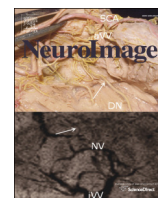




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# Distinct and distributed functional connectivity patterns across cortex reflect the domain-specific constraints of object, face, scene, body, and tool category-selective modules in the ventral visual pathway

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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 tool-related 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

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-of-interest (ROIs). While a few previous studies have examined the FC patterns pertaining to single, or in some cases, two types of category-selective 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 category-selective 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, 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, participants 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 inter-stimulus 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 inter-stimulus 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.

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