The Time Varying Networks of the Interoceptive Attention and Rest

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Abstract

Focused attention to spontaneous sensations is a phenomenon that demands interoceptive abilities and a dynamic character of attentive processes. The lack of its control has been linked to neuropsychiatric disorders, such as illness-anxiety disorder. Regulatory strategies, like focused attention meditation, may enhance the ability to control attention particularly to body sensations, which can be reflected on functional neuroanatomy. Adopting a systems-level approach, we aimed at estimating the recurring fMRI functional connectivity (FC) patterns between regions of the dorsal attention network, default mode network, and frontoparietal network during 20 minutes of an attentional task to spontaneous sensations, and during rest before and after the task, in fifteen experienced meditators. Dynamic functional connectivity analysis was performed using sliding windows and k-means clustering. On the rest data, we observed three FC patterns. The task data were associated to five FC patterns, three of them presenting the rest patterns characteristics. The time spent in the rest states varied depending on whether the subjects had or not performed the task. We conclude that interoception performance does not suppress the FC found at rest. Rather, is associated to a more diverse FC organization in time, probably to achieve the task-cognitive demands. The impact of task performance over the subsequent rest period suggests an underlying mechanism probably involved in the learning process linked to cognitive training.

Keywords: Attention, Interoception, Networks, Dynamic, Functional connectivity

Introduction

In our everyday life, numerous stimuli surround us, requiring their selection and processing through attention (Posner, 2012). Once a stimulus is attended, it will be more likely for it to influence the brain systems and to guide our behavior (Dehaene & Changeux, 2005; Webb & Graziano, 2015). Attention also exerts an important modulation of the body representation in the somantosensory cortex. It is associated with the facilitation of the conscious perception of the external stimuli and also can increase or decrease the perception of spontaneous sensations occurring without any external stimulus (Boly et al., 2007; Michael & Naveteur, 2011). Spontaneous sensations are closely related to interoception, the sensing of the body's physiological condition, essential for body awareness (Michael, Naveteur, Dupuy, & Jacquot, 2015).

As a property of multiple cognitive processes (Bartolomeo & Chokron, 2000; Golomb & Turk-Browne, 2010), the lack of regulation in the control of attention is linked to different psychiatric disorders (Donald, Abbott, & Smith, 2014; White & Shah, 2006), like panic disorder, somatization and illness anxiety disorders which are distinguished by an excessive attention and increased concern in body sensations (Stern et al., 2017; Stins, Kempe, Hagenaars, Beek, & Roelofs, 2015). Regulatory strategies, like focused attention meditation (FAM) practices, considered a form of cognitive training (Tang, Hölzel, & Posner, 2015), may enhance the ability to control the attention particularly to body sensations, producing an improvement in the attentional skills. FAM requires to focus the attention to an object and bring the attention back to the object when it is lost (Manna et al., 2010), resulting in a better identification of the attention/inattention states (K. Fox et al., 2016; Lutz, Slagter, Dunne, & Davidson, 2008). A meditation practice involving focus attention is Vipassana meditation, characterized by focusing the attention on present-moment sensory awareness. This practice laid the basis for the foundation of mindfulness meditation techniques which has been used in the clinical setting (Cahn & Polich, 2009; Goyal et al., 2014). Evidence suggests that such control of attention leads to changes in the functional neuroanatomical organization measured by modulations in functional connectivity (FC) (Hasenkamp & Barsalou, 2012; Kilpatrick et al., 2011; Rabipour & Raz, 2012). FC is an estimation of the communication across distant brain regions, which results in the integration of information (Friston, Frith, Liddle, & Frackowiak, 1993; van den Heuvel & Hulshoff Pol, 2010), a fundamental principle for cognitive processes. Various FC systems have been linked to attention tasks and FAM, primarily the frontoparietal network (FPN), the dorsal attention network (DAN) and the default mode network (DMN) (Corbetta & Shulman, 2002; Raz, 2004; Vossel, Geng, & Fink, 2014). Focusing the attention to spontaneous sensations is also associated with changes in the functional connectivity of regions related to these three networks, according to previous studies (Bauer, Díaz, Concha, & Barrios, 2014; Hasenkamp & Barsalou, 2012; Kilpatrick et al., 2011). However, most of these fMRI studies have implicitly considered FC as stationary, i.e. representing an average of the FC from the scanning session (Hutchison et al., 2013; Preti, Bolton, & Van De Ville, 2017), therefore, ignoring the dynamic character of attention and FAM (Fell, Axmacher, & Haupt, 2010; Hairston, Jung, Ko, Komarov, & Lin, 2017).

We here aimed at quantifying the dynamic variations of FC during rest and during a spontaneous sensations attention task of 20 minutes in experienced meditators. The decision to include experienced meditators in FAM was given to evidence showing that the expertise in this practice is related to improved ability to control and sustain the attentional processes, features that could facilitate the required attentional stability of the subjects for the performance of our task (Lutz et al., 2008; Raffone & Srinivasan, 2010). This allowed us to describe the characteristic patterns of FC associated to the dynamic attention process and interoception, as well as the determination of differences between these patterns with the resting state patterns. We hypothesize that differences between the FC patterns of rest and task will be found, with the task patterns showing a high connectivity in networks usually associated to attention, as the DAN and FPN. On the other hand, we proposed that in the rest patterns we will find a higher connectivity in regions from the DMN, which is usually associated to undirected cognition.

