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ORIGINAL ARTICLE

Task-specific preparatory neural activations in low-interference contexts

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Abstract How the brain prepares for forthcoming events is a pivotal question in human neuroscience. In the last years, several studies have suggested that expectations of perceiving upcoming stimuli engage relevant perceptual areas. Similarly, some experiments manipulating the task to be performed with targets have also found pre-activations in task-related brain areas. However, the usual configuration of this type of paradigms entails high levels of interference and/or working memory load, together with a small set of target stimuli. We designed a cued task paradigm in which interference was reduced to a minimum, as evidenced by behavioral indices of performance, and that included a high number of targets to avoid their anticipation. This was achieved using a large set of uni-valent target stimuli preceded by fully valid cues in a functional magnetic resonance imaging experiment. We found category-specific patterns of activity in which semantic cues engaged the left inferior frontal gyrus whereas spatial cues preactivated the right superior parietal lobe. Together with functional connectivity analyses, the activation maps showed the specific involvement of semantic and spatial processes upon the presentation of the cues that are coherent with previous literature. Our results thus suggest that even in contexts of low interference that prevent the anticipation of specific targets, our brain takes advantage of current information to deal with upcoming demands.

Keywords Preparation · Cognitive control · Interference · Task set

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Introduction

One of the most adaptive human abilities is to plan and control future behavior based on goals. Rather than merely responding to sensory stimulation in an automatic manner, our brain has the capacity to enter task states that guide the processing of relevant stimuli according to behavioral requirements (e.g., Gilbert and Sigman 2007). Preparation, that is, the anticipation of a given context before it occurs (Brass and von Cramon 2002, 2004; Bode and Haynes 2009), is an important process underlying this ability. As an example, imagine you are expecting a call from your boss and another from a close friend. In this scenario, reading the name of the caller on the screen of the ringing phone would allow you to anticipate your response in a context-dependent manner. In a related area of research (Summerfield and Egner 2009), predictive coding theories propose that our perception depends on iterative processes between bottom-up and top-down information along the cortical hierarchy (Friston 2005). At each step of this hierarchy, top-down expectations are met with bottom-up sensory information that updates the expected input and reduces prediction errors.

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Our knowledge of how top-down templates are implemented in the brain has improved substantially in recent years, due in part to the progressive refinement in neuroimaging methods and analyses. In particular, event-related functional magnetic resonance imaging (fMRI) allows the separation of the brain activations related to cues, which can initiate top-down states, and to the subsequent targets, which are processed according to task requirements. Research in the field of selective attention has suggested that top-down settings are able to modify activity at different stages of information processing according to task goals (e.g., Baldauf and Desimone 2014; Kastner and Pinsk 2004). Selective attentional modulations may increase the tonic state of relevant brain areas before the stimulation is presented (e.g., Ruz and Nobre 2008a), which is accompanied by further increases in responses evoked by targets (e.g., Chawla et al. 1999). These modulations may reflect in part the filtering of irrelevant information (Kastner and Pinsk 2004), and/or enhancement of task-relevant processes (e.g., Corbetta et al. 1990; Ruz et al. 2005; Ruz and Nobre 2008b; Wylie et al. 2006).

In task cueing paradigms (for other approaches, see Manelis and Reder 2013), participants have to prepare for alternating tasks that imply different rules. A large amount of studies has pointed to the prefrontal cortex (PFC) as a key area for set preparation (see Sakai 2008, for a review) within a more general frontoparietal control network involved in task implementation (Ruge et al. 2013). Although the majority of the studies have focused on the difference between switch and non-switch trials, other investigations highlight the specificity of preactivations for certain types of task sets. On a seminal paper, Sakai and Passingham (2003) showed how in a working memory (WM) task in which participants were cued in advance to hold in mind and manipulate spatial vs. semantic material, the preparatory cues modulated the pattern of connectivity between the anterior PFC and other frontal structures, suggesting a domain-specific role of the latter during the preparation stage. In addition, these authors showed that semantic cues elicited preactivation of the left inferior frontal gyrus (LIFG) and temporal areas (superior and middle temporal gyrus), whereas the superior frontal sulcus and the superior parietal lobe (SPL) were selective for spatial cues. This line of results, in which goal-related activity during task preparation is observed within and outside the core control network, has been supported by further evidence (e.g., Sakai and Passingham 2006; Donohue et al. 2008; Yamagata et al. 2012). Altogether, neuroimaging evidence suggests that different brain regions and networks working at different levels of specificity support the brain's ability to prepare for forthcoming events.

