NÖRO PSİKİYATRİ ARŞİVİ
ARCHIVES OF NEUROPSYCHIATRY

RESEARCH ARTICLE

Arch Neuropsychiatry 2025;62:100–108
https://doi.org/10.29399/npa.28795

Intrinsic Functional Connectivity Patterns of The Object-Selective Visual Areas

Ulaş AY[1,2], Tamer DEMİRALP[3]

[1]Department of Neuroscience, Aziz Sancar Institute of Experimental Medicine, Istanbul University, İstanbul, Türkiye
[2]Hulusi Behcet Life Sciences Research Laboratory, Neuroimaging Unit, Istanbul University, İstanbul, Türkiye
[3]Department of Physiology, Istanbul Faculty of Medicine, Istanbul University, İstanbul, Türkiye

ABSTRACT

Introduction: It has been shown by numerous investigations that the occipitotemporal area has a particular object perception area called the lateral occipital complex, which is composed of lateral occipital (LO) and posterior fusiform (pF) cortices. The aim of this study is to examine the intrinsic functional connectivity (iFC) patterns of the object-selective LO and pF regions in order to shed light on the underlying neural mechanisms of object recognition.

Methods: 15 healthy participants were included in the study. A standard localizer task was used to identify LO and pF regions. Magnetic resonance imaging (MRI) data were collected using two different imaging protocols: high-resolution anatomical image and functional MRI (fMRI) data. Data preprocessing steps were carried out in accordance with standard procedures. After determining the LO and pF regions with activation analyses on the task-based fMRI data, the iFCs of these regions were investigated with functional connectivity analyses carried out on the resting-state fMRI recording.

Results: iFC analyzes revealed that LO and pF regions have different connectivity patterns. Lateral occipital had a widely distributed connectivity network, whereas pF showed a more localized connectivity pattern. Lateral occipital had more extensive occipitotemporal, occipitoparietal and motor connections compared to pF. In contrast to this distribution pattern, the connections of the right and left LO were generally concentrated on the ipsilateral sides, while the connections of the pF were bilateral.

Conclusion: The results of the study revealed complex iFC patterns of the LO and pF differentiating their functional roles in object perception/recognition. While the pF revealed bilaterally distributed iFC along the ventral visual stream, the extensive and lateralized iFC of the LO suggests its role in integrating visual information including object-related attention and action recognition.

Keywords: Intrinsic functional connectivity, lateral occipital complex, lateral occipital cortex, object perception, posterior fusiform cortex

Cite this article as: Ay U, Demiralp T. Intrinsic Functional Connectivity Patterns of The Object-Selective Visual Areas. Arch Neuropsychiatry 2025;62:100–108.

INTRODUCTION

The human brain, owing to its ability to recognize objects quickly and reliably, seamlessly integrates sensory input to create a coherent representation of the external world. One of the biggest factors underlying this success can be considered as the presence of areas specialized for object recognition in the visual cortex. In the human brain, the lateral occipital complex (LOC), a critical cortical area for object recognition, was first identified by Malach et al. (1995)(1). The researchers localized this cortical region on the lateral shore of the fusiform gyrus with the posterior border of motion-sensitive MT/V5, which shows stronger activation to photographs of everyday objects compared to visual texture images without obvious shape interpretations. Therefore, they suggested that this region has an important role in object recognition. A similar result was reported by Kanwisher et al. (1996) using drawings: the LOC responded more strongly to three-dimensional objects depicted by drawings, whether familiar or new, compared to scrambled drawings in which no clear shape could be identified (2). Later neuroimaging studies also confirmed the object selectivity of this region, finding that the LOC showed stronger activation to images of various objects compared to scrambled images of these objects (3,4).

Highlights

- **The iFC of the LO is more widespread than that of the pF.**
- **The iFC of LO encompasses dorsal and ventral visual streams and the motor cortices.**
- **The iFC of pF is more localized compared to that of LO.**
- **The iFC of the LO was more pronounced within the same hemisphere.**
- **The iFC of LO with the motor cortex may be associated with action recognition.**

Grill-Spector et al. (1999) suggested that the LOC consists of two components that differ anatomically and functionally (5). The caudal-dorsal component was distinguished from the anterior-ventral component based on its size and position sensitivity, and the anterior-

Correspondence Address: Ulaş Ay, Hulusi Behcet Life Sciences Research Laboratory, Neuroimaging Unit, Istanbul University, 34093, Istanbul, Türkiye • **E-mail:** psk.ulasay@gmail.com
Received: 15.04.2024, **Accepted:** 22.04.2024, **Available Online Date:** 08.06.2025
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ventral component appeared to be more sensitive to changes in object position compared to the caudal-dorsal component. Since then, the distinction between two functionally and anatomically distinct components of the LOC has been demonstrated in many studies. The caudal-dorsal component, the lateral occipital cortex (LO), was defined based on anatomical (within the lateral occipital cortex) and functional (posterior to middle temporal gyrus) boundaries (1,6). On the other hand, the anterior-ventral component is located within the fusiform gyrus anterior to areas V4/V8, and extends to the occipitotemporal sulcus (6). Although the ventral temporal component of the LOC has been variously labeled as posterior fusiform sulcus, ventral temporo-occipital cortex, posterior fusiform, anterior lateral occipital, and ventral lateral occipital complex, a recent study defined this object selective area as posterior fusiform (pF) (6).

