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Monitoring mechanisms in visual search: an fMRI study

Antonino Vallesi^{1,2,3,#}

¹ Department of Neurosciences: SNPSRR, University of Padova, Italy

² Centro di Neuroscienze Cognitive, University of Padova, Italy

³ International School for Advanced Studies (SISSA), Trieste, Italy

[#]Corresponding Author's address:

Antonino Vallesi

Department of Neurosciences: SNPSRR

University of Padova

Via Giustiniani, 5, 35128 Padova

Tel +39 049 821 ext. 4450

Fax +39 049 821 8988

E-mail: antonino.vallesi@unipd.it

Abstract

This fMRI study investigates the neural underpinning and the cognitive factors associated with monitoring in visual search. A visual search task was designed by pseudo-randomly mixing four experimental conditions, which were obtained through the factorial combination of salience (pop-out vs. non pop-out) and target presence (present vs. absent). The fastest responses were obtained when a salient target was presented, while responses were slowest with target-absent conditions, which required extensive evaluation of the visual scene. Partial Least Square multivariate analysis was used to analyze the fMRI data. The first Latent Variable revealed a set of fronto-parietal and occipital regions, which was cohesively activated especially when the presence of the target stimulus was not easy to discard, such as when all stimuli in the visual scene were non-targets or when one stimulus among the rest was salient (pop-out) but not a target. The most extensive and robust activation within this cohesive set of regions was located in the right inferior/middle frontal gyrus. This finding corroborates evidence in favor of a role of the right lateral prefrontal cortex, and associated regions, for evaluative operations, extending previous findings to the visual search domain.

Keywords: Salience, Relevance, Monitoring, Prefrontal Cortex, Partial Least Square, Visual Search.

1. Introduction

Different high-level cognitive functions have been attributed to specific neural networks with important nodes in the prefrontal cortex (e.g., Badre, 2008; Koechlin & Summerfield, 2007; Petrides, 2005; Stuss, 2011). In particular, the right lateral prefrontal cortex has been shown to be important in checking for the occurrence of critical events especially when this occurrence is not self-evident (e.g., Langner & Eickhoff, 2013; Stuss & Alexander, 2007; Vallesi, 2012).

Cognitive operations such as checking and evaluating, which we will refer to as ‘monitoring’ throughout this article, have been shown to be right-lateralized in the prefrontal cortex in many domains, such as goal evaluation (Camus et al., 2009; Knoch et al., 2006), time preparation (Stuss et al., 2005; Vallesi et al., 2007a), problem solving (Reverberi, D’Agostini, Skrap, & Shallice, 2005; Turner et al., 2004), semantic and episodic memory (Hayama & Rugg, 2009; Henson, Shallice, & Dolan, 1999) and perceptual decision-making (Fleck, Daselaar, Dobbins, & Cabeza, 2006). A related construct is that of alertness, defined as the continuously scanning of the environment for behaviorally relevant stimuli, which has also been reported to heavily rely on right hemispheric regions (Langner et al., 2012).

The present fMRI study aimed at extending this accumulating evidence to the visual search domain, by investigating whether a right-frontally based neural network is involved in a visual search task, especially in the conditions when monitoring is mostly required. During visual search, monitoring is unlikely to be required when the critical event is salient. If the critical event was salient (e.g., with a different color with respect to distractors), indeed, it would pop out through bottom-up perceptual processes and would not need further monitoring. Salient stimuli, however, might require monitoring if they are non-targets for the task at hand. That is, when it is ambiguous to determine whether a salient object, which attracts attention in a bottom-up (pop-out) manner, belongs to the target category or not, evaluating the target status of an item becomes crucial to prevent false alarms. In our task, as we will see below, this condition was approximated by using a conjunction of features (color and letter identity) to distinguish the target from non-targets.

Therefore it would be difficult to quickly identify a color-deviant pop-out stimulus as target or non-target only on the basis of its color, as its status should be carefully checked when the feature integration operation would be completed.

An exhaustive visual search, accompanied by a more effortful and extensive monitoring, would be necessary when scanning for the presence of the critical item, but only distractors with similar characteristics as the potential target are encountered in the visual scene (i.e., target-absent and non-salient items). Controlled visual search processes are also expected when the critical object is embedded in a set of similar distractors, that is, conditions with non-salient targets only (e.g., Treisman & Gelade, 1980). This condition is more likely to be associated to intense and extensive monitoring than a pop-out target-present condition, but less so with respect to non pop-out conditions with no target, since monitoring for the target-presence would be on average terminated earlier in the former condition than in the latter.