Methods

Subjects

We included meditation practitioners in Vipassana meditation. All participants were evaluated for exclusion criteria: fMRI contraindications, history of psychiatric or neurological disorder, or medical illness. Subjects answered digital versions of the Symptom Checklist 90 and Edinburgh Inventory to exclude psychiatric symptoms and to evaluate handedness respectively. All participants signed an informed consent from the experiment in accordance with the Declaration of Helsinki and approved by the Bioethics Committee of the Neurobiology Institute (Comité de Bioética del Instituto de Neurobiología, Universidad Nacional Autónoma de México).

Experimental design

Functional images where acquired in one session per subject. The session started with 10 minutes of resting state fMRI Pre-task (rs pre-task), followed by 20 minutes of the attention task fMRI and finally, 10 minutes of resting state fMRI Post-task (rs post-task).

The attention task is a focus attention meditation technique, which consisted of focusing the attention to spontaneous sensations (e.g. numbness, pulsation, tingling, warming, cooling, itching, tickle, vibration, flutter, skin stretch, stiffness, etc.) in five specific anatomical regions: nostrils, right thumb, left thumb, right great toe, left great toe, always in the same order, cyclically and counterbalanced. Once participants started to feel a spontaneous sensation (i.e. pulsation) in the respective region, they were asked to sharpen focus more and more until they had a clear, distinct and uninterrupted sensation. When this level of felt sensation was reached, they were instructed to sustain it for about 3-5 seconds and then press a button (Nordic Neurolab MR compatible button system). This button press signaled both the end of clear and distinct focus of felt sensation and shift of attention to the next anatomical region *(Fig. 1)*. This was repeated at the participants own pace throughout the scan until the end. During the MRI session the subjects laid supine and remained relaxed with their eyes closed and avoided any motion. The time and the quantity of the responses were registered.

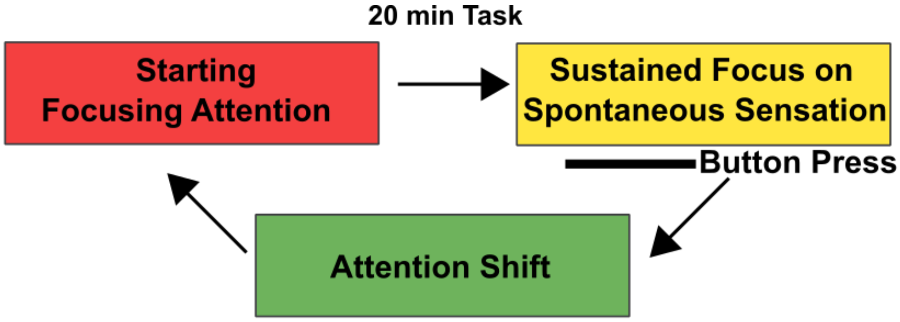

Figure 1.-The task consisted in focusing attention to spontaneous sensations starting in the nostrils. Once a clear spontaneous sensation was felt, subjects sustained the focus on it for 3-5 seconds. Then, pressed a button to signal the shift of attention to the next target.

MRI acquisition

Images were obtained using a 3.0T GE Discovery MR750 scanner (General Electric, Waukesha, WI) with a 32 channel head coil. We acquired three fMRI scans during one session per subject; A resting state scan before the task (rs pre-task), then, the task scan and finally a rest scan after the task (rs post-task). The attention task scan was obtained using a T2* EPI pulse sequence of 20 minutes, with TR/TE= 1500ms/27ms, 64x64 matrix, spatial resolution 4x4x4 mm3, 35 slices/volume, obtaining 804 volumes. The resting state fMRI scans consisted in an EPI pulse sequence of 10 minutes in duration each one, with TR/TE= 2000 ms/40ms, obtaining 300 volumes in the rs pre-task and 300 volumes in the rs post-task. During rest, subjects were asked to remain awake and with their eyes closed. After the fMRI acquisition a high resolution 3D T1 SPGR structural sequence was acquired (voxel size of 1x1x1 mm3, 256x256 matrix, TR/TE= 8.156 ms/3.18 ms).

Preprocessing

The functional images including the task fMRI and the rsfMRI pre and post task, were preprocessed using FSL (Smith et al., 2004) and for this the structural images were required. The steps for this preprocessing were: Extraction and discarding of skull and other non-brain tissue from the structural and functional image using BET of FSL (Smith, 2002) and reorientation. Slice timing correction, motion correction using MCFLIRT tool (Jenkinson, Bannister, Brady, & Smith, 2002), linear corregistration with FLIRT tool and nonlinear with FNIRT to the MNI152 standard space, segmentation of white matter and cerebrospinal fluid, regression of the signal from CSF, white matter and motion, artefact extraction with aCompCor, band-pass filtering of 0.01-0.08 Hz. We did not perform the global signal regression since previous studies suggest that this may lead to false anticorrelations.

