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Distinct and distributed functional connectivity patterns across cortex reflect the domain-specific constraints of object, face, scene, body, and tool category-selective modules in the ventral visual pathway



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ABSTRACT

Primate occipitotemporal cortex (OTC) is composed of a mosaic of highly specialized brain regions each involved in the high-level visual analysis and recognition of particular stimulus categories (e.g., objects, faces, scenes, bodies and tools). Whereas theories attempting to account for this modular organization of category-selective responses in OTC have largely focused on visually driven, bottom-up inputs to OTC (e.g., dimensions related to the visual structure of the world and how it is experienced), other proposals have instead focused on the connectivity of OTC's outputs, emphasizing how the information processed by different OTC regions might be used by the rest of the brain. The latter proposals underscore the importance of interpreting the activity (and selectivity) of individual OTC areas within the greater context of the widely distributed network of areas in which they are embedded and that use OTC information to support behavior. Here, using resting-state fMRI, we investigated the functional connectivity (FC) patterns of OTC regions associated with object-, face-, scene-, body- and toolrelated processing defined from task-based localizers acquired in the same cohort of participants. We observed notable differences in the whole-brain FC patterns, not only across OTC regions, but even between areas thought to form part of the same category-selective network. Furthermore, we found that the neuroanatomical location of OTC regions (e.g., adjacency) had little, if any, bearing on the FC networks observed. FC between certain OTC areas and other regions traditionally implicated in sensory-, motor-, affective- and/or cognitive-related processing and the associated theoretical implications is discussed.

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Introduction

Convergent evidence from a wide variety of methodologies, ranging from non-human primate (NHP) neurophysiology to human functional MRI (fMRI), transcranial magnetic stimulation (TMS), and neuropsychology, suggests that occipitotemporal cortex (OTC) contains a constellation of highly specialized brain regions involved in the high-level perceptual analysis of different categories of visual stimuli (see Grill-Spector and Malach, 2004). For instance, human fMRI work has identified a number of regions – some of which have also been reported

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in the NHP (see for example, Nasr et al., 2011; Tsao et al., 2003, 2006; Wachsmuth et al., 1994) – that maximally respond to the viewing of particular object categories. These areas include the lateral occipital (LO) area and posterior fusiform sulcus (pFs) for basic objects (Malach et al., 1995), the occipital face area (OFA) and fusiform face area (FFA) for faces (Kanwisher et al., 1997), the retrosplenial cortex (RSC) and parahippocampal area (PPA) for scenes (Epstein and Kanwisher, 1998; Maguire et al., 1998), the extrastriate body area (EBA) and fusiform body area (FBA) for bodies (Downing et al., 2001; Peelen and Downing, 2005a) and the posterior middle temporal gyrus (pMTG) for tools (reviewed in Lewis, 2006). Consistent with this fMRI evidence, disruption to the normal activity of these regions, either via brain lesions or stimulation, selectively impairs the perceptual processing of specific object categories (e.g., Mahon et al., 2007; Moro et al., 2008; Parvizi et al., 2012; Pitcher et al., 2009, 2012; Urgesi et al., 2004).

Several theories have been proposed to account for this highly modular arrangement of category-selective neural responses in OTC, with the majority suggesting that this organization largely reflects the visual



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structure of the world and/or how it is experienced (e.g., Gauthier et al., 1999; Haxby et al., 2001; Levy et al., 2001). Given that many projections to OTC arise from early visual areas of the brain (Felleman and Essen, 1991), it is not surprising that most theories should attempt to account for its organization based on this connectivity. However, there is mounting evidence that visual stimulation, by itself, is not actually required for the typical patterns of category-selective responses in OTC to be normally expressed (e.g., Mahon et al., 2009; Pietrini et al., 2004). Thus, if visual experience is not necessary for the modular arrangement in OTC to be observed, then what other factors might influence its organization?

One particularly compelling alternative view, called the 'distributed domain-specific hypothesis', suggests that the category-selective organization of OTC, in addition to partially reflecting the constraints imposed by connectivity with early visual cortex, is an emergent property of the distinct connectivity patterns that OTC areas share with the rest of the brain, particularly the structures and pathways that use the information to guide behavior (Mahon and Caramazza, 2009, 2011). The key idea of the proposal is that the organization of OTC reflects a manifestation of the connectivity constraints imposed by a much more widely distributed network of areas (i.e., beyond that of visual cortex alone), with each network specialized for processing all types of information related to particular aspects of that object category (e.g., perceptual, sensory, motor, cognitive, and affective). The hypothesis, although difficult to test without significant developmental or genetic interventions (e.g., examining how networks may re-organize during development if key neural structures that have reciprocal connections with OTC are lesioned or eliminated), nevertheless captures the importance of considering the activity of single OTC areas within the context of a more widely distributed network of interconnected areas that use the information to support actions and behavior. This raises the simple question: What is the connectivity among different OTC regions and between each region and other structures in the brain?

Based on the notion that some insights into OTC functional organization might be revealed from the brain's functional connectivity (FC), here we used resting-state functional MRI (RS-fMRI) to directly compare the whole-brain FC patterns of localizer-defined OTC regions-ofinterest (ROIs). While a few previous studies have examined the FC patterns pertaining to single, or in some cases, two types of categoryselective areas (e.g., Baldassano et al., 2013; Bracci et al., 2012; Davies-Thompson and Andrews, 2012; Mahon et al., 2007; Nir et al., 2006; Stevens et al., 2012; Turk-Browne et al., 2010; Zhu et al., 2011), what has been largely missing in the literature is a systematic and detailed investigation of the FC relationships that each of these areas has not only with each other, but also with the rest of the brain. Here, we provide such an investigation and examine several key questions, each pertinent to gaining a better understanding of the functional organization of OTC:

- (1) How does the neuroanatomical proximity of different categoryselective ROIs correspond to their FC patterns? For instance, do areas situated more closely to one another in cortex show more similar patterns of FC?
- (2) Are there systematic differences in the FC of category-selective areas across the two hemispheres? For instance, does the typically stronger right-hemispheric activity in certain OTC areas, such as face- and scene-processing regions, translate to a more robust, extensive, and long-range pattern of FC for those right-hemisphere ROIs than their left-hemisphere counterparts?
- (3) What are the similarities and/or differences in the FC patterns of areas thought to form part of the same category-selective network? For instance, given their shared role in face processing, do distinct category-selective areas, such as the OFA, located in lateral-occipital cortex, and the FFA, located in ventro-temporal cortex, show similar patterns of whole-brain FC?

(4) Where in cortex are common 'convergence zones' for the different category-selective OTC networks? For instance, do face- and scene-processing networks, despite clear regional differences at the level of OTC, eventually converge upon common substrates elsewhere throughout the brain?

Material and methods

Participants

Twenty-three right-handed volunteers (12 females; mean age = 24.8 years), recruited from the Western University (London, Ontario, Canada; N = 11) and Queen's University (Kingston, Ontario, Canada; N = 12), participated in the resting-state and localizer experiments. Informed consent was obtained in accordance with procedures approved by each University's Health Sciences Research Ethics Board. Participants were naïve with respect to the hypotheses being tested.

Localizer experiments

Each participant took part in two types of functional localizer runs. The first included stimulus blocks of black-and-white photos consisting of faces, scenes, objects, and scrambled versions of these stimuli (modified from Cant and Goodale, 2007, 2011, see FSO localizer details below). The second included stimulus blocks of color photos consisting of headless bodies, tools, non-tool objects, and scrambled versions of these stimuli (Valyear and Culham, 2010, see BOT localizer details below). In both localizers, participants were required to maintain fixation on a dot (small black circle) superimposed on the center of each image. Each image subtended approximately 15° of the visual angle. Photos were repeated across runs, and the stimulus and epoch orders were pseudo-randomized and balanced across runs. To encourage participants to maintain attention throughout the localizer scans, they performed a 1-back task throughout, whereby responses were made, via a right-handed button press, whenever two successive photos were identical.

The purpose of these localizer scan sessions was to independently identify well-documented category-selective OTC ROIs involved in object-, face-, scene-, body-, and tool-related processing and then examine, using resting-state data, the convergent and divergent patterns of connectivity between these areas and with other regions of the brain (see Fig. 1 for an overview of the methods and general experimental approach employed).

Face, scene, and object (FSO) localizer

Stimuli were organized into separate 16-s blocks, with 16 photos per block, presented at a rate of 400 ms per photo with a 600 ms interstimulus interval. Each run lasted 450 s and was composed of four stimulus blocks per condition, with each stimulus block separated by a scrambled block. Two fixation/baseline blocks (20 s) were placed at the beginning and end of each run. All participants took part in three or four FSO localizer scans. Each stimulus block included two repeated photos.

Body, object, and tool (BOT) localizer

Stimuli were organized into separate 16-s blocks, with 18 photos per block, presented at a rate of 400 ms per photo with a 490 ms interstimulus interval. Each run lasted 450 s and was composed of six stimulus blocks per condition, seven scrambled blocks, and two fixation/ baseline blocks (20 s) placed at the beginning and end of each run. Stimulus blocks were organized into sets of three, separated by scrambled blocks and balanced for prior-block history within a single run. All participants took part in three or four BOT localizer scans. Each stimulus block included either three or four repeated photos, balanced across conditions.