Thus, we adopted a 2 by 2 factorial design with salience and target-presence as the critical factors, since this experimental design could help determining which of these factors (or which interaction between them) is critical for obtaining an activation of right lateral prefrontal regions and a related network.

Previous fMRI studies have already investigated similar issues. Kim and colleagues (Kim, Eliassen, Lee & Kang, 2012) for instance used a visual search task with experimental manipulations aimed at distinguishing between efficient and inefficient visual search. By means of an fMRI block design, the authors identified several clusters, including subcortical, superior occipito-parietal and prefrontal regions, which were quantitatively more activated during inefficient vs. efficient visual search. Similar results had been obtained in a previous fMRI study, which found overlapping brain activations for the two search conditions, apart from a bilateral superior frontal activation unique for inefficient visual search (Leonards, Sunaert, Van Hecke, & Orban, 2000). In both studies, which adopted an fMRI block design, there was no clear lateralization of activations associated with inefficient search. In our study, we adopted an event-related design to avoid steady-state task-set

effects and tax monitoring demands more when inefficient visual search conditions unpredictably appear in the visual display, with the aim to detect more right-lateralized brain networks.

Our main prediction was that a right-lateralized network, with an important node in the right lateral prefrontal cortex, would be involved in visual search proportionally with the monitoring demands of the task. Other regions involved in the task, such as those responsible for visual perception in the occipital cortex, spatial attention in the parietal cortex and motor preparation processes in the dorso-medial frontal cortex and precentral gyrus, are also expected to participate to the same network in evaluative task contexts.

2. Results

A schema of the different task conditions is illustrated in figure 1a-1d.

2.1 RTs. Participants were faster in detecting target-present letter matrices than target-absent ones [target presence main effect, $F(1, 15)=37.2$, $p=.00002$]. They were also faster in detecting salient items than non salient ones [salience main effect, $F(1, 15)=10.5$, $p=.005$]. The 2-way target presence by salience interaction was also significant [$F(1, 15)=29.4$, $p=.00007$; see Figure 1e]. Tukey's post-hoc tests (Ryan, 1959) showed that RTs were fastest for the “target-present & salient” condition than for any other condition (for all, $p<.001$), and then for the “target-present & non-salient” condition than for the “target-absent & salient” and “target-absent & non-salient” ones (for both, $p<.001$).

---- *Insert Figure 1 about here* ----

2.2 Accuracy. The accuracy level was very high, ranging from 98.2% in the target-present and salient condition to 99.71% in the target-present and non-salient one, with the two target-absent conditions in between. No comparison was significant for the analysis concerning accuracy (for all, $p>.22$).

2.3 *fMRI Data*. The first Latent Variable (LV) of the Partial Least Square (PLS) analysis was significant (explained cross-block variance: 45.98%, $p=.041$). This LV describes a set of regions which were co-activated, in a decreasing order, for target-absent and non-salient, target-absent and salient, target-present and non-salient, and target-present and salient conditions, as it can be appreciated by looking at the brain scores plot (Figure 2). A 2x2 ANOVA with salience and target presence as the within-subjects factors and the brain scores as the dependent variable demonstrated a main effect of target presence [$F(1,15)=30.2$, $p<.0001$], with target-absent conditions being associated to higher brain scores than target-present ones. No other effect was significant.

---- *Insert Figure 2 about here* ----

Most of the reliable saliences and bootstrap ratios were positive and occurred between lags 2 and 3 (from 2 to 6 seconds post-stimulus), that is, around the typical peak of the Hemodynamic Response Function (HRF; see Table 1). Figure 3 shows the pattern of brain clusters co-activated with the task conditions in the first Latent Variable, as shown in Figure 2.

---- *Insert Table 1 about here* ----

---- *Insert Figure 3 about here* ----

The most robust activation (peak bootstrap ratio) with the largest cluster was obtained in the right inferior/middle frontal gyrus (roughly corresponding to BA 45/9; see Figure 4), but the cohesive network whose activation was reflected in the first LV also included: on the right hemisphere, inferior parietal lobule, thalamus and superior occipital lobe; bilaterally, superior frontal gyrus, insula, inferior-middle occipital gyrus and cerebellum; on the left hemisphere, supplementary motor area and pre-central gyrus. The only negative bootstrap ratios were observed

in the first TR and included the left caudate body, the superior medial frontal gyrus and the right cerebellum.

---- *Insert Figure 4 about here* ----

3. Discussion

The present fMRI study investigated the neural underpinning of the monitoring process during various visual search contexts, created by factorially crossing salience and target-presence. Monitoring is a long-lasting process, which has been shown to be right-lateralized in the prefrontal cortex in many other domains (e.g., Henson et al., 1999; Stuss & Alexander, 2007; Vallesi, 2012). Based on the existing literature on the anatomo-functional basis of monitoring, we hypothesized that this cognitive process would engage right lateral prefrontal regions, together with a prevalently right-lateralized network.

