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Functional connectivity at rest captures individual differences in visual search

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ABSTRACT

Brain functional connectivity is supposed to capture personal and lifetime learning experiences and contribute to generating individual differences in cognitive abilities. We tested this possibility by using the visual search task as a measure of visual information processing and the functioning of the visual attention control system. Forty-two undergraduate students completed a functional MRI study with a resting-state session and a visual search task scan. The visual attention and control systems were studied by investigating the functional connectivity of the primary visual area, the posterior parietal cortex, the dorsolateral prefrontal cortex, and the dorsal anterior cingulate cortex, because these areas have been closely related to the visual search task. A pairwise resting-state functional connectivity analysis was conducted between these regions, followed by a correlation analysis with the behavioral measures from the visual search task. Results showed that higher connectivity values between the posterior parietal cortex and the dorsal anterior cingulate cortex were positively correlated with faster response speed. The posterior parietal cortex has been related to the formation of priority maps and the integration of sensory and executive information. Inhibitory control, performance monitoring during top-down cognitive tasks, and target detection have been associated with the dorsal anterior cingulate cortex. In light of these results, we suggest that the a priori enhanced connectivity between these regions defines individual differences in visual information processing and the ability to adapt to cognitive demands.

KEYWORDS

1. Introduction

Human brain functional connectivity has been continuously studied since the observation of temporally correlated, low-frequency, spontaneous fluctuations in blood oxygen level-dependent (BOLD) signals (Biswal et al. 1995; Raichle et al. 2001). Specifically, resting-state functional connectivity (rs-FC) has emerged as a neuroimaging paradigm to characterize how individual brain areas work together as networks (Bressler and Menon, 2010). This method is based on the study of the neural activity patterns of brain areas that are anatomically separated, but functionally related; in other words, the activity of these areas is synchronized (Gusnard et al. 2001; Greicius et al. 2003; Buckner and Vincent, 2007). It is worth mentioning that rs-FC, which measures *signal synchronicity*, differs from other resting-state derived measures such as the amplitude of low frequency fluctuations (ALFF), which measures *signal periodicity*. A number of authors have suggested that rs-FC reflects the prior history of co-activation of brain regions (Miall and Robertson, 2006; Buckner and Vincent, 2007; Dosenbach et al. 2007; Seeley et al. 2007; Fair et al. 2009; Guerra-Carrillo et al. 2014). If rs-FC captures individual life experiences, it can be used as a measure of individual variability on cognitive tasks. The objective of the present functional magnetic resonance imaging (fMRI) study was to investigate whether rs-FC is able to predict individual differences in the visual search capacity.

Visual search is a quite versatile laboratory paradigm that has been used to study the basic aspects of vision, and it involves a wide range of cognitive functions such as attention, memory, or decision making (Nakayama and Martini, 2011). It allows us to study attention control and examine the orientation and selection processes involved in locating and detecting target objects among distractors (Eimer, 2014) – otherwise known as an object recognition task (Nakayama and Martini, 2011). Different fMRI studies have found associations between the variability in rs-FC patterns and better cognitive performance on a variety of visual search tasks. Baldassarre et al. (2012) used a perceptual task and found that an increased rs-FC between dorsal and ventral areas of the visual cortex covaried with better task performance. However, better task performance was also associated with reduced rs-FC between a right dorsal visual region (i.e., V3A–lateral occipital complex) and the left anterior insula, or between a right ventral visual region (i.e., V1–V2) and the right ventral medial prefrontal cortex. On an efficient visual search task where stimuli shape was manipulated (e.g., the target stimuli's shapes were salient

compared to the distractor stimuli's shape), faster response speed was associated with increased rs-FC between: the postcentral gyrus and the different regions of the orbitofrontal cortex (e.g., gyrus rectus, lateral orbital gyrus), the postcentral gyrus and the striatum nucleus, the middle cingulate gyrus and the striatum nucleus, and, lastly, the parahippocampal gyrus and the striatum nucleus (Chou et al. 2013). In addition, there is evidence that the rs-FC between the posterior parietal cortex and the primary visual area is modulated by the response speed during non-efficient visual search controlled by efficient visual search, regardless of whether the stimuli are letters or numbers (Bueichekú et al. 2015).

Associations have also been found between rs-FC and behavioral performance in other domains closely linked to visual search. In the working memory domain, Hampson et al. (2006) examined the brain temporal activity during a working memory task and the rs-FC between the posterior cingulate cortex and the medial frontal gyrus/ventral anterior cingulate cortex. They found that the strength of the connectivity between these two areas was positively correlated with performance on the 3-back task. In another rs-FC study, Sala-Llonch et al. (2012) found that the anti-correlation between the default mode network and the working memory networks (i.e., fronto-parietal or executive networks) was positively correlated with better task performance (e.g., 2-back or 3-back task conditions). In the attention domain, Kelly et al. (2008) studied the relationship between the individual variability in response time and the dorsal attention network or the default mode network. They found that the participants with a more consistent pattern of responses showed a stronger anti-correlation between the dorsal attention network and the default mode network.