Understanding the intrinsic functional connectivity (iFC) of LOC can provide valuable insights into its functional organization, and shed light on the underlying neural mechanisms of object recognition. The iFC refers to the ongoing activity patterns within the brain that are temporally correlated, providing insights into the intrinsic organization and communication of different brain regions. Such iFC patterns that can be observed in resting state data reflect the functional connections between brain areas, independent of the presence of external stimuli or specific task demands (7). In a study examining the iFCs of category-selective regions in the occipitotemporal cortex (8), many regions in the occipitotemporal cortex have been examined. Although this study reported different connectivity patterns of the LO and pF, the functional significance of these differences were not specifically evaluated in terms of their relationship to object recognition and related processes. The present study aims to elucidate and compare the iFC patterns of the LO and pF regions specifically regarding their functional specialization in object perception.

METHODS

Participants

The sample size was determined using the software R (version 4.2.2, https: //www.rproject.org). The power was set to at least 0.8 and the alpha to 0.05. The smallest sample size of 14 was calculated based on the effect size in a previous pilot study (9). Fifteen healthy participants were recruited. Inclusion criteria for participation were defined as: a) being aged between 18 and 40 years, b) right-handedness, c) having normal or corrected-to-normal vision, d) writing an informed consent, and e) Beck Depression and Anxiety Inventory scores under 17 and 16, respectively. Exclusion criteria for the study were: a) the presence of any pathology in sensory systems that could not be corrected, b) having any neurological or psychiatric disorder, c) the use of medication affecting the central nervous system, d) history of head trauma resulting in prolonged loss of consciousness, e) presence of any material in the body incompatible with magnetic resonance imaging (MRI), and f) claustrophobia. The Addenbrooke's Cognitive Examination-III (ACE-III) screening test was used to evaluate the general cognitive status of the participants. The study was approved by the Clinical Research Ethics Committee of Istanbul University Istanbul Faculty of Medicine (Protocol Number: 2021/670). This study was performed in accordance with the ethical principles of the latest version of the Declaration of Helsinki.

Localizer task

A standard localizer task was employed to identify object-selective areas, wherein participants were presented with black-and-white images of objects, scenes, human faces, and scrambled objects in four distinct blocks. Participants were instructed to press a button if they saw the same image twice in a row throughout the experiment, thus providing them with a simple working memory task frequently used in relevant literature to ensure sustained attention during the experiment. The experiment design was created using E-prime software. The localizer task was created in a block design, which consisted of two runs created in a palindromic order. Each run comprised 16 blocks (4 objects, 4 scenes, 4 faces, 4 scrambled objects), each lasting 16 seconds and preceded and followed by 16-second fixation blocks. Each photograph presented in the blocks was presented for 350 ms followed by a 450 ms fixation. Thus, each run lasted 5 minutes 36 seconds and the total duration of the localizer task was determined as 11 minutes and 12 seconds.

Object stimuli were selected from the Bank of Standardized Stimuli (BOSS) Phase II database (10). These stimuli were categorized into four categories (kitchen items, furniture, clothing, vehicles), with each category containing 20 stimuli. Then, scrambled object stimuli were created from objects selected from the BOSS database by applying the "scramble" plugin (https: //www. telegraphics. net/sw/product/Scramble) in Adobe Photoshop, resulting in scrambled images of 20×20 pixels. Thus, a total of 320 stimuli were selected for the localizer task. All stimuli were saved in black-and-white on a gray background with dimensions of 500×500 pixels.

MRI acquisition parameters

Magnetic resonance imaging was performed at the Istanbul University Hulusi Behçet Life Sciences Research Laboratory, Neuroimaging Unit using a 3T scanner (Philips Achieva, The Netherlands) equipped with a 32-channel head-coil. T1-weighted turbo field echo sequence was utilized to acquire high-resolution anatomical images (TR=8.4 ms, TE=3.9 ms, FOV=250×250 mm, 180 axial slices, voxel size=1 mm^3, flip angle=8°). Resting-state fMRI data were collected using a T2*-weighted echoplanar imaging protocol with the following parameters: TR=2000 ms, TE=30 ms, FOV=224×240 mm, number of slices=36, voxel size=2×2×4 mm, flip angle=77°. After acquiring 10 dummy volumes, 214 axial volumes were collected, resulting in a total scan time of 448 s. The parameters used in the localizer task were the same as the resting-state, however, a total of 2 runs with 168 functional images were recorded in one run. All subjects were advised to relax while keeping their eyes closed and to refrain from sleeping throughout the duration of the scan.

Activation analyses and region of interest definition

Following preprocessing, a general linear model was conducted using SPM software (version 12.7771) to identify activations arising from the localizer task. In first-level analyses, the BOLD signal was modeled separately for each participant by convolving with a canonical hemodynamic response function, incorporating four block conditions and a multiple regressor, to estimate parameters. Object-selective regions were identified using the object > scrambled object contrast. To account for effects, six motion parameters (three translations and three rotations) and outlier images identified with ART during preprocessing were included in the model. Subsequently, a high-pass filter with a 128-second cutoff was applied to remove slow oscillating signals, and *t*-contrast was defined to be used in second-level analyses. To prevent interindividual differences in the anatomical locations of regions of interest (ROIs), a one-sample t-test was conducted at the group level in second-level analyses. Statistical significance in second-level analyses was considered uncorrected at $p < 0.001$, and two ROIs (LO and pF) were determined bilaterally.

Preprocessing of resting-state fMRI data

The preprocessing of neuroimaging data was performed with the CONN functional connectivity toolbox (11). Initially, functional images were realigned to the first image to correct individual head movements. Subsequently, functional volumes were compared with the previous

image using the ART toolbox to identify outliers in participant head movements and signal changes. Outliers in signal changes were determined based on the condition of exceeding a global signal z-value threshold of ±5 standard deviations or a motion change greater than 0.9 mm from the previous image. Participants with more than 20% outlier images in each session were planned to be excluded; however, no participants exceeded this threshold, therefore, all data were included in the analyses. Then, functional and structural co-registration was performed to align high-resolution anatomical images with functional images. Following this process, structural images were segmented into white matter, gray matter, and cerebrospinal fluid compartments and normalized to the Montreal Neurological Institute (MNI) standard space. Using the resulting transformation matrix, functional data were spatially normalized and resampled to isotropic 2 mm^3 voxels. Finally, functional data were smoothed with an isotropic Gaussian kernel (full width at half maximum=6 mm).