A multivariate PLS analysis showed that many regions were co-activated more in target-absent conditions (which required more visual search-related monitoring) than in target-present ones, including fronto-parietal and high-level occipital regions. Statistical analyses performed on the brain scores of the first latent variable extracted with the PLS analysis showed a significant main effect of target-presence. While a significant salience main effect and a target-presence by salience interaction could be detected behaviorally (with the fastest RTs for salient targets), these effects did not show up in the fMRI data, suggesting that salience per se is not predictive of the activation of this network of regions, which is effortfully engaged in monitoring for the target occurrence in target-absent visual search contexts.

Importantly, among a cohesive set of brain regions, the cluster that resulted to be most extensively and robustly modulated by the experimental manipulations was located in the right lateral prefrontal cortex. The minimum activation level was observed in this set of regions for a pop-out condition that did not require any monitoring, that is, when a target-present and salient

stimulus was presented (e.g., red ‘O’ among other green non-target letters). The highest activation levels were instead obtained for target-absent and salient trials, when the pop-out stimulus should be carefully evaluated to prevent false alarms, and for target-absent and non-salient trials, when the cognitive system should be engaged more extensively in visual search to check that the target stimulus is absent from the visual scene (i.e., matrix of letters). These right frontally-based evaluative, checking operations which were engaged in different target-absent visual search conditions could be interpreted as manifestations of the monitoring construct. Similar findings have been reported in the time domain: checking the non-occurrence of targets during variable preparatory time intervals has also been shown to require right lateral prefrontal regions (e.g., Vallesi et al., 2007a; Vallesi, Shallice, & Walsh, 2007b; but see Triviño, Correa, Arnedo & Lupiañez, 2010, for evidence of bilateral prefrontal involvement).

In an interesting fMRI study by Indovina and Macaluso (2007), the presentation of highly salient checkerboards in one hemi-field did not activate the fronto-parietal network if spatial attention was endogenously oriented elsewhere, suggesting that salience per se is not a sufficient condition for its engagement. The cognitive determinants of a fronto-parietal involvement in the evaluation of the visual scene are further unveiled by our data. In the present work, indeed, individuals had to pay attention to each centrally presented matrix of letters (i.e., spatial attention demands were equally spread to the whole visual scene), in order to decide whether the target was present or absent. The factorial design (salience x target-presence) of the present study allowed us to isolate target-absence as the critical factor, independently of salience status (which was manipulated in two levels) and spatial attention (which was held constant).

In apparent contrast with the present results, another fMRI study with rhesus monkeys (Wardak, Vanduffel, & Orban, 2010) showed that even target-present and salient targets may involve the right ventral prefrontal cortex (BA 45). However, in that case the contrast was with baseline conditions that did not involve visual search. Even if one assumes that a similar activation pattern may occur in the human brain to that reported in monkeys, our data are not necessarily in

conflict with those of Wardak and colleagues (Wardak et al., 2010), because also in our case there could be an involvement of this region in pop-out target conditions. Our design however allowed us to show that an analogous region with respect to that investigated in the monkey's study (Wardak et al., 2010) was relatively more involved in visual search conditions in which the target was absent and evaluation of the visual scene was more extensively required as compared to pop-out target conditions.

The activation of the inferior parietal lobule in the conditions which taxed monitoring was partially overlapping (although more inferiorly) with that reported in studies of visual attention (e.g., Wojciulik & Kanwisher, 1999), especially when involving feature integration tasks (Corbetta, Shulman, Miezin, & Petersen, 1995), similar to our study. This activation was completely right-lateralized, consistent with the right hemispheric dominance reported for the ventral parietal regions during color-shape feature integration (Albert, Sheremata, Silver, & Robertson, 2013), especially within a visual search mode (Shafritz, Gore, & Marois, 2002; c.f., Nobre, Coull, Walsh, & Frith, 2003). The involvement of parietal regions in inefficient visual search, such as non pop-out conditions, is also corroborated by neuropsychological evidence (e.g., Aglioti, Smania, Barbieri, & Corbetta, 1997; Friedman-Hill, Robertson, & Treisman, 1995).

The involvement of regions from the ventral visual stream, such as V4, could be expected based on monkey studies (Bichot, Rossi, & Desimone, 2005; Chelazzi, Miller, Duncan, & Desimone, 2001) showing an involvement of V4 neurons in biasing visual search by filtering out non-target stimuli on the basis of non-spatial features. It is likely that this ventral region, being cohesively activated for the same effortful visual search conditions as fronto-parietal regions, is guided by the latter through top-down and task-related signals in favor of one of the competing populations coding for the target features, and this interaction is more intense when the search for a target is harder to stop, such as during target-absent conditions. This interpretation should be tested more directly in future studies.