However, different sources of interference, such as target ambiguity, invalid cues or cue-target compounds, require increased cognitive control and may affect specific preparatory activity, a hypothesis that has been not been tested yet. For instance, the use of bivalent targets in task-switching experiments, that is, when the same target stimulus can be processed according to either task, has been related to higher switching costs (e.g., Kiesel et al. 2010). In a typical task cueing paradigm, targets are common across tasks, and thus the ignored dimension triggers the activation of the irrelevant information, therefore, generating interference. For instance, in Shi et al. (2014), a cue signaled whether participants should perform a face or a number task with the next target, which was a composition of a face and a superimposed number. These authors found that after a face task trial, regardless of which task had to be performed on the following trial, there was residual activity in brain areas associated with face processing. Likewise, they found a significant positive correlation between the amount of this residual activity and switching costs. This residual activity in switch trails has been attributed to the competition between the two tasks to gain control (Wylie et al. 2006). In bivalent contexts, compared to univalent ones, control demands are high due to interference between tasks, and thus the need for selective attention is increased (e.g., Stokes et al. 2013). In fact, Yeung et al. (2006) found that task-set inertia in task-switching paradigms accounts for a large portion of switching effects, which, crucially, affected both frontoparietal and category-specific preparatory activations.

Evidence for category-specific preactivations with univalent targets (i.e., each task is linked to a specific type of target) also comes from visual attention studies, in which participants are prompted to classify stimuli in categories rather than to perform a given task with it. For instance, Puri et al. (2009) used a task in which participants had to prepare for perceiving faces or houses images, cued in a 70 % of trials by a valid cue (e.g., the word "FACE" in a face image trial). These authors found that the mere cuing of a category (face or house) activated the associated perceptual brain region (fusiform face area, FFA, or parahipocampal cortex, PPC, respectively) prior to the presentation of the image and enhanced the target-related activity in these areas. Moreover, the magnitude of the preactivations in these category-specific areas correlated with the activity of the aforementioned frontoparietal network. This effect supported the idea of a top-down modulation from this network towards sensory cortices (see also Esterman and Yantis 2009). In this study, however, a percentage of the cues was invalid, which also generates interference. When a cue is valid, that is, when it adequately signals the upcoming task, it engages attentional mechanisms that allow for a better response to the next target. As for invalid cues, interference arises due to the mismatch between the cued and the actual task, which

requires a disengagement of attentional resources upon target presentation. As seen with other sources of interference, this may influence the extent and selectivity of preparatory activity (De Baene and Brass 2014). Interestingly, some authors have shown the utility of using only valid cues to reduce the interfering task-set inertia in univalent contexts (Elchlepp et al. 2012). Therefore, despite suggestive evidence of cue-related activations with univalent targets, the effect of cue validity on these preparatory mechanisms is still unknown.

Moreover, an additional source of potential selectivity of preparatory activity in switching experiments is the use of a small set of stimuli. This allows for the creation of cue-target compounds (explicit responses encoded in episodic memory for a given cue-target conjoint; Logan and Bundesen 2004), which could trigger cue-related activation due to repeated association of specific cues and targets (e.g., the cue "red circle" always signals a square or triangle target, whereas the cue "green circle" is linked to a blue or yellow shape). Moreover, using small set of target stimuli allows for the imagination and rehearsal of the forthcoming task upon the presentation of the cue (Klauer and Zhao 2004). These strategies involve modality-related working memory processes, such as articulation for phonological demands, or visual imagery for visual tasks (Baddeley 2003). Thus, when few visual stimuli are used, as in the case of most studies revised here (e.g., Esterman and Yantis 2009), visual imagery entails additional working memory demands, which usually engage selective maintenance activity in the prefrontal cortex (e.g., Curtis and D'Esposito 2003), potentially confounding task and item preparatory activity.

In sum, previous studies have used task-switching paradigms that imply different sources of interference. Importantly, these can affect the consistency of the neural correlates of preparatory mechanisms, since interference affects the interplay between top-down and bottom-up information. The extent to which task-specific preparatory activity also takes place in contexts of low interference remains unknown. The aim of the present study was to investigate the existence of specific preparatory activity in a paradigm designed to keep interference between tasks and item-specific visual anticipation to a minimum. To do so, we employed a task in which (1) targets were univalent and fully distinct, (2) cues always provided valid information, (3) a large set of targets was used, to prevent visual imagery and avoid cue-target compounds. Cues were symbolic and asked participants to perform within-category classifications. Although we could have used different target modalities, such as visual and auditory, to reduce interference even more, we chose two visual categories, semantic and spatial, that are "maximally distinct" (Ruge et al. 2013) and whose specific activation and connectivity patterns are well mapped (e.g., Sakai and Passingham 2003). Our approach allowed us

to study a consistent pattern of activation and connectivity associated with category-specific preparatory processes under conditions of low interference.

Materials and methods

Participants

Twenty-four participants (16 females; mean age 22; range 19–26) took part in the experiment. All participants reported normal or corrected-to-normal vision and no history of neurological disorders. They all signed a consent form approved by the local ethics committee and received money in exchange of their participation.