Functional images underwent further preprocessing steps to eliminate physiological noise from the BOLD signal. A denoising step was first performed, which involved linear regression of possible confounding effects in the BOLD data and the use of a band-pass filter (11). Linear regression was used to assess and eliminate the possible noise effects observed for each voxel in the brain. An anatomical component-based correction approach (aCompCor) was used after the default denoising procedure in CONN to reduce any confounding effects. This approach assessed and incorporated possible noise components arising from white matter and cerebrospinal fluid signals as confounding factors in the denoising stage. Furthermore, the six motion parameters (three translations and three rotations) acquired for each participant during realignment were considered possible confounding factors in the study. Additionally, outlier images observed during the ART preprocessing stage were considered confounding factors. Finally, a band-pass filter of 0.01–0.1 Hz was used to reduce the impact of noise sources in functional images.

Intrinsic functional connectivity analyses

The seed-to-voxel iFC analysis was performed on the resting-state fMRI data with the four ROIs (bilateral LO and pF) obtained in the activation analyses. Subject level iFC analysis was conducted by computing the bivariate correlation coefficients between the mean time series of individual seeds, utilizing unsmoothed data, and the time series of all other voxels in the brain, employing smoothed data. Following this, all correlation values underwent Fisher's *z*-transformation. The *z*-score for each participant was included in a voxel-wise one-sample t-test to identify clusters exhibiting significant connectivity with each seed during the resting state. Cluster-level inferences were based on nonparametric statistics from permutation analyses with 5000 residual-randomization iterations. Results were thresholded using a combination of cluster-forming p <0.001 voxel-level threshold, and family-wise corrected p (p_{FWE}) <0.001 cluster-mass threshold.

RESULTS

Sample characteristics

Fifteen healthy participants, meeting the inclusion and exclusion criteria, were recruited (5 female; age: 27.7±4.3, range: 21–36 years; education: 17.9±2.5, range: 15–22 years). Scores on the ACE-III screening test assessing participants' overall cognitive status ranged from 90 to 100 (mean: 97.3±3.0). Further sample characteristics are given in Table 1.

Activation analyses results

As visualized in Fig. 1, the localizer task revealed bilateral LO regions in the lateral occipital cortices and pF regions on the ventral visual streams (right LO: t (14)=8.25, p=0.0002; left LO: t (14)=6.97, p=0.0001; right pF: t (14)=86.76, p=0.0004; left pF: t (14)=8.5.99, p=0.0007). These regions obtained as the result of the second level analysis of the task-based fMRI data were used as regions of interest in iFC analyses performed on the resting-state fMRI data.

Intrinsic funcitonal connectivity results

LO functional connectivity

Similar iFC patterns were obtained for both the right and left LO, however, with a predominantly unilateral distribution (Fig. 2). The connections of both LOs with bilateral occipitotemporal and occipitoparietal regions, bilateral inferior temporal and bilateral motor cortices were significantly higher than zero (Both LOs Mass p_{FWE}: $<10^{-6}$, Table 2). However, the comparisons between the iFC patterns of the right and left LOs pointed to a rather unilateral predominance of the connectivities (Fig. 3 and Table 3). Hence, the left LO exhibited stronger connections with the left fusiform gyrus, left inferior and middle temporal gyrus, left inferior and middle occipital gyrus, left lingual gyrus, left parahippocampal gyrus, left superior parietal and occipital gyrus, left precuneus, and left inferior parietal gyrus compared to the right LO (Cluster 1 Mass p_{FWE}: $<10^{-6}$, Cluster 2 Mass p_{FWE}: <0.0002). Conversely, the right LO showed stronger connections with the right inferior, middle, and superior occipital gyrus, right inferior and middle temporal gyrus, right fusiform gyrus, right lingual gyrus, and right calcarine fissure compared to the left LO (Mass p_{FWE}: $<10^{-6}$). Thus, we found that the left LO exhibited stronger connections predominantly with the left while the right LO exhibited stronger connections with the right hemisphere.

Table 1. Sample characteristics

Characteristics	Values
Number of participants	15
Age mean ± SD (range)	27.7±4.3 (21–36 years)
Sex	5 female (33,3%), 10 male (66,7%)
Education mean ± SD (range)	17.9±2.5 (15–22 years)
Beck Depression Inventory mean ± SD (range)	7.9±4.7 (0–15)
Beck Anxiety Inventory mean ± SD (range)	5.9±3.6 (1–12)
ACE-III total score mean ± SD (range)	97.3±3.0 (90–100)

ACE-III: Addenbrook Cognitive Examination-III; SD: standard deviation.