The bilateral insula was also activated in target-absent conditions, which were the most demanding in terms of attentional resources, as we can infer from the RT results. This result is compatible with previous studies, which have already demonstrated that increasing task demands produce increased interaction between the anterior insula and regions responsible of executive control, independently of the stimulus and response modality (e.g., Eckert et al., 2009), possibly due to the optimal regulation of arousal levels by this structure.

The conditions that activated the fronto-parietal network most were those associated with a longer visual search duration (target-absent conditions, see Figure 1b), that is those with the longest average RTs. Therefore, duration of the critical processes or general effort, in addition to evaluative mechanisms, may conceivably have influenced the reported fMRI effects (cf. Yarkoni, Barch, Gray, Conturo, & Braver, 2009). However, the described PLS effects on HRF, especially those concerning the right lateral prefrontal cluster, started already in the first and second TR (1-4 sec post-stimulus), that is, with an excessively early onset to be solely due to generally longer lasting processing in target-absent conditions. Moreover, while target-present and non-salient conditions were statistically in between with respect to the other three conditions in terms of RTs, this was not reflected in the neuroimaging data (which only showed a main effect of target-presence), again suggesting that an explanation solely concerning difficulty could not be sufficient to account for our data. Nevertheless, future studies should try to disentangle more directly between the role of time-on-task and general effort, on the one side, and that of monitoring demands, on the other side.

A possible alternative explanation of the functional meaning of the regions activated in the first latent variable, and especially right ventro-lateral prefrontal cortex, concerns the need to keep the response system in check in the conditions in which the visual search process lasts longer, that is target-absent conditions. An inhibitory role of this region has indeed been advocated in previous studies (Aron, Robbins, & Poldrack, 2004). No overt behavioral evidence could corroborate this possible account in the present study, since no excessive false alarms were present in target-absent conditions, and the accuracy level was equally at ceiling for all the four conditions. Moreover, a

response inhibition account of the right lateral prefrontal involvement even in some classical inhibitory tasks (e.g., stop-signal, go/nogo) has been recently criticized, as activations in this region are task-dependent and more easily interpreted in terms of working memory or monitoring requirements (e.g., Mostofsky & Simmonds, 2008). Moreover, many findings showed that left lateral (e.g., Swick, Ashley, & Turken, 2008) and superior medial prefrontal (e.g., Picton et al., 2007) regions, and not so consistently the right ventro-lateral prefrontal cortex, are causally involved in response inhibition. However, to better settle this issue, future studies should more directly disentangle a monitoring role of right lateral prefrontal regions from an inhibitory one.

No region was more activated for stimuli that were both behaviorally relevant (target-present) and perceptually salient (pop-out) than for the other conditions, with the exception of a few regions with negative bootstrap ratios during the first TR only. The low level of involvement of brain regions in this condition is in agreement with psychophysical studies that demonstrate that pop-out target stimuli do not require many attentional resources (e.g., and do not engage much the fronto-parietal network (e.g., Indovina & Macaluso, 2007) or high-level occipito-temporal areas (Kourtzi, Betts, Sarkheil, & Welchman, 2005).

4. Conclusion

The present study showed that a set of brain regions, with the most extensive cluster located in the right inferior/middle prefrontal cortex, is engaged when an intensive evaluation of the target/non-target status is required by the task demands during visual search (target-absent contexts). This finding extends previous literature on the relationship between the right lateral prefrontal cortex and evaluative, monitoring processes to the visual search domain. Data from patients with brain lesions in this and other brain regions activated here during monitoring-demanding conditions will be critical in order to definitely test whether this right prefrontal region,

as well as the other nodes of the network highlighted in the present study, are not only associated with monitoring in visual search, but also necessary for this key cognitive process.

5. Methods and Materials

5.1 *Participants*

Sixteen healthy volunteers (9 females; mean age: 27 years, range: 21-35) took part in the study after signing an informed consent. An extra female participant was discarded because her accuracy was below 2.5 SD with respect to the group average in some conditions. All participants had normal or corrected-to-normal vision. All were right-handed, as assessed with the Edinburgh Handedness Inventory (Oldfield, 1971; average score: 86, range: 60-100). None reported any history of psychiatric or neurological disorders. Participants received 25 Euros in compensation for their time. The study was approved by “IRCCS La Nostra Famiglia” (Udine, Italy) ethical committee.

