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Community Analysis of Brain Functional Networks Reveals Systems-Level Integration in Olfactory Hedonic Perception

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***Abstract*— Olfactory hedonic perception involves complex interplay among an ensemble of neurocognitive systems implicated in sensory, affective and reward processing. However, the mechanisms of these inter-system interactions have yet to be well-characterized. Here, we employ directed functional connectivity networks estimated from source-localized EEG to uncover how brain regions across the olfactory, emotion and reward systems integrate organically into cross-system communities. Using the integration coefficient, a graph theoretic measure, we quantified the effect of exposure to fragrance stimuli of different hedonic values (high vs low pleasantness levels) on inter-systems interactions. Our analysis focused on beta band activity (13-30 Hz), which is known to facilitate integration of cortical areas involved in sensory perception. Higher-pleasantness stimuli induced elevated integration for the reward system, but not for the emotion and olfactory systems. Furthermore, the nodes of reward system showed more outward connections to the emotion and olfactory systems than inward connections from the respective systems. These results suggest the centrality of the reward system—supported by beta oscillations—in actively coordinating multi-system interactivity to give rise to hedonic experiences during olfactory perception.**

***Index Terms*—Olfactory perception, Community detection, Integration, Reward system, EEG**

I. INTRODUCTION

Odors have the ability to evoke a medley of subjective states, including positive emotions [1], as well as vivid feelings of liking and wanting. Such a multifaceted phenomenology points towards the fact that the hedonic perception of olfactory stimuli implicates several neural structures, each contributing to a holistic affective experience.

There are three dominant neurocognitive systems involved in olfactory hedonic perception: the Olfactory, Emotion and Reward systems [2]. After sensory registration in the nasal epithelium and olfactory bulb, stimulus information is perceptually encoded in the *olfactory system* whose key hubs include the primary olfactory (pyriform) cortex and the anterior temporal cortices that contribute to olfactory object analysis. The olfactory cortex projects to the *emotion system* comprising limbic structures such as the amygdala, hippocampus, parahippocampal gyri and insula, to decode the emotional content of the stimuli. There are also projections to the *reward system* represented by the orbitofrontal and cingulate cortices, in which the stimuli undergo reward evaluation that drives experiences of liking and wanting.

These strong structural links amongst the three neurocognitive systems support the tight functional co-ordinations amongst them during online exposure to olfactory stimuli. Odors have been observed to increase haemodynamic activity concurrently across key sites representing the three cognitive systems, as well as induce robust patterns of functional connectivity amongst them as a function of olfactory pleasantness [3].

These findings demonstrate that there are no clear functional partitions dividing these cognitive systems, owing to the fact that some neural sites have multiple functional roles. Therefore, it is of interest to uncover how these brain regions, during olfactory stimulation, organise themselves organically into communities that transcend their classical system allegiance. These have yet to be examined empirically, thus forming the basis of our present research. Recently, the study of olfactory hedonic perception has gained increasing interest due to a wide range of applications ranging from consumer [4], [5] to clinical research [6], [7].

The aim of this study is to characterize how the three neurocognitive systems functionally integrate with each other during olfactory hedonic processing and to quantify the effect of the hedonic value during exposure to high versus low pleasantness fragrance stimuli. To achieve this, we employ community detection analysis (using the Leiden algorithm [8]) on directed connectivity data based on source-localised EEG, which will be recorded during presentations of high- and low-pleasantness fragrances. These analyses will focus within the beta frequency band (13-30 Hz), as beta oscillations are known to support integration of various cortical areas involved in sensory perception and have been linked to significant brain mechanisms relevant to reward [9], [10] and olfactory processing [11]. It is hypothesised that when perceiving high- versus low-pleasantness olfactory stimuli, there will be an increase in probability for nodes of the reward, emotion or olfactory systems to reconfigure into functional communities with nodes of the other systems.

II. METHODS

A. Experiment Procedure

Eighteen participants (age range 21-42) took part in the experiment held at the National University of Singapore. To minimise gender-related effects, only female subjects participated [12]. The local Institution Review Board (IRB) approved all procedures. In a pre-screening stage, participants were presented with a series of six fragrance samples, and

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the top two and bottom two samples in terms of pleasantness ratings were identified. In the main experiment, participants wore a blindfold and were presented with the 4 samples for 10 trials each, all in random sequence. Each sample was contained in a small bottle, which was opened only during the trial duration of 8 seconds and presented at a consistent distance from the nose. Immediately after, participants were asked to rate the pleasantness on a 11-point (0-10) balanced scale, followed shortly by the presentation of coffee grounds which acted as an odor neutralizer. Short breaks separated the trials to prevent temporary noseblindness.