ROI Selection

According to the literature, focused attention is associated with changes in functional connectivity in the DAN, DMN and FPN regions, therefore, for the analysis we decided to include the regions of these three networks. In order to obtain the ROI masks of these three networks for each subject, we made an independent analysis, using the rs pre-task and the Functional Connectivity Toolbox (CONN) v.16.b (Whitfield-Gabrieli & Nieto-Castanon, 2012). First, these images where preprocessed using a default preprocessing in CONN; this included motion correction, slice timing correction, segmentation, corregistration, artefact detection, regression and spatial smoothing of 6 mm. Then, this preprocessed data was used to perform a first level fMRI connectivity analysis in each subject. For this connectivity analysis we used 4mm spheres, created with SPM in MATLAB, centered for the DMN, DAN and Executive control network (ECN) regions according to the coordinates of Raichle (Raichle, 2011). We obtained a pFDR map for each of these three networks in each subject. Then, to eliminate voxels out of these regions of interest that could have survived to the threshold, we used FSLmaths to multiply these maps with the regions of interest that CONN uses for its connectivity analysis of those networks. After this, we observed in the results, that in some of the subjects the DAN mask did not contain one of the frontal eye fields since there were no significant voxels in these regions. Therefore, to homogenize the DAN maps in the group, the DAN ROI masks of each subject only contained 2 regions, left and right intraparietal sulcus. Finally, we obtained 10 ROIS belonging to the three networks, that were combined in one map for each subject. These were the left and right intraparietal sulcus, the medial prefrontal cortex (MPFC), posterior cingulate cortex (PCC), left and right lateral parietal cortex (LPl, LPr), the left and right lateral prefrontal cortex (LPFCl and LPFCr), and the left and right posterior parietal cortex (pPCl, pPCr) *(Fig. 2)*.

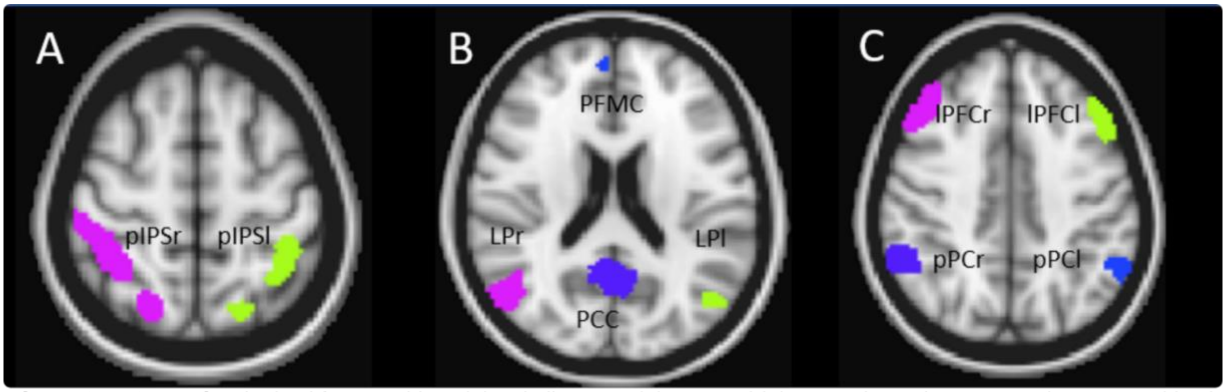

Figure 2.- ROI masks obtained from a subject. (A) Including DAN, (B) DMN and (C) FPN regions. The 3 ROI masks were combined into a single ROI mask containing the 10 ROIS which was used for the DFC analysis of this subject.

Dynamic functional connectivity analysis

Sliding windows is a strategy applied to explore the time dynamic nature of the FC and in conjunction with a clustering approach such as k-means, allows to identify patterns of FC that may reoccur in time across subjects, defined as dynamic FC states (DFCS) (Chang & Glover, 2010; Damaraju et al., 2014).

Applying a similar approach of previous studies (Damaraju et al., 2014; Mooneyham et al., 2017), we used sliding windows in order to determine the time varying functional connectivity (Sakoğlu et al., 2010) between the ROIs and then, to determine the average reoccurring connectivity patterns, defined as dynamic functional connectivity states (DFCS), we used the k-Means algorithm for clustering (Allen et al., 2014; Chang & Glover, 2010). For the analysis we used FSL tools, R software (3.4 version) (R Foundation for Statistical Computing., 2016) and different packages in this software. We decided to apply the approach separately for the task data and for the rest data, this to be able to find the task and rest characteristic states *(Fig. 3).*