Fig. 1. General methods overview. Category-selective regions for objects, faces, scenes, bodies, and tools were identified within occipitotemporal cortex via separate block-design localizer tasks and then whole-brain resting-state FC analyses were performed on each area using spherical ROIs (radius = 3 mm) centered on the peak voxel of activity in each region. A) Block design localizer tasks employed. Using the face, scene, and object (FSO) localizer (top), object-selective regions were identified using the contrast object > scrambled stimuli, face-selective regions were identified using the contrast face > scene stimuli and scene-selective regions were identified using the contrast scene > face stimuli. Using the body, object and tool (BOT) localizer (bottom), body-selective regions were identified using the contrast tool > object stimuli. B) ROI locations (in black), for left and right retrosplenial complex (RSC) and parahippocampal place area (PPA), overlaid atop a contrast map for scene > face stimuli generated using the localizer tasks. C) Time series form each ROI was correlated with the time series from every other voxel in the brain to generate a whole-brain correlation map, demarcating the FC of that ROI during the resting-state scan. LH = left hemisphere, RH = right hemisphere.

Resting-state experiments

A single resting-state scan was acquired for each participant in which they were instructed to rest with their eyes open while fixating at a central location. RS-fMRI exploits the correlations of slow bloodoxygenation-level-dependent (BOLD) oscillations between distinct brain areas in the absence of any task paradigm to provide reliable connectivity maps in both humans (Beckmann et al., 2005; Damoiseaux et al., 2006) and NHPs (Hutchison et al., 2011, 2012a,b; Margulies et al., 2009; Vincent et al., 2007). The low-frequency fluctuations (LFFs; ~0.01-0.1 Hz) of the BOLD signal are presumed to be a hemodynamic manifestation of coupling between slow fluctuations in neuronal activity (Fox and Raichle, 2007; Shmuel and Leopold, 2008; for review, see Leopold and Maier, 2012). It is important then to consider that the recorded signals represent an indirect measure of the underlying brain activity and further, that one cannot fully delineate the effects of modulation or interaction with other regions that may bias the estimated pairwise correlation between two ROIs.

Ongoing work has demonstrated that the FC patterns are shaped (though not fully determined) by anatomical connectivity. Brain regions

that are connected via white-matter tracts tend to show strong FC between those regions; however, FC does not guarantee a direct structural link between the two (Greicius et al., 2009; Honey et al., 2009; Shen et al., 2012; van den Heuvel et al., 2009; Vincent et al., 2007 for review, see Damoiseaux and Greicius, 2009). FC networks are also much more malleable than the underlying structural connectivity (SC) patterns in the sense that they can be modified by repeated evoked co-activation of regions on a relatively short timescale (e.g., over the course of learning a task, for reviews see Deco and Corbetta, 2011; Deco et al., 2011; Fox and Raichle, 2007) and thus, extend beyond existing structural connections. It has also been recently demonstrated that FC can vary even within the period of a standard scan, allowing for substantial deviation from the SC architecture (for review, see Hutchison et al., 2013). Taken together, interpreting the physical connections between regions identified to be functionally interconnected must be done with caution and consideration of previous diffusion imaging and animal neuroanatomical tracing studies. The value of FC measures should not, however, be seen as ancillary to non-invasive diffusion techniques that could be applied to explore OTC connectivity (e.g., Saygin et al., 2012). Beyond limitations of diffusion imaging in regard to delineating the origins,

crossings, and terminations of pathways, FC captures information about the ongoing temporal (and spatial) features of the brain's organization that cannot be gleaned from the SC matrix alone (Behrens and Sporns, 2012).

MRI acquisition and preprocessing

Imaging was performed on 3 T Siemens TIM MAGNETOM Trio MRI scanners located at the Centre for Functional and Metabolic Mapping (CFMM; at Western University) and the Centre for Neuroscience Studies (CNS; at Queen's University). For each participant, all functional data was collected using a T2*-weighted single-shot gradient-echo echoplanar imaging (EPI) acquisition sequence (repetition time [TR] = 2000 ms; slice thickness = 3 mm; in-plane resolution = 3 mm \times 3 mm; echo time [TE] = 30 ms; field of view [FOV] = 240 mm \times 240 mm; matrix size = 80×80 ; flip angle = 90°) with 32-channel (at CFMM) and 12-channel (at CNS) receive-only head coils. Each volume was comprised of 34 contiguous (no gap) oblique slices acquired at a ~30° caudal tilt with respect to the plane of the anterior commissure and posterior commissure (AC-PC), providing near whole brain coverage. For resting state scans, 1 run of 360 continuous functional volumes was collected (acquisition time of each scan was 12 min.). A T1-weighted high-resolution anatomical image was collected using an ADNI MPRAGE sequence (TR = 2300 ms; TE = 2.98 ms; FOV = 192 mm \times 240 mm \times 256 mm; matrix size = 192 \times 240 \times 256; flip angle = 9°; acquisition voxel size = $1 \times 1 \times 1$ mm). The resting-state scans and a second anatomical image were acquired in a separate session in four participants due to time constraints imposed during the initial imaging session.

All preprocessing and analysis for localizer and resting-state scans was implemented using the FMRIB Software Library toolbox (FSL, http://www.fmrib.ox.ac.uk, Smith et al., 2004; Woolrich et al., 2009) and included slice time correction for interleaved acquisitions (using Fourier-space time-series phase shifting), motion correction (six parameter affine transformation), brain extraction, spatial smoothing (Gaussian kernel of full-width at half-maximum [FWHM] 6 mm applied to each volume separately), high-pass temporal filtering (Gaussianweighted least-squares straight line fitting with sigma = 100 s), and normalization (12 degrees-of-freedom linear affine transformation) to the standard 152-brain MNI template (voxel size $= 2 \times 2 \times 2$ mm). Resting-state scans were additionally low-pass temporal filtered (halfwidth at half-maximum [HWHM] = 2.8 s, Gaussian filter). Global mean signal regression was not implemented in this study because it can artificially introduce negative correlations into the connectivity maps (Murphy et al., 2009) and the global mean signal may in fact have an underlying neural component (Scholvinck et al., 2010).

Region of interest (ROI) selection

For the localizer experiments we used a general linear model (GLM) with predictors created from boxcar functions convolved with a double-gamma hemodynamic response function. A boxcar function was aligned to the onset of each stimulus block with its duration dependent on stimulus block length (i.e., 8 volumes for both the FSO and BOT localizers). The baseline/fixation epochs were excluded from the model; therefore all regression coefficients (betas) were defined relative to the baseline activity during these time points. The subject-level analysis was carried out using FILM with local autocorrelation correction (Woolrich et al., 2001). A group-level GLM was carried out using FMRIB's Local Analysis of Mixed Effects (FLAME, Beckmann et al., 2003; Woolrich et al., 2004). Corrections for multiple comparisons were implemented at the cluster level using Gaussian random field theory (z > 2.3; cluster significance: p < 0.05, corrected).

At the group level, the most significantly active voxel, or peak, was identified based on a particular contrast, constrained by the anatomical location expected from previous reports (see below for details). This approach ensured that regions were selected objectively and could be reliably segregated from adjacent activations (see also Downing et al., 2006). We opted to select the ROIs at the group-level rather than at the single-subject level, for two important reasons. First, individuals can fail to show consistent and statistically significant activity in an intended ROI for a particular stimulus class (i.e., some ROIs can be localized consistently in nearly all participants whereas others are less robust). Accordingly, such participants would not be included in the FC analysis, resulting in different numbers of participants being used for different ROIs. Although on its own this is not inherently problematic, it would, however, significantly complicate the interpretation of differences (or similarities) between the patterns of FC across ROIs, as it would be unclear the extent to which they reflect real FC differences versus differences in the statistical power (i.e., number of participants) used to obtain those maps. Second, at the single-subject level, some object categories can produce multiple foci of activity that are difficult to disentangle (e.g., multiple face-selective regions along the fusiform gyrus, see Weiner and Grill-Spector, 2010). By selecting ROIs at the group-level based on well-established criteria (Downing et al., 2006) we avoid any such issues of ambiguity and are able to robustly and reliability identify the ROIs.

We defined the lateral occipital (LO) area and posterior fusiform sulcus (pFs) based on their selective response to objects (Malach et al., 1995), the occipital face area (OFA) and fusiform face area (FFA) based on their selective response to faces (Haxby et al., 2000; Kanwisher et al., 1997), and the retrosplenial complex (RSC) and parahippocampal area (PPA) based on their selective response to scenes (Epstein and Kanwisher, 1998; Maguire et al., 1998) in both hemispheres using the FSO localizer data. We defined the extrastriate body area (EBA) in both hemispheres and fusiform body area (FBA) in the right hemisphere (it was not active in the left hemisphere at the group level with a mixed effects analysis) based on their selective response to bodies (Downing et al., 2001; Peelen and Downing, 2005a) and the posterior middle temporal gyrus (pMTG) in the left hemisphere (it is typically a leftlateralized area) based on its selective response to tools (Lewis, 2006; Valyear and Culham, 2010), using the BOT localizer data. For specific details, see below.

Object-selective activity (LO and pFs) was localized based on the contrast of objects > scrambled. LO was defined by the peak voxel of activity near the lateral occipital sulcus (Grill-Spector et al., 1999, 2001; Malach et al., 1995). pFs was defined by the peak voxel of activity in the posterior aspect of the fusiform gyrus, extending into the occipitotemporal sulcus (Grill-Spector et al., 1999, 2001).