5.2 *Experimental material & task*

The background color was constantly a light grey. Visual stimuli consisted of 9 capital letters presented in a 3x3 invisible matrix. The letters were written in Arial (font size: 22) and were either green or red, depending on the condition. All the letters of the Italian alphabet but “O” (the possible target) and “Q” (which was too similar to the target) were used as distractors (19 letters in total).

The participants’ task was to press the button under their right index finger if they detected a “red O” (target) among the 9 letters, and that under the right middle finger if there was no “red O”. The association between response finger and condition was counterbalanced between subjects. There were 4 possible conditions which occurred pseudo-randomly and equally often during the run. For half of the participants these conditions were defined as follows (see Figure 1a-1d):

- Target-present & Salient: “red O” among green letters
- Target-present & Non-salient: “red O” among red letters

- Target-absent & Salient: 1 red letter among 8 green letters or 1 green letter among 8 red letters (with no target letter)

- Target-absent & Non-Salient: all red letters with no "O".

For the other half of the participants, the target was instead defined as a “green O”, and the letter colors in the 4 conditions described above were inverted accordingly. Each trial started with a blank screen lasting for an inter-trial interval, which was continuously jittered between 2 and 8 seconds. The letter matrix was then centrally shown for 2 seconds, which corresponded to the response deadline.

Eight practice trials were also presented before 80 test trials. After each practice trial, different visual feedbacks were shown to the participants according to whether they had responded accurately (“Bene”, that is, “well done” in Italian), not accurately (“Sbagliato, attenzione”, “wrong, be careful”) or they did not respond (“Sii più veloce”, “try to be faster”). No feedback was shown after each test trial.

5.3 Acquisition and Pre-processing of fMRI data. The fMRI data were acquired at the S. Maria della Misericordia Hospital in Udine on a 3T Achieva Philips whole-body scanner with an 8-channel head coil. Cushioning was applied to minimize head movements. Functional scans were obtained using a whole head T2*-weighted echo-planar image (EPI) sequence (repetition time, TR: 2 sec; echo time, TE: 35 ms; 34 transverse axial slices with interleaved acquisition; flip angle: 90; 3.59x3.59x4 mm voxel size; field of view, FOV: 230 mm, acquisition matrix: 64x64; SENSE factor: 2 in anterior-posterior direction). After a short practice phase without image acquisition, 288 scans were acquired in a single run, which lasted 9.6 minutes. While lying in the scanner, participants also performed two other tasks (in a counterbalanced order), which are not reported in the present study. Anatomical images (TR/TE: 8.2/3.7, 190 transverse axial slices; flip angle: 8; 1 mm³ voxel size; FOV = 24 cm; acquisition matrix: 240x240; no SENSE factors) were also acquired in the middle of the whole scanning session. Stimulus presentation and response collection were

managed using Presentation (<http://www.neurobs.com/>) and delivered within the scanner by means of MRI-compatible goggles mounted on the head coil. Manual responses were recorded using an MRI-compatible response pad.

The pre-processing of fMRI data was performed with SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>). A dummy period of 4 TRs was discarded to allow the MR signal to reach a steady-state. Functional scans were spatially realigned and unwarped to compensate for participants' head movements during the experiment using a 4th degree B-Spline interpolation. For normalization, a transformation matrix between the mean image of realigned volumes and a standard functional template from the Montreal Neurological Institute (EPI.nii) was generated with a 4th degree B-spline algorithm and applied to re-slice volumes with a 2 mm³ voxel-size. The normalized images were spatially smoothed with an 8 mm full-width-at-half-maximum Gaussian filter to decrease residual anatomical variability.

5.4 Behavioral data analysis. RT data were analyzed by means of a 2x2 repeated measures ANOVA with salience (salient vs. non-salient) and target-presence (present vs. absent) as the within-subjects variables. Tukey's HSD test was used as the post-hoc test. Since accuracy was not normally distributed due to ceiling effects, paired comparisons were run with non-parametric Wilcoxon's test.

5.5 FMRI data analysis. A multivariate approach was used here to characterize a cohesive set of regions involved in the different visual search conditions at the whole brain level. Multivariate statistical analyses were performed with Partial Least Square (PLS, pls.rotman-baycrest.on.ca), a software which assesses the relations between any set of independent measures, such as the experimental design, and a set of dependent measures, such as the brain voxels (see McIntosh, Bookstein, Haxby, & Grady, 1996, for a full description of this approach). PLS carries out the computation of the optimal least squares fit to cross-block correlation between independent and

dependent measures, to identify patterns of brain voxels whose signal change co-varies with the experimental manipulations. All the 4 task conditions of the design (2 target presence x 2 salience) were included in this analysis.