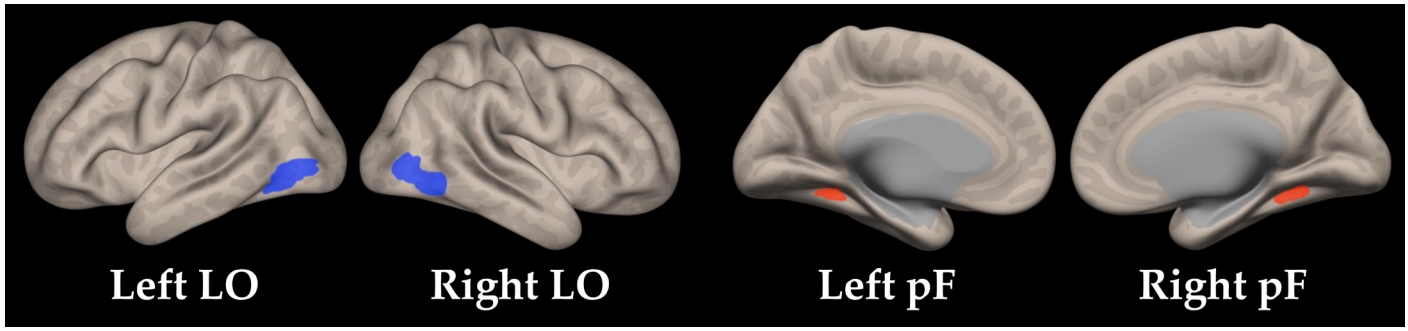


Figure 1. Bilateral lateral occipital (LO) and posterior fusiform (pF) object-selective cortices identified as a result of activation analyses.

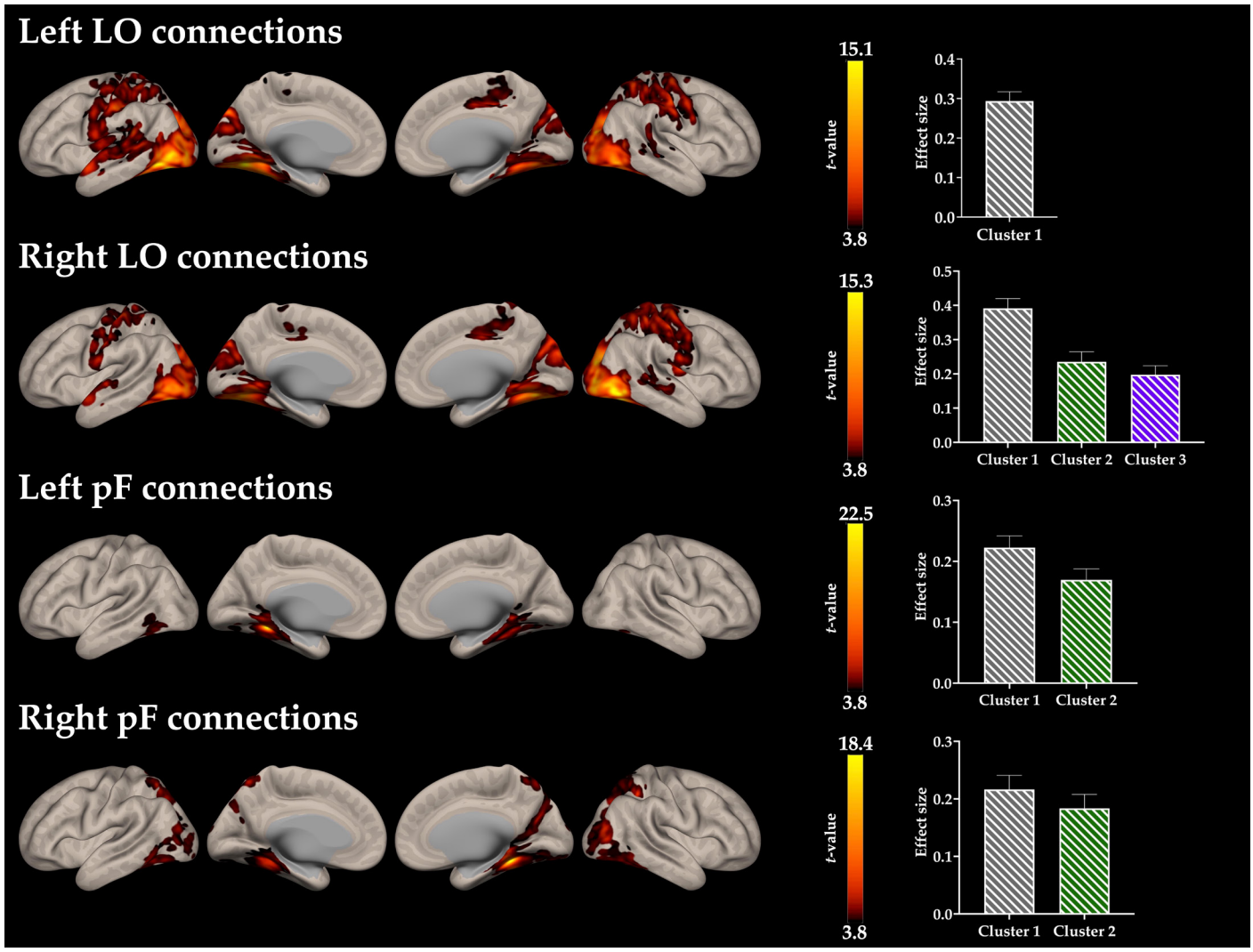


Figure 2. Intrinsic functional connectivity of the object-selective lateral occipital and posterior fusiform cortices.
Clusters in the effect size graphs in the right column correspond to the clusters defined in Table 2

pF funcitonal connectivity

We found that the iFCs of pFs were predominantly limited to more local regions (Fig. 2, Table 2). One of the two clusters functionally connected with each of the right and left pFs was exclusively localized in the left hemisphere, while the other was exclusively localized in the right hemisphere. Specifically, we identified that the left pF exhibited significant iFC with two distinct bilateral clusters, comprising bilateral fusiform gyri, bilateral lingual gyri, bilateral parahippocampal gyri, bilateral hippocampi, left inferior and middle temporal gyri, and left inferior occipital gyrus. Similarly, the right pF also showed significantly stronger iFC with two distinct clusters. These clusters included bilateral fusiform gyri, bilateral middle occipital gyri, bilateral superior parietal gyri, bilateral parahippocampal gyri, bilateral inferior occipital gyri, bilateral middle temporal gyri, bilateral cuneus, right inferior temporal gyrus, right superior occipital gyrus, right calcarine fissure, right hippocampus, right postcentral gyrus, right angular gyrus, left lingual gyrus, left precuneus, and left inferior parietal gyrus (Both pFs Mass p_{FWE}: $<10^{-6}$, Table 2). However, we did not find any differences between the iFCs of the right and left pFs.