Face-selective activity (OFA and FFA) was localized based on the contrast of faces > scenes. OFA was defined by the peak voxel of activity in the inferior occipital gyrus (Calder and Young, 2005; Gauthier et al., 2000; Haxby et al., 2000; Puce et al., 1996), inferior and more medially located than the activity for LO. FFA was defined by the peak voxel of activity in the fusiform gyrus (Kanwisher et al., 1997).

Scene-selective activity (PPA and RSC) was localized based on the contrast of scenes > faces. PPA was defined by the peak voxel of activity located medially along the collateral sulcus and parahippocampal gyrus (Epstein and Kanwisher, 1998). RSC was defined by the peak voxel of activity located medially and ventrally in the posterior cingulate area, posterior to the corpus callosum, lying near the inferior junction of the occipital and parietal lobes (near the point where the calcarine sulcus joins the parieto-occipital sulcus, see Epstein and Higgins, 2007; Epstein et al., 2007; O'Craven and Kanwisher, 2000).

Body-selective activity (EBA and FBA) was selected based on the contrast of bodies > objects. EBA was defined by the peak voxel of activity in the posterior inferior temporal sulcus/middle temporal gyrus (Downing et al., 2001; Peelen and Downing, 2005b), superior to LO and OFA. FBA was defined by the peak voxel of activity in the fusiform gyrus (Peelen and Downing, 2005a; Schwarzlose et al., 2005), close to that selected for FFA (note that FBA was only selected in the right hemisphere as it was not active at the group level in the left hemisphere). Tool-selective activity (pMTG) was localized based on the contrast of tools > objects. pMTG was defined by the peak voxel of activity on the posterior middle temporal gyrus (Lewis, 2006; Martin et al., 1996; Valyear and Culham, 2010), positioned more lateral, ventral, and anterior to EBA. For details about MNI coordinates of all ROIs see Table 1.

Statistical analysis for functional connectivity of localizer-defined ROIs

Following selection of the category-selective peak voxels at the group level, spherical seeds (radius = 3 mm, volume = $\sim 113 \text{ mm}^3$) were centered at the peak locations and the mean time course for each seed ROI was extracted for every participant from their respective resting-state scan. It is critical to note, that the spherical seeds selected for each ROI did not overlap, barring the exception of R-FFA and R-FBA, which overlapped by (shared) a single voxel. The extracted time courses of each ROI was then used as predictors in a regression model for multiple regression at the individual participant level in which nuisance covariates for white matter, cerebrospinal fluid (both derived using the averaged time course from voxels contained within segmented MNI-template masks), and six motion parameters were included. This was followed by a second-level mixed-effects group-level analysis between participants. Images were thresholded using clusters determined by z > 2.3 and a (corrected for multiple comparisons) cluster threshold of p = 0.05. The group-level analysis produced thresholded z-statistic maps showing brain regions significantly correlated with each localizer-defined ROI across all participants. The group z-scores were projected from volume data to the PALS-B12 cortical surface (Van Essen, 2005) using the CARET (http://www.nitrc.org/projects/ caret) enclosed-voxel method (Van Essen et al., 2001). For the sake of clarity and interpretation, voxels that were negatively correlated with the ROI time courses are not displayed in the figures or discussed. These are, however, accounted for in the cross-correlation matrix of ROIs time series and whole-brain FC patterns and included in the clustering analysis (see below).

A third-level analysis was computed across relevant ROI pairs using both mixed and fixed effects analysis (z > 2.3; cluster significance: p < 0.05, corrected). The analysis allows for the calculation of differing (i.e., ROI A > ROI B) and shared (i.e. ROI A + ROI B) FC between the ROIs. The fixed effects analysis was implemented to show those regions whose z-scores did not pass the stringent statistical significance

Table	1
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Seed-region locations.

Area	MNI atlas space
Object areas	
R-LO	48/-74/-8
L-LO	-50/-82/-6
R-pFs	32/-40/-22
L-pFs	-32/-42/-22
Face areas	
R-OFA	44/-80/-14
L-OFA	-44/-82/-16
R-FFA	42/-44/-26
L-FFA	-46/-54/-22
Scene areas	
R-PPA	28/-44/-14
L-PPA	-26/-42/-16
R-RSC	16/-56/8
L-RSC	-18/-58/8
Body areas	
R-EBA	50/-64/-4
L-EBA	-52/-74/6
R-FBA	42/-40/-28
Tool areas	
L-MTG	-54/-68/-2

Note: Abbreviations are indicated in the main text.

required by the mixed effects analysis, but nonetheless may reveal important similarities and divergences. The results of these analyses are included in the Supplementary material.

Examining temporal and spatial relationships

Unweighted average-linkage hierarchical cluster analysis was applied to identify the functional clustering of both the OTC ROIs and their whole-brain FC patterns based on their temporal and spatial relationships. The algorithm utilizes a pairwise distance matrix to form a hierarchy of clusters, progressively merging clusters from the individual data elements based on the mean distance between elements.

Temporal relationships

To first construct the distance metric for the OTC ROIs, we calculated the correlations among the 16 ROIs. The extracted time course for each ROI was correlated with the time course of all other ROIs to obtain a correlation matrix (while partialling out the nuisance co-variables). Each element of the matrix was then z-transformed, averaged across participants, and then converted back to correlation values. The Euclidean distance between each pair of group-averaged correlations was then computed to assess the similarity among the OTC ROIs. A hierarchical cluster tree, referred to as a dendrogram, was then derived by applying the linkage criterion to the Euclidean distance matrix (Michener and Sokal, 1957) to allow for the relationships between the elements to be visualized. The method does not require the a priori selection of the cluster number. However, to determine cluster assignments, a distance threshold must be chosen-combining linked elements below that value into clusters. It is also important to note that the clustering will force elements (i.e., ROIs) to be eventually linked together at some level. To assess the quality of the clustering, we implemented a permutation test in which 10,000 randomly ordered pairwise distance matrices between ROIs were each evaluated using the cophenetic correlation coefficient and then we compared this randomized distribution of coefficients (n = 10,000) to that obtained from the original matrix. The cophenetic correlation coefficient value captures the correlation between the linking of elements (cophenetic distance) in the cluster tree and the distances between elements of the original distance vector. The closer the value of the cophenetic correlation coefficient is to 1, the more accurately the clustering solution reflects the underlying data.

Spatial relationships

The above procedure was then repeated, but instead the spatial correlation matrix of the group-level whole-brain connectivity patterns for each ROI was used. Each of the brain-masked FC maps was thresholded such that values above a z-score of 2.3 were assigned a 1, those below -2.3 were assigned a -1, and all other voxels were given a zero value. This was done to better delineate the spatial extent of significantly connected voxels and quantify the spatial overlap between the seed-defined networks. The spatial correlation between all FC maps was then calculated.

To further interpret the spatial and temporal relationships of the ROIs and their FC maps, each was also represented in graph form using a Kamada–Kawai algorithm (Kamada and Kawai, 1989). The process arranges the network nodes such that highly correlated nodes are closer together and weakly correlated nodes are further apart. The distance was calculated based on the absolute values of correlation coefficients. The graphs' edges were then thresholded at $r \ge |0.3|$ and $r \ge |0.1|$ for the temporal and spatial correlations, respectively. Degree centrality, the number of edges of a node that connect it to other nodes, was also calculated and represented by the size of the node.

Finally, using the same procedure as described above, temporal correlation values were also calculated between each OTC ROI and the averaged time course of voxels contained within select brain areas of interest defined using the automated anatomical labeling (AAL) template (Tzourio-Mazoyer et al., 2002). The AAL regions were selected a priori based on the previously established sensory, motor, emotional and cognitive processing roles of the regions. The connectivity of the ROI with the AAL regions was then represented as a "connectivity fingerprint" for each OTC ROI. This allows for the similarities and differences of connectivity patterns between seed regions to be highlighted and immediately identified. While the selection of AAL regions can determine the shape of the fingerprint and highlight specific similarities/differences, the connectivity of the seed region with all brain areas is captured in the figures from the voxel-wise seed based results that display the whole-brain FC maps.

Additional control seed regions

To investigate possible partial volume effects of the selected OTC seed regions (e.g., to test whether the OTC seeds contain residual nonvisual signals that could fully account for the observed connectivity patterns), additional seeds were selected within the gray matter, directly adjacent and anterior to the task-localized regions. Statistical analysis of the anterior seeds was performed in the same way as described above for the task-defined regions. The thresholded functional maps were then binarized and directly compared to the respective OTC FC pattern (see Fig. 11).