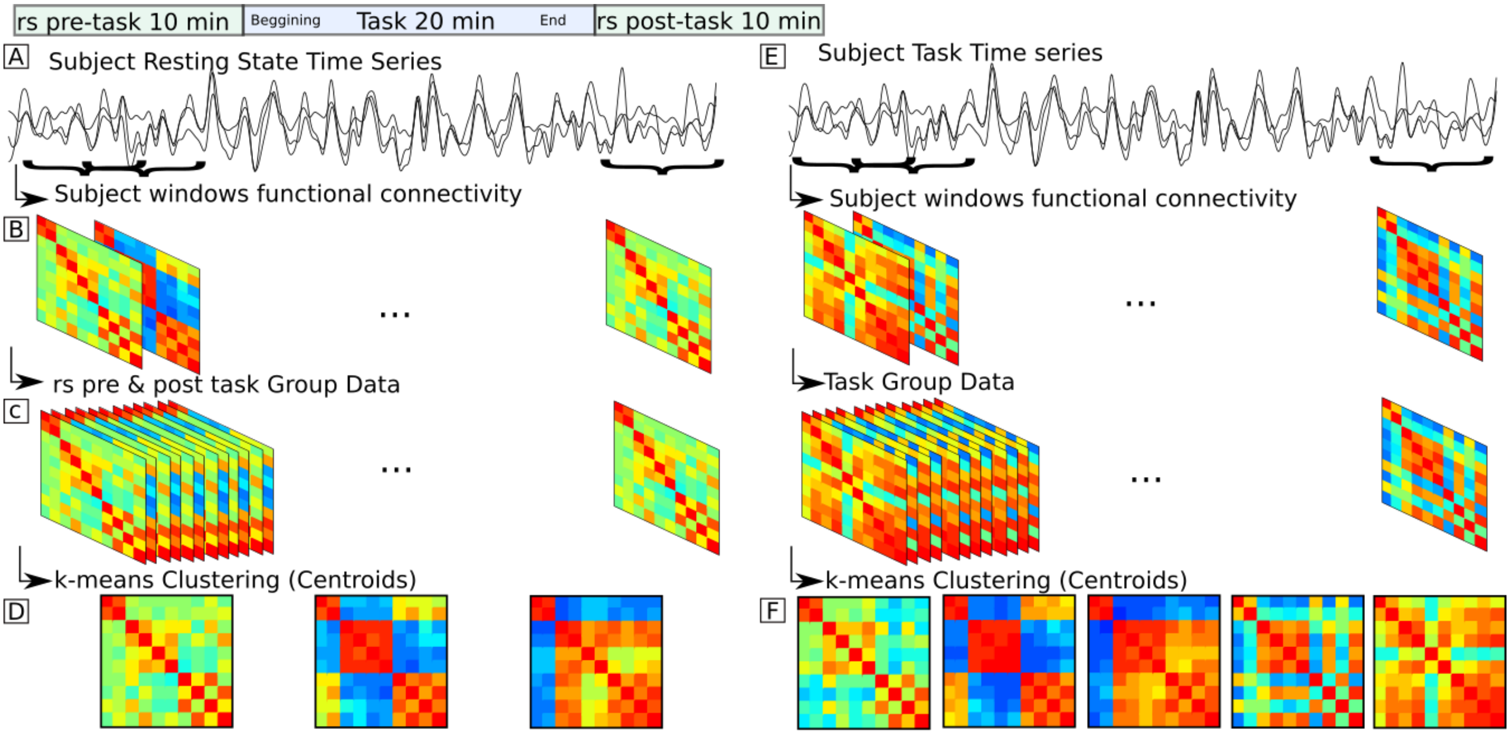

Figure 3.- DFC Analysis.- (A)The time courses at rs pre-task and rs post-task, where used for the siliding widows analysis (B) In each 30s window was calculated the FC for the 10 ROIS. (C) All the rs data were joined into a group data set. (D) The cluster solution of 3 was applied and k-means clustering was used to obtain the centroid for each cluster. (E)Separately the same process was used for the 20min task data.(F)Obtaining 5 centroids after the clustering.

Sliding windows and clustering approach

For the task data we established windows of 30s width (20 TRs) and steps of 15 s (10TR), which resulted in 79 windows per subject, representing the 20 minutes of the task scan. For the group task data, we obtained 1185 windows. In each window we estimated the functional connectivity between the ten regions of the three networks, calculating the Pearson's R for each pair of ROIs and then transformed it to z values, obtaining a 10x10 matrix of connectivity for each window, this means 1185 matrices of task connectivity for the group.

For the rest data, we also stablished windows of 30 s width (15 TR) and steps of 15 s (7TR), resulting in 39 windows in the 10 min of the rs pre-task and 39 windows in the 10 min rs post-task per subject. Therefore, we obtained 585 windows from the rs pre-task data of the 15 subjects and 546 windows for the rs post-task data of 14 subjects, since one subject did not conclude the rs post-task scan. We grouped this rs pre and post-task data, resulting in 1131 windows and we applied the same functional connectivity analysis as in the task data, obtaining 1131 matrices of rest connectivity for the group.

The 1185 task FC matrices were grouped into a data set and applied the k-Means clustering. For this, first we determined the ideal number of cluster of the task data set using the NbClust package (Charrad, Ghazzali, Boiteau, & Niknafs, 2014) from R software. NbClust is a package that determines the optimal number of clusters in a data set using 30 indexes which according to the majority rule, the best number of clusters for our task data set was five clusters. Then, we applied the k-Means clustering to obtain the centroids of these five clusters. These five centroids represented the five task dynamic functional connectivity states. This analysis also allowed us to allocate each FC matrix from the task data set to one of this clusters.