Apparatus and stimuli

The stimuli consisted of 56 concrete noun words (average number of letters 5.7, range 5–7) and 56 different overlapped rectangles and oval shapes containing leftward or rightward oriented lines (see Fig. 1). Half of the words represented natural items (e.g., agatha) and the other half referred to man-made objects (e.g., fork). The rectangle and oval overlapped figures contained lines in the same direction in half of the shapes and in opposite directions in the other half. Two different squares, colored in blue and green, were used as cues. A PC running Presentation 0.70 displayed the stimuli through MR-compatible goggles.

Design and procedure

Both tasks were performed in an interleaved single run. The (blue, green) cue (100 % valid) instructed participants
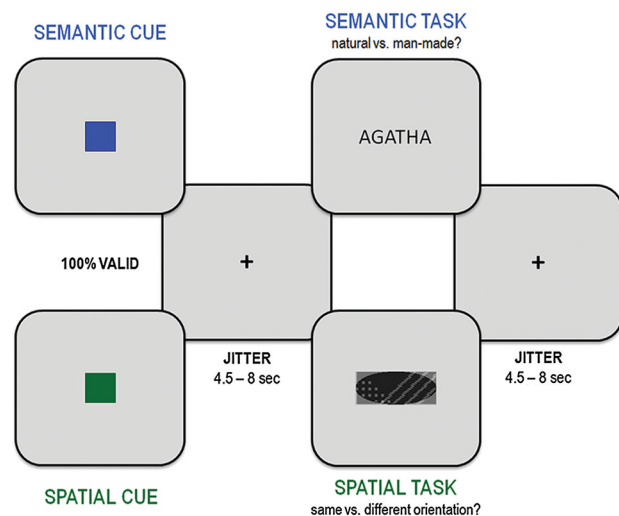

Fig. 1 Sequence of events in a trial for the event-related fMRI design

on a trial-by-trial basis about the task they had to perform on the upcoming target (either a word or a complex shape). They had to judge the semantic content of the words (decide whether the items represented something natural or man-made) or the spatial orientation of the lines in the complex shapes (whether the lines of the superimposed rectangle and oval were oriented in the same or in the opposite direction). Participants were encouraged to respond as accurately and as fast as possible. In addition, they were asked to use the cue to prepare as much as possible before target onset, as this would help them to respond more efficiently. To encourage this preparation, before the experiment participants were informed that the three persons with the highest performance scores (taking into account both accuracy and speed) would be rewarded with 25 Euros extra.

The association between cues and tasks, as well as the response options, was counterbalanced across participants. In the event-related run (50 min approximately), the delays between cue and target, and between trials, were jittered to allow for the deconvolution of cue- and target-related signals. Each trial comprised the following events (see Fig. 1). A cue was flashed in the center of the screen for 500 ms, followed by an interval displaying the fixation point with a 4.5–8 s duration that varied randomly in steps of 500 ms (mean 6.25 s). The target then replaced the fixation point for 500 ms, after which another variable interval was presented, with the same structure as the previous one. On average, a trial lasted 13.5 s. In total, there were 224 trials (112 per condition), ran in a pseudo-random order that presented all items once before displaying them for the second time (every item was used twice) and thus avoided immediate item repetitions.

During the whole experiment, participants used the index and middle fingers of their right hand to make speeded discrimination responses to targets by pressing one of two buttons on a custom-made MRI-compatible button box. Before performing the task in the scanner, participants completed a short training session with a different set of stimuli to become familiar with the tasks.

Prior to the fMRI experiment, we conducted a behavioral pilot study to ensure that with the current design cues received attention and participants used them to prepare in advance. All details of the design and stimuli were the same except cues were invalid in 20 % of the trials.

Data acquisition and analysis

Magnetic-resonance images were acquired using a 3T Trio scanner at the Hospital Clinic of Barcelona (Spain). Functional images were obtained with a one-shot T2*-weighted echo planar imaging (EPI) sequence [time until echo (TE) = 29 ms, flip angle = 80°, repetition time (TR) = 2 s]. Thirty-eight interleaved sagittal slices with a thickness of 3.0 mm (no gap) covered the entire brain (64 × 64 matrix with a field of view of 240 mm, voxel size of 3 × 3 × 3 mm). The event-related experiment was performed in one run consisting of 1540 volumes. The first 5 images were discarded to allow for saturation of the signal. In addition, we acquired a standard structural image of each participant using a high-resolution T1-weighted sequence (TR = 2300 ms; TE = 2.98 ms; 1 × 1 mm in-plane resolution and 1 slice thickness).

We used SPM8 (http://www.fil.ion.ucl.ac.uk/spm) to preprocess and analyze the images. First, we used slice timing to correct for differences in the time of slice acquisitions. Images were then realigned and unwarped using a least-squares approach and a six-parameter (rigid body) spatial transformation to correct for motion artifacts. Afterwards, images were normalized to the standard EPI template included in SPM8. Images were spatially smoothed using an 8 mm full-width at half-maximum isotropic Gaussian kernel. A 128 s high-pass filter was used to remove low-frequency artifacts.