Unlike previous research that focused on finding a relationship between rs-FC and behavioral performance on a variety of tasks, the aim of the present research is more specific and less exploratory. Thus, the novelty of our research lies in using a different strategy, and our goals differ from the abovementioned studies. First, we departed from the visual attention model by Petersen and Posner (2012) and the empirical evidence collected in previous research that associated visual search tasks with cortical areas devoted to visual attention (Bueichekú et al. 2016). On goal-directed visual attention cognitive tasks, a relationship has been found between posterior and anterior brain systems. In other words, the orienting system (exerting active control on the attentional focus when orienting to external stimuli) has been related to the activity of the parietal cortex and regions forming an executive system, which included frontal regions and the

anterior cingulate cortex (Petersen and Posner, 2012; Posner and Petersen, 1990). The posterior attention system, the PPC, is in charge of establishing and managing the priority maps for controlling the focus of attention (Fecteau and Munoz, 2006; Serences and Yantis, 2006; Bisley et al., 2011; Ipata et al., 2009; Bisley and Goldberg, 2010; Zelinsky and Bisley, 2015), and the anterior attention system regions, such as the dorsal ACC, influence the PPC in a top-down manner, selecting the relevant stimuli for the task goal (Petersen and Posner, 2012). The dorsal ACC is a superior control center that has been linked to task-set maintenance and cognitive monitoring, and it plays a leading role during the selection process (Dosenbach et al. 2006; et al. 2015; Heilbronner and Hayden 2016). In addition, the processing of visual stimuli generally recruits occipital areas, and strong activity in the primary visual area has been observed throughout the visual search task performance. Second, in order to investigate the individual differences, we selected brain cortical areas that have already been associated with visual attention. In this case, we used previous findings that allowed us to isolate which brain regions are specifically related to the visual search task (Bueichekú et al. 2016). The main idea is to study how the combined activity of these regions could potentially reflect the individual differences observed at the behavioral level (e.g., measures collected during the visual search task performance). Finally, we will try to link the empirical evidence found here with a current hypothesis on the relationship between behavioral measures and spontaneous brain activity.

In light of the growing evidence supporting the existence of spontaneous spatiotemporal activity patterns in the brain and their correlation with behavior measures, but without a supporting theory, the Spontaneous Trait Reactivation (STR) hypothesis was proposed to explain the functional role of the spontaneous fluctuations observed in the brain (Harmelech and Malach, 2013). The STR hypothesis proposes that spontaneous fluctuations reflect a priori individual cognitive biases, which basically refer to individual differences in cognitive aptitudes. One straightforward implication is that, if rs-FC successfully captures these spontaneous fluctuations, it can be used to measure individual differences on cognitive tasks. This hypothesis questions the role of the spontaneous activity observed in the brain during periods of apparent lack of activity (i.e., resting-state). In our case, we will use the visual search task to measure individual behavioral differences in a cognitive ability and investigate the brain-behavior relations between resting-state functional connectivity and this cognitive aptitude.

Prior to the formulation of the STR hypothesis, some authors had already indicated that the functional interdependence between brain areas seems to reflect lifetime learning

experiences (Miall and Robertson, 2006; Buckner and Vincent, 2007; Dosenbach et al. 2007; Seeley et al. 2007; Fair et al. 2009). Specifically, rs-FC networks may reflect common configurations of brain areas that reconfigure to adapt to recent experiences and current tasks (Albert et al. 2009; Shirer et al. 2012; Buckner and Vincent, 2013). Indeed, rs-FC is a good predictor of brain organization during task performance (Smith et al. 2009), but it also offers the advantage of not requiring a task-fMRI session to study individual differences in brain-behavior relations. Moreover, rs-FC could be understood as a biomarker of individual cognitive variability, due to the fact that rs-FC networks are inherent and stable and, thus, reflect inter-individual and group differences (Fox and Raichle, 2007; Shehzad et al. 2009). Therefore, if rs-FC is sensitive to individuals' biases, it should be linked to behavioral outputs, as some investigations have pointed out (Baldassare et al. 2012; Chou et al. 2013; Bueichekú et al. 2015).

With the objective of investigating the relationship between individual differences in visual search and visual attention systems, and based on visual attention models (Petersen and Posner, 2012; Posner 2012), we obtained the seed-based pairwise rs-FC measures in four brain areas: the primary visual cortex, the posterior parietal cortex, the dorsolateral prefrontal cortex, and the dorsal anterior cingulate cortex. Then, we studied the association between pairwise rs-FC and the behavioral measures obtained from visual search task performance. Drawing on previous research, we expected to find a performance facilitation effect; that is, the participants with higher rs-FC between these brain regions would have better accuracy scores and/or faster response speed on a visual search task. The main implication of this investigation lies in supporting the role of spontaneous brain activity fluctuations as a biomarker of cognitive individual variability.

2. Methods

2.1. Participants

Functional MRI data were collected from 42 healthy undergraduate students at the Universitat Jaume I. The sample consisted of 22 females and 20 males with a mean age of 20.79 (SD=1.63) years. All the participants were right-handed (Oldfield, 1971), had normal or corrected-to-normal vision, and reported no neurological or psychiatric history or past or current use of any drugs. All the participants completed the Matrix Reasoning Test (WAIS-III-R) to ensure similar intellectual level throughout the sample (M=21.24 SD=2.16). All the participants provided written informed consent prior to the scanning, and they received monetary compensation for their time and effort. The study was

approved by the Ethics Committee of the Universitat Jaume I and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

2.2. Experimental procedure

2.2.1. Task and stimuli

A letter-based consistent mapping visual search paradigm was adapted to a block design (**Supplementary Figure 1**). The task consisted in one control condition and two visual search conditions. One advantage of using two visual search conditions is to minimize the development of automaticity intra-session due to task repetition.

Task overview. The task consisted of 42 active blocks and 42 passive blocks. The active blocks consisted of: 14 control task blocks, 14 search blocks that corresponded to targets *B C D F G H* and 14 search blocks that corresponded to targets *L M N P Q R*. The distractors were always *J K Ñ S T V W X Y Z*. Each active block started by presenting the instruction display indicating the targets, which remained on the screen for 3000 ms. The active blocks had 12 trials, which consisted of 300 ms of a fixation point, 1500 ms of a search frame, and 200 ms of a blank screen. All the passive blocks consisted of periods of 8000 ms when the screen remained completely blank. During the search conditions, the search frame consisted of the presentation of either six distractors or five distractors and one target, which were arranged circularly around a fixation cross. During the control condition, the search frame where either a six *A-letters* array or a six *X-letters* array. Participants had to give manual responses only with their right hand: target detection was indicated with their right thumb, and target absence with their right forefinger. During the control condition, the six *A-letters* array was a target and the six *X-letters* array was a no-target frame. During task performance, there were no restrictions to eye movement. However, considering the distance between the fixation point and the stimuli (visual angle = 1.32º), eye movements were not strictly needed to perform the task. Participants were asked to answer as quickly as possible, but without compromising accuracy.

