attended to (that is, it makes no sense to inhibit an area that is not activated when responding to words). Hence, we would expect to find inhibition-related activation in the same areas that were activated by this contrast during attention to letters. Results show, however, that there is no region overlap for this contrast between the two attention conditions. On the other hand, there is no reason to suspect that words were generating interference when they were ignored as none of the performance indices obtained is sensitive to this word–nonword variable when attention was focused on drawings. That is, accuracy, RT and d prime (and conversely false alarm rate) were statistically equivalent for the attend drawings condition regardless of the lexical nature of the ignored letter strings. Such findings fail to support an explanation of the critical UW > US activation contrast in terms of differential interference or semantic competition upon the primary task.

There are other considerations relevant to further interpretation beyond evidence of lexical sensitivity for ignored letter strings. The use of a block design, compelled by our replication strategy, leaves open the question of the time-course of the effects. For example, it is currently unknown whether our results are specifically induced by each ignored word or represent more tonic processes present throughout the block, perhaps related to overall differences in block context (see Chawla et al., 1999 for discussion). Although the current fMRI design cannot resolve such issues, our previous ERP study using the same task however, demonstrated rapid processing differences time-locked to stimulus onsets of ignored words and nonwords presented during the same block (Ruz et al., 2005). On the other hand, nonwords are harder to process than words. This pattern was confirmed by behavioral data when letters were attended. Note, however, that when attention was tied to drawings, the presentation of words vs. nonwords did not affect any behavioral index of performance. Thus, differences in difficulty between the two kinds of stimuli could be contributing to attended word vs. nonword BOLD differences but not to those revealed when letters were ignored. Another consideration for interpreting the neuroimaging results is that the paradigm required the items to be repeated frequently (but see Ruz et al., 2005, Experiment 2). Stimulus repetition is known to enhance explicit memory of attended items and to change brain activations in several ways (see Henson, 2003), and thus this manipulation should be relevant to our results. However, stimulus repetition was constant across our variables, so it does not represent a source of contamination.

More generally, the finding of different brain pathways in performing a task under conditions that manipulate effortful vs. automatic processing is not unprecedented, as similar effects have been frequently demonstrated in learning situations (see Petersen et al., 1998). For example, practice-related effects in the verb generation task described by Raichle et al. (1994) are paradigmatic in the field. In this landmark study, participants were asked to verbally generate uses for common nouns (vs. a control task of reading the nouns aloud). Brain regions recruited during the initial unpracticed state included left inferior prefrontal and cerebellum. However, after a few minutes of practice, overt responses became faster and stereotyped, and BOLD indices in these regions were no longer sensitive to the instructional manipulation (i.e. generate vs. read), yet other regions including the left insula demonstrated increased sensitivity to verb generation. Similar practice related

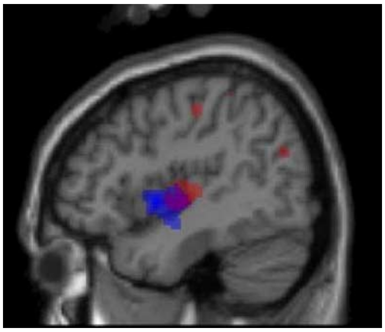

Fig. 5. Mid-saggital image ($x = -45$) showing the partial overlap between the global contrast of attention to drawings > attention to letters (in red) and the specific contrast of words > nonwords under the attend drawings condition (in blue). Note that the main region of overlap between these two findings lies in insular regions.

changes in brain pathways have been replicated several times in other learning paradigms (e.g. Van Mier et al., 1998; Korman et al., 2003). Explanations for this phenomenon rely on differences in computations used when performing an attention-demanding novel task and the easier automatic processing that takes place after practice. When participants are not skilled with a task, a set of effortful processes is employed to cope with the situation. With practice, however, a more automated processing strategy is adopted, which leads to a more accurate and faster performance. This processing shift is accompanied by a change in neural pathways recruited to support the altered processing strategy.

In the present study, practice levels were the same in the two attention conditions. However, attention was tightly focused in the letter domain in one situation and fully withdrawn from it in the other. The fact that both letters and drawings were presented in overlapping spatial positions in a highly demanding task most likely led to strong competition between the two dimensions (Desimone and Duncan, 1995). This competition could have been heightened by the foveal position of items, as it has been previously shown that suppression of information in inattentional blindness paradigms is much more pronounced when items are presented at fixation relative to more peripheral locations (see Mack and Rock, 1998). In our experiment, attention to letters and drawings directed resources to different brain regions to successfully perform the task. This distribution of resources could be responsible for allowing only a set of brain regions to respond to the word–nonword contrast, in the sense that only regions activated by the attention task would have available resources to differentiate between words and nonwords. Results provide some support for this notion, given that there was a partial overlap between the regions more activated when attention was directed to drawings and those more active for ignored words than nonwords in this attention condition (see Fig. 5). The reverse is also true, although to a lesser extent, when attention was focused on letters. This hypothesis is reinforced by the fact that even when the threshold was reduced to $P < 0.05$ uncorrected, none of the regions more active for attended letter blocks were involved in the unattended word–nonword contrast, and vice versa when drawings were the focus of attention.

Our results suggest that in conditions of high attentional load, brain resources route to different pathways in response to task demands. The analysis of word stimuli by these different processing pathways produces different behavioral and neural effects. In the present study, attention to letters activated a set of language-relevant areas, partially overlapping with those more activated for words than nonwords. This generated more efficient responses to words than nonwords and allowed a consolidation in explicit memory for attended words.[5] In contrast, when attention was directed to drawings, the competition with letters directed resources to a different set of brain regions and this allowed a different and nonoverlapping subset of areas to respond differentially to words and nonwords, although these activations did not have any effect on behavioral measures, most likely because in that condition behavior was being guided by regions related to the processing of the drawings.

In summary, the present study adds to previous literature suggesting the existence of some level of word processing even in strict inattention situations that lead to symptoms of inattention amnesia. Critically, we find that pathways responsive to word processing may change depending on the focus of attention. Future research will need to show whether this dramatic effect of attention on brain dynamics and performance is limited to the fast presentation parameters and stimulus contrasts (words vs. nonwords) of the present experiment or can be generalized to other high perceptual load task paradigms dealing with domains outside language.

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