Applying this same approach, we determined a three cluster solution for the 1131 rest connectivity matrices. After the k-Means clustering, we obtained the three centroids, which represented the three rest dynamic functional connectivity states. The 1131 matrices were allocated to one of this three clusters and therefore to a representative DFCS.

The decision to apply this approach separately between the rsfMRI data and the task fMRI data, was to be able to obtain the characteristic FC states or patterns of each condition and to describe the differences. Furthermore, each FC matrix represented 30s of time, therefore, this enabled us to estimate the time spent in a state for each subject during task and rest, according to the number of matrices assigned to a DFCS, that is, the more matrices assigned to a DFCS, the more time spent in that state. This also allowed us to make comparison of the time spent in each state during task and rest.

Results

We included fifteen Vipassana meditation practitioners, 6 females, with a mean age of 40 +/- 12 years old and an average number of hours of meditation practice at 1677 +/- 367. For each subject we acquired 10 minutes of rs pre-task, followed by 20 minutes of attention task fMRI, and 10 minutes of rs post-task. The obtained images were preprocessed *(Methods)* and as a part of this preprocessing, motion correction was performed. This resulted in an average of 1 volume deleted in the rs pre-task data from the subjects, an average of 3 volumes in the task data and an average of 1 volume in the rs post-task data.

After the dynamic functional connectivity analysis, we obtained three DFCS for the rest fMRI data, described here as rest states 1 to 3, whereas for the task fMRI data we obtained five DFCS, described here as task states 1 to 5 *(Fig. 4)*.