Search frames. The search frames consisted of black ink letters on a white background. Each search frame had six stimuli arranged circularly around a fixation point (visual angle: letters = 0.50º; fixation point = 0.24º; distance between letters and fixation point = 1.32º). Targets and distractors were always letters. Thus, search frames were always "within-category searches". There were two sets of target stimuli: *B C D F G H* and *L M N P Q R*. Distractors were always *J K Ñ S T V W X Y Z*. The role of targets and

distractors did not change across tasks (consistent mapping search). Each search frame consisted of the presentation of either six distractors or five distractors and one target. Stimuli locations were randomized in all the conditions. Finally, no stimulus appeared twice in a row in the same location.

Control task. A control task was included in the experimental paradigm to measure a baseline response time and a baseline cerebral response, and it matched the visual array used in the search frames of the visual search conditions. The control task displays consisted of black ink letters on a white background. There were only two types of frames: a six *A-letters* array and a six *X-letters* array. *A's* and *X's* were arranged circularly around a fixation point (visual angle: letters = 0.50º; fixation point = 0.24º; distance between letters and fixation point = 1.32º). *A's* and *X's* were never mixed on the display.

Information display. At the beginning of each block, a display informed participants which task they should perform. The information display presented targets in black ink on a white background in a single centered row (visual angle: letters = 0.50º). There were three different displays: 1) *A,* which indicated that participants would perform the control task; 2) *B C D F G H,* which indicated that they would search for these letters; 3) *L M N P Q R,* which indicated that they would search for these letters.

In-scanner visual search task. The experimental task lasted 25 minutes. The task consisted of 42 active blocks and 42 passive blocks. The active blocks consisted of: 14 control task blocks, 14 search blocks that corresponded to targets *B C D F G H* and 14 search blocks that corresponded to targets *L M N P Q R*. These blocks were counterbalanced throughout the experiment. In all the blocks, fifty per cent of the trials constituted a target-present frame. Each block had 12 trials, which consisted of 300 ms of a fixation point, 1500 ms of a search frame, and 200 ms of a blank screen. Each block started by presenting the information display, which remained on the screen for 3000 ms. All the passive blocks consisted of periods of 8000 ms when the screen remained completely blank.

Practice task before fMRI. For the practice task, an identical laptop was used, with the same display configuration as the one used to present the in-scanner visual search task. The same hardware was used for manual responses with identical settings. Participants received written instructions about how to do the task. The practice task

lasted 7 minutes and consisted of: 4 control task blocks, 2 search blocks that corresponded to targets *B C D F G H*, 2 search blocks that corresponded to targets *L M N P Q R,* and 8 passive blocks (blank screen). Regarding stimulus design, block organization, block timing and information displays, the practice task was identical to the in-scanner task. In the case of the search frames, none of the search templates that appeared during the practice task were used later during the in-scanner task or the training task (i.e., *C T G D B R*, with C in the top center position and the rest of the letters organized circularly and clockwise).

Software. Stimulus presentation was controlled by the E-Prime software (Schneider et al., 2002), professional version 2.0, which was installed in a Hewlett–Packard portable workstation (screen-resolution 800×600, refresh rate of 60 Hz). Participants watched the laptop screen through MRI-compatible goggles (VisuaStim, Resonance Technology, Inc., Northridge, CA, USA), and their responses were collected by MRI compatible response-grips (NordicNeuroLab, Bergen, Norway). Stimulus presentation timing and duration, and participants' accuracy and reaction times (RTs) to each stimulus were saved in the E-Prime's logfile.

2.2.2. Experiment and MRI acquisition procedure

Before the MRI session, participants performed a practice session of the visual search task, which lasted 7 minutes. Participants had to obtain 80% correct responses on the practice task in order to participate in the MRI experiment. All the participants included in this study reached this criterion (percentage of hits: M = 85.75 SD = 4.17 N=42).

The MRI data were acquired in a 1.5 T Siemens Avanto scanner (Erlangen, Germany). All the participants were placed in the scanner in the supine position. Fixation cushions were used to reduce head motion. All the scanner acquisitions were performed in parallel to the anterior commissure-posterior commissure plane (AC-PC), and they covered the entire brain. First, one high-resolution T1-weighted magnetization-prepared rapid gradient echo imaging (MPRAGE) anatomical image was obtained per participant (TR = 2200 ms, TE = 3.8 ms, 256 x 256 x 160 matrix, 1 x 1 x 1 mm in-plane voxel size) and took 10 minutes. Then, a gradient-echo T2*-weighted echo-planar magnetic resonance imaging sequence was used to obtain 270 volumes for the resting-state fMRI acquisition (24 interleaved ascending slices, 3.5 x 3.5 mm in-plane voxel size, slice

thickness 4 mm, interslice gap 0.8 mm, repetition time (TR) = 2000 ms, echo time (TE) = 48 ms, flip angle 90º, 64 x 64 matrix). The resting-state acquisition lasted 9 minutes. Finally, for the task-fMRI, a gradient-echo T2*-weighted echo-planar sequence was used to obtain 602 volumes, recorded in 25 min (29 interleaved ascending slices, 3.5 x 3.5 mm in-plane voxel size, slice thickness 3.6 mm, interslice gap 0.4 mm, TR = 2500 ms, TE = 50 ms, flip angle 90 º, 64 x 64 matrix).

