



How thoughts arise from sights: inferotemporal and prefrontal contributions to vision

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We are rapidly approaching a comprehensive understanding of the neural mechanisms behind object recognition. How we use this knowledge of the visual world to plan and act is comparatively mysterious. To fill this gap, we must understand how visual representations are transformed within cognitive regions, and how these cognitive representations of visual information act back upon earlier sensory representations. Here, we summarize our current understanding of visual representation in inferotemporal cortex (IT) and prefrontal cortex (PFC), and the interactions between them. We emphasize the apparent consistency of visual representation in PFC across tasks, and suggest ways to leverage advances in our understanding of high-level vision to better understand cognitive processing.

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Introduction

Of the features differentiating the primate brain from brains of ancestral mammals, two have received a disproportionate amount of attention. First, the primate brain has an expanded visual system. This visual system likely evolved to process input from primates' frontally directed eyes [1]. Second, primates have an expanded prefrontal cortex. Many primate prefrontal regions appear to be 'new,' in the sense that no clear homologues exist in rodents [2]. Given the simultaneous expansion of these two systems, it is possible that these new prefrontal areas have a role in

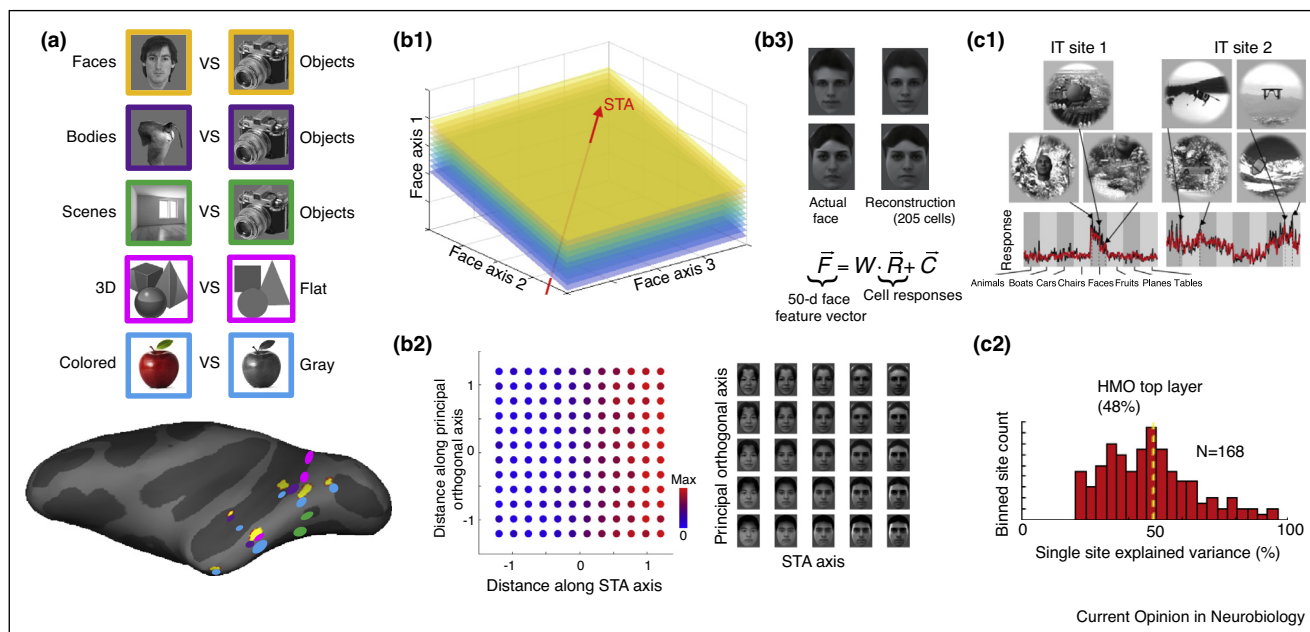
perceiving the visual world. Indeed, stimulation of prefrontal cortex in human patients produces complex visual hallucinations [3]. Alternatively, primate prefrontal cortex may have developed to take advantage of the opportunities that the sophisticated primate visual system provides. An influential theory of prefrontal cortex suggests that it plays a critical role in tasks requiring flexible mapping between sensory input and action that is guided by internal states [4]. In either case, it is natural to ask how the primate visual system interacts with prefrontal cortex. In this review, we summarize current knowledge regarding representation of visual information in inferotemporal cortex, located at the apex of the visual hierarchy, and prefrontal cortex, as well as their interactions during cognitive tasks.