LO versus pF funcitonal connectivity

In the comparison between the iFCs of the LO vs pF, we found that both right and left LO exhibited a stronger and wider iFC pattern compared to

Table 2. The intrinsic functional connectivity of the lateral occipital and posterior fusiform cortices

Seed	Cluster	Regions showing stronger connections at baseline	Peak MNI coordinate	Cluster size	Mass p_{FWE}
Left LO	1	Bilateral precentral gyrus, bilateral postcentral gyrus, bilateral middle occipital gyrus, bilateral fusiform gyrus, bilateral middle temporal gyrus, bilateral lingual gyrus, bilateral superior temporal gyrus, bilateral superior occipital gyrus, bilateral inferior occipital gyrus, bilateral cuneus, bilateral inferior temporal gyrus, bilateral superior parietal gyrus, bilateral inferior parietal gyrus, bilateral calcarine fissure, bilateral supramarginal gyrus, bilateral paracentral lobule, bilateral superior frontal gyrus, bilateral precuneus, bilateral parahippocampal gyrus, right middle cingulate gyrus, left superior temporal pole, left rolandic operculum, left insula, right middle frontal gyrus	-36 -64 -10	30815	$<10^{-6}$
Right LO	1	Bilateral middle occipital gyrus, bilateral lingual gyrus, bilateral fusiform gyrus, bilateral cuneus, bilateral superior occipital gyrus, bilateral middle temporal gyrus, bilateral inferior occipital gyrus, bilateral inferior temporal gyrus, bilateral calcarine fissure, bilateral middle temporal gyrus, bilateral precuneus, right superior temporal gyrus, right parahippocampal gyrus,	38 -62 -10	17500	$<10^{-6}$
	2	Right postcentral gyrus, right precentral gyrus, right superior parietal gyrus, right rolandic operculum, bilateral middle cingulate gyrus, right paracentral gyrus, right insula, right inferior parietal gyrus, right superior frontal gyrus, right middle frontal gyrus, bilateral supplementer motor area, right precuneus, left paracentral lobule, right superior temporal gyrus,	50 -12 14	5996	$<10^{-6}$
	3	Left postcentral gyrus, left precentral gyrus, left superior temporal gyrus, left superior temporal pole, left middle temporal gyrus, left superior parietal gyrus, left inferior parietal gyrus, left rolandic operculum, left paracentral lobule	-52 6 -14	2721	$<10^{-6}$
Left pF	1	Left fusiform gyrus, left lingual gyrus, left parahippocampal gyrus, left inferior temporal gyrus, left middle temporal gyrus, left inferior occipital gyrus, left hippocampus	-32 -46 -8	1784	$<10^{-6}$
	2	Right fusiform gyrus, right parahippocampal gyrus, right lingual gyrus, right hippocampus	26 -20 -22	1101	$<10^{-6}$
Right pF	1	Right fusiform gyrus, right middle occipital gyrus, right inferior temporal gyrus, right superior parietal gyrus, right superior occipital gyrus, right parahippocampal gyrus, right inferior occipital gyrus, right middle temporal gyrus, right cuneus, right calcarine fissure, right hippocampus, right postcentral gyrus, right angular gyrus	34 -44 -12	6201	$<10^{-6}$
	2	Left fusiform gyrus, left middle occipital gyrus, left superior parietal gyrus, left inferior occipital gyrus, left lingual gyrus, left precuneus, left middle temporal gyrus, left parahippocampal gyrus, left inferior parietal gyrus, left cuneus	-24 -64 54	3402	$<10^{-6}$

LO: Lateral occipital; pF: Posterior fusiform.

pF (Table 3, Fig. 4). Specifically, we observed that the left LO has stronger iFC with bilateral occipital areas (Mass p_{FWE}: $<10^{-6}$), the left motor cortex (Mass p_{FWE}: $<10^{-6}$), the right motor cortex and frontal regions (Mass p_{FWE}: $<10^{-6}$), and left occipitotemporal regions (Mass p_{FWE}: 0.0002) compared to the left pF. The right LO also demonstrated stronger connections with bilateral occipital and temporal regions (Mass p_{FWE}: $<10^{-6}$) and the right motor cortex and frontal regions (Mass p_{FWE}: 0.0004) compared to the right pF.

DISCUSSION

This study focused on the complex intrinsic functional connectivity patterns of the LO and pF cortices, which are critical regions for object perception and recognition. Our findings revealed considerable differences in iFC patterns across different brain areas, shedding light on their particular functions of these areas in visual processing.

The significant functional connectivity seen in both the right and left LO areas is consistent with previous studies demonstrating the LO's critical role in integrating visual information across diverse cortical regions (5,12). Previous investigations using functional magnetic resonance imaging (fMRI) have repeatedly found strong links between the LO and the occipitotemporal and occipitoparietal regions, demonstrating its importance in object recognition tasks (8,13,14). These connections most likely aid in the integration of visual characteristics and the construction of coherent object representations (15,16).