Results and discussion

Functional connectivity of object-selective ROIs LO and pFs

LO functional connectivity

We observed much more extensive FC for L-LO than R-LO (see Fig. 2A; for statistical comparisons, see Supplementary Fig. 1). L-LO connectivity extended dorsally into bilateral parieto-occipital sulcus (POS) and posterior IPS (pIPS) as well as ventrally into bilateral posterior fusiform gyrus. In contrast, the connectivity of R-LO extended only unilaterally into lateral dorsal visual areas and near the junction of the POS and IPS. Assuming the sharing of information within functionally interconnected circuits, the general pattern of LO-pIPS FC corresponds well not only with previous observations of object-selective responses in and around the posterior IPS (Konen and Kastner, 2008), but also with findings reporting the decoding of object-directed grasping-related signals from both pIPS (Gallivan et al., 2011) and LO (Gallivan et al., 2013b).

pFs functional connectivity

In contrast to the asymmetrical FC patterns found with L-LO and R-LO, L-pFs and R-pFs showed largely symmetrical FC maps (see Fig. 2B; for statistical comparisons, see Supplementary Fig. 1). Both L-pFs and R-pFs connectivity extended unilaterally into the surrounding fusiform and parahippocampal gyri, superior temporal sulcus (and surrounding gyrus; STS and STG, respectively), and with small patches extending into insular cortex. In addition, R-pFs also showed FC with ipsilateral posterior middle temporal gyrus (pMTG) and with small patches of contralateral fusiform gyrus. Notably, both L-pFs and R-pFs showed distinct connectivity with several subcortical structures including the thalamus, neostriatum, and amygdala. Convergent evidence suggests that 1) the occipitotemporal-medial temporal pathway, extending into the parahippocampal gyrus, may be important for longterm object memory, 2) the occipitotemporal-neostriatal pathway, extending into basal ganglia structures, for visually dependent habit formation and skill learning, and 3) the occipitotemporal-amygdaloid pathway, extending into the amygdala, for emotional processing (see Kravitz et al., 2013 for an in-depth review of these different OTC pathways).

Functional connectivity overlap between LO and pFs

Consistent with the notion suggested above that LO and pFs might route object-related information along separable pathways in the brain (i.e., LO to parietal cortex and pFs to ventral OTC and nearby subcortical structures), in both the left and right hemispheres we found very little overlap between their whole-brain patterns of FC (see Figs. 2C–D; for statistical comparisons, see Supplementary Fig. 1). In fact, we only observed small FC overlap in the patches of cortex that lie directly in between the two ROIs. Note that, in the very least, this small level of overlap should be expected given the 1) spatial blurring inherent in the hemodynamic response, and 2) spatial smoothing applied to the data. Thus, despite both LO and pFs showing the 'same' type of object-selectivity (and localized accordingly based on the common contrast of objects > scrambled), these FC results suggest that these two ROIs may communicate object-related information with rather distinct pathways in the brain.

Differences between correlation- and localizer-defined spatial maps

In light of previous evidence indicating a close correspondence between the brain maps defined using task-based and RS-connectivity analysis methods (Laird et al., 2011; Smith et al., 2009; Toro et al., 2008; though see Mennes et al., 2013), we directly examined the extent to which this correspondence would hold between the networks localized using standard subtraction contrast approaches and the resultant RS-connectivity maps generated from well-documented categoryselective nodes within these task-evoked networks. We found that RSconnectivity analyses revealed unique activity dorsally in and around the POS, subcortically (in the regions already noted above), and in the STS/STG and insular cortex (see Fig. 2E).

While noteworthy, these unique sites of FC must be interpreted with some level of caution. Comparisons of resting-state maps with taskevoked maps necessarily hinge on the exact contrast performed with the localizer data. For example, face-selective areas (discussed in the next section) can be defined via a multitude of contrasts (e.g., faces > scenes, faces > objects, faces > scrambled stimuli, and faces > baseline/ fixation) and these different contrasts may - depending on the stringency of the contrast criteria - either reveal less or more of the underlying network that shows selectivity for faces. That is, one would expect far less, but more focused face-related activity, for the contrast of faces > scenes than the contrast of faces > baseline/fixation, with much of the activation in the latter contrast simply being attributable to the general effects of visual stimulation, attentional demands, and/or the task performed rather than face-selective processing as such (recall that during the localizer scans participants performed a one-back detection task, but during fixation/baseline epochs they simply maintained fixation). To fully account for the effect of contrast and aid comparisons between the RS-connectivity and task-based maps (as well as related interpretations), here we have chosen to overlay activity for all three of the aforementioned maps (see Fig. 2E). This way, it can be clearly seen the unique areas revealed with the RS-connectivity analyses (Fig. 2E, in red) versus those areas activated by the contrasts used to define the object-selective ROIs (Fig. 2E, in blue; objects > scrambled) and those areas active simply due to the general effects of task, visual stimulation, and/or attention (Fig. 2E, in green). Note that because comparisons between the FC- and localizer-defined maps, though informative, constitute a somewhat minor component of this study, we only return to a discussion of these comparisons at the very end of the Results and discussion section.

Functional connectivity of face-selective ROIs OFA and FFA

OFA functional connectivity

We observed a more extensive pattern of FC for L-OFA than R-OFA (see Fig. 3A; for statistical comparisons, see Supplementary Fig. 2). Whereas the network connectivity for R-OFA was constrained bilaterally to lateral occipital and surrounding cortex, the connectivity of L-OFA was far more expansive. It not only encompassed larger bilateral swaths of activity in lateral occipital cortex, but also extended dorsally into bilateral POS, posterior and medial IPS and superior parietal lobule



Fig. 2. Functional connectivity of object-selective LO and pFs ROIs. Group averaged whole-brain correlation maps and their overlap are shown for left and right LO and pFs separated according to putative subdivisions (A–B) and cortical hemisphere (C–D). E) Overlap comparison of the activation maps generated using FC methods from all the ROIs (FC of all Object ROIs, shown in red, generated by combining connectivity maps across the four ROIs), the subtraction contrast used to identify the object-selective regions (shown in blue), and the sub-traction contrast of object stimuli versus fixation (shown in green). ROI locations are shown in black and differentiated according to their shapes (denoted by the legend in B). All statistical maps are threshold at a z-score of 2.3. LH = left hemisphere, RH = right hemisphere. White lines on the flat maps indicate major sulci. CoS = collateral sulcus, ITS = inferior temporal sulcus, POS = parieto-occipital sulcus, IFS = intraparietal sulcus, CiSm = marginal ramus of the cingulate sulcus, POCes = postcentral sulcus, CiS = cingulate sulcus, SF = sylvian fissure.

(SPL), and even into the medial precentral gyrus/superior cingulate cortex and medial superior frontal gyrus (SFG). Notably, this bilateral medially-extending frontal cortex FC closely corresponds with the well-documented representation of the face and upper body found with stimulation studies in the medial supplemental motor cortex of both humans and monkeys (Penfield and Welch, 1951; Woolsey et al., 1952).

FFA functional connectivity

We found a far more extensive network of FC for L-FFA than R-FFA (see Fig. 3B; for statistical comparisons, see Supplementary Fig. 2). The observed connectivity of R-FFA was completely unilateral, and extended into the MTG, STG and inferior parietal lobule as well as frontally along the inferior frontal gyrus (IFG) and anterior insular region. In contrast, the connectivity of L-FFA extended into the contralateral hemisphere



Fig. 3. Functional connectivity of face-selective OFA and FFA ROIs. Maps are computed and shown as in Fig. 2.

along the fusiform gyrus, anterior STG and paracentral lobule medially (i.e., supplementary motor area, SMA) and showed quite extensive unilateral connectivity. Included among these unilateral areas is FC with MTG, STS and STG (the latter two being regions commonly activated by the viewing of faces, see Atkinson and Adolphs, 2011; Kanwisher and Yovel, 2006), IPL, posterior and medial IPS, postcentral and precentral gyri, supplementary motor region, junction of the SFS and precentral sulcus [frontal eye fields (FEF)/dorsal premotor (PMd) cortex in humans], middle and inferior frontal gyri (MFG and IFG), insular cortex, and lastly, a frontal region located anteriorly along the IFS, often referred to as the IFS face patch (IFSFP), frequently reported in both humans (Avidan et al., 2005; Huth et al., 2012) and monkeys (Tsao et al., 2008a,b). Functional connectivity overlap between OFA and FFA

The FC maps of OFA and FFA showed very little overlap, with the exception of L-pIPS for the face-selective ROIs seeded in the left hemisphere (i.e., L-OFA and L-FFA) and the small patch of cortex bordered by the two ROIs bilaterally (Figs. 3C–D; for statistical comparisons, see Supplementary Fig. 2). With regard to the overlap found in pIPS, others have recently reported sensitivity for face stimuli in pIPS in addition to that of OFA and FFA (Kietzmann et al., 2012). One possibility, based on the FC observed here, is that OFA and FFA may in some way contribute to these previous reports of face-sensitive responses in pIPS. Beyond this quite small overlap, however, substantive differences in the FC patterns of OFA and FFA indicate that these two regions may be performing unique roles in the representation of face stimuli (for review of task-

based data, see Taylor and Downing, 2011) and transmitting this information to different sites in the brain.