2.2.3. Behavioral analysis

Descriptive analyses were conducted with SPSS (IBM SPSS Statistics software, version 23 Armonk, New York, USA), obtaining the mean, standard deviation, and range (minimum and maximum) of the visual search task performance during fMRI for each participant. The behavioral variables included in the analysis were: the accuracy and RTs of the control condition and the averaged accuracy and averaged RTs of the two visual search conditions. Only correct trial data were used. For subsequent brain-behavior correlation analysis, the control condition was used as a control measure; therefore, the behavioral variables were calculated as a subtraction: *visual search minus control condition*. The normality of the variables was tested using the Shapiro-Wilk test.

2.2.4. Image preprocessing for rs-FC

For the purposes of this study, only the anatomical and resting-state fMRI data were analyzed. Each subject's rs-fMRI data set was aligned with the AC-PC plane by using its own anatomical image (Statistical Parametrical Mapping, SPM 12; Wellcome Department of Imaging Neuroscience, London, England). Then, standard image data pre-processing was carried out with the Data Processing Assistant for Resting-State fMRI (DPARSF v4.1; Chao-Gan and Yu-Feng, 2010). Preprocessing included: (*i*) slice timing (24th slice as reference); (*ii*) two-step procedure realignment; (*iii*) anatomical and functional data co-registration; (*iv*) reduction of nuisance through nuisance co-variate regression (regression of the constant, linear, and quadratic trends); (*v*) head motion correction by using a six-parameter rigid body transformation (regression of three translation and three rotation variables); (*vi*) scrubbing, which consisted of regressing the acquisition's bad time-points with a framewise displacement threshold of 0.2 (Jenkinson et al., 2002) (specific options were: scrubbing time points before bad time = 1; scrubbing time points after bad time=2); (*vii*) regression of the global mean signal, the white matter signal, and the cerebrospinal fluid signal; (*viii*) spatial normalization by using the SPM's

echo-planar image template (voxel size resampling to 3 mm^3) to the Montreal Neurological Institute (MNI) space; (*ix*) spatial smoothing with a 6-mm full-width-at-half-maximum (FWHM) Gaussian kernel; (*x*) and band-pass temporal filtering (0.01 – 0.08 Hz).

2.2.5. Definition of the ROIs

Based on visual attention models (Posner and Petersen, 1990; Petersen and Posner, 2012), we centered the rs-FC in four brain regions within the dorsal stream pathway: the primary visual area (rVisual), right posterior parietal cortex (rPPC), right dorsolateral prefrontal cortex (rDLPFC), and dorsal anterior cingulate cortex (dACC). The coordinates were all peak maxima cortical activations from the task contrast from our previous visual search task fMRI study (see Figure 3, Bueichekú et al., 2016), which studied the brain areas involved in the performance of this task (contrast: *pre-ttraining session: visual search conditions minus control condition*). The definition of the regions of interest (ROIs) was carried out using SPM Wake Forest University PickAtlas software (Maldjian et al., 2003). Four 6-mm radius spheres, or seed regions, were defined as: rVisual MNI: 15 -70 13; rPPC MNI: 27, -64, 46, rDLPFC, MNI: 42, 38, 22 Brodmann area 46; and dACC MNI: 6, 23, 49 (see **Figure 1**). We verified that the region identified as V1 was mainly assigned to the primary visual cortex by using the SPM Anatomy Toolbox ("Overlap between structure and function" toolkit, Eickhoff et al. 2005; Eickhoff et al. 2006; Eickhoff et al. 2007), finding that the probability for V1 = 63% and for V2 = 27%. In addition, task-fMRI data from current sample was analyzed to confirm that the neural correlates involved in the task are valid for the functional connectivity analysis (see "*Task-fMRI pre-processing and post-processing*" details in **Supplementary Materials: Supplementary methods** and **Supplementary Figure 2**).

2.2.6. Pairwise seed base rs-FC analysis

The pairwise rs-FC analysis was conducted with DPARSF Advanced software (Chao-Gan and Yu-Feng, 2010). The DPARSF toolbox extracts the mean time course of all the voxels in each seed region for each session and subject. Then, the toolbox calculates pairwise linear Pearson's correlations, obtaining the *r*-values and *p*-values for each pair of seed regions. Afterwards, individuals' *r*-values were normalized to *z*-values using Fisher's z-transformation. The *z*-values were stored in a SPSS database and used to study brain/behavior relations.

2.2.7. Brain-behavior correlation analysis

To study the relations between rs-FC and behavioral task performance, we used SPSS to conduct Pearson correlation analysis (N=42) between either the visual search task averaged RT values or the accuracy values and the behavioral variables. The Bonferroni correction was applied after the correlation analyses: for an alpha value = 0.05 / 6 tests, the corrected p-value was set as $p < 0.008$. Following this main correlation analysis, different analyses were performed to ensure the quality of our approach. First, a partial correlation analysis was conducted, introducing age and gender as covariates (N=42, degrees of freedom=38), to find out whether the brain-behavior correlation analysis results were explained by age or gender. Second, a Pearson correlation analysis (N=42) was carried out between the Matrix Reasoning Test scores and the behavioral variables to find out whether the cognitive measures were related to the visual search task performance. Finally, we investigated the relationship between the rs-FC z-values and the accuracy scores collected during the practice task that took place before the fMRI scanner acquisition. When necessary, the Bonferroni correction was applied after the correlation analyses: for an alpha value = 0.05 / 6 tests, the corrected p-value was set as $p < 0.008$.