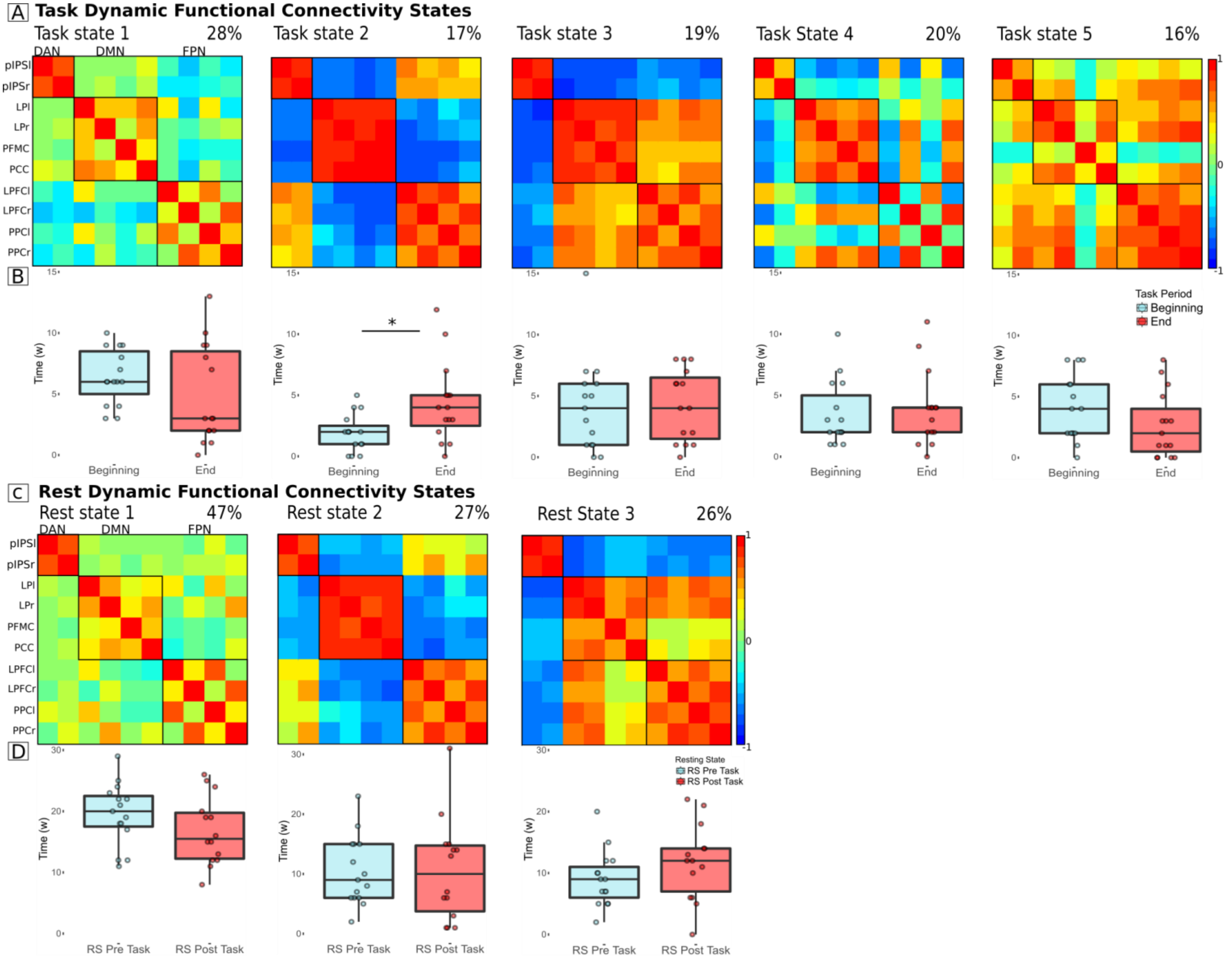

Figure 4.- DFC States (A)After the clustering approach using the Task data five states were obtained, with 10 ROIs from DAN/DMN/FPN. Percentage of ocurrence during task is above the centroid. (B)Differences in the time spent in each state at the beginning and at the end of the task for all subjects. Significantly increase (p-value 0.01 uncorrected) in the time spent in state 2 is showed. (C)Three states were obtained for the rs data (Pre and post task). (D)Differences in the time spent in each state at rs pre-task vs post-task for all subjects. Time is represented for the number of windows (30s) assigned to a state. The color bar indicates the Pearson's r value.

Resting Dynamic Functional Connectivity States

Three patterns of connectivity were obtained for the rs pre-task and post-task grouped data *(Fig. 4)*. Rest state 1 was characterized by low internetwork connectivity between the three networks with a preservation of the intranetwork connectivity. Rest state 2 showed high connectivity between the DAN and the FPN regions and an anticorrelation of these two networks with the DMN, this last with high intranetwork connectivity values. Rest state 3 demonstrated high connectivity between the DMN and the FPN regions and an anticorrelation of these two networks with the DAN regions, with this last presenting high intranetwork connectivity.

Using the clustering approach, each of the 1131 windows of FC obtained from the rest pre-task and post-task condition were assigned to one of the three rest states. We obtained that 47% of the windows were assigned to the rest state 1. Since each window represents 30s in time, this means that subjects spent 47% of the time in the rest state 1. A total of 27% of the time was spent in the rest state 2 and 26% of the time in the rest state 3.

We evaluated if there were differences between the rs post-task FC and the rs pre-task FC, expressed as differences in the time spent in the rest states. This in order to assess if the task condition influenced the succeeding resting connectivity. For this, we estimated the time spent in each of these three rest states during the rs pre-task and during the rs post-task condition. For this, we used the number of windows of the subjects assigned to each of the three states in each condition.

In the case of the rest state 1, we observed that subjects spent less time in this state during the rs Post-task compared to the rs Pre-task *(Fig. 4)*, and after calculating the percentage change we obtain a percentage decrease of 19.79%. This implies that after the performance of the task, subjects spent less time in this low connectivity state. With respect to the rest state 2 we obtained a percentage decrease of 6.36%, which indicates that subjects spent less time in this state after the performance of the task. For the rest state 3, characterized for a high connectivity between DMN and FPN regions, we obtained a percentage increase of 21.48%. This indicates that subjects spent more time in this state after the performance of the task compared to the rs pre-task.

In order to define if these differences were significant, we applied the mixed effects linear model using the lme function from the nlme package in R (Pinheiro, Bates, DebRoy,

& Sarkar, 2017). This test was chosen instead of t-test since one of the subjects did not complete the 10 min of the rs post-task, having 15 subjects in the rs pre-task data and 14 subjects in the rs post-task data. We applied this analysis in each rest state, to compare the time spent in the rs pre-task against the rs post-task using the number of windows. The time spent in the rest state 1 decreased after the task condition, but the test showed this difference was no significant, obtaining a p=0.07. The time spent in rest state 2 before and after the task did not show significant differences (p=0.95). The time spent in rest state 3 increase after the performance of the task, nevertheless, the test showed no significant difference (p= 0.11).

Task Dynamic Functional Connectivity States

Five connectivity states were obtained for the task data *(Fig. 3)*. The task states 1, 2 and 3 had a high similarity with the rest states, in contrast, the task state 4 and 5 were only found during the task. Task state 1 showed the lowest connectivity between the regions of the three networks and a high intranetwork connectivity in the DAN. Task state 2 was characterized by the highest intranetwork connectivity in the three networks and by a high connectivity between the DAN and FPN regions; this state was also characterized by a segregation of the DMN and a high intranetwork connectivity between the regions of this network. Task state 3 presented a strong internetwork connectivity between the DMN and the FPN and a segregation of the DAN which also showed the highest intranetwork connectivity in this state compared to the others. On the other hand, task states 4 and 5 where distinctive of the task data. Task state 4 showed low values of internetwork connectivity, similar to the task state 1, however, unlike the task state 1, task state 4 presented positive correlation values between the right regions from the FPN with the DMN and positive correlation values between the left regions of the FPN with the DAN. The highest intranetwork connectivity in task state 4 was presented in the DMN. Finally, task state 5 was characterized by the highest internetwork connectivity between the three networks and by high intranetwork connectivity, predominantly in the FPN. During task state 5, the medial prefrontal cortex showed a correlation value near to 0 with the DAN and FPN regions.