B. EEG Data Acquisition and Analysis

1) Acquisition: ANT Neuro WaveguardTM caps (CA-142) with a 64 Ag/AgCl sensors montage (10-10 system) were used to record the EEG signals at a 512-Hz sampling rate (acquisition software: AsaLabTM, ANT Neuro). Each channel had an impedance $< 15k\Omega$. Horizontal and vertical electroculogram (hEOG and vEOG) were obtained with electrodes on the bilateral temples, and above and below the right eye, respectively.

2) Preprocessing: The raw EEG signals were digitally filtered (0.3 - 40 Hz), resampled (256 Hz) and re-referenced (common average). Epochs corresponding to the 8-sec trials were extracted and Independent Component Analysis (ICA) was run, so as to remove components related to eye and muscle movement artefacts. Recombining the other components produced the cleaned EEG signal.

3) Source Localisation: Source localisation was performed using the standardised-Low Resolution Electromagnetic Tomography (sLORETA) algorithm to estimate the current source density at each of 6239 voxels at the gray matter and hippocampus of the brain [13]. The data was then parcellated into 116 regions of interest (ROIs) using the Automatic Anatomical Labeling (AAL) atlas to measure functional connectivity. 26 cerebellar and 10 sub-cortical ROIs were removed from further analysis. Thus, further analyses were conducted on a 80 $\times$ 80 connectivity matrix.

4) Functional Connectivity Network: With the source-localized data, Partial Directed Coherence (PDC) was used to estimate functional connectivity, generating an 80 x 80 directed connectivity matrix that defines our functional connectivity network. Each entry in the connectivity matrix defines the pairwise adjacencies between network nodes (ROIs) for each second in a 8-sec trial. As a frequency-domain approach of Granger Causality, PDC describes the outflow from source node *j* to node *i* as a ratio of all the outflows from node *j* [14]. The connectivity matrix was then thresholded using Orthogonal Minimum Spanning Trees (OMSTs) to obtain a more sparse and meaningful connectivity network. Using OMSTs, the network topological configuration that maximizes network efficiency while minimizing cost can be found [15].

5) Community Detection: The Leiden algorithm was applied to the connectivity matrix to perform temporal community detection. Using this algorithm, network nodes were partitioned into communities based on the maximisation of the modularity quality function. An equation for modularity maximisation for directed graphs is given by Leicht and Newman [16]:

$$Q = \frac{1}{m}\sum_{ij}(A_{ij} - \gamma\frac{K_i^{out}K_j^{in}}{2m})\delta(\sigma_i, \sigma_j) \quad (1)$$

where K_i^{out} and K_i^{in} refer to the out-degree and in-degree of node i, A_{ij} refers to an edge from i to j with a value of 1 when there is an edge and 0 otherwise. σ_i denotes the community of node i, γ is the resolution parameter and δ $(\sigma_i, \sigma_j) = 1$ if $\sigma_i = \sigma_j$ and 0 otherwise.

The Leiden algorithm guarantees to yield connected communities and, when used iteratively, it converges to a partition where all subsets of all communities are locally optimally assigned [8]. As such, for each 1-sec slice in a 8-sec trial, using the Leiden algorithm, membership vectors for time slices were obtained. For each slice, an 80 $\times$ 80 co-occurrence matrix was created based on the community partition of each node pair, with the element of the co-occurrence matrix having a value of 1 if two nodes were in the same community and 0 if the nodes were in different communities. The allegiance matrix, representing the probability that each pair of nodes belong to the same community, was then computed by averaging the co-occurrence matrices across the 8 slices in a trial.

6) Cognitive System Assignment: In order to calculate the integration coefficient for each node of the network, based on previous literature, 28 regions of interest (ROIs) involved in olfactory perception, emotion and reward processing were selected [17], [18], [19], [20]. Based on literature evidence on their predominant function, these ROIs were assigned to one system, out of the 3 possible systems: olfactory, emotion and reward. Fig. 1 shows the assignment of nodes to the 3 systems.