2.2.8. Additional brain functional connectivity analysis

To investigate the relationship between the rs-FC and other resting-state derived measures such as: amplitude of low frequency fluctuations (ALFF), the fractional amplitude of low frequency fluctuations (fALFF), the degree centrality (DC); we used the ALFF, the fALFF and the DC modules within the DPARSF Advanced. For each ROI (rVisual, rPPC, rDLPFC and dACC) and for each individual we extracted the normalized values for ALFF, fALFF or DC. We then used SPSS software to conduct bivariate Pearson's correlation analysis (N=42) between: (1) the ALFF and rs-FC z-values where the Bonferroni correction was set as $p<0.0021$ (alpha value = 0.05 / 24 tests); (2) ALFF, fALFF or DC z-values and the behavioral measures where the Bonferroni correction was set as $p<0.0125$ (alpha value = 0.05 /4 tests).

In addition, the relationship between the rs-FC and task-fMRI data was investigated. In this case, task-fMRI data was processed using SPM 12 (Wellcome Department of Imaging Neuroscience, London, England) (see Supplementary Materials for details on pre-processing and post-processing). After pre-processing and individual data post-

processing, a whole-brain one-sample t-test with the individuals' contrast images was conducted at the group level. We then used the SPM 12 eigenvariate method, which extracts mean value of the time series for each ROI (rVisual, rPPC, rDLPFC and dACC) and for each individual. Then, we conducted bivariate Pearson's correlation coefficient analysis between the task activity values and the pairwise rs-FC z-values. The Bonferroni correction was applied after the correlation analysis: for an alpha value = 0.05 / 24 tests, the corrected p-value was set as $p<0.0021$.

3. Results

The results of the descriptive analysis conducted with the accuracy and RTs of the behavioral variables appear in **Table 1**.

The means and standard deviations of the pairwise rs-FC measures appear in **Table 2** (above the diagonal). The table shows that the range measures (minimum and maximum) reveal a great degree of individual variability in the rs-FC measures in all the pairs of seed regions.

The results of the correlation analysis between the rs-FC *z*-values of each pair of seed regions and the RT values (i.e., *visual search minus control task*) appear in **Table 2** (below the diagonal). A statistically significant correlation was found between the response speed and the connectivity between rPPC and dACC ($r =$-.532, $p<.001$, N=42, Bonferroni corrected), indicating that the higher the connectivity, the faster the task performance (see **Figure 2**). When graphically representing the correlation, we observed that one participant had very low connectivity values in comparison with the other participants. Because this person could be an outlier, we again conducted the correlation analysis, excluding this participant's data, and we found similar results ($r = -.501$, $p=.001$, N=41, Bonferroni corrected). No other statistically significant correlations were found after the Bonferroni correction was applied.

The results of the correlation analysis between the rs-FC *z*-values of each pair of seed regions and the accuracy values (i.e., *visual search minus control task*) appear in **Supplementary Table 1**. No statistically significant correlations were found.

The results of the partial correlation analysis between the rs-FC z-values of each pair of seed regions and the RT values appear in **Supplementary Table 2**, and for the accuracy values, see **Supplementary Table 3**. As these results show, the participants'

age and gender had little influence in controlling for the relationship between the brain and behavior variables. The results of the bivariate Pearson's correlation coefficient analysis between the individual Matrix Reasoning Test scores and the accuracy scores or the RT values did not reveal any statistically significant results (Accuracy: r-value=0.131, p-value=0.410 N=42; RTs: r-value=-0.039, p-value=0.805 N=42).

Additional analyses were carried out to further investigate the relationship between individual differences in visual search task and resting-state. Specifically, it was studied ALFF, fALFF and DC. When studying the relationship between ALFF and rs-FC, a statistically significant correlation was found between rPPC-rDLPFC (rs-FC) and rPPC (ALFF): r-value=0.499, p-value=0.001 (Bonferroni corrected) (**Supplementary Table 4**). No other correlations survived the Bonferroni correction. On the other hand, no statistically significant correlations were found between ALFF, fALFF or DC and the behavioral data acquired during the task (**Supplementary Tables, 5, 6** and **7**) or between the rs-FC and the behavioral data acquired during the practice task (**Supplementary Table 8**).

Finally, we also studied the relationship between the time series for each ROI (during task-fMRI) and pairwise rs-FC. In this analysis, no correlations survived the Bonferroni correction (**Supplementary Table 9**).

4. Discussion

In the present study, rs-FC data were collected before the participants completed a visual search task in the fMRI scanner, with the aim of testing the association between rs-FC values and individual behavioral differences in visual search task performance. We expected higher connectivity between brain areas involved in visual attention control in participants who performed better on the task. This hypothesis was confirmed for one pair, rPPC and dACC, which showed more synchronized activity in the participants who performed the task faster. This result supports the general hypothesis that rs-FC could reflect the prior history of co-activation of brain regions. In other words, areas that co-work show enhanced connectivity (e.g., Miall and Robertson, 2006; Buckner and Vincent, 2007; Fair et al., 2009), thus supporting the STR hypothesis (Harmelech and Malach, 2013). Our main conclusion is that rs-FC is a valuable tool as a biomarker of individual differences in performance on cognitive tasks such as the visual search task.