In the analysis examining the iFC differences between the left and right LO regions, it was found that the left LO exhibited greater iFC with the left occipitotemporal and occipitoparietal regions, while the right LO showed stronger iFC with the right occipitotemporal regions. Of significance is the observation that one of the two clusters where the left LO displayed greater iFC compared to the right LO was centered around the fusiform and parahippocampal gyrus. This cluster is observed to overlap with the other object-selective posterior fusiform (pF) cortex, indicating its involvement in object recognition. Numerous studies on object recognition have underscored the importance of the LOC, comprising LO and pF, in processing various object categories and encoding the low-level and complex visual features and shapes within the ventral visual

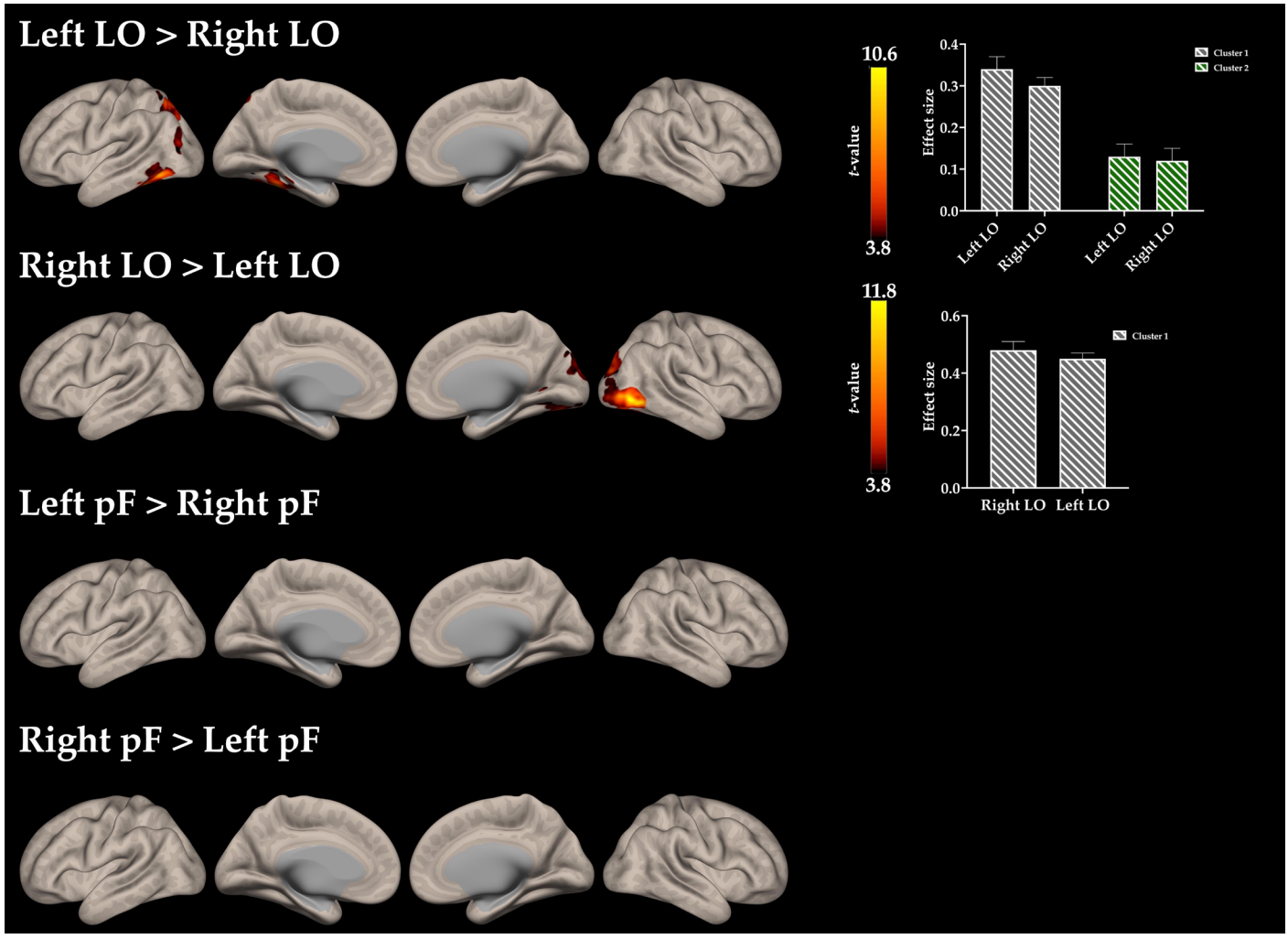


Figure 3. Differences in the intrinsic functional connectivity between the object-selective cortices of the right and left hemispheres (R: right, L: left).

Table 3. Comparison of intrinsic functional connectivity between right and left object-selective cortices and lateral occipital vs posterior fusiform cortices

Contrast	Cluster	Regions showing connectivity changes	Peak MNI coordinate	Cluster size	Mass p_{FWE}
Left LO > Right LO	1	Left fusiform gyrus, left inferior temporal gyrus, left inferior occipital gyrus, left middle temporal gyrus, left lingual gyrus, left parahippocampal gyrus	-38 -50 -22	1552	$<10^{-6}$
	2	Left middle occipital gyrus, left superior parietal gyrus, left superior occipital gyrus, left precuneus, left inferior parietal gyrus	-20 -66 52	710	0.0002
Right LO > Left LO	1	Right inferior occipital gyrus, right middle occipital gyrus, right middle temporal gyrus, right superior occipital gyrus, right fusiform gyrus, right inferior temporal gyrus, right lingual gyrus, right calcarine fissure	46 -66 -2	2534	$<10^{-6}$
Left LO > Left pF	1	Bilateral middle occipital gyrus, bilateral fusiform gyrus, bilateral lingual gyrus, bilateral inferior occipital gyrus, bilateral superior occipital gyrus, bilateral middle temporal gyrus, bilateral cuneus, bilateral inferior temporal gyrus, bilateral calcarine fissure	-38 -62 -8	13264	$<10^{-6}$
	2	Right postcentral gyrus, right precentral gyrus, right inferior parietal gyrus, right superior parietal gyrus, right supramarginal gyrus, right superior frontal gyrus, right middle frontal gyrus	18 -22 78	3350	$<10^{-6}$
	3	Left postcentral gyrus, left precentral gyrus, left inferior parietal gyrus, left superior parietal gyrus, left supramarginal gyrus, left paracentral lobule	-34 -42 64	2442	$<10^{-6}$
	4	Left superior temporal pole, left superior temporal gyrus, left postcentral gyrus, left rolandic operculum, left middle temporal gyrus	-54 10 -10	603	0.0008
Right LO > Right pF	1	Bilateral middle occipital gyrus, bilateral fusiform gyrus, bilateral lingual gyrus, bilateral inferior occipital gyrus, bilateral cuneus, bilateral superior occipital gyrus, bilateral middle temporal gyrus, bilateral inferior temporal gyrus, bilateral calcarine fissure	40 -60 -14	8995	$<10^{-6}$
	2	Right precentral gyrus, right postcentral gyrus, right middle frontal gyrus	22 -40 46	1270	0.0004