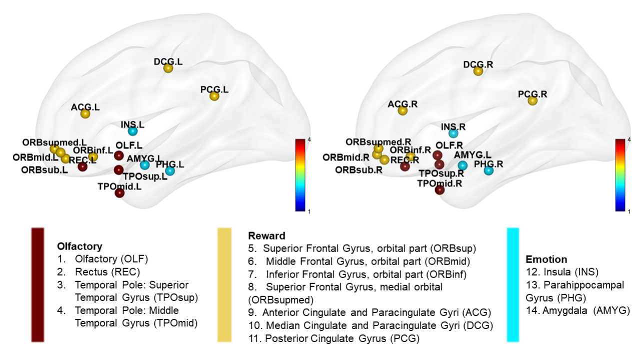

Fig. 1. Assignment of brain regions into nodes responsible for Olfactory (red), Reward (yellow) and Emotion processing (blue).

7) Integration Metric: In order to quantify how the three cognitive systems functionally integrate as a result of olfactory stimulation to generate different olfactory hedonic percepts, we estimated an integration metric. The metric is defined as the average probability that a node (brain region) is in the same network community as nodes from other cognitive systems. Thus, integration quantifies the time-dependent probability that a brain region will associate with different cognitive systems [21]. Using the allegiance matrix and the cognitive system assignment, the integration coefficient of each node was obtained for all trials across all subjects for the beta frequency band. The equation for integration (I_i^s) of region i with respect to system S is given as follows:

$$I_i^s = \frac{1}{N - n_s} \sum_{j \notin S} A_{ij} \tag{2}$$

where N is the total number of brain regions, n_s is the size (number of regions) of system S and A_{ij} is an element of the module allegiance matrix [22]. A brain region that has a high integration coefficient is thus more likely to be found in communities of other systems, besides its own, pointing to a tighter functional integration of the system in which that region acts.

III. Results

A. Functional Connectivity

In this study, the directed functional connectivity measure, PDC, was used to characterize directed connectivity between brain regions in the beta frequency band and when perceiving high pleasantness and low pleasantness olfactory stimuli. The strength of functional connections for nodes in the olfactory, emotion and reward networks were visualised using BrainNet viewer [23], as shown in Fig. 2. Reward processing brain regions, such as the Right Middle Frontal Gyrus (ORBmid.R), Left and Right Inferior Frontal Gyrus (ORBinf.R and L), Anterior Cingulate and Paracingulate Gyri (ACG.L and R), Left and Right Posterior Cingulate Gyrus (PCG.R and L) were observed to display strong connections with emotion and olfactory systems.

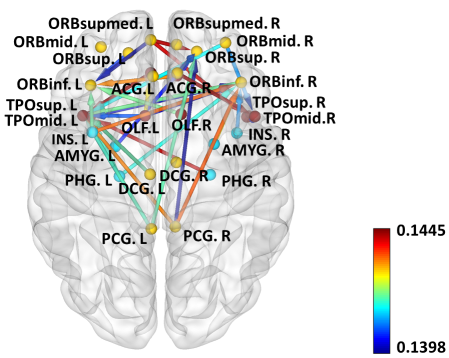

Fig. 2. Top 5% of directed connections, in terms of PDC connections strength visualised as edges along with olfactory, emotion and reward nodes on an anatomical brain sketch

B. Systems Level Analyses

For the analysis at cognitive systems level, we estimated the integration coefficient, in the beta frequency band, of the nodes assigned to the 3 systems of interest in our analysis: olfactory, emotion and reward. We observed a statistically significant difference in integration between the high pleasantness and low pleasantness conditions, for the reward system, $t(26) = 0.944$, $p = .019$ (FDR-corrected), $d = 0.357$ (Fig. 3). This result suggest that brain regions involved in reward processing have a significantly higher probability of being in the same functional community with regions from other systems when perceiving high pleasantness odor stimuli, as compared with low pleasantness odor stimuli. There were no statistically significant differences in integration for regions in the olfactory and emotion systems.