Before focusing the discussion on the implications of the main results of our research, it is worth discussing the general rs-FC results found here. The mean FC values indicate that brain regions commonly involved in the visual search task were related to each other (e.g. rDLPFC-PPC (*i.e.,* M=0.20) and rDLPFC-dACC (*i.e.,* M=0.43), which means that they usually work synchronously on several cognitive tasks, including visual attention tasks. The rDLPFC has been related to top-down executive attentional control (Dosenbach, 2008; Petersen and Posner, 2012), and so it could be a key region for studying the behavioral differences in the performance on the visual search task. However, to determine whether rs-FC reflects the individual differences on a specific task, it is necessary to assess how rs-FC is modulated by the differences in performance; therefore, the brain-behavior relations have to be studied. Although these two pairs involving the rDLPFC had the strongest mean rs-FC values, they were not influenced by behavioral performance (no statistically significant brain-behavior correlations were found for these pairs). On the other hand, the connection between the posterior and the anterior visual attention systems – established between PPC-dACC –, albeit displaying the weakest mean rs-FC value (*i.e.*, M=0.06), is actually the connection most influenced by the individuals' performance, showing the strongest brain-behavior relation (*i.e., r =*-.532, *p*<.001, N=42, Bonferroni corrected). This means that rs-FC is sensitive to individualities: individuals with the strongest rs-FC between PPC-dACC had better performance (with the shortest RTs preserving good accuracy), and, conversely, individuals with the weakest FC had poorer performance. Even more importantly for understanding individual differences in cognitive tasks and how rs-FC is a valuable tool for this purpose, we had to evaluate not only the synchronicity between the regions, but also when the relations between them are sensitive to the individual's performance.

The STR hypothesis proposes that the spontaneous fluctuations observed in the brain at rest reflect a priori individual cognitive biases. The specific predictions of this hypothesis are: first, that spontaneous fluctuations are the result of daily life experiences (i.e., *average training of cortical networks throughout daily life*); second, that individual differences during the performance of cognitive tasks are captured by spontaneous fluctuations; and third, that it should be possible to modify the pattern of spontaneous fluctuations with cognitive training because prior training (i.e., life experiences) shaped these rs-FC patterns (Harmelech and Malach, 2013). In this investigation, visual search was used as an example of a goal-directed task because individuals can use different

approaches to cognitively process and manage information, and so this paradigm makes it possible to investigate connectivity modulations through behavioral performance. Visual search is a commonly used, everyday human ability (Eckstein, 2011), and differences in performance are expected among individuals (Vogel and Awh, 2008; Kanai and Rees, 2011). Indeed, its performance can be improved through training (Kelly and Garavan, 2005; Kübler et al. 2006; Bueichekú et al. 2016), and changes at the behavioral level can be accompanied by brain changes, such as decreased activation in specific and task-related areas and increased connectivity in local and large-scale attention and control networks (Bueichekú et al. 2016; Bueichekú et al. 2018). In the present study, high individual variability was found in the response speed during visual search, as well as in the rs-FC values obtained prior to task performance. Moreover, a strong correlation was found between the rs-FC of rPPC and dACC and the response speed: the more synchronized the activity between these two brain regions, the faster the response speed of the participants. These findings essentially support the STR hypothesis.

The STR hypothesis agrees with previous authors who pointed out that rs-FC reflects lifetime learning experiences (Miall and Robertson, 2006; Buckner and Vincent, 2007; Dosenbach et al. 2007; Seeley et al. 2007; Fair et al. 2009). Indeed, Buckner et al. (2013) highlighted that rs-FC is not only a reflection of the functional organization of the brain areas recruited and used during task execution (Deco and Corbetta, 2011), but it is also a brain state defined by both anatomical connectivity constraints and dynamic properties motivated by task states. Moreover, there seems to be good correspondence between resting and task-related connectivity patterns (Smith et al. 2009). One of the main advantages of rs-FC is its sensitivity to coupling dynamics, which allows us to study the relations between areas and networks (Buckner et al. 2013) without the need for a task-scan, which can be difficult to obtain in certain populations. The usefulness of rs-FC lies in the possibility of generating hypotheses about brain functioning (Buckner et al. 2013), for instance, in relation to brain/behavior correlations. In this regard, several years ago, Fox and Raichle (2007) remarked that spontaneous fluctuations are stable across brain states, but capture inter-individual variability, because they arise from the variability in task performance and brain activation during task performance. This means that spontaneous fluctuations are a result of learning through life experiences, where doing a task over and over gives shape to the functional relations between brain areas.

The specific role of spontaneous fluctuations has been and continues to be a matter of debate (Fox and Raichle, 2007; Buckner et al. 2013; Harmelech and Malach, 2013). Among the different positions, it has been proposed that connectivity patterns could be structures for organizing brain activity because more activity coherence is found between areas that co-work (Salinas and Sejnowski, 2001; Buzsáki and Draguhn, 2004). Another possibility is that the brain functional connectivity systems could be preparation schemas for current or future cognitive requirements; thus, these systems continuously predict, sustain, and adjust (Raichle, 2011). In this study, the fact that the connectivity between rPPC and dACC strongly correlated with response speed during visual search shows that rs-FC could be indicating adaptation to the dynamics of the task and its demands in areas that usually co-work during this task (Kastner and Ungerleider, 2000; Posner and Petersen, 1990; Petersen and Posner, 2012). It should be kept in mind that participants performed a practice task outside the scanner before the fMRI session, and that participants knew that they would have to complete a visual search task after the anatomical and resting-state scans. Therefore, the brain could have entered "a preparation mode" state, even though the participants were instructed to remain calm and not think about anything in particular.