LO: Lateral occipital; **pF:** Posterior fusiform.

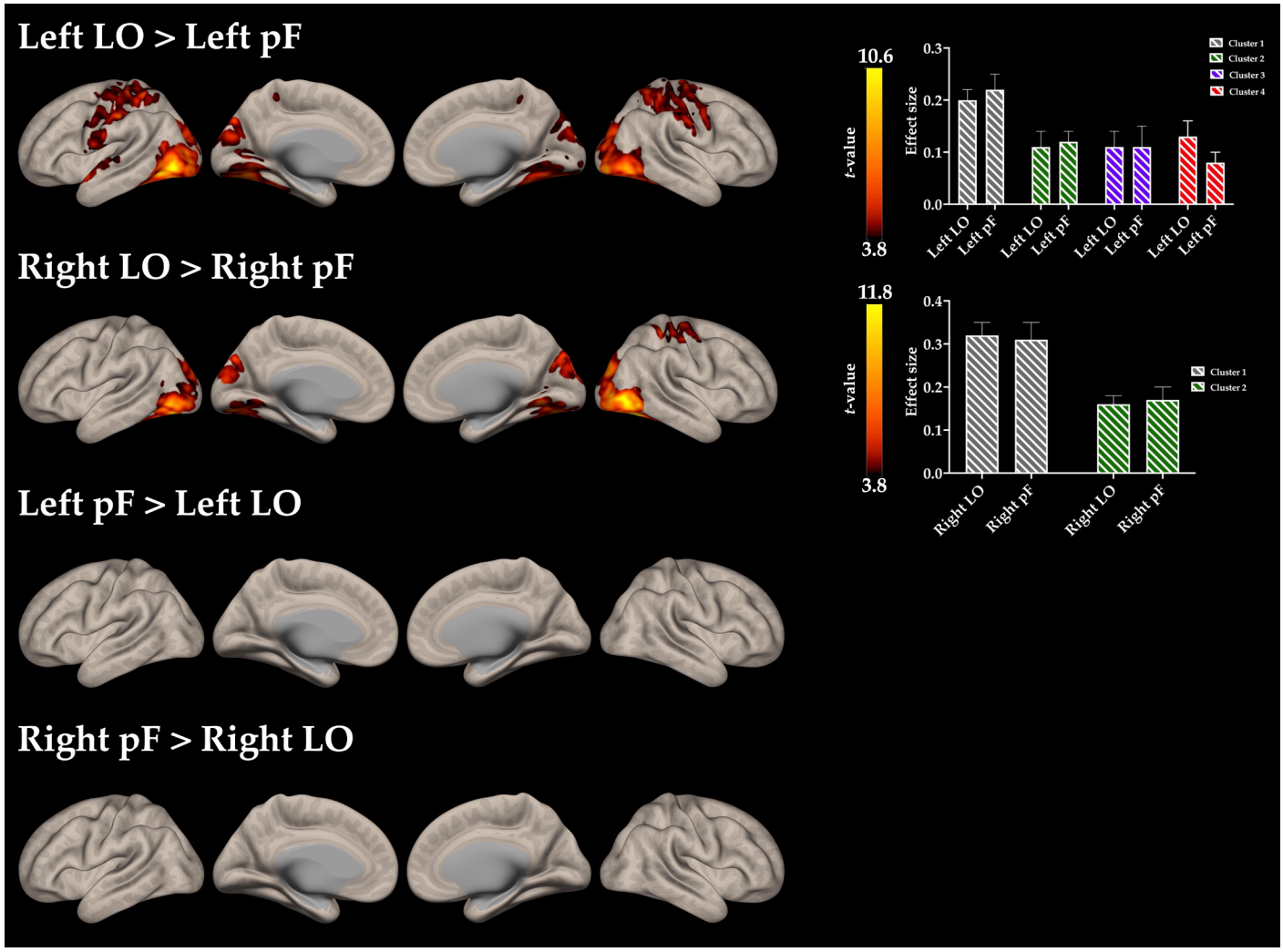


Figure 4. Differences in the intrinsic functional connectivity between the lateral occipital and posterior fusiform areas. Clusters in the effect size graphs in the right column correspond to the clusters defined in Table 3 (R: right, L: left).

hierarchy (12,15,17,18). Furthermore, although both LO and pF are sensitive to objects, it is known that these two regions exhibit differential functional sensitivity based on object size and position (5). Additionally, when examining regions where the right LO demonstrates greater iFC compared to the left LO, a cluster comprising solely the right hemisphere's LO and pF is obtained. Thus, it can be posited that both the right and left LO exhibit greater connectivity with their respective hemisphere's pF. The observed hemispheric lateralization may contribute to accelerating the processing of information during object perception.