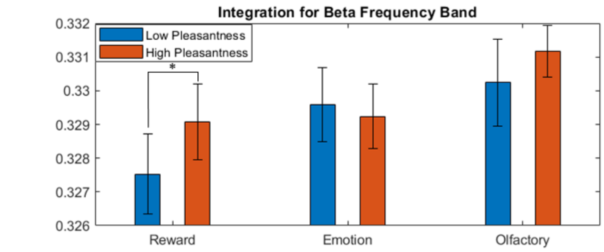

Fig. 3. (A) Bar plots of average integration coefficient between high pleasantness and low pleasantness conditions in the Beta frequency band for Olfactory, Emotion and Reward across all subjects and trials. Error bars indicate ±1 standard error. (* indicates $p < .05$, after FDR correction)

C. Reward System Out-degree vs. In-degree

Next, we sought to determine if reward-system nodes are driving the integration with other systems (or vice versa), by estimating nodal out- and in-degree across the 3 systems. Nodal degree is defined as the number of connectivity edges connecting the respective node to other nodes in the functional network. Averaging across nodes within each system, the mean Reward→Emotion out-degree was higher than mean Reward←Emotion in-degree across both low-pleasantness ($t(17) = 9.18$, $p = 1.34 * 10^{-8}$, $d = 2.16$) and high-pleasantness ($t(17) = 9.75$, $p = 5.64 * 10^{-9}$, $d = 2.30$) conditions. Similarly, the mean Reward→Olfactory out-degree was higher than the mean Reward←Olfactory in-degree across both low-pleasantness ($t(17) = 7.97$, $p = 9.58 * 10^{-8}$, $d = 1.88$) and high-pleasantness ($t(17) = 7.90$, $p = 1.08 * 10^{-7}$, $d = 1.86$) conditions. Fig. 4 shows the reward-system nodes with the highest out-degree difference (Love – Like) towards the emotion system and towards the olfactory system. Overall, the orbitofrontal cortex has high predominance in outward connections with other systems.

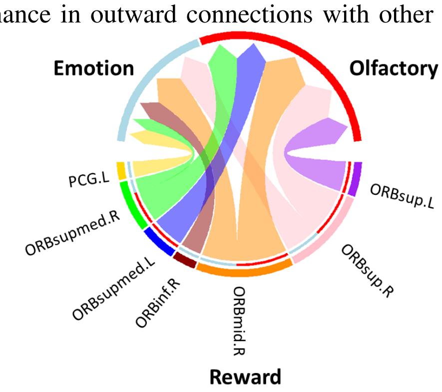

Fig. 4. (A) Circular plot showing the top 5 specific nodes in the reward systems found to have highest difference in out-degrees towards the emotion and olfactory systems between high pleasantness and low pleasantness conditions. Thicker connections indicate nodes with higher difference in out-degrees between high pleasantness and low pleasantness conditions.

IV. Discussion

The current study sought to characterize the patterns of directed functional connectivity among olfactory, emotion and reward brain systems during perception of olfactory stimuli of different hedonic levels. Two central findings emerged from the analyses. First, within the beta frequency band, nodes in the reward system exhibited elevated average integration during exposure to higher-pleasantness stimuli. This is congruent with prior studies which have documented significant modulations in beta-band EEG activity with regards to reward-based processing of monetary reward [24]. Additionally, beta oscillatory activity have been known to facilitate informational integration across cortical areas in sensory perception. This suggests that the increased beta-band integration observed here reflects reward processing brain areas coordinating information spanning multiple neurocognitive mechanisms during olfactory hedonic perception.

Second, the nodes of the reward system showed more outward connections to the emotion and olfactory systems than inward connections from the respective systems. This sheds more light on the systems-level analysis: the significant increase in integration for reward processing could mean a greater probability of nodes with outward connections to emotion and olfactory systems that form functional communities with these systems, driving hedonic perception. Further, we found that the orbitofrontal cortex nodes dominate the outward connections to the emotion and olfactory systems. This scenario agrees with the hypothesis that the orbitofrontal cortex mediates the coupling of reward processing with other brain areas during hedonic perception [24].

These are reinforced by our findings in the context of olfactory hedonic processing. There are also proposals where beta oscillations are thought to promote learning from positive experience and are also involved in memory, attention and motivation [10]. Thus, if nodes in the reward system have a high integration with other systems like the olfactory system and the emotion system when experiencing high pleasantness olfactory stimuli, it can also be speculated that reward system nodes will have high integration with other networks such as in learning and attention, forming communities that facilitate the transfer of information to other brain areas. We plan to investigate these in future work.

V. Conclusions

In this paper, changes in a metric of directed functional connectivity, PDC, in response to high pleasantness and low pleasantness olfactory stimuli were investigated. It was found that in the beta frequency band, there was a statistically significant difference in the integration coefficient for the reward system which could reflect the reward system as one of the main drivers of brain processing involved in olfactory hedonic perception.

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