Functional connectivity of scene-selective ROIs RSC and PPA

RSC functional connectivity

We observed a far more extensive pattern of whole-brain FC for R-RSC than for L-RSC (see Fig. 4A; for statistical comparisons, see Supplementary Fig. 3). The connectivity of L-RSC was largely constrained bilaterally to areas of surrounding precuneus, fusiform, and parahippocampal gyri, as well as unilateral STG and posterior MTG. In contrast, the connectivity of R-RSC, in addition to spanning these same general regions, extended unilaterally into the SPL, lateral IPS (LIP), STG and surrounding auditory cortex, insula, medial post- and precentral gyri, medial SFG, FEF/PMd and ventral premotor (PMv) cortex, as well as contralaterally into the precuneus and posterior and anterior cingulate cortices. Anatomical connectivity studies in non-human primates are largely consistent with this observed pattern of FC. RSC and the posterior cingulate region are reciprocally connected with parietal regions, such as 7a and LIP, as well as the medial temporal lobe (MTL), making it ideally positioned to interface between the allocentric coding of space in MTL and the egocentric coding of space in parietal cortex (Epstein, 2008; Maguire, 2001; Vogt et al., 1992). These patterns of functional and anatomical connectivity, combined with functional neuroimaging task-based evidence (as reviewed in Epstein, 2008), support the notion that RSC might be particularly involved in spatial memory processes for the



Fig. 4. Functional connectivity of scene-selective RSC and PPA ROIs. Maps are computed and shown as in Fig. 2.

purposes of orienting and navigating oneself within environments (Epstein, 2008).

in Kravitz et al., 2013). This pattern of anatomical connectivity in nonhuman primates corresponds well with the patterns of FC observed here.

PPA functional connectivity

We found diametrical differences between L-PPA and R-PPA in the amount and extent of FC (see Fig. 4B; for statistical comparisons, see Supplementary Fig. 3). Whereas R-PPA showed significantly larger amounts of FC, it was constrained to both OTC and parietal cortex; by contrast, L-PPA showed less overall amounts of FC, but it extended into frontal cortical regions (for findings of a similar nature, see Stevens et al., 2012). Specifically, R-PPA showed bilateral FC extending into the posterior cingulate, POS, precuneus, SPL, and medial IPS, as well as ipsilateral FC with the right MTG and STG. By contrast, L-PPA showed bilateral FC with anterior cingulate cortex (ACC) and the fusiform and parahippocampal gyri, as well as ipsilateral FC with precuneus and insular cortex and contralateral FC with MFG, near the frequently reported functional location of dorsolateral prefrontal cortex (DLPFC, Curtis and D'Esposito, 2003).

It is worth further noting that L-PPA, in addition to showing significant FC with MTL structures, also showed subcortical ipsilateral FC with the basal ganglia (pallidum and the tail of the putamen) and anterior thalamus—a set of interconnected nuclei that, among other things, coordinate movements of the body and gait (Kandel et al., 2000). In nonhuman primates, a putative homologue of PPA has recently been identified (monkey PPA, mPPA, see Nasr et al., 2011; Rajimehr et al., 2011), and lies immediately anterior to monkey area TEO in inferotemporal (IT) cortex. Anatomical studies show that anterior TEO and its anterior neighboring area, TE, project directly to the putamen as well as the tail of the caudate, and with TE in particular projecting to PFC (as reviewed

Functional connectivity overlap between RSC and PPA

Connectivity maps between the scene-selective ROIs, RSC and PPA, showed very little overlap (Figs. 4C-D; for statistical comparisons, see Supplementary Fig. 3). For L-RSC and L-PPA, the connectivity overlap was constrained bilaterally to the fusiform and parahippocampal gyri and the precuneus unilaterally. For R-RSC and R-PPA, the overlap was greater, extending bilaterally into the fusiform and parahippocampal gyri, POS, pIPS and SPL. These general patterns of FC overlap support observations of a parieto-medial temporal pathway in primates that supports spatial navigation, which courses medially through posterior cingulate cortex and RSC to the medial temporal lobe (MTL), where PPA is located. Again, however, consistent with our observations of the FC patterns for object- and face-selective ROIs, we generally observed very little overlap between the RSC and PPA FC maps. This adds mounting evidence to the notion that RSC and PPA may support complementary, yet distinct, mechanisms in the core cognitive ability of spatial navigation (see Epstein, 2008 for review).

Functional connectivity of body-selective ROIs EBA and FBA

EBA functional connectivity

We observed very similar levels, yet in some regions quite distinct, whole-brain FC patterns for both L-EBA and R-EBA (see Fig. 5A; for statistical comparisons, see Supplementary Fig. 4). L-EBA showed bilateral FC with the post- and precentral gyri, anterior SFG, MTG, STG and



Fig. 5. Functional connectivity of body-selective EBA and FBA ROIs. Maps are computed and shown as in Fig. 2. Note that no ROI was defined for L-FBA as this region was not active at the group-level with mixed-effects statistical criteria.

surrounding auditory cortex, IPL, and cingulate cortex, as well as ipsilateral FC in anterior IPS (aIPS), IFG and FEF/PMd. R-EBA showed bilateral FC with mid-to-anterior cingulate cortex, FEF/PMd, post- and precentral gyri, STG, insular cortex as well as ipsilateral FC in pIPS, aIPS, and SPL. EBA-insular FC seems noteworthy given that the insula has been implicated in a wide-range of cognitive processes ranging from hand and eye movement control (Fink et al., 1997; Pelphrey et al., 2005) to bodily selfawareness (Craig, 2009; Karnath et al., 2005) and a sense of body ownership (Nieuwenhuys, 2012; Tsakiris et al., 2007). For R-EBA, we also found FC with subcortical regions, specifically with the right anterior thalamus and basal ganglia (posterior putamen and pallidum).

In addition to these observations, in frontal cortex we found notable separation in the FC patterns of L-EBA versus R-EBA. L-EBA showed bilateral FC with the ACC and rostral region of SFG, areas typically associated with executive functions, decision-making, and cognitive control (Rushworth et al., 2007), whereas R-EBA showed bilateral FC with the well-described cingulate motor areas (Picard and Strick, 2001). To speculate, these patterns of FC, when taken together, suggest a variety of pathways through which EBA may share visual information about the body with areas involved in sensing, selecting, and exerting cognitive control over the body's various effectors (legs, limbs, eyes, etc.)

FBA functional connectivity

R-FBA showed extensive bilateral FC that was largely constrained to the occipital, temporal, and parietal cortices (although in the right hemisphere, there was some small frontal connectivity, see Fig. 5A; for statistical comparisons, see Supplementary Fig. 4). Specifically, R-FBA showed bilateral connectivity with much of OTC, precuneus and POS, posterior-to-middle cingulate cortex, SPL, IPS, IPL, STG and surrounding auditory cortex, as well as ipsilateral FC with ventral premotor and insular cortex and contralateral FC with anterior temporal cortex.

Functional connectivity overlap between EBA and FBA

We observed several key nodes of FC overlap between L-EBA, R-EBA, and R-FBA in 1) the STG near primary auditory cortex bilaterally, 2) the aIPS/hand-area of primary somatosensory cortex bilaterally, and 3) near the R-EBA (overlap denoted in white, Fig. 5A). While the overlap in R-EBA simply suggests convergence in the integrated circuits underlying visual-perceptual body processing, the former two observations are of particular interest as they suggest a convergence of bodyrelated information upon areas frequently implicated in the sensory encoding of sound and speech (Hickok and Poeppel, 2007; Okada et al., 2010; Peelle et al., 2010) and areas implicated in sensorimotor processing for hand movements and object manipulation (Cavina-Pratesi et al., 2010; Culham et al., 2003; Frey et al., 2005b; Gallivan et al., 2011; Tunik et al., 2005), respectively.

In addition to these convergence zones in the FC patterns of the body-selective ROIs, it is worth noting that several FC differences were also revealed. For instance, one noteworthy observation is that R-FBA largely showed FC constrained within the parietal, temporal, and occipital lobes whereas the FC of L-EBA and R-EBA extended further and far more extensively into frontal cortex. These FC differences suggest that EBA and FBA may be performing complementary, yet distinct, neural computations in body-related processing. Task-based fMRI findings offer some support for this notion, showing stronger body part selectivity in EBA than FBA and a relative bias in FBA for more complete images of the body (Taylor et al., 2007). With regard to the EBA versus FBA FC patterns observed here, one possibility, though speculative, is that this stronger body part selectivity in EBA emerges due to its more prominent FC with the body part maps represented in the somatosensory and motor cortices.

Functional connectivity of tool-selective ROI pMTG

Fig. 6 shows the full-brain network connectivity of the tool-selective ROI, L-pMTG. For the sake of allowing direct comparisons, we have also

overlaid the FC map corresponding to L-EBA, a ROI location located a mere ~1 cm from the ROI seed location of pMTG (for statistical comparisons, see Supplementary Fig. 4). Two observations are immediately apparent: 1) the FC map of pMTG is not quite as extensive and distributed as that of EBA, and 2) in consideration of their close anatomical proximity, there is very little overlap in the whole-brain FC maps of the two regions. Taken together, it is clear that anatomical vicinity alone cannot fully capture nor explain the distribution of FC that each categoryselective OTC has with the rest of the brain (otherwise one would expect far more graded than discrete transitions in the patterns of whole-brain connectivity between adjacent OTC areas).

pMTG functional connectivity

pMTG showed connectivity with many of the brain areas shown to be engaged in the visual processing of tools, pantomiming of tools, the use of tools and accessing knowledge associated with their use (Frey, 2007; Frey et al., 2005a; Gallivan et al., 2013a; Lewis, 2006; Mahon et al., 2007; Martin, 2007; Valyear et al., 2012). In particular, pMTG showed bilateral connectivity with POS, precuneus, posterior cingulate, pIPS, SPL, MTG, superior STS, insular cortex, MFG and IFG, as well as ipsilateral connectivity with middle-to-anterior IPS, IPL, lateral postcentral gyrus, PMv, PMd/FEF, and medial fusiform gyrus. Notably, these latter ipsilateral areas are all robustly activated in the context of viewing tools and the performance of tool-related tasks (Lewis, 2006). This pattern of FC suggests that the brain areas involved in the viewing of tools, like pMTG, are functionally interconnected with the brain networks involved in pantomiming and imagining tool use, naming tools, and hearing tool-related sounds (for review, see Lewis, 2006).