Statistical analysis was performed with a General Linear Model for each participant with corrections for serial autocorrelations using the AR(1) model. The model included regressors for the cues and targets in both switch and non-switch situations, which were convolved with the standard hemodynamic response function. Duration and onset vectors for each condition were introduced as regressors into a standard General Linear Model (GLM). The two different cues (Semantic, Spatial) were modeled as events with a duration that encompassed the whole cue-target interval, which allowed us to capture the sustained anticipatory activity generated by each type of cue. Targets were modeled as events with zero duration. Jittered intervals between trials were used as implicit baseline, and trials with errors and missing responses were grouped together as separate events with an extended duration for the whole trial (encompassing both cue and targets). Contrasts of interest (i.e., cues vs. baseline; semantic vs. spatial cues: CUE_SEM > CUE_SPA and viceversa; semantic vs. spatial targets: TARGET_SEM > TARGET SPA and viceversa; switch vs. non-switch cues and targets) were obtained for each participant and then entered into a second-level analysis, where t tests were used to contrast conditions. Only clusters surviving a family wise error (FWE) correction thresholded at a 0.05 cluster-level (initial uncorrected cluster-forming threshold was $p < 0.001$) are reported. In the figures, we used Caret software (Van Essen 2005) to project the images on to inflated PALS surface (population-average, landmark- and surface-based) and help visualization.

General and specific cue- and target-related activations

We first identified the brain areas that were engaged by cues (contrast CUES > BASELINE) to map the preactivations across tasks. Then, we sought to isolate the regions that were engaged by each cue type in a task-selective manner. For this, we calculated the contrasts CUE_SEM > CUE_SPA and vice versa, to obtain category-specific clusters. Additionally, we used results from the contrasts TARGET_SEM > TARGET_SPA and vice versa to look for category-specific activity at the target period. To further explore whether target-related clusters were pre-activated at the cue stage, we conducted a conjunction analysis (Nichols et al. 2005) to test which precise brain areas were active in both cue and target periods of a given task. This analysis allowed us to look for clusters specific to each task that were active both in the cue and the target periods. For conjunction analyses, we performed one-way ANOVAs using first-level contrast images of interest. Only conjunction clusters surviving an MS/CN test (Minimum Statistic compared to the Conjunction Null; Nichols et al. 2005) are reported.

Psychophysiological interactions

To assess the networks involved in the advance preparation to perform semantic vs. spatial computations, we conducted a psychophysiological interaction analysis (PPI; Friston et al. 1997) using SPM8. The GLM analysis described above identified the left inferior frontal gyrus (LIFG; −48, 26, 1) and the right superior parietal lobe (RSPL; 24, −67, 52) as key regions of preactivation for the semantic and spatial cues. These two coordinates were the center of 6-mm radius spherical seeds in the two PPI analyses during the preparation period. A first-level GLM analysis was then performed using the specific ROI time course, the psychological variable (cue type) and the interaction term (PPI) obtained in SPM8 as regressors. After obtaining a contrast image of the interaction for each subject, we performed a second-level t test analysis. Clusters surviving the statistical threshold corresponded to areas whose temporal activation pattern correlated with that of the ROIs, upon presentation of a given cue.

Results

Behavioral

Six participants performed a behavioral pilot study that used univalent targets but included cue validity as a factor. Results showed that whereas accuracy did not change as a function of validity ($F < 1$), participants were faster on valid ($M = 773$ ms, SD = 160) than on invalid ($M = 860$ ms, SD = 186) trials, $F_{1,5} = 9.37$, $p < 0.05$. This significant validity effect indicates that participants paid attention to the cues and prepared to respond accordingly, even though these were not fully reliable and all targets were associated unequivocally with only one task.

During the fMRI session, accuracy analyses showed a main effect of task, as participants were more accurate in the perceptual (97 %) than in the semantic task (94 %), $F_{1,23} = 10.1$, $p < 0.01$ (all other $Fs \leq 1$). The ANOVA on reaction times (RT) showed a main effect of task, $F_{1,23} = 137.41$, $p < 0.001$, as RT were faster in the spatial (751.9 ms) than in the semantic (918.4 ms) condition. Neither the main effect of switch, $F_{1,23} = 1.19$, $p > 0.28$, nor the interaction between the two factors, $F_{1,23} = 2.8$, $p > 0.1$, were significant.

GLM

First, we used the CUES > BASELINE contrast to look for preparation across tasks during the cue period (Fig. 2, left panel). We found strong activation in several regions, including right (33, 53, 28; $k = 131$) and left (−27, 38, 28; $k = 177$) anterior lateral prefrontal cortex (PFC, BA 10), right mid-dorsolateral PFC (48, 14, 22; $k = 23$), posterior cingulate cortex (PCC, −3, −25, 28; $k = 783$), supplementary motor area (SMA, −6, 5, 58; $k = 513$), bilateral insula (−33, 20, 1, and 31, 17, 1; $k = 228$), thalamus (−3, −22, 1; $k = 446$), left somatosensory cortex (−42, −31, 61; $k = 83$), right (30, −52, 52; $k = 40$) and left superior parietal lobe (SPL, −27, −58, 55; $k = 456$), and visual areas such as BA 17−18 (−27, −97, −8; $k = 213$) and BA 19 (36, −88, −8; $k = 255$).