For each condition, the hemodynamic response function (HRF) of each voxel was defined as the intensity difference from trial onset during 7 successive post-stimulus repetition times (2 sec each) averaged across trials. The data matrix, which included all voxels and associated temporal segments (in columns) for all conditions and subjects (in rows), was mean-centered column-wise with respect to overall grand average. The matrix was decomposed using singular-value decomposition (SVD) to produce a set of mutually orthogonal latent variables (LVs) with a decreasing amount of explained covariance.

Each latent variable consisted of: (i) a singular value, (ii) a pattern of design scores, which identifies the contrasts between task conditions, and (iii) a singular image, which shows how the spatio-temporal distribution across the brain relates to the identified contrasts. The numerical weights within the singular image are called saliences and can be positive or negative, depending on their relation to the task design scores. An advantage of PLS, with respect to other multivariate approaches, is that coefficients of salience are computed for each voxel and can be used to test localization even though they have not been computed independently but in a multivariate manner (McIntosh et al., 1996). By multiplying the raw images by the singular image on a particular LV for each brain, PLS additionally produces brain scores that indicate how strongly each individual subject expresses the patterns on the LV.

A permutation test is used to determine the significance for each LV. The data matrix rows are randomly reordered at each permutation and a new set of LVs is calculated each time. The singular value of each new LV is compared to the singular value of the original LV. A probability is assigned to the initial value based on how frequently a statistic from the permuted data exceeds this original value (McIntosh et al., 1996). For the current experiment, 1000 permutations were used. The LV was considered significant if the probability was < 0.05 .

Voxel saliences indicate how strongly a given voxel contributes to a LV. To determine the reliability of the voxels' saliences, all data were submitted to a bootstrap estimation of the standard errors, by randomly re-sampling subjects with replacement 200 times. PLS was recalculated for each bootstrap sample to identify those saliences whose value remains stable independently of the chosen sample (Sampson, Streissguth, Barr, & Bookstein, 1989). The ratio of the salience to the bootstrap standard error (bootstrap ratio, BSR) is approximately equivalent to a z score, given a normal bootstrap distribution (Efron & Tibshirani, 1986). For each TR, clusters with at least 50 contiguous voxels with a $BSR \geq \pm 4$ (approximately equivalent to a z-score corresponding to $p < .0001$) were considered as reliable. Coordinates of the voxel with the peak BSR within each cluster were obtained in MNI space. Approximate brain areas were then identified using Anatomy toolbox in SPM (Eickhoff et al., 2005).

To understand the relation between the polarity of the saliences (and bootstrap ratios) in the singular image and the direction of HRF change in the clusters reliably activated in each LV, it is useful to relate the saliences to the design scores. For instance, positive saliences would indicate areas that are relatively more active in conditions with positive weights in the design scores. Conversely, negative saliences would indicate areas that are relatively more active in conditions with negative weights in the design scores.

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Figure legends

Figure 1. Panels A to D show the different task conditions: Target-present & Salient, Target-present & Non-salient, Target-absent & Salient, Target-absent & Non-Salient. Panel E: Response Times (RTs, in ms) and Standard Errors of the Mean, according to salience and target presence.

