



# Preferential coding of eye/hand motor actions in the human ventral occipito-temporal cortex



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## ABSTRACT

The human ventral occipito-temporal cortex (OTC) contains areas specialized for particular perceptual/semantic categories, such as faces (fusiform face area, FFA) and places (parahippocampal place area, PPA). This organization has been interpreted as reflecting the visual structure of the world, i.e. perceptual similarity and/or eccentricity biases. However, recent functional magnetic resonance imaging (fMRI) studies have shown not only that regions of the OTC are modulated by non-visual, action-related object properties but also by motor planning and execution, although the functional role and specificity of this motor-related activity are still unclear. Here, through a reanalysis of previously published data, we tested whether the selectivity for perceptual/semantic categories in the OTC corresponds to a preference for particular motor actions. The results demonstrate for the first time that face- and place-selective regions of the OTC exhibit preferential BOLD response to the execution of hand pointing and saccadic eye movements, respectively. Moreover, multivariate analyses provide novel evidence for the consistency across neural representations of stimulus category and movement effector in OTC. According to a 'spatial hypothesis', this pattern of results originates from the match between the region eccentricity bias and the typical action space of the motor effectors. Alternatively, the double dissociation may be caused by the different effect produced by hand vs. eye movements on regions coding for body representation. Overall, the present findings offer novel insights on the coupling between visual and motor cortical representations.

## 1. Introduction

The human ventral visual stream coursing through the occipito-temporal cortex (OTC) contains a set of regions highly specialized for the analysis of stimulus categories, such as faces, places and body parts, that have an intrinsic biological significance (reviewed in [Op de Beeck et al., 2008](#)). Based on neuropsychological evidence (i.e. category-specific agnosic and semantic deficits), this neural specificity has been linked to object recognition/perception ([Goodale and Milner, 1992](#); [Milner and Goodale, 2008](#)), conceptual knowledge and semantic representations ([Mahon and Caramazza, 2009](#)). However, the principles driving such an organization are still strongly debated. Whereas dominant accounts explain the organization of OTC as dependent on basic principles of visual processing organization, i.e. similarities in object visual shape ([Haxby, et al., 2001](#)) or visual field eccentricity biases ([Hasson et al., 2002](#); [Levy et al., 2001](#)), a more recent proposal suggests that categorical specificity in OTC may emerge from connectivity constraints with downstream fronto-parietal regions ([Mahon](#)

and [Caramazza, 2011](#)). This provocative theory focuses on interconnections between areas of the dorsal and ventral visual streams and is supported by a series of findings, like the recent observation that object representations in OTC are shaped by non-visual, action-related object properties ([Bracci et al., 2012](#); [Bracci and Peelen, 2013](#); [Mahon, et al., 2007](#)). More relevantly, a series of fMRI studies have recently highlighted an unexpected BOLD response in the ventral visual pathway to motor preparation/execution. For example, the extrastriate body area EBA ([Downing et al., 2001](#)) responds to the execution of unseen, voluntary movements of the subject's hands and feet ([Astafiev et al., 2004](#)). Furthermore, unseen movements performed by different effectors activate sub-regions of the OTC with somatotopic correspondence ([Orlov et al., 2010](#)). Finally, upcoming hand motor actions can be decoded from preparatory fMRI activity patterns in OTC ([Gallivan et al., 2013](#)). However, although this latter study excludes a purely sensory feedback (i.e. proprioceptive) interpretation, the functional role and specificity of this motor-related activity are still unclear.

The present study tested whether the specificity for perceptual/

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semantic categories in OTC corresponds to a preference for particular motor actions through a reanalysis of previously published experiments (Sestieri et al., 2014; Tosoni et al., 2014, 2008). We first analyzed the response of face- and place-selective regions during the motor execution phase of a perceptual decision experiment (PD-1) (Tosoni et al., 2008), showing for the first time that the fusiform face area (FFA) and the parahippocampal place area (PPA) also exhibit a preference for hand and eye movements, respectively. These results were confirmed by data from a functional localizer conducted on a larger sample (Sestieri et al., 2014; Tosoni et al., 2014) to identify movement-specific activity. The double dissociation also generalized to other face- and place-selective regions of the OTC, as demonstrated by further analyses of perceptual (PD-2) (Tosoni et al., 2014) and memory (MD) (Sestieri et al., 2014) decision-making experiments, and did not appear to be explained by task design, low level sensory modulations or a spread of motor-related activity from the cerebellum. Finally, multivariate analyses provided novel evidence for a partial similarity in the neural representation of stimulus category and movement effector in OTC. According to a ‘spatial hypothesis’ these findings are the result of the strong association between visual field eccentricity biases in OTC and the typical action space of hand and eye movements. Alternatively, this double dissociation may result from the association between body-selective visual representations and actions that affect the representation of the actor’s body (‘body representation hypothesis’).

