



# Visual areas PPA and pSTS diverge from other processing modules during perceptual closure: Functional dichotomies within category selective networks



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## ABSTRACT

The nature of neural processing within category-preferring visual networks remains an open topic in human neuroscience. Although the topography of face, scene, and object-preferring modules in the human brain is well established, the functional characterization, in terms of dynamic selectivity across their nodes is still elusive.

Here, we use long trials of perceptually impoverished images of faces and objects to assess the dynamics of BOLD activity and selectivity induced by perceptual closure within these regions of interest. Departing from paradigms involving immediate percepts, we used ambiguous images favoring holistic search and independence from low level stimulus properties.

By assessing the neural responses to images that go beyond the preferred category of the studied ROIs we could dissect the specificity of these processes as a function of the timing of perceptual closure and contribute to the debate regarding specialization of these modules.

We found that pSTS is a notable exception to the observation that category selective high-level visual areas also participate on the perceptual closure of their non-preferred category. A similar observation was found for PPA responses to faces. Most importantly, these observations directly link the pSTS region with the social processing network, which cannot be engaged by object stimuli.

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## 1. Introduction

Since the first fMRI studies involving the fMRI response to objects (Malach et al., 1995) many neuroimaging studies have attempted to identify regions that preferentially process a few given image categories. Among these, particular focus has been given to the study of neural responses to images of objects, scenes and faces (Malach et al., 1995; Epstein & Kanwisher, 1998; Kanwisher, McDermott, & Chun, 1997). Recent work has emphasized methodological issues, standardization of paradigms and analyses, which has helped to establish the cortical topography and general organization of these high-level selective visual regions in the ventral stream (Fox, Iaria, & Barton, 2009; Rossion, Hanseeuw, & Dricot, 2012).

The core face-preferring network (Haxby, Hoffman, & Gobbini, 2000), comprises the Fusiform Face Area (FFA) (Kanwisher et al.,

1997), the Occipital Face Area (OFA) (Gauthier et al., 2000), and a region on the posterior bank of the Superior Temporal Sulcus (pSTS) (Puce, Allison, Bentin, Gore, & McCarthy, 1998). According to Haxby's model, the OFA is thought to drive other face-selective regions by analyzing lower-level features of a face, while the FFA underlies holistic processing and the STS extracts higher level social and emotional aspects.

Regarding object processing in the visual cortex, an extensive area comprising parts of the inferior temporal and the lateral occipital cortex, called the lateral occipital complex (LOC) (Malach et al., 1995) shows larger responses to objects than textures or scrambled images. (Grill-Spector et al., 1999a). This area can be subdivided into a fusiform region and a lateral occipital region. Mimicking the OFA and FFA hierarchy, while the lateral occipital region performs lower-level analysis and extraction of features, the posterior fusiform region shows more invariance to basic properties such as viewpoint.

Scene selective regions include the parahippocampal place area (PPA) (Epstein & Kanwisher, 1998), the retrosplenial cortex (RSC) (Maguire, 2001) and the Transverse Occipital Sulcus (TOS) (Nakamura et al., 2000), which is also known as the Occipital Place Area (OPA) (Dilks, Julian, Paunov, & Kanwisher, 2013). While the

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PPA is more concerned with scene processing and individuation, the RSC is more directly involved in visual navigation and integration (Park & Chun, 2009).

However, these functional specializations and processing at each node of the networks do not go without controversy, (for a review on the face-network architecture see Atkinson & Adolphs, 2011) and the degree to which they can be engaged by non-preferred categories is still controversial. In fact, the assessment of how truly specialized is the processing in these high-level regions is fundamental to the understanding of the concept of selectivity in visual areas.

Here, we addressed this question by studying temporal dynamics of activity using images that imply delayed perceptual closure and categorization. We compared closure across categories for all networks irrespective of their preference.

Perceptual closure refers to the well known Gestalt principle of perceptual organization that reflects the ability to perceive an incomplete pattern or object as complete or whole. In other words, coherent perception of an image content occurs under circumstances when the visual information is incomplete (Grützner et al., 2010). Such a methodological approach allows assessing the degree to which the selectivity of each node is affected by perceptual rather than stimulus related factors, given the impoverished content of the image. This is because the impact of perceptual decision on dynamic selectivity provides a window to understand the nature of processing occurring before and after perceptual closure. Moreover, the assessment of each region-of-interest (ROI) beyond its categorical preference reveals into which extent dedicated processing indeed occurs in the visual cortex.

Previous studies addressing closure through impoverished images used pure noise images which change throughout time into a coherent object or face (Jiang et al., 2011; Ploran et al., 2007) or the popular alternative of Mooney images (Mooney, 1957). These latter binarized black–white versions of normal grayscale images can appear devoid of any meaning other than a simple set of blobs until holistic perception occurs. Accordingly, Mooney stimuli have been used to study face perception but not in the context of the impact of perceptual closure on response selectivity. McKeef and Tong (2007) focused on the FFA to highlight its role in face perception while also showing an absence of decision-related activity in nonface-selective visual areas. In turn, a study by Andrews and Schluppeck (2004) found differential FFA activation when subjects reported seeing a face compared to perceiving the image as a collection of blobs, but found no difference in magnetic resonance response between face and no-face perceived events either in the superior temporal sulcus, a face selective area, or in the PPA and LOC. These studies are relevant and intriguing by studying these phenomena either at short time scales (Andrews & Schluppeck, 2004) or by focusing on a few pivotal regions (McKeef & Tong, 2007), using faces or scrambled controls.