High-level vision in inferotemporal cortex

Great progress has been made in recent years unraveling mechanisms for high-level object representation in inferotemporal (IT) cortex, with key insights coming from studies in both humans and macaques. Early lesion and electrophysiology studies in macaques pointed to the importance of IT cortex for high-level object vision, revealing behavioral deficits specific to object recognition following IT lesions, and the existence of cells in IT cortex selective for various complex forms such as hands, faces, and trees. Later, fMRI studies in humans revealed the existence of specific areas in the human temporal lobe selective for various ethologically important categories such as faces, bodies, and scenes [5]. These patches appear to develop through a combination of preexisting selectivity and visual experience: With training, juvenile monkeys develop patches selective for artificial stimuli, but patches arise in stereotyped locations determined by the visual shape of the stimuli [6*].

Studies of patches in the temporal lobe selective to faces have yielded a plethora of insights regarding its organization and computational mechanisms, befitting the importance of faces to primate behavior. While earlier studies reported face-selective neurons in various parts of temporal cortex, without an anatomical framework, it was unclear how face information was represented and transformed. More recent studies have targeted specific face patches identified using fMRI (Figure 1a). In all six face patches in the macaque temporal lobe, nearly all neurons respond substantially more strongly to faces than to non-face objects [7–9]. However, their neural codes differ substantially. In the middle face patches ML and MF, neurons respond similarly to faces at specific viewpoints regardless

Figure 1



Functional architecture and coding principles of IT cortex. **(a)** Multiple specialized networks exist in macaque IT cortex, including for faces [13], bodies [14], scenes [15,16], 3D objects [17], and color [18]. The approximate location of these networks are shown on the inflated left hemisphere of the macaque brain. **(b)** The code for facial identity in the macaque face patch system (adapted from [12]). **(b1)** A single cell in a face patch linearly projects incoming faces onto a specific axis (the 'STA axis' shown in red). Across the population, these axes tile a high-dimensional face space, specifically, a 'shape-appearance' space. This model predicts that single cells should show the same response to all faces in planes orthogonal to the STA (i.e., the yellow plane). **(b2)** Experimental confirmation that single face cells have a large null space of face metamers. Left: Responses of an AM cell to 144 faces evenly sampled from the 2D space spanned by the STA axis and principal orthogonal axis, synthesized specifically for this cell, are color coded and plotted. Right: A subset of 743 the faces presented to this cell, spanning $([-1.2 -0.6 0 0.6 1.2] \times [-1.2 -0.6 0 0.6 1.2])$. **(b3)** Face feature vectors in shape-appearance space can be accurately reconstructed by a simple linear transformation of face cell population response vectors. Shown on the left are two actual faces presented to a monkey, and on the right are the reconstructions using responses of 205 cells from face patches ML/MF and AM. **(c)** Comparison of IT activity and predictions based on a linear model operating on the top layer of a CNN, adapted from [22]. **(c1)** IT responses (black trace) and model predictions (red trace) and for 1600 test images not used to fit the model. **(c2)** Distribution of explained variance of linear models trained to predict multi-unit activity based on the top layer of the CNN to the presented stimulus, for 168 recorded IT sites. Yellow line indicates the median. (b) is reprinted from *Cell*, vol. 169, L. Chang and D.Y. Tsao, The code for facial identity in the primate brain, p. 1013–1028, Copyright 2017, with permission from Elsevier. (c) is reprinted from *Proc Natl Acad Sci U S A*, vol. 111, D.L.K. Yamins, H. Hong, C.F. Cadieu, E.A. Solomon, D. Seibert, and J.J. DiCarlo, Performance-optimized hierarchical models predict neural responses in higher visual cortex, p. 8619–8624 (2014).

of the identities of those faces, while in the most anterior face patch AM, neurons respond similarly to different face identities regardless of viewpoint. Neurons in the intermediate face patch AL are tuned for both face viewpoint and identity, responding to views of faces in a mirror-symmetric fashion (i.e., left and right profile faces elicit similar responses) and displaying a level of invariance for identity between that of ML and AM [7]. Although face patches cannot be distinguished from surrounding portions of IT on the basis of cytoarchitecture alone, the patches form an anatomically interconnected network, with strong connections between patches, but little connectivity with other parts of IT [10,11].

One of the key insights about face processing to emerge from electrophysiological recordings in IT face patches is that cells in these regions are *measuring* faces, they are not yet explicitly *classifying* them. The key evidence for this is

the fact that single cells in both ML/MF and AM are tuned along a specific dimension in face space, with completely flat tuning in the hyperplane orthogonal to this dimension (Figure 1b) [12]. A consequence of this is that each face cell has a vast null space of face metamers, highly distinct faces which all elicit the same strong response in a particular face cell. This is true even of highly sparse AM cells that might *prima facie* be suspected to encode identities of specific individuals. It seems clear that IT cortex does not contain any cells that are explicitly selective for specific individuals. Rather, the computational mission of IT face patches is to generate a robust, efficient, and invariant code for faces, which can then be read out for any behavioral/cognitive purpose downstream. While details of face encoding strategies may differ significantly between face patches and other parts of IT cortex specialized for representing other types of objects, we think that this general principle of

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