Convergence and divergence in the whole-brain functional connectivity patterns across category-selective networks

Functional connectivity in lateral-occipital cortex

As can be clearly seen in Figs. 7A and B (for statistical comparisons, see Supplementary Fig. 5), two major conclusions can be readily drawn from the overlap in the FC patterns between the various ROI examined in lateral occipital cortex (LO, OFA and EBA): 1) that EBA, in both the left and right hemispheres, shows by far the most extensive full-brain FC and, 2) despite the three ROIs being situated in such close proximity to each other in cortical space (see ROIs denoted by black symbols), they show considerably little overlap in their FC patterns across the whole brain (note that we made this very same observation above when considering the FC overlap between the toolselective pMTG and the body-selective EBA). With regard to this second point, it is worth noting that the *only* zone in which the FC maps of the three different ROIs converged was in the middle temporal gyrus of both hemispheres (overlap denoted in white). Considering the spatial blurring inherent in the hemodynamic response and the spatial smoothing applied to the fMRI data, this area of overlap - in the very least - is to be expected.

In the left hemisphere ROIs (Fig. 7A), we found a good degree of overlap between the FC of L-LO and L-OFA in the fusiform and parahippocampal gyri ipsilaterally, the parahippocampal gyrus contralaterally, and the lateral occipital cortex and dorsal occipital cortex bilaterally (denoted in pink). Between L-LO and L-EBA we only observed FC overlap in a small patch of cortex between their ROI seed locations (as well as a corresponding location in the contralateral hemisphere, denoted in cyan). However, as a notable departure from FC overlap being constrained to the occipital and temporal cortices, in both hemispheres the FC of L-OFA and L-EBA showed small overlap on the superior medial wall of the cingulate, in the plane of the central sulcus, saddling the border between the primary somatosensory and motor cortices (denoted in yellow). With regard to the homunculus represented in primary motor cortex, this site of overlap approximately corresponds to the shoulder/trunk area and with regard to the homunculus in primary sensory cortex, this site additionally corresponds to the neck/head area



Fig. 6. Functional connectivity of the tool-selective left pMTG ROI. For comparison, the FC map generated from the left EBA ROI is overlaid with that generated from the left pMTG ROI (in A). B is computed and shown as in Fig. 2E.

(Kandel et al., 2000). Using this site of overlap as a neuroanatomical frame of reference, the unique site of L-OFA connectivity located more anteriorly (in superior cingulate/SFG) may correspond to the neck and head representations of the body contained in primate SMA (Penfield and Welch, 1951; Woolsey et al., 1952).

Between the FC maps of the right hemisphere ROIs we found quite little FC overlap (Fig. 7B; for statistical comparisons, see Supplementary Fig. 6). For instance, for R-LO and R-OFA we observed overlap in posterior ITG (within lateral occipital cortex) and dorsal occipital cortex (denoted in pink). For R-LO and R-EBA, we found small overlap in dorsal occipital cortex near pIPS and in lateral occipital cortex (denoted in cyan). Lastly, for R-OFA and R-EBA, in contrast to the frontal FC overlap noted with their left hemisphere counterparts (briefly discussed above), we observed rather small overlap along the ITG and the fusiform gyrus (denoted in yellow), the latter in the vicinity of the category-selective ventro-temporal seed regions.

Functional connectivity in ventro-temporal cortex

Figs. 7C, D and E (for statistical comparisons, see Supplementary Figs. 7 and 8) allow for two further conclusions to be drawn: 1) of the ventro-temporal cortex areas, both L-FFA and R-FBA show the most extensive full-brain FC, and 2) as was observed for lateral-occipital cortex, the three ventro-medial ROIs display very little overlap in their FC profiles (as indicated by the very small patches of activity denoted in white). This latter observation is perhaps best exemplified in the markedly distinct whole-brain FC maps of R-FFA and R-FBA (Fig. 7E), which, due to their near anatomical proximity (Peelen and Downing, 2005b; Schwarzlose et al., 2005), actually have ROI seed voxels lying directly adjacent to one another on cortex. This outcome, combined with several of the findings already discussed above, clearly suggests that the close neuroanatomical proximity of different ROIs on cortex does not translate into similarities in the patterns of whole-brain FC observed from these regions.

In the left hemisphere ROIs (Fig. 7C), we found only small overlap between the FC maps of L-pFs and L-FFA along ipsilateral IFG and fusiform gyrus (denoted in yellow). Between L-pFs and L-PPA FC maps we observed only small overlap in the ipsilateral fusiform gyrus extending into the parahippocampal gyrus (denoted in pink). Lastly, between L-FFA and L-PPA, we found no FC overlap (except for the areas in white, as already indicated above). This is consistent with the notion that these latter two brain regions engage largely distinct circuitry for stimulus processing (Kanwisher, 2000, 2010, see also Nir et al., 2006; Zhu et al., 2011). Note that even in the cases where FC overlap was observed (Fig. 7C), it did not occur outside OTC.

In the right hemisphere ROIs (Fig. 7D), we found only small FC overlap between R-pFs and R-FFA in ipsilateral ITG and near their ROI seed locations (denoted in yellow). Between R-pFs and R-PPA we observed only small FC overlap in the ipsilateral fusiform and parahippocampal gyri and posterior MTG (denoted in pink). Lastly, between R-FFA and R-PPA, we only observed very small connectivity overlap in the ipsilateral MTG (denoted in cyan). Again, note that none of these areas of overlap extended outside of OTC.

Lastly, while there are several notable differences in the patterns of whole-brain FC between R-FFA and R-FBA (despite their close proximity), of particular interest are the sites in which connectivity overlap was observed: ipsilateral MTG, pSTS, SMG and IFG (see Fig. 7E). In the case of



Fig. 7. Overlap of functional connectivity of all category-selective regions across OTC. Whole-brain correlation maps and their overlap are shown for lateral occipital areas on the left (A) and right (B) and ventro-temporal areas on the left (C) and right (D). E) Overlap of FC between right FFA and FBA. ROI locations are shown in black and differentiated according to their shapes (denoted by legends associated with each cortical map). All statistical maps are threshold at a z-score of 2.3. Note that the FC of pMTG is not shown in A. LH = left hemisphere, RH = right hemisphere.

FC with MTG and pSTS, these areas have been implicated in voice recognition and speech processing (Davis and Johnsrude, 2003), are commonly activated in face discrimination tasks (Haxby et al., 2000) and have recently been shown, through combined fMRI and diffusion-weighted imaging, to have direct structural connectivity with FFA (Blank et al., 2011). In addition, pSTS, has been implicated in the processing and recognition of biological motion (for review, see Peelen and Downing, 2007).

Differences between RS- and task-based maps

Previous work has demonstrated considerable correspondence between the brain networks derived from task- and RS-based data (Smith et al., 2009; Toro et al., 2008), suggesting that the spontaneous intrinsic activity of the brain at rest can provide a framework for understanding its responses to the external world (Fox et al., 2006; Raichle, 2010). Consistent with this notion, the patterns of OTC FC observed in the current study converge upon many of the same regions activated in a wide variety of semantic knowledge tasks, such as the MTG, parahippocampal and fusiform gyri, IPL, prefrontal cortex, and the posterior cingulate gyrus (see Binder et al., 2009 for a recent meta-analysis of 120 fMRI studies). There is mounting evidence, however, that RS-based analyses alone cannot provide a complete account of task-evoked networks, and vice versa (see Mennes et al., 2013). As suggested by Mennes et al. (2013), part of this discrepancy may result from fundamental differences in the analyses employed. Whereas task-based analyses tend to average responses over several repetitions of stimuli (i.e., trial-based averaging) and, in essence, ignore any changes in the temporal dynamics across trials, RS-based analyses fully capture covariations in the spontaneous fluctuations of the BOLD signal. In addition to this basic methodological difference, substantial differences in what the two approaches actually measure should further dictate that they need not always be in perfect alignment. Whereas the task-independent nature of RS-analyses has the potential to reveal the full underlying architecture that can be utilized at any given moment to support the processing of information related to all aspects of the object category (e.g., perceptual, sensory, motor, cognitive, and affective), the brain networks activated by a particular task (e.g., in the localizer tasks employed here, detecting the same image on successive trials) should be largely composed only of those areas required for performing the task (i.e., perceptual discrimination of the particular object category). As such, it follows that RS-analyses have the capacity to provide unique, yet complementary insights into the latent pathways that flexibly support the utilization of object knowledge in accordance with task demands.

Cluster and network analysis

In order to provide a more quantitative analysis of the FC between different OTC ROIs (i.e., temporal correlation relationships) as well as similarities and differences between their whole-brain FC patterns (i.e., spatial correlation relationships), here we provide complete correlation matrices and the results of hierarchical cluster analyses (see the Material and methods section) for the ROI time courses and resulting spatial connectivity maps (see Fig. 8).