Another cluster where the left LO exhibited higher connectivity than the right LO was identified around the posterior parietal cortex, which is part of the dorsal attention network (19). Neuroimaging experiments utilizing tasks requiring participants to shift or maintain their attention to one of two objects have demonstrated activation of the fronto-parietal regions involved in object-based attention. Furthermore, the importance of the left posterior parietal cortex and left intraparietal sulcus regions in object-based attention has been highlighted in previous studies (20,21). Additionally, it has been found that stroke patients with lesions in the left hemisphere exhibit deficits in object-based attention (22). Taken together, these findings suggest that the connectivity between the left LO and left posterior parietal regions may represent the neural underpinnings of object-based attention processes.

In contrast, the more localized functional connectivity patterns observed in pF regions underscore their specialization in processing specific object categories. pF, situated amidst the extrastriate cortex and higher-level visual cortex, is considered an optimal locus for processing moderately complex object features (23). Additionally, pF has been shown to represent object-based shapes, parts, and category-specific features that are independent of low-level visual features (24,25). According to the hierarchical framework, areas in both the occipitotemporal and occipitoparietal pathways are organized hierarchically, allowing low-level inputs to be transformed into more abstract representations through successive processing stages. Nearly all visual processing tasks engage V1 and V2. However, as one progresses from one area to another, neuronal response properties become increasingly complex. Within this framework, it is thought that pF plays a role, particularly in the subdivision of object categories based on semantic properties (26,27). Findings from this study suggest that, while encompassing ventral stream areas known to be crucial for processing various object categories, bilateral hippocampi are also connected to pF (not LOs). These connections likely facilitate distinguishing between different object categories, thereby contributing to efficient object recognition processes and long-term object memory. The more localized connectivity of pF with specific regions implicated in object recognition further emphasizes its specialization in processing visual stimuli within a constrained neural circuitry. Additionally, akin to the

findings of Hutchison et al., (2014) we found no iFC difference between the bilateral pF in contrast to lateralized iFC pattern of the LO. The absence of this difference indicates that object perception processes running in the pF are equally contributed by both hemispheres.

Comparative analysis of functional connectivity between LO and pF regions underscores the broader involvement of LO in distributed neural networks underlying object perception compared to pF. When examining the topography of these connectivity differences, it is particularly evident that the motor cortex prominently emerges, as illustrated in Figure 3. A recent study delineated two regions encompassing object-selective areas we refer to as LO and pF, as the lateral occipitotemporal cortex (LOTC) and the ventral occipitotemporal cortex (VOTC), respectively. They emphasized their functional specializations by proposing a network for action recognition (28). Specifically, the study posited an additional lateral stream for processing visual information, alongside the established dorsal and ventral streams, that is responsible for the neural basis of the action recognition. Furthermore, they proposed the representation of conceptual action in the left LOTC. Considering the iFC differences, particularly between the left LO and left pF in our study, we propose that the connections extending from LO to the motor cortex through the intraparietal sulcus may reflect an intrinsic characteristic of the action recognition network. The strong lateralization of the iFC pattern of LO in contrast to a bilateral distribution of that of the pF supports this proposal. It is known that various conceptual representations of actions such as tool use and language are lateralized to the left hemisphere (29,30). Conversely, various studies demonstrated that regions sensitive to facial and bodily cues, such as the fusiform face area and extrastriate body area, are right-lateralized (31). A reasonable interpretation of this lateralization is that action recognition and representation are primarily associated with the left LO, whereas processing of bodily cues crucial for other aspects of social perception constitutes a function of the right LO (28).

Limitations and future prospects

Although our study has provided valuable insights on object and action recognition, there are some limitations worth considering. First, our study focused only on intrinsic functional connectivity patterns of the LO cortex and pF regions, ignoring possible interactions with other brain networks involved in visual processing. Additionally, although our results revealed distinct connectivity profiles of the LO and pF in the resting-state, causal inferences regarding the functional role of these regions require additional experimental manipulations in well-designed task-based studies. Finally, examining the connectivity patterns of individuals with neurological or psychiatric disorders that affect object or action recognition may provide additional support regarding the functional specialization of these object-selective areas and also valuable insight into the neural mechanisms underlying these disorders.

As a result, our study has elucidated complex patterns of intrinsic functional connectivity in the LO cortex and pF regions that are critical for object perception and recognition. The apparent differences in functional connectivity underscore the subtle role of these brain regions in visual processing. Specifically, the extensive connectivity demonstrated by the LO, particularly with occipitotemporal and occipitoparietal regions, is consistent with its established role in integrating visual information across cortical areas, facilitating coherent object representation. Furthermore, the lateralization of the iFC of the LO and its extension to motor areas support the perspective that LO may be an important node of the network responsible for action recognition.

Acknowledgements: This study was produced from Ulaş Ay's doctoral thesis (Thesis No: 844813) and has not been presented anywhere before. Ulaş Ay acknowledges the support of Turkish Council of Higher Education for 100/2000 CoHE doctoral scholarship. This study was funded by the Scientific and Technological Research Council of Turkey (TUBITAK) grant #122S654.

Ethics Committee Approval: The study was approved by the Clinical Research Ethics Committee of Istanbul University Istanbul Faculty of Medicine (Protocol Number: 2021/670).

Informed Consent: Informed consent form was obtained from the participants.

Peer-review: Externally peer-reviewed.

Author Contributions: Concept- UA, TD; Design- UA, TD; Supervision- TD; Resource- TD; Data Collection and/or Processing- UA; Analysis and/or Interpretation- UA, TD; Literature Search- UA; Writing- UA, TD; Critical Reviews- TD.

Conflict of Interest: The authors declared that there is no conflict of interest.

Financial Disclosure: Authors declared no financial support.

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