Afterward, we located brain areas engaged by category-specific target processing, which included those commonly reported during semantic and spatial computations. Target words (TARGET_SEM > TARGET_SPA) activated a typical left-lateralized language network, including the left inferior frontal gyrus (IFG, −42, 26, −11; $k = 704$), left superior frontal gyrus (−3, 14, 52; $k = 153$) and the left fusiform gyrus (−54, −49, −17; $k = 100$), as well as the right IFG (30, 29, −1; $k = 315$), right dorsolateral pre-frontal cortex (RDLPF; 54, 32, 31; $k = 93$), and occipital regions (−6, −85, 10; $k = 169$). On the other hand, spatial targets (TARGET_SPA > TARGET_SEM) engaged different parietal regions such as the right SPL (12, −73, 58; $k = 234$) and the left inferior parietal lobe (IPL, −33, −91, 19; $k = 119$), as well as the right fusiform gyrus (36, −56, −12; $k = 205$) and BA 19 (36, −85, 13; $k = 357$).

The analysis of semantic cues (CUE_SEM > CUE_SPA) revealed a large cluster of activation in the LIFG
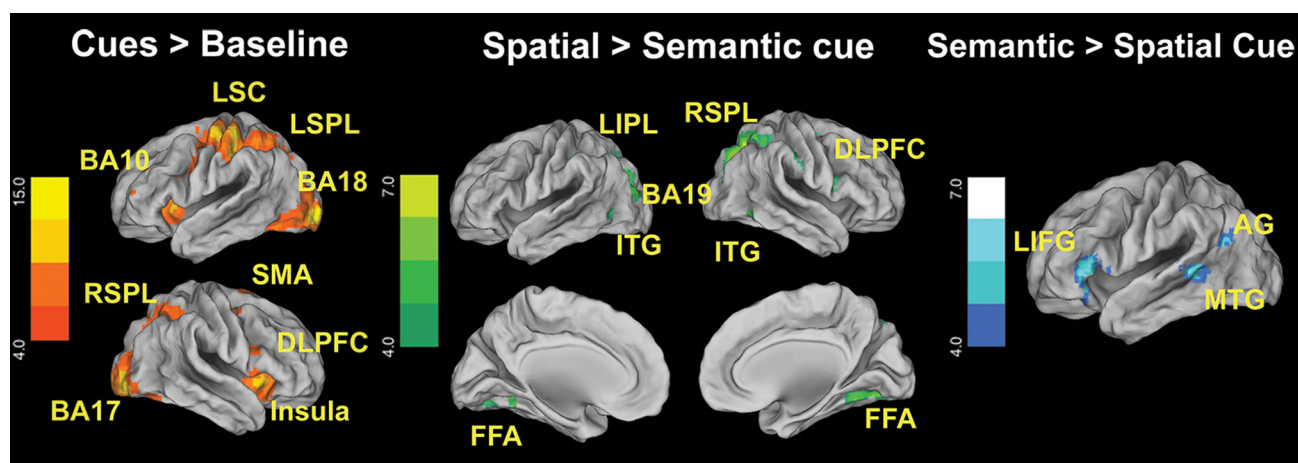
Fig. 2 Activation common for cues across tasks (*left*), and specific for spatial (*middle*) and semantic (*right*) cues. The Cues > Baseline contrast revealed significant activation in bilateral BA 10 (brodmann area 10), right DLPFC (dorsolateral prefrontal cortex), bilateral insula, SMA (supplementary motor area, LSC (left somatosensory cortex), bilateral SPL (superior parietal lobe), BA 17 (brodmann area 17) and BA 18 (brodmann area 18). Spatial cues engaged right DLPFC, RSPL, LIPL (left inferior parietal lobe), bilateral ITG (inferior temporal gyrus), bilateral FFA (fusiform face area) and BA 19 (brodmann area 19). Semantic cues activated the LIFG (left inferior frontal gyrus), left MTG (middle temporal gyrus) and left AG (angular gyrus). *Scales* represent peaks *t* values