After the clustering approach, each of the 1185 windows of FC of the task condition were assigned to one of the five task states. We obtained that 28% of the windows were assigned to the task state 1, which means that subjects spent 28% of the time in this state during the task. For the other task states, we obtained subjects spent 17% of the time in task state 2, 19% in the task state 3, 20% in task state 4 and 16% of the time in task state 5, being this last the less prevalent.

Since FC changes in short periods of time as in seconds, we were interested to know if the time spent in each task state changed significantly when comparing this time between the beginning of the task (first five minutes) and the end of the task (last five minutes). For this estimation we used the number of windows of FC assigned to each task state from the first five minutes and the last five minutes of the task in the group. Differences according to this data were observed and are showed in Figure 3. In respect to task state 1, subjects spent less time in this low connectivity state at the end of the task as compared to the beginning, obtaining a percentage decrease of 23.95%. For task state 2 there was an increase in the time spent in this state at the end of the task with a percentage increase of time of 124.13%. The time spent in task state 3 was very similar at the beginning and at the end of the task, obtaining a percentage increase at the end of the task of 1.58%. For task state 4, we obtained an increase in the time spent in this state at the end of the task of 11.53%. Finally, for task state 5 there was a decrease in the time spent in this state at the end of the task with a percentage decrease of 33.33%. To estimate the significance in these differences, we applied a t-test comparing the number of windows assigned to the beginning and to the end of the task of the fifteen subjects for each task state *(Fig. 3)*. We obtained that for the Task state 2, there was a significant difference with a p value of 0.01, between the time spent at the beginning versus at the end of the task. Nevertheless, after the Bonferroni correction we obtained an adjusted p-value of 0.085. The results of the t-tests obtained for the other task states did not show any significant value.

Discussion

Attention is a fundamental process of human adaptability (Tang & Posner, 2009), allowing to the selected signal to increase its cortical representation and to affect the content of awareness (Farb, Segal, & Anderson, 2013a). This sensory cortical activation generated by focused attention on the body without inputs, has been suggested as the underlying process in spontaneous sensations, relevant to interoception and body awareness (Ferentzi, Drew, Tihanyi, & Köteles, 2018; Tihanyi, Ferentzi, & Köteles, 2017).

The impaired attention control, particularly in body focus, is a feature that has been linked to several psychiatric disorders (Asmundson, Abramowitz, Richter, & Whedon, 2010; Fergus, Wheless, & Wright, 2014). This has led to the use of a varied set of cognitive training techniques to enhance the control of attention, although not exclusively for these disorders (Fergus & Bardeen, 2016; Tang & Posner, 2009). This is the case of FAM, which improves the stability and control of attention, with the interoceptive attention as the underlying process in the cognitive change (Farb, Segal, & Anderson, 2013b).

On this basis, a growing interest in studying focus attention to interoception and cognitive training techniques that may improve its control, as FAM, has been evident. Until now, studies have shown changes in functional connectivity related to these processes, however the approach used in these studies assumed a constant FC in their results. Recent functional connectivity studies have shown the dynamic nature of the brain activity at rest, demonstrating FC patterns that evolve in time and even organize in a hierarchical way (Demertzi et al., 2019; Hutchison et al., 2013; Vidaurre, Smith, & Woolrich, 2017). Therefore, during task performance, the modulation of these dynamics may be subjected to specific characterization as brain activity is related to cognitive demands, such as attention (Gonzalez-Castillo & Bandettini, 2017). The objective of this work was to determine the DFCS including the DAN, FPN and DMN regions during an attention to spontaneous sensations task, and to describe the differences of these states with the DFCS obtained at rest.

Our main finding was that there are different patterns of FC characterizing the rest and the task condition, each state with a specific connectivity between the three networks, confirming our main hypothesis. For the rest condition, three rest states were found, although these where very similar to three of the five task states in terms of inter-areal connectivity. This finding agrees with previous studies showing that brain activity during resting conditions is not abolished, instead, it was characterized for a varied set of patterns of FC. It was interesting to find that the time spent in each of the three rest states varied depending on whether the subjects had or not performed the task. This was particularly evident for the rest state 1, with the subjects spending less time in this low connectivity state after the performance of the task. This led us to suggest that the performance of the task had some influence in the rs post-task connectivity.

The task condition was characterized for five patterns of FC or task states with differences in the time spent in each task state during the 20 minutes for the group. In addition, there were also differences in the time spent in these task states depending whether it was the beginning or the end of the task. These results suggest that FC organization varies according to the cyclical attention states which are present during the task, in line with previous studies that propose that variabilities in FC may correlate with changes in behavior and cognitive demands (Tagliazucchi & Laufs, 2015). The similarity between three of the five task states with the three rest states, suggest that the characteristic rest connectivity continues during task, which is in line with previous studies suggesting that rest FC is not extinguished but rather modulated through task, with the task FC representing a combination of spontaneous activity and the task-related responses (M. D. Fox & Raichle, 2007; Fransson, 2006).