## 2. Methods

### 2.1. Subjects

The present study is based on a reanalysis of BOLD data from a total sample of 50 subjects that participated in a series of fMRI studies conducted in our institute between 2007 and 2013. All participants gave informed consent in accordance with guidelines set by the Human Studies Committee of G. d’Annunzio University, Chieti. All subjects performed a passive viewing localizer session in which they passively observed pictures of faces and places (Face/Place Passive viewing Localizer) and an active localizer session in which they executed delayed saccadic eye and hand movements to visual targets (Hand/Eye Movements Localizer). In addition, distinct subgroups of subjects participated in one or more decision experiments (see Table 1). In particular, data from 11 out of 50 subjects were collected on a 1.5 T scanner in a perceptual decision experiment (PD-1) described in (Tosoni et al., 2008) (one subject was excluded from the original sample for missing data on the Face/Place Passive Localizer session). Data from the remaining 39 subjects were collected on a 3 T scanner. Among them, a total of 15 subjects (6 males, mean age  $25 \pm 4$ ) participated in a perceptual decision experiment (PD-2) described in (Tosoni et al., 2014) and a total 24 subjects (11 males, mean age  $25 \pm 3$ ) in a memory decision experiment (MD), described in (Sestieri et al., 2014). Nine subjects participated in both PD-2 and MD experiments.

**Table 1**

The table indicates the different subgroups of subjects that participated in the functional localizers (passive and active) and the decision experiments. Eleven subjects participated in the functional localizers and a perceptual decision experiment (PD-1) in a 1.5 T scanner (Tosoni, et al., 2008). The remaining 39 subjects performed at least one paradigm in a 3 T scanner. All of them participated in the functional localizers (passive and active). In addition, 6 of them performed a perceptual decision (PD-2, (Tosoni, et al., 2014)) experiment, 15 of them performed a memory decision (MD, (Sestieri, et al., 2014)) experiment and 9 of them performed both decision experiments (PD-2+MD).

Subjects	1.5 T	3.0 T
11	Localizers + PD-1	
9		Localizers + PD-2 + MD
6		Localizers + PD-2
15		Localizers + MD
9		Localizers

### 2.2. Functional Localizers

#### 2.2.1. Face/place passive viewing localizer

In a block fMRI design, observers passively viewed eight alternating blocks (16 s) of faces and places images presented for 300 ms every 500 ms, interleaved with fixation blocks of variable duration (mean duration =15 s (Tosoni et al., 2008), mean duration =13 s (Sestieri et al., 2014; Tosoni et al., 2014)). The images (shades of gray, 240×240 pixels) were selected from a larger set developed by N. Cohen (University of Illinois) and used in previous experiments (Corbetta, et al., 2005; Epstein and Kanwisher, 1998; Kelley et al., 1998). Two runs were collected in each subject, each including 16 blocks of faces and places images. Visual stimuli were displayed using an in-house toolbox for MATLAB (The Mathworks).

#### 2.2.2. Hand/eye movements active localizer

In a blocked fMRI design, observers alternated blocks of delayed hand pointing or saccadic eye movements to visual targets (duration=16 s (Tosoni et al., 2008), duration=18 s (Sestieri et al., 2014; Tosoni et al., 2014)) with blocks of visual fixation of variable duration (mean duration=13 s). Each block started with a written instruction (FIX, EYE, HAND) and contained 4 trials. Each trial began with observers maintaining central fixation while holding down a button on a response pad. On each trial, a peripheral target indicating the location for the upcoming movement appeared for 300 ms in one of 4 radial locations ( $1/4, 3/4, 5/4, 7/4 \pi$ ) at an eccentricity of  $8^\circ$  of visual angle. The targets were filled white circles of diameter  $0.9^\circ$  in size. After a variable delay (1.5, 2.5, 3.5, or 4.5 s), the fixation point turned red and participants either released the button and rotated their wrist (without moving the shoulder or the arm) to point with their right hand while keeping central fixation (hand pointing blocks) or moved the eyes while continuing to hold the button (saccadic eye blocks) toward the remembered target location. Subjects were instructed to immediately return back to resting position after movement execution.

We opted for hand pointing rather than point-to-grasp movements for two main reasons. First, point-to-grasp movements are more frequently associated with head movements, with a negative impact on signal to noise ratio. Second, the apparatus for the recording of point-to-grasp movements (Culham et al., 2003) in fMRI is incompatible with eye-movement recording (Singhal et al., 2013), which was used in our decision experiments to monitor whether subjects correctly executed eye movements to peripheral targets. Two runs were collected in each subject, each including 8 blocks of hand pointing and saccadic eye movements. Visual stimuli were displayed using an in-house toolbox for MATLAB (The Mathworks).

### 2.3. Decision tasks

The three decision tasks shared several common features. First, they employed fast-event related designs in which subjects were instructed to provide decisions based on perceptual (place/face or male/female) or mnemonic (old/new) information by executing specific motor responses (eye/hand) following a go signal. The movements, described in the eye/hand localizer section, were directed toward the remembered position of a peripheral target, which was indicated by a white dot presented at the beginning of each trial. Second, in order to separate the BOLD response associated with the decision process from that evoked by movement execution, the tasks employed a delay paradigm in which the selected movements were executed in response to a go-signal (change in the color of the fixation cross) after a fixed delay period. In the present study, we were primarily interested in this latter execution phase. Third, the paradigms included a manipulation of the amount of evidence for a particular decision. However, to minimize possible effect of decision uncertainty on action execution signals, here we limited the analyses of the current study to high evidence correct trials, i.e. easy decisions, as

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