In this study we followed a different approach, because we were specifically interested in the temporal dynamics of selectivity before and after perceptual closure. We did therefore use long time scales, to dissect selectivity along time and its dependence on perceptual closure. We used 12 s trials of rotating Mooney images of faces and objects to assess the dynamics of activity and selectivity in category-preferring networks. In this manner we could investigate BOLD activity in selected regions of interest (ROIs) in response to different categories irrespective of their preference.

## 2. Materials and methods

### 2.1. Subjects

13 right-handed subjects (6 females, 7 males, ages 20–32, mean age  $23.8 \pm 3.5$  years) participated in the study after providing informed consent. All had normal or corrected to normal vision.

The study followed the tenets of the Declaration of Helsinki, informed consent being obtained from all subjects for the protocol, which was approved by our local Ethics Committee.

### 2.2. Stimuli

The stimuli for our experiment were comprised of Mooney images. These images are simply impoverished black and white (two-value only, no grayscale) versions of regular images. Sixty Mooney faces were built from thresholding online images of faces, with a wide range in lighting, angle and face size properties, thus maximizing ambiguity. The same procedure was adopted for building 60 Mooney images of objects. Due to the broader span of the object category, images of objects were restricted to three sub-categories: utensils, means of transportation and musical instruments.

Mooney stimuli were chosen because they provide a classical way of generating ambiguous perception (which is enhanced if stimuli are viewed upside down). These stimuli may appear devoid of any recognizable content for several seconds until the observer suddenly becomes aware of the emergence of a holistic percept. Stimuli characteristics were thus suited to the research goal of uncoupling sensation from perception because the sudden global awareness of the content leads to temporally contained perceptual events (perceptual closure), separable from initial local sensory processing. Also, differential onset of activity on “early” and “late” detection trials is a distinguishing characteristic of a neural encoder of perceptual closure processes, a property which can advantageously be used in identifying the networks involved in this perceptual phenomenon. Finally, interpretation of the image content cannot be easily achieved through local visual analysis, and renders high-level processing impossible in the pre-perceptual period, which therefore serves as a sensory control/baseline.

The 120 Mooney images were converted into movies that consist of the rotation of such images. Starting from the inverted position, the image slowly rotates  $20^\circ$  per second until it reaches the upright position where it rests for 3 s. There were no repeated movies. Stimuli were presented in a black background and subtended approximately  $12.40^\circ$  of the visual field. Difficulty levels were adjusted in pilot experiments to guarantee variability in perception times.

### 2.3. Task: the dual categorical paradigm

Subjects performed two-tasks, each of which comprised a run with faces and a run with objects. Task choice was based on Rebola, Castelhan, Ferreira and Castelo-Branco (2012). In each experimental run subjects were requested to search for either faces or objects. In the case of objects runs, these were divided into three blocks, before which a cue was presented centrally for 4 s with the sub-category to search for. Since objects are a broader category than faces, implying more uncertainty in content, shapes and viewpoints, using this cue to specify the sub-category in the object runs allowed us to limit and equate this variability to the face runs, so that activity differences are not driven by different levels of expectancy.

In the first task, subjects were instructed to respond when they were confident they had perceived the content of the images. Response was achieved through a response box, by pressing of a button with a finger of the left hand. This task is referred to as the “Simultaneous Response Task”.

In the second task, the image foreground (the white part of the Mooney image) changes color every TR (2 sec) in the following order (white, blue, yellow, pink, green, and light gray). Upon content perception, instead of responding immediately, subjects withheld their response until the end of the trial, when they were instructed to identify from a list the color of the foreground (in case of detection) that was present at the moment of perceptual closure. Thus, the selected color encoded the time of perception, which was decoupled from response processes. Selection was made by using two buttons in one hand to move a cursor up or down until the correct color was highlighted and then pressing a button with the other hand to confirm the choice. When the subject responded the color list disappeared, followed by fixation. A simplified timeline of this dual-task paradigm is shown in Fig. 1 (see also Rebola et al. (2012)).

In total, there were four runs: two for the “Response Task” and two for the “Color Task”.

The order of the runs was counterbalanced across subjects. Given that both tasks lead to comparable modulation across visual areas (Rebola et al., 2012), activity in high-level visual ROIs was consequently pooled across tasks.

### 2.4. Localizer scans to map selective regions for ROI analysis

Localizer stimuli consisted of grayscale images of faces, places (buildings, landscapes, and skylines), objects (tools, cars, and chairs), and scrambled versions of objects. Stimuli were presented in a black background and subtended approximately  $9.48^\circ$  of the visual field.

Localizer scans consisted of two runs of alternately viewed blocks of stimuli from a given class (faces, places, objects, and scrambled images). Each run had 12 blocks and each block lasted 20 s (20 images, 800 ms each, 200 ms gap), separated by 10 s fixation baseline intervals. During each block subjects performed a 1-back task to keep stable attention levels. Three repetitions per block were employed. The definition of contrasts to identify distinct brain regions of interest (ROIs) is shown in Table 2.

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