The rest state 1 and task state 1were very similar and mainly characterized for low internetwork connectivity. Both were the most prevalent in terms of time spent during rest and during task respectively. Nevertheless, at the end of the task subjects spent less time in task state 1 and it seems that this decreasing tendency continued in the rs post-task. Evidence suggests that the time spent in these DFCS is not random and that it might be associated with behavioral traits (Vidaurre et al., 2017). Therefore, the generally high prevalence but the decrease in time as a possible effect of the task, lead us to assume that this state is a basal and a transitioning configuration. This agrees with a similar study which obtained three DFCS including the executive control network (CEN), salience network (SN) and DMN regions, during a breathing attention task. One of the states of this study showed low correlations between the regions of the three networks and a preservation of the intranetwork connectivity during the task, similar to our rest state 1 and task state 1. They argued that this could represent a transitioning state (Mooneyham et al., 2017).

Rest state 2 and task state 2 were also very similar, showing high connectivity between the DAN and FPN region and an anticorrelation of these networks with the DMN. We found a significant increase in the time spent in the task state 2 at the end of the task with a trend (p= 0.08) after the Bonferroni correction. On the other hand, the time spent on it, remains practically unchanged between rs pre-task and rs post-task conditions. This led us to consider this pattern as an attention state. Task performance has been associated with higher connectivity between the networks required by the task, that in the case of attention and cognitive control tasks, the DAN and FPN regions are usually involved (Madhyastha, Askren, Boord, & Grabowski, 2015; Tang & Posner, 2009), which agrees with our findings in this task state. Furthermore, a very similar state of strong internetwork connectivity between SN and CEN regions and low correlation between these networks with the DMN was also previously found during an attention task (Mooneyham et al., 2017), which was interpreted as a focused attention state.

Rest state 3 and task state 3 showed similar FC characteristics such as: strong connectivity between DMN and FPN regions with segregation of the DAN. The time spent in this task state 3 was about the same whether the subjects were at the beginning or the end of the task. However, we found an increase in the time spent in the rest state 3 in the rs post-task condition compared to rs pre-task, suggestive of a task-mediation effect. We consider that this pattern of connectivity could represent a state of inattention. This is supported by previous evidence that the coupling of the DMN with the FPN regions, usually assumed to work in opposition, is associated with the inability to focus attention during task performance (Crockett, Hsu, Best, & Liu-Ambrose, 2017; Hsu et al., 2014) and have been also linked to mind wandering and spontaneous thought process (Christoff, Gordon, Smallwood, Smith, & Schooler, n.d.; K. C. R. Fox, Spreng, Ellamil, Andrews-Hanna, & Christoff, 2015).

Task states 4 showed the right FPN regions interacting with the DMN and the left FPN regions with the DAN. This “dissociation” of the FPN connectivity was interesting since evidence suggests that the FPN is composed of hubs, giving it a flexible interaction with a variety of functional networks and that the sequential interaction of it, is fundamental for the control and adaptation in task demands (Cole et al., 2013; Harding, Yücel, Harrison, Pantelis, & Breakspear, 2015). Since the dissociation of the FPN connectivity characteristic of this state has been associated to control in tasks, this could be associated to the shift of attention required in the task.

Task state 5 showed a high internetwork connectivity, preserved intranetwork connectivity, and a decoupling of the MPFC with the DAN and FPN. MPFC supports self-related processing and emotional adaptive responses (Euston, Gruber, & Mcnaughton, 2013; Jang et al., 2011).According to recent findings its connectivity is associated with conscious awareness and conscious recovery (Luo et al., 2017). With regards to meditation, studies have found MPFC activity linked to mind wandering during focused attention to breath while at rest a decoupling between the MPFC and the PCC is associated to higher meditation experience (Hasenkamp & Barsalou, 2012; Hasenkamp, Wilson-Mendenhall, Duncan, & Barsalou, 2012). We consider that the decoupling of the MPFC with the DAN and FPN regions found in our study might play a key role that enables the final interaction between the three networks, required for fulfillment of this task demands.

Due to the characteristics of the task we consider that beyond the description of the FC in attention, our results are representative of the FC associated to interoception and body processing. It was interesting to find that such form of interoception task is linked to a FC that changes notoriously over time, involving regions of networks usually associated to cognitive control. We suggest that this might consist in a top-down control from these cognitive networks to primary cortical regions linked to interoception, such as the insula and somatosensory cortex (Bauer et al., 2014; García-Cordero et al., 2017). This conclusion is supported by anatomic findings indicating inputs from parietal and occipital cortices to primary cortical regions which in turn integrates somatosensory information (Namkung, Kim, & Sawa, 2017).

Conclusions

In conclusion, our study shows that performance of an interoception task does not suppress the FC states found at rest. Rather, beside the persistence of these rest states, the task is associated to a more diverse functional organization between the DMN, the DAN and the FPN regions. These varied task states, including patterns of interaction between functionally opposed networks, are probably required to achieve the demands for attention and interoceptive processes. Further, it is interesting to observe the impact of task performance over the subsequent resting period. Indeed, although the task was over, FC in the rs post-task had certain similarity with the task FC in terms of the time spent in the patterns. This leaves the question of whether the effect would persist beyond the 10 minutes of the rs Post-task and if the duration of these subsequent changes after a task are an underlying mechanism associated with the learning process linked to cognitive training.

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