(-48, 26, 1; $k = 373$), as well as in other language-related areas (see Fig. 2, right panel), such as the left middle temporal gyrus (BA22; -54, -43, 1; $k = 151$) and the left angular gyrus (BA 39; -42, -64, 25; $k = 151$). An additional cluster was found in the right middle occipital gyrus (BA 19; 33, -97, -8; $k = 68$). For spatial cues (CUE_SPA > CUE_SEM), the statistical map depicted a pattern of activation in areas related to spatial processing (see Fig. 2, middle panel), namely a large cluster in the parietal lobe, with a local maxima at the RSPL (24, -67, 52; $k = 759$), and LIPL (-33, -37, 43; $k = 147$), as well as in bilateral inferior temporal gyri (-51, -67, -2; $k = 84$; and 54, -61, -11; $k = 68$) and bilateral fusiform gyri (-27, 52, -14; $k = 141$; and 30, -55, -11; $k = 182$). Additionally, we found activations in bilateral BA 19 regions (-33, -86, 19; $k = 354$; and 36, -85, 22; $k = 59$) and in the RDLPFC (51, 8, 19; $k = 127$). However, although these areas showed higher levels of activation for one of the tasks, it could be the case that the other task also engaged them although to a lesser degree. To rule out this scenario, we selected the peak clusters in both tasks (RSPL for the spatial and LIFG for the semantic task) to create ROIs. Then, we used these two ROIs to query activity in the opposite task contrasts (e.g., for the RSPL ROI, CUE_SEM > CUE_PER and Cue_SEM > BASELINE). This analysis did not yield significant results for any of the contrasts even when the correction was lowered to $p < 0.1$ uncorrected.

None of the contrasts involving the switch factor (i.e., switch vs. non-switch cues and targets) survived the FWE threshold (neither a $p < 0.001$ uncorrected, 10 voxel-extent threshold). To confirm the absence of switching effects, we conducted ROI-based (FWE corrected) comparison of Switch > Repeat trials for all clusters identified in the CUES > BASELINE contrast. This did not yield significant results even after lowering the correction to an uncorrected 0.1 cluster-level threshold. We also computed the Switch > Repeat contrast for each task separately in the regions showing the strongest task-specific preparatory activation effects (i.e., IFG and SPL). Again, no significant effects were found even at an uncorrected $p < 0.1$ cluster-level threshold.

Conjunction analysis

To isolate the brain areas involved in target processing that were pre-activated by preparatory cues, we performed a conjunction analysis ([CUE_SEM > CUE_SPA] > [TARGET_SEM > TARGET_SPA] and vice versa) as described in Methods section. A large portion of the LIFG (-51, 29, -2; $k = 365$) was engaged by both semantic cues and word targets (Fig. 3, right panel). Spatial targets (Fig. 3, left panel), on the other hand, activated the RSPL (24, -67, 49: $k = 112$), the left BA 19 (-33, -88, 16; $k = 190$), and the right fusiform gyrus (30, -58, -14; $k = 154$).

PPI analyses

The pattern of connections of the two key regions during the preparation period changed according to the task that participants were expecting (Fig. 4). Preparing to perform a semantic task increased the connectivity of the LIFG with the anterior part of the left insula (-36, 26, 4; $k = 110$), the SMA (-3, 17, 52, $k = 185$) and the left SPL (-33, -49, 52; $k = 469$). The LIFG also increased its
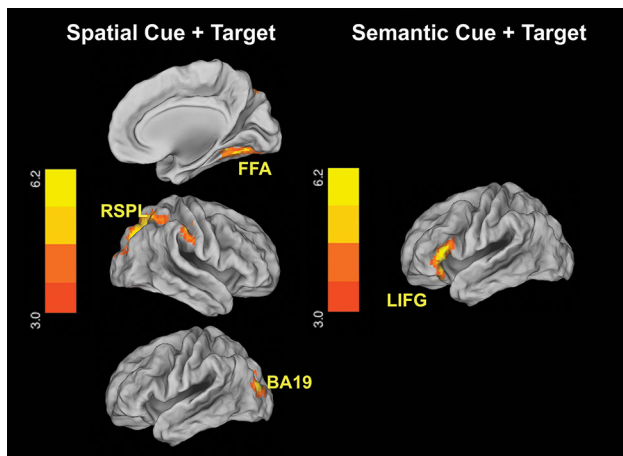
Fig. 3 Cue and target conjunction results for spatial (*left*) and semantic (*right*) trials. The right SPL (superior parietal lobe), right FFA (fusiform face area) and left BA19 (brodmann area 19) were active both for spatial cues and targets, whereas the left IFG (left inferior frontal gyrus) was the only area engaged during semantic cues and targets. *Scales* represent peaks *t* values

connectivity with a large perceptual cluster ($k = 581$) including the left fusiform gyrus in the vicinity of the Visual Word Form Area ($-42, -58, -14$; McCandliss et al. 2003), as well as left and right BA 18 ($-24, -94, -8$; $k = 99$; $24, -97, -5$; $k = 92$).

On the other hand, preparation to perform a spatial task enhanced the connectivity between the RSPL and neighboring regions such as the IPL ($48, -31, 55$; $k = 118$) as well as homologous areas in the left hemisphere ($-39, -43, 52$; $k = 189$). Additionally, the RSPL also increased its coupling with several occipital regions such as the left and right BA 19 ($-33, -73, -17$; $k = 121$; $36, -91, 13$; $k = 61$), and posterior right temporal areas ($57, -61, -14$; $k = 110$).