Within-OTC connectivity

The top panel in Fig. 8A shows a complete correlation matrix of the time courses of each ROI correlated with that of every other ROI, averaged across all participants. To further show the relations between the time courses, we performed average-linkage hierarchical cluster analysis of these ROIs (see Fig. 8A, middle panel). Here, we observed cluster separations (cophenetic correlation coefficient = 0.8969, p < 0.00001, based on non-parametric permutation statistics, see the Material and methods section) largely based both on the categorical selectivity and anatomical proximity of the different ROIs. For instance, a cluster separation at a Euclidean distance of 1.2 was found to distinguish 2 major clusters within OTC: the first, composing bilateral RSC, pFs and PPA, and the second, composing all remaining ROIs. Notably, this general separation conforms not only to the general anatomical arrangement of the ROIs in OTC (i.e., with the former group all being located more ventro-medially whereas the second group is located from ITS extending laterally), but also with the general types of lateral-to-medial gradients of functional response properties observed in the region, as measured with task-based fMRI (for review, see Chao et al., 1999; Mahon et al., 2007; Martin, 2007; Miceli et al., 2001; Noppeney et al., 2006). At more fine-grain cluster separations, a Euclidean distance of 0.6 for example, we found that clusters were even further segregated along the dimensions of categorical selectivity and ROI location. For instance, we found that L-EBA and L-pMTG, given their close anatomical proximity, were clustered together but, importantly, only as a pair of areas clustered together with R-EBA.

The bottom panel of Fig. 8A provides another visualization (graph representation) of the relationship between OTC ROIs based on their temporal correlation patterns. Note that the close proximity of bilateral homologues is evident across all ROIs. Taken together, these correlation metrics and network analyses largely re-affirm the types of functional relationships to be expected based on a combination of both neuroanatomical proximity and categorical-selectivity.

Whole-brain connectivity

The top panel in Fig. 8B shows a complete spatial correlation matrix of the whole-brain spatial connectivity maps generated from each OTC ROI. In this figure, ROIs showing more similar patterns of whole-brain connectivity have higher correlation values (see the Material and methods section for specific details as to how these correlation metrics were derived) [note that interpreting the relationships displayed in Fig. 8B requires reference to the patterns of network convergence and divergence across the different OTC ROIs, shown in Fig. 7]. Following average-linkage hierarchical cluster analysis of the ROI-based spatial maps (cophenetic correlation coefficient = 0.7923, p < 0.00001, based on non-parametric permutation statistics) we found that the cluster separations looked markedly different from those based on the timeseries correlations within OTC alone (compare Fig. 8B middle with that of Fig. 8A middle). While caution should be applied when attempting to infer hierarchical relationships of areas based on spatial FC patterns alone, the pattern of separations indicates that the FC relationships of specific OTC ROIs with the rest of the brain cannot be simply explained on the basis of either 1) the categorical-selectivity of the ROIs (e.g., all face-selective regions showing a common profile of full-brain connectivity) or 2) their neuroanatomical proximity to one another within OTC (e.g., more similar full-brain connectivity patterns for ROIs located adjacent to one another on cortex).

The bottom panel of Fig. 8B provides the equivalent visualization graph display to that seen in the bottom of Fig. 8A. In this case, interpreting the spatial arrangement is limited in the sense that these are based on whole-brain spatial similarities and not temporal relationships (the graph representation then serves merely to offer a complementary visualization of the relationships seen above). Taken together, the spatial correlation metrics converge upon the same conclusion readily derived from viewing the whole-brain FC patterns in Figs. 2–7: The whole-brain FC of OTC significantly varies not only across ROIs with different category-specificities (e.g., faces versus scenes), but also even across areas showing the same general category-specificity (e.g., OFA versus FFA), both as a function of seed hemisphere and location along the OTC posterior–anterior axis.

For a different visualization of the extent to which the wholebrain FC patterns of the different OTC ROIs converge and diverge across cortex, we have created 'connectivity fingerprints' for each of the ROIs (see Fig. 9). Here, the group-averaged, z-normalized correlation values between each ROI and select AAL areas are displayed (note that AAL areas were selected based on their typical roles in sensory-, motor-, cognitive- and affective-related processing and based on the general observation that these areas appear to be important sites of convergence or divergence in the patterns of OTC FC across the brain; see Figs. 2-7). While the z-score values presented appear low, it is important to consider that each predefined AAL region is quite large and thus, the signal to be correlated with the activity of each OTC seed ROI is averaged across a large number of voxels, necessarily decreasing the levels of specificity that can be observed. As such, the plots are only meant to provide a comprehensible visualization of the FC profiles across key non-OTC regions.

Network convergence

Though much of the present study has emphasized the many cases of divergence in the whole-brain networks correlated with the restingstate activity of different OTC regions, it is worth noting that we do in fact observe, outside of the lateral-occipital and ventro-temporal cortices, a few prominent sites of convergence (these 'convergence zones' are shown in Fig. 10, with the different colors indicating the number of OTC functional maps that overlap at each voxel in the brain). In particular, in the PPC we found significant overlap in the POS, pIPS, and medial IPS across the OTC FC maps (Fig. 10). Based on previous DTI work, these PPC regions are thought to form part of a structural core that links other structural modules in the brain and thus play a critical role in the functional integration of information across cortex (Hagmann et al., 2008). Beyond these convergence sites in PPC, however, the findings presented in Fig. 10 largely serve to reinforce the extent to which the OTC whole-brain networks are differentiated.



Fig. 8. Correlation metrics of within-OTC and whole-brain functional connectivity maps. A) (top) Average pairwise correlation matrix of resting-state BOLD time series between OTC ROIs. The upper triangular part of the graph displays the coefficient values according to the color bar on the right and the lower triangular part (mirror image) of the graph displays the corresponding absolute numerical correlation coefficient values. (Middle) Dendrogram plot of the hierarchical binary cluster tree of OTC ROIs following cluster analysis (based on Euclidean distance of the correlation coefficients in the left panel). (Bottom) Graph representation of the correlation matrix in the top panel in which each ROI represents a node and where each edge represents a pairwise temporal correlation nutrix ($r \ge |0.3|$). The size of the node represents is degree centrality. B) (top) Average pairwise correlation matrix of maps generated from each OTC ROI (shown the same as in A). (Middle) Dendrogram plot of the hierarchical binary cluster tree of whole-brain correlation matrix in the top panel in which each ROI representation matrix in the top panel in which each OTC ROI (shown the same as in A). (Middle) Dendrogram plot of the hierarchical binary cluster tree of whole-brain correlation matrix in the top panel and prepresentation correlation matrix in the top panel in which each OTC ROI (shown the same as in A). (Middle) Dendrogram plot of the hierarchical binary cluster tree of whole-brain correlation matrix in the top panel in which each ROI FC map represents a node where each edge represents a pairwise spatial correlation value ($r \ge |0.1|$). The size of the node represents its degree centrality.



Fig. 9. Functional connectivity fingerprints of OTC ROIs. The polar plots show the object (A), face (B), scene (C), body (D), and tool (E) ROIs connectivity with select AAL-defined brain regions. The values indicate the absolute z-scores averaged across participants (inner dashed circle = 0.125; outer circle = 0.250).

Additional control seed region analyses

One possible explanation for much of the anterior extensions of FC seen with many of the seed ROIs is that it may reflect the problem of partial voluming of seed regions. That is, our original selection of seed



Fig. 10. Conjunction analysis across the functional connectivity maps of all categoryselective OTC regions. Color maps represent the number of OTC functional maps that have significant functional connectivity (z-score > 2.3) at each voxel. For interpreting which FC maps are driving overlap effects, see Fig. 7. LH = left hemisphere, RH = right hemisphere. regions based on the task-based functional localizer visual stimuli may, in addition to selecting visual voxels, also select non-visual voxels in the region and this may affect (and inadvertently explain) some of the long-range parietal and frontal FC patterns seen with our original seed regions. To address this possibility, we examined the whole-brain FC patterns associated with neighboring seed regions, located adjacent and just anterior to our original seed regions. It stands to reason that if the original visual network ROIs are completely segregated functionally from neighboring non-visual networks then, at least to a certain extent, this should manifest as a largely non-overlapping set of FC patterns for the original and control (anterior) ROIs.

Visual inspection of the FC maps generated from the control anterior seed ROIs revealed patterns of FC that were, depending on the area in question, either different or similar to the patterns of FC generated from the original task-based seed regions (see Fig. 11). Notably, for some of the ROIs these differences in the outside-OTC distributed FC patterns (i.e., throughout parietal and frontal cortices) were far more pronounced (e.g., R-PPA) than for other ROIs (e.g., L-EBA). Also, we found cases in which the anterior seed ROIs showed much greater long-range FC than the corresponding original ROI (e.g., left and right LO). On the one hand, these differences are to be expected based on the different voxels being sampled while, on the other hand, some of the similarities in the FC maps are to be expected based on the proximity and shared functions of the control and original seed locations. While the outcome of this control analysis approach can be somewhat difficult to interpret, these additional analyses have been included so that interested readers can be left to make their own judgments on the selectivity of the original localizer-defined FC maps.



Fig. 11. Overlap of functional connectivity of task-localized OTC regions and anterior control regions. Whole-brain correlation maps from OTC seed regions (red) and seeds placed directly adjacent and anterior to these regions (blue) are displayed (binarized with a z-score threshold 2.3) on flat maps of both hemispheres for all category-selective regions. Spatial overlap is denoted by pink.