Both PPC and dACC are key regions in visual search (Fecteau and Munoz, 2006; Serences and Yantis, 2006; Ipata et al., 2009; Bisley and Goldberg, 2010; Zelinsky and Bisley, 2015; Posner and Petersen, 1990; Posner 2012; Petersen and Posner, 2012), and because they co-work during the search, it is likely that their connectivity provides some information about individual differences in the search. In fact, some fMRI studies have found that the PPC and dACC share roles (Egner et al. 2008), and other studies have found that functional connectivity between these areas is mediated by behavioral performance (Prado et al. 2011). Egner et al. (2008) used a cued visual search task in which the spatial or feature-based information about the next target was parametrically modulated. The authors found that, before each search, the brain representations of spatial and feature-based information highly overlapped and were located in intraparietal sulcus, frontal eye field, anterior insula / ventrolateral prefrontal cortex, and dACC / pre-supplementary motor areas. Prado et al. (2011) used a selective attention control task where the participants had to manually detect visual letters as quickly as possible without compromising their accuracy, while ignoring the presentation of irrelevant auditory letters. The results showed that slower participants (i.e., long response speed values) had

reduced connectivity between dACC and right DLPFC or bilateral PPC. Our findings are consistent with these investigations because we found that increased connectivity between dACC and rPPC is associated with accurate and fast performance (i.e., short response speed values). In general, these results seem to support the STR hypothesis, and rs-FC could be a biomarker of individual variability, not only on a visual search task, but also on other goal-directed tasks with similar visual attention selection components.

On visual attention tasks, representations of the visual world are combined in *priority maps* where the combination of bottom-up information (i.e., sensory information or the features of the stimuli) and top-down information (i.e., cognitive information or the identity of the stimuli) occurs in order to complete the processing of the visual scene or perform a specific goal-directed task (Bisley, 2011). It has been proposed that priority maps are located in cortical association areas such as the PPC – and also the frontal eye field or the DLPFC – (Fecteau and Munoz, 2006; Serences and Yantis, 2006; Bisley et al., 2011; Ipata et al., 2009; Bisley and Goldberg, 2010; Zelinsky and Bisley, 2015). During visual search, the main function of the PPC priority maps is to direct the focus of attention, based on priority signals originating in both bottom-up and top-down information and other sources (Zelinsky and Bisley, 2015), in order to eventually complete the selective attention process (Fecteau and Munoz, 2006). On the other hand, dACC has been associated with top-down executive control because it has been found to be active during goal-directed tasks that require cognitive control (Ridderinkhof et al., 2004; Nee et al., 2007; Shackman et al., 2011; Niendam et al., 2012; Cieslik et al., 2015), and it has been linked to conflict and reward monitoring, motor control, cognitive adaptation, and learning (Heilbronner and Hayden, 2016). Indeed, dACC activity has been linked to supporting executive control functions, such as task-set maintenance or monitoring, during a wide variety of control-demanding tasks, including the visual search task (Dosenbach et al., 2006). Accordingly, theories about the functioning of the attention system link the PPC and dACC to the orienting and executive systems (Petersen and Posner, 2012; Posner 2012). The orienting system is devoted to attention shifts to external stimuli. The PPC and frontal eye field belong to the dorsal attention system, which controls overt attention shifts (Petersen and Posner, 2012). Research focused on stimulus-driven visuo-spatial attention supports the proposal that the activity of the dorsal attention system (e.g., PPC) is predicted by the strength of external stimuli (e.g., complex visual and auditory events) and modified by the continuous variation in the salient stimulus

within the environment (Nardo et al. 2011; Nardo et al. 2014). The executive system is related to the task control system, which operates in a top-down manner, and it is supported by lateral frontal and parietal regions and by the dACC and anterior insular regions (Petersen and Posner, 2012). One hypothesis is that dACC and DLPFC have different roles within top-down task control; whereas dACC is devoted to performance monitoring, the DLPFC is related to implementing control per se (Dosenbach, 2008; Petersen and Posner, 2012). Recently, dACC has been proposed as a core region that monitors several variables, serves as a buffer that stores relevant information about the task, and produces signals to control action (Heilbronner and Hayden, 2016).

Keeping in mind the main result found in this study, rs-FC could contribute more empirical evidence to theoretical visual attention models, integrating rather than segregating the role of multifaceted areas such as dACC into models focused on fronto-parietal networks as top-down sources of attentional control (Deco and Rolls, 2005; Petersen and Posner, 2012). For example, Egner et al. (2008) found that the PPC, dACC, and prefrontal cortex are devoted to the integration of spatial and feature-based information before each search, and so these areas are involved in different kinds of visual search tasks. Womelsdorf and Everling (2015) propose an integrative model of attention selection that includes six separate, but interrelated, components of attention subdivided into two processes. The first process controls and guides stimulus selection, and the second process implements it. The areas that aid in target selection processes are, for example, the DLPFC, dACC, and different subcortical areas (i.e., endogenous control sources or top-down influence), and the areas that implement target selection are those that hold the priority maps, such as the PPC, the frontal eye field, or the superior colliculus, which are linked to sensory cortices. Therefore, future studies on rs-FC could contribute more empirical evidence to integrative models of attention.

The main limitation of our study is the use of a reduced set of regions of interest for investigating the relationship between individual differences in visual search and the variability of rs-FC. It is always a challenge in seed-based rs-FC research to find the equilibrium in the fair representation of the relevant brain regions when studying the brain function. Furthermore, the use of different analysis methods (FC, ALFF, fALFF, DC) and different parameters within those methods for analyzing the fMRI BOLD signal offer complex and different descriptions about how the brain functions. In this case, FC helped us to understand more brain-behavior relationships, but ALFF, fALFF and DC did not

contribute more empirical evidence. Regarding the methods, another controversial topic is the use of global signal regression (GSR): because global signal is composed of neural and non-neural signals, similar or different results can be obtained after GSR. The fact that the statistical results obtained after GSR are dissimilar does not mean these results are not valid (e.g., it cannot be assured that the signal is artefactual) (Murphy and Fox, 2017). There is recent research that still supports GSR use (Power et al. 2016; Burgess et al. 2016; Satterhwaite et al. 2013). GSR removes the shared variance between the global signal (*e.g.*, motion, cardiac and respiratory cycles, arterial CO_2 concentration, blood pressure, etc.) and the time course of each individual voxel. Without GSR the distribution of FC is positively skewed, after GSR the distribution of FC values is within a range of positive and negative values. Future research may improve the approach used in this research taking into account these limitations.