Discussion

The current investigation revealed that expectations about an upcoming stimulus category activate some of the brain regions that are involved in target processing later on. These

areas include the LIFG for linguistic expectations and the RSPL for abstract figures, which suggests that key regions for semantic and spatial processing (e.g., Jefferies 2013; Husain and Nachev 2007) are already engaged when expecting to encounter items belonging to these categories. Crucially, these activations were found in a setting with minimal interference, in which a large set of univalent targets were preceded by fully valid cues. The different manipulations we introduced were able to abolish switching effects (both at behavioral and neural levels). The use of univalent targets alleviates interference between tasks (Kiesel et al. 2010), probably by decreasing automatic task inertia in the patterns of activations (Yeung et al. 2006). Also, we avoided the use of invalid cues as they increase interference, a potential source of switching costs (Yeung et al. 2006). Although the use of 100 % valid cues could impair the mobilization of attentional resources during the preparatory stage, it has also been suggested that invalid cues could hinder preparatory activations by minimizing the perceived utility of the cue (Wendt et al. 2012). Crucially, our behavioral pilot data showed validity effects in a setting where cues were even less likely to be processed than in the fMRI paradigm, given the presence of 20 % of invalid cues. Still, the fMRI patterns strongly suggest that cues preactivated brain regions relevant for subsequent target-specific processing.

Preparing in advance for upcoming demands is a well-documented human ability. This ability relies on different brain networks, which include a frontoparietal one as the most prominent (Ruge et al. 2013). This network is not only linked to preparatory processes but also to cognitive control and attention in general (e.g., Corbetta et al. 2008). Since preparation depends on control mechanisms, the implication of frontoparietal nodes seems quite coherent. The present study adds to previous research about the neural correlates of this process by finding task-specific brain patterns of both activity and connectivity under conditions of low interference.

Regarding activations common to cues, we found significant clusters in anterior and posterior parts of the PFC and premotor areas, and generic areas of maintenance of
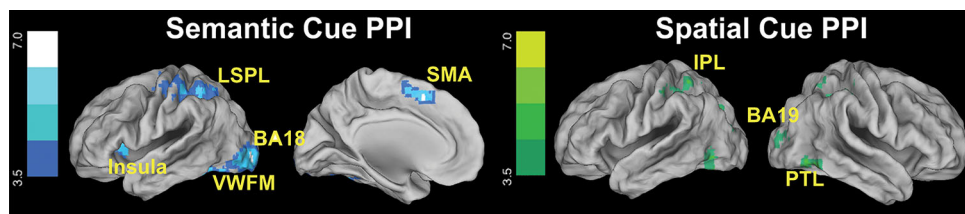

Fig. 4 PPI analysis results for semantic (*left*) and spatial (*right*) cues. Upon the presentation of a semantic cue, the seed (LIFG; left inferior frontal gyrus) enhanced its connectivity with the left Insula, SMA (supplementary motor area), left SPL (superior parietal lobe), left fusiform gyrus (visual word form area) and BA 18 (brodmann area 18). On the other hand, the spatial seed (RSPL; right superior parietal lobe) increased its connectivity with the left IPL (inferior parietal lobe), bilateral PTL (posterior temporal lobe) and BA 19 (brodmann area 19) during spatial cue processing. *Scales* represent peaks *t* values

control sets (i.e., the insula; Dosenbach et al. 2008), and some motor and visual regions. Anterior frontal activations have been related to active maintenance of task sets, which could potentially increase WM load in long cue-target interval designs due to anticipatory visual imagery when a small set of stimuli is used (Baddeley 2003; Ruge et al. 2013). However, we used a wide variety of stimuli that made not possible for participants to image them in advance, thus abolishing the impact of anticipatory item maintenance during the cue-target interval. Moreover, in our task participants could not form explicit cue-target compounds, and thus they could not prepare direct responses upon the presentation of the cue. The implication of the mid-dorsolateral PFC near the Inferior Frontal Junction together with premotor areas is consistent with the activation of the abstract (not item-related) task sets (Ruge et al. 2013; Baldauf and Desimone 2014) needed. On the other hand, our pattern of results seems to be in line with previous studies on switch probability, which suggest that differences between switch and non-switch trials might be related to particular preparatory strategies. De Baene and Brass (2013, 2014) revealed a dissociation between strategy-dependent and independent areas in preparation, in which the LPFC, the LIPL and the left MTG seemed to be involved in low switch-probability contexts (probably reflecting the increased control required in unexpected switch trials), whereas the preSMA and the SPL were insensitive to the probability-related strategy. A relatively high switch probability scenario such as ours (i.e., 50 % switch trials) may have reduced the activation of the LFPC, LIPL and left MTG, since the strategy could have moved "to an intermediate neutral control state" (De Baene and Brass 2013). Interestingly, the high switch-probability scenario is thought to erase both neural and behavioral switch-specific results. This, together with the other experimental manipulations that reduced interference between tasks, could help explain the absence of switching effects in our results.