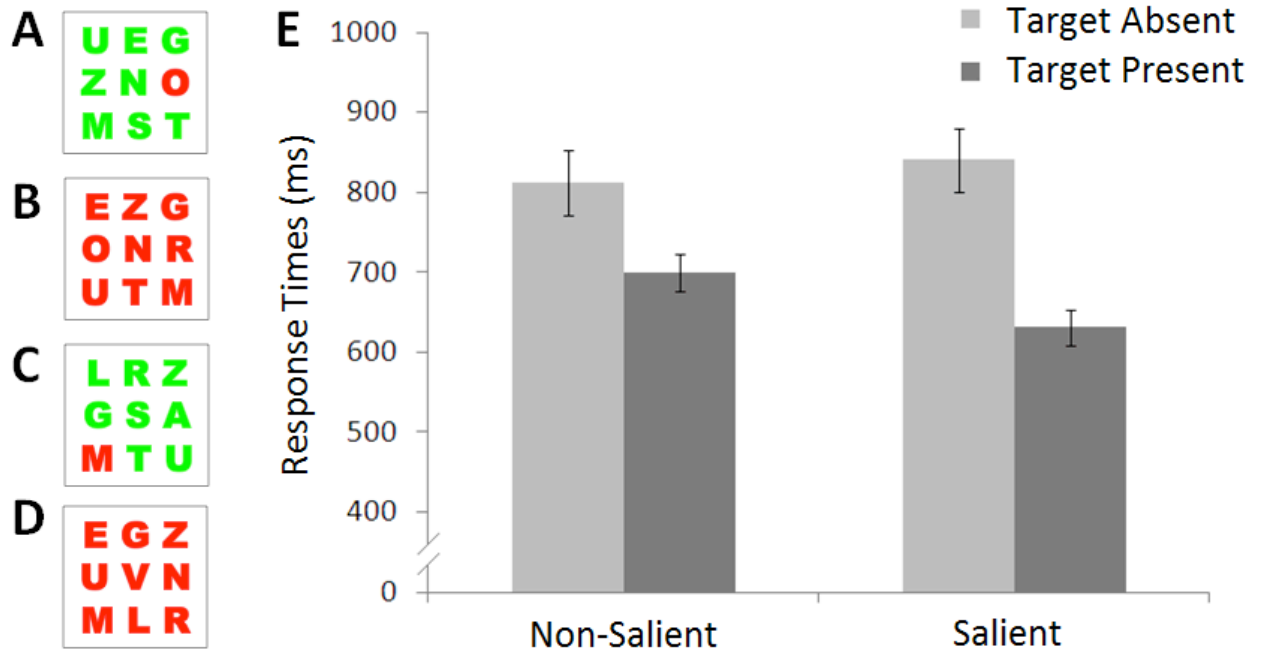


Figure 2. Brain Scores (and confidence intervals) as a function of task conditions. Brain Scores indicate how strongly each individual subject expresses the patterns on the LV

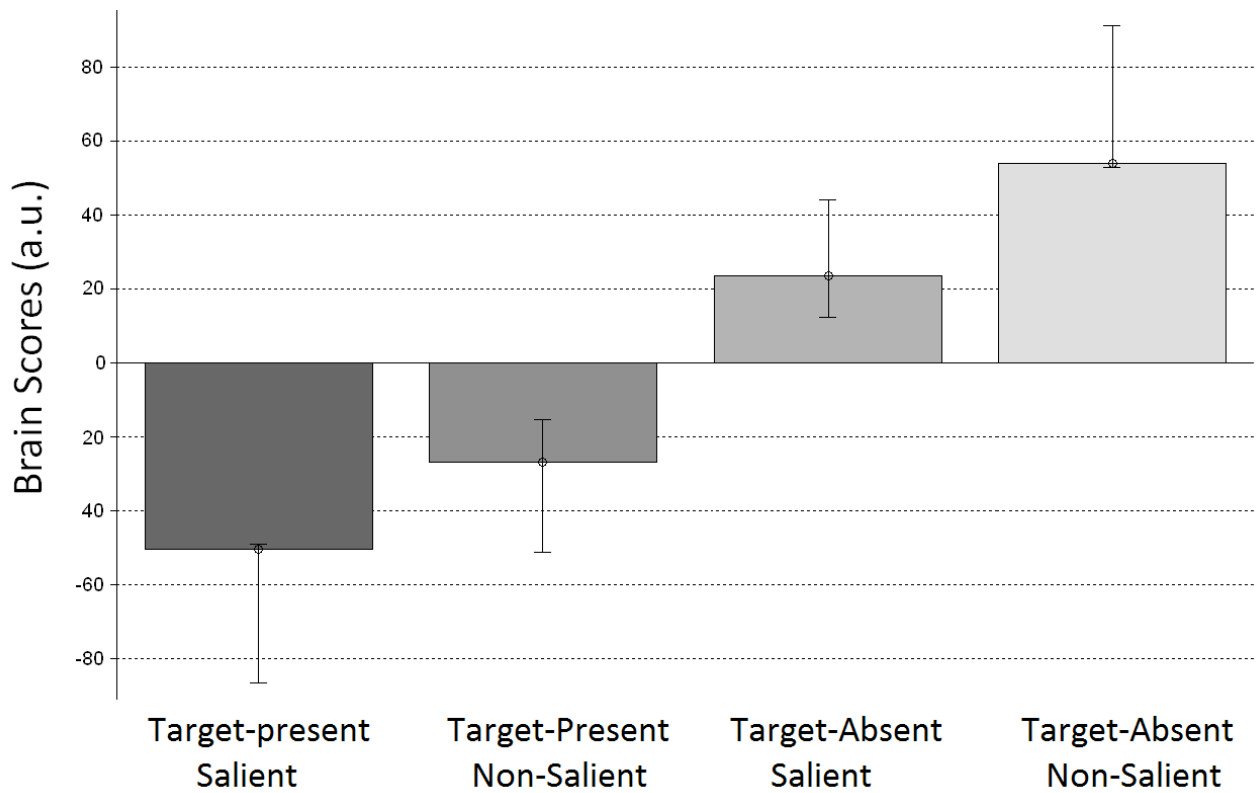


Figure 3. Panel A: Singular image, with the Bootstrap Ratios below -4 and above 4, which shows how the spatio-temporal distribution across the brain relates to the identified contrasts in Latent Variable 1 across the seven repetition times (2 sec each) used to estimate the average Hemodynamic Response Function. Panel B: Right inferior/middle prefrontal cluster (40 30 24) showing reliable and positive bootstrap ratios in Latent Variable 1, lag 2.