5. Conclusions

In agreement with previous authors, the present study found that rs-FC is a powerful tool to generate and test hypotheses about brain functioning because it captures the relationships between functionally-related brain areas at rest and makes it possible to describe brain/behavior relations by studying inter-individual differences in task performance. We found that rs-FC was associated with individual differences in visual search; specifically, higher connectivity between rPPC and dACC was strongly correlated with a faster response speed during the search. This result favors the existence of brain-behavior relationships that allow us to describe individual differences in cognitive tasks. In the long run, descriptions of brain-behavior relationships could provide empirical evidence to the STR hypothesis: functional connectivity is able to capture lifetime learning experiences, including the cognitive abilities.

6. Ethical standards

All procedures performed in the present research, which involved human participants, were in accordance with the ethical standards of the institutional Review Board of the Universitat Jaume I and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

7. Conflicts of interest

The authors declare that they have no conflicts of interest.

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9. Tables

Table 1 Descriptive analysis results. A summary of the mean (M), standard deviation (SD), and range (min: minimum, max: maximum) values for the accuracy measures (maximum score = 12) and reaction time measures (RTs in milliseconds) of the control condition and the averaged visual search task conditions is presented. In addition, the descriptive measures of the *visual search minus control condition* variable are included, along with the results of the normality test for this variable

	Control condition	Visual search conditions	Visual search minus Control	Shapiro-Wilk test
Accuracy	M =11.98 SD =0.15 Min =11 Max =12	M=10.85 SD =0.47 Min =10 Max =12	M = -1.1 SD = 0.45 Min = -2 Max = 0	W=.91 gl=42 *p*=.002
RTs	M =424.81 SD =67.04 Min = 310 Max =596	M=886.86 SD =107.76 Min = 671.5 Max =1100	M = 462.05 SD = 84.38 Min = 311.5 Max = 641.5	W=.97 gl=42 *p*=.200

Table 2 Results of the rs-FC and response speed correlation analyses. A statistically significant correlation was found between the response speed and the rs-FC between rPPC and dACC, indicating that faster participants had enhanced connectivity between these regions. Above the diagonal: means (M), standard deviation (SD), and range (min: minimum, max: maximum) values of the pairwise rs-FC measures. Below the diagonal: Pearson correlation analysis results expressed in *r*-values (*r*) with their *p*-values (*p*). The correlation analysis (N=42) was performed between the pairwise rs-FC *z*-values and the visual search task RTs, controlled by the control condition RTs (i.e., *visual search conditions reaction times minus control condition reaction times*). Bonferroni correction was applied. * $p < .05$, uncorrected; ** $p < .008$, corrected for multiple comparisons. Abbreviations: rVisual = right primary visual area; rPPC = right posterior parietal cortex; rDLPFC = right dorsolateral prefrontal cortex; dACC = dorsal anterior cingulate cortex

	rVisual	rPPC	rDLPFC	dACC
rVisual	-	M =.055 SD = .19 Min = -.39 Max = .42	M =-.06 SD =.14 Min = -.37 Max = .25	M =-.10 SD =.15 Min = -.42 Max = .35
rPPC	r = .160 p = .311	-	M =.20 SD =.23 Min = -.28 Max = .72	M =.06 SD =.24 Min = -.53 Max = .55
rDLPFC	r = -.317 * p =.041	r = -.300 p =.054	-	M =.43 SD =.19 Min = .09 Max = .93
dACC	r = -.060 p =.704	r = -.532 ** p < .001	r = -.081 p =.610	-

10. Figure captions

Fig. 1 Brain regions used as seed regions in pairwise rs-FC analysis. Abbreviations: rVisual = right V1; rPPC = right posterior parietal cortex; rDLPFC = right dorsolateral prefrontal cortex; dACC = dorsal anterior cingulate cortex
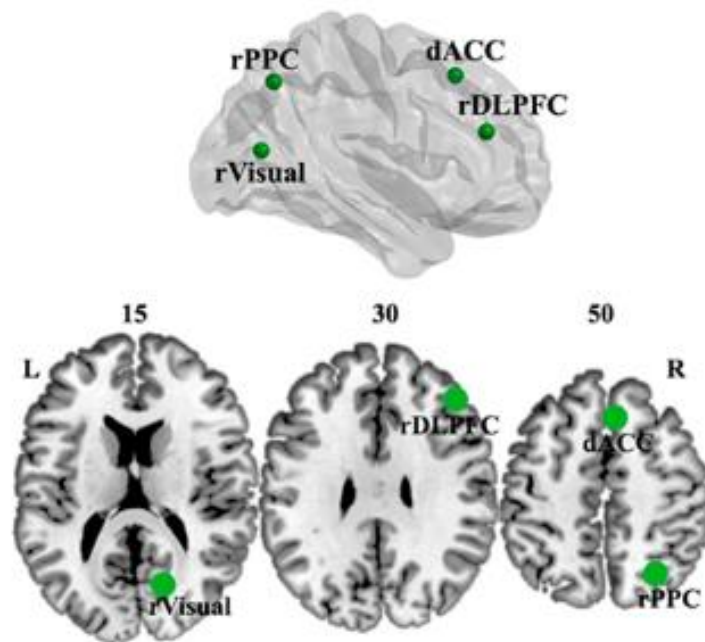
Fig. 2 Pairwise rs-FC between rPPC and dACC are associated with task performance. A statistically significant correlation was found between the visual search performance and the rs-FC between rPPC and dACC, indicating that the fastest participants had enhanced connectivity between these regions ($r = -.532$ ** $p < .001$ N=42). This suggests that participants with higher connectivity between PPC and dACC will perform better on tasks that require fast information processing, searching, target detection, and task adaptation.