Furthermore, the GLM revealed coherent-specific activity for each cue category. The activation of the rostral LIFG has often been related to the selection of task-relevant semantic information (e.g., Fiez 1997; Wagner et al. 2001). Our experiment replicates previous findings (Sakai and Passingham 2003) showing that this brain region is engaged by semantic cues, before any target word is presented. This represents further evidence for the role of this area in maintaining a preparatory state for subsequent semantic processing. Our analyses showed that semantic cues also activated the middle temporal lobe and the angular gyrus. These areas, together with the LIFG, are thought to conform a crucial network for semantic control (Binder et al. 1997; Price 2000; Jefferies 2013). Some authors (Noonan et al. 2013) propose that the middle temporal gyrus tunes the semantic processing to the appropriate aspects required by the context, while the angular gyrus may be in charge of selecting goal-related semantic features (Jefferies 2013). In addition, conjunction analysis revealed that the LIFG was activated both during the semantic cue and during word targets, which support its role in semantic-controlled processes. However, the other two areas contributed exclusively upon the presentation of the cue, suggesting that these control processes might help LIFG in facing semantic stimuli successfully by contributing to an adequate preparatory state before target appearance.

Additionally, the pattern of connectivity of the LIFG showed how even before the presentation of the word, this area connected with others such as visual regions in the vicinity of the Visual Word Form Area. This region is a key component of visual word recognition due to its role in bridging word perceptual aspects with higher order semantic information (McCandliss et al. 2003). On the other hand, the LIFG was also functionally coupled with the insula, having a core role in language processing (see Ardila et al. 2014 for a recent review). Pivotal theories (e.g., Dosenbach et al. 2008) argue the additional involvement of the insula and the frontal operculum in control processes. In fact, the cluster we found was in the more dorsal part of the anterior insula, which has been related to control processes such as switching, inhibition and conflict (Chang et al. 2012).

On the other hand, the two types of task conditions showed a clear pattern of lateralization. Whereas semantic cues engaged left hemisphere areas, spatial ones preactivated more bilateral regions with a general right hemisphere dominance. While the RSPL has been related to the relocation of top-down attention to relevant stimuli (Corbetta et al. 2008), its inferior part is closely involved in visuo-spatial perception (Constantinidis 2006; Husain and Nachev 2007) and orientation coding (Harris et al. 2008). The activation of this region, together with prominent visual ones, is coherent with the nature of the spatial task, in which participants had to tell the orientation of several lines superimposed in complex shapes. Although word perceptual analysis was also a requirement in the semantic task, which may be related to the increased connectivity of the LIFG with left fusiform regions, the type of fine visuo-spatial discriminations required in the spatial condition may explain the involvement of the RSPL in this condition. Moreover, the pattern of connectivity of this area during the cue period emphasizes the role of a dorsal occipito-parietal processing stream in preparation for upcoming demands of spatial perception (Husain and Nachev 2007; Goodale and Milner 1992).

Several theories propose the existence of common brain networks underlying preparation across categories. For

instance, Dosenbach et al.'s (2008) cognitive control model posits the existence of two differentiated networks, one for initiation (frontoparietal) and a different one for the maintenance of task sets (cingulo-opercular). Other prominent theories, such as Duncan's (2010) Multiple Demand system, also support the implication of frontoparietal networks in flexible reorganization of cognitive states, such as those required in our task. Our results strongly suggest the presence of both general and task-specific preparatory processes for both categories in low-interference contexts. These are reflected in differential patterns of activation and connectivity for semantic and perceptual cues, which are coherent with later target-related activity in both cases.

Our results are coherent with previous literature on task preparation (see Sakai 2008) and, most importantly, they advance knowledge in the field showing specific task-related preactivations in a low-interference context. It could be argued, however, that our symbolic cues still required a certain memory load to be maintained during the cue-target interval. In addition, due to scanner equipment constraints the same fingers were used for both tasks, which could have induced some interference due to potential updates of response mappings (Meiran 2000). Indeed, achieving a complete lack of prospective memory load and interference in settings designed to study preparation is difficult, if not impossible. Preparing for something requires maintaining a set across time, and thus removing maintenance altogether would entail abolishing preparation. Thus, it is highly likely that the process of preparation, per se, is inextricably linked to prospective memory to a certain degree. The inclusion of a large target set in our design, however, minimized the role of working memory per se, in the sense of controlled manipulation of item information. Cue-target compounds could not be formed and thus cues could not trigger the anticipated imagination or manipulation of specific stimuli. Our results, obtained in a paradigm minimizing the influence of these factors, show that clear preparatory effects are nevertheless observed.

Conclusions

The current investigation represents a step forward in our understanding of selective preparatory processing in the brain. Our data are in line with predictive coding theories, which propose that the brain anticipates upcoming scenarios by creating a potential template of stimulation that is later on compared against the actual sensorial information (e.g., Friston 2003). Just like our brain represents the prediction of the perception of a face before its appearance (Summerfield et al. 2006), it also seems to recruit in advance areas needed for category-specific computations over stimuli whose specific content is unpredictable.

Compliance with ethical standards

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