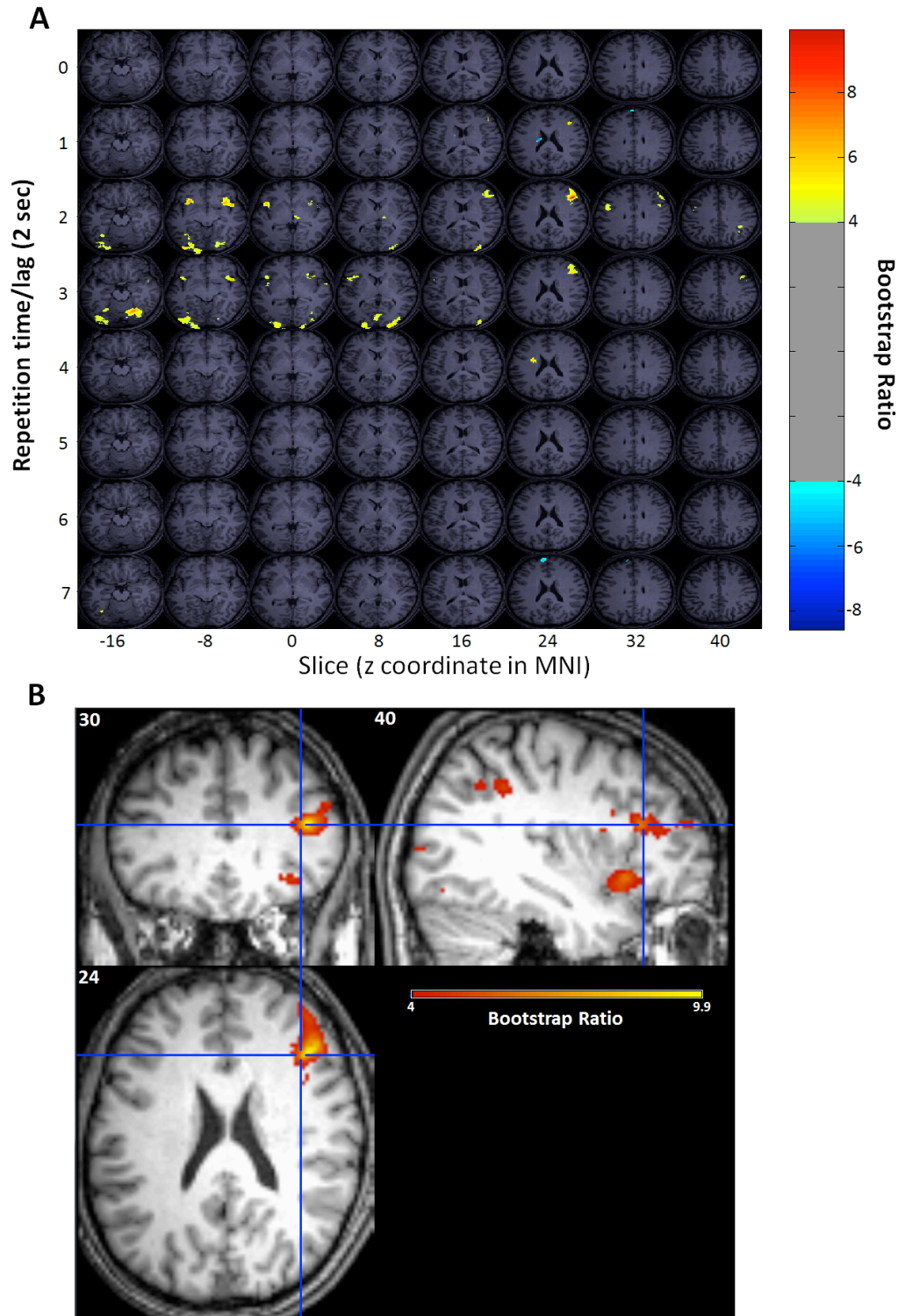


Figure 4. Modulation of Hemodynamic Response Function in the right inferior/middle prefrontal cluster by the different task conditions (average of peak voxel at MNI coordinates x: 44, y: 30, z: 24, and its 27 neighboring voxels).