General discussion

Just as the architecture of the mind might be inferred from the brain's functional organization (Kanwisher, 2010) there is mounting evidence that significant insights into the brain's functional organization can be revealed from its patterns of connectivity (Behrens and Sporns, 2012). Thus, part of understanding the functional organization of category-selective responses in OTC requires gaining a better understanding of how the visual-perceptual information processed by OTC might be used by the rest of the brain. To investigate this issue, we used rs-fMRI to compare the FC patterns of several well-documented localizer-defined OTC regions involved in object-, face-, scene-, body-and tool-related visual-perceptual processing, both with each other and with structures elsewhere in the brain. As detailed in the Results and discussion section above, we found notable differences between the whole-brain FC patterns of different OTC ROIs, not only between

the different object categories (e.g., faces versus scenes), but also between areas thought to form part of the same processing network (e.g., OFA versus FFA). To our knowledge, this work is the first to systematically compare the different resting-state FC networks across the majority of category-selective regions in OTC. To the extent that different OTC regions have distinctive patterns of whole-brain functional connectivity, our results support interpretations of these regions not only as distinct entities in high-level visual–perceptual analysis (Kanwisher, 2010) but also as components of a greater, more widely distributed and integrated network of areas specialized for processing specific object domains (Mahon and Caramazza, 2009, 2011).

Key questions

Much of the present investigation, as noted at the outset in the Introduction section, is focused on examining several main questions concerning the FC of different category-preferring OTC regions. Here, we briefly discuss the extent to which the current findings may offer insights into addressing these questions, each in turn.

Is there correspondence between the neuroanatomical proximity of different OTC ROIs and their whole-brain FC patterns?

A key theme explored in the current study, though not explicitly tested, is the idea that the modular arrangement of category-selective responses in OTC emerges as a result of an organization not only at the level of visual cortex connectivity with OTC, but also at the level of its connectivity with the non-OTC brain structures that ultimately use the information to produce behavior. In this view, the categoryselective organization of OTC reflects the instantiation of, and constraints imposed by, a widely distributed network of areas that includes several other regions (Mahon and Caramazza, 2009). One prediction that naturally follows from this idea is that there might be a tight coupling between the locations of category-preferring regions in OTC and their corresponding whole-brain patterns of FC (Mahon and Caramazza, 2011). We examined this possibility in our resting-state data and found support for this prediction, but only to a matter of degree. For instance, as would be predicted by the hypothesis, we found that the FC patterns of FFA and PPA, located a good distance from each other in OTC, were fully distinct. Likewise, while we observed fairly distinct FC patterns when considering ROIs located directly adjacent to one another, such as L-EBA and L-pMTG, both regions showed substantial FC with somatomotor cortex (Fig. 6), as predicted by the hypothesis (Mahon and Caramazza, 2011). However, when considering the activity of two areas located in even closer proximity to each other, R-FFA and R-FBA, we observed significantly different FC patterns: FC for R-FBA was extensively distributed throughout the entire brain whereas R-FFA showed FC with only a very small subset of those areas showing FC with R-FBA. Thus, while it is clear that some predictions from the hypothesis are borne out in the data, additional organizational principles (and further experimentation) may be required to help account for the patterns of FC observed.

Are there systematic differences in the FC of OTC ROIs across the two hemispheres?

Based on ample evidence that category-selective responses in OTC tend to be stronger in the right than left hemisphere (e.g., Downing et al., 2001; Epstein and Kanwisher, 1998; Kanwisher et al., 1997; Malach et al., 1995), we initially predicted that this might translate to (or perhaps reflect) a more extensive and distributed pattern of FC for right-hemisphere ROIs. Here, if anything, we found evidence for the opposite pattern (although it is worth noting that the scene-selective areas, RSC and PPA, appear to be exceptions). Why might the lefthemisphere seeds have more extensive FC? Neuropsychological and neurophysiological investigations indicate that the left hemisphere may be particularly specialized for the visual-motor control of action (Frey et al., 2005a; Grafton et al., 2002; Haaland et al., 2000; Heilman et al., 1997; Perenin and Vighetto, 1988; Rushworth et al., 2001; Schluter et al., 2001; Verstynen et al., 2005) as well as speech processing and communicative behavior (Davis and Johnsrude, 2003; Hickok and Poeppel, 2007; Kandel et al., 2000; Kimura, 1982). Given that the visual-motor and speech processing centers in left frontoparietal cortex are expected to be particularly well developed in the right-hand dominant participants tested here (Bethmann et al., 2007; Dassonville et al., 1997; Hugdahl et al., 1997; Kim et al., 1993; Kloppel et al., 2007; Wada and Rasmussen, 1960), one intriguing possibility is that the FC of left hemisphere OTC ROIs may be organized from the standpoint of implementing behavior and aiding communication.

How do the FC patterns of ROIs forming components of the same category-selective network compare?

We had initially expected that areas forming key core components of a category-preferring hub in OTC (as evidenced by their routine coactivation during visual-perceptual tasks) would show very similar whole-brain patterns of FC. This prediction directly follows from the notion that each of these core areas (e.g., OFA and FFA), functioning as part of a highly distributed and integrated network involved in processing a specific object domain (e.g., faces), might also show FC with the entire network of areas in which they are thought to be situated. We found this to be true only when considering the FC of ROIs within OTC. That is, object-, face-, scene-, and body-related areas generally tended to show strong temporal correlations with the homologous areas in the opposite hemisphere as well as with areas showing the same category-selectivity (see Fig. 8A, see also Nir et al., 2006; Zhu et al., 2011). However, when considering the whole-brain patterns of FC across the different OTC ROIs - the most important and unique contribution of the current study - this was clearly not the case. Indeed, perhaps one of the most consistent and noteworthy findings of the current study was the considerably small degree of overlap in the whole-brain FC patterns of ROIs belonging to the same category-selective network (see Figs. 2–6). The specific insights gained by this observation have already been addressed in the appropriate sections of the Results and discussion section (above). Here, we only re-emphasize that these findings fully align with the notion that ROIs belonging to the same category-selective network likely perform separable, yet complementary roles as part of a stepwise hierarchy involved in transforming localized visual information into a more abstract and invariant representation for a particular object category (Grill-Spector and Malach, 2004; Taylor and Downing, 2011).

Where in cortex do the different category-selective OTC networks converge?

Despite differences in the locations in which certain object categories are represented in OTC (e.g., faces versus scenes), we had initially expected that, once outside of OTC, there might be several different sites of convergence in the patterns of FC. This expectation was based on the assumption that common neural substrates (e.g., frontal areas traditionally implicated in executive control or short-term memory) might be frequently recruited for processing several different object categories and that these shared underlying circuits and pathways might then be revealed via FC with rs-fMRI. A major theme to emerge in the current study, however, is that once outside of OTC, we observed strikingly little convergence in the FC patterns of different categorypreferring ROIs (see Fig. 10 for verification). From the vantage point of whole-brain FC, these results lend further support to the notion that these different OTC regions form distinct entities in the processing of different object categories (Kanwisher, 2010).

Limitations to interpretation

In describing the FC patterns in the Results and discussion section above we have attempted, where appropriate, to situate the current findings within the context of previously published work. Like all connectivity studies (e.g., neuroanatomical tracing studies and DTI), this entails speculating on the types of cortical processes that certain patterns of FC may help enable or support (called 'reverse inference', see Poldrack, 2006). We appreciate that the claims made using reverse inference can be both limited and context-dependent (Hutzler, 2013; Poldrack, 2011) and this may be particularly true with regard to the current study for two reasons. First, the current results were obtained during the resting-state, and thus, any inferences about the cognitive functions that may be supported by the FC networks observed rely on assumptions of stationarity in the brain between task and rest (which may or may not be true, see Toro et al., 2008; Smith et al., 2009; Mennes et al., 2013). Second, whereas the current findings are based on correlation metrics, the cognitive and/or network processes that may be supported by the patterns of FC often require reference to previous reports of neural activation. This necessitates the assumption that some of the shared variance between two regions stems from the typical task-related processing of one region on its own. For these and other reasons, we acknowledge that suggestions concerning the functional processes supported by the networks derived via resting-state analyses remain speculative. For further discussion, readers can also see the Supplementary material.

One point worth acknowledging is that the current paper largely presents and discusses the FC findings with reference to a more modular view of stimulus category representations in OTC (Kanwisher, 2010). However, there are also suggestions, brought forward from other studies, that OTC represents different object categories through widely distributed and overlapping patterns of activity across the whole of OTC rather than through category-selective modules (Haxby et al., 2001). Though it is unclear where the current findings would be situated within these two extremes, it is compelling that we observe quite distinct patterns of FC across the different category-selective ROIs and even between areas thought to form core components of the same category-selective network. Insofar as these FC findings bear some insights into the functional organization of the ventral visual pathway, these findings suggest a more modular representation in OTC. Nevertheless, we suspect that future studies and techniques will be required to more definitively weigh-in on this important and ongoing debate.

Conclusion

In conclusion, our OTC FC findings complement and extend results from previous studies of anatomical and task-evoked patterns and, when taken together, they lend support to the notion that categoryselectivity at the level of OTC is in part a reflection of the connectivity constraints imposed by a widely distributed network of areas (Mahon and Caramazza, 2011). More generally, these findings also offer insights into how category specificity is realized throughout the brain and ultimately used to generate cognition and behavior.

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.neuroimage.2014.03.068.

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