Task-related top-down modulations are more pronounced in inner cortical depths of human visual cortex

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Abstract:

Face processing is a challenging computational problem, yet the human brain processes this rich visual category effortlessly. Here we address one specific aspect of face processing, namely how task-related top-down modulations shape neural responses to face stimuli. Crucially, we use Ultra-High Field (UHF) fMRI to measure neural activation to face stimuli across stimulus-relevant and stimulus-irrelevant tasks in a cortical depth-dependent fashion. Our results show that top-down attentional modulations are most prominent in the inner depths of face-selective regions and in V1. Thus, with the use of UHF fMRI, we can successfully probe the neural response of distinct cortical depths in humans. Future investigations can exploit this cortical depth sensitivity to build quantitative models of information processing at a layer-specific level.

Keywords: Face processing; Cortical depths; Ultra-High Field fMRI.

Introduction

Face processing represents a computational challenge. For example, changes in low-level properties such as lighting or viewing angle substantially alter the image statistics of a face without changing higher-level visual information, such as identity or gender. Yet the human brain is able to extract this information effortlessly. Empirical data highlight the existence of a cortical face network comprising a number of core and peripheral regions dedicated to processing this rich visual category. However, how these regions process visual information—including whether responses are purely stimulus-driven—remains unclear.

Here we aim to characterize the extent to which BOLD responses are modulated by task demand and stimulus manipulations. To this end, we manipulated the phase coherence of face stimuli, thus altering the "visibility" of the faces (see Methods), and instructed our participants to perform two stimulus-relevant tasks (face detection and gender categorization) and one stimulus-irrelevant task (fixation) during scanning. We focused on two core regions of the face network, namely the Fusiform Face Area (FFA) and the Occipital Face Area (OFA), as well as V1.

Crucially, we measured BOLD responses using 7T fMRI at sub-millimeter resolution, enabling us to resolve differences in functional properties across cortical layers. Invasive animal electrophysiology studies show that feed-forward (FF) input arrives in the middle layers, while the innermost and outermost layers are dominated by feedback (FB) (Markov et al., 2013). We therefore expect task demands to affect activity predominantly in the innermost and/or outermost layers.

Methods

Participants. Four healthy adults between the ages 19–36 participated in the experiments.

Stimuli. We used grayscale images of faces (20 male and 20 female). We manipulated the phase coherence of each face, from 0% to 40% in steps of 5%, resulting in 360 images (9 visual conditions x 20 identities x 2 genders). We equated the amplitude spectrum across all images.

Task. In the scanner, subjects were required to perform three tasks. Two tasks were stimulus-relevant, involving perceptual judgment of the visual stimuli (face detection and gender categorization). In the third task, to isolate bottom-up stimulus-driven responses, subjects engaged in a difficult fixation task that required responding to a specific color change of the fixation cross. Visual stimuli were identical across tasks to ensure that any differences observed were related solely to top-down processes. Four runs were acquired for each task. Within each run, participants viewed ninety images (9 phase coherence levels x 5 identities x 2 genders) randomly interspersed with six blank trials. Stimuli were shown for 2000ms with an ISI of 2000ms, in randomized order to minimize priming and adaptation effects.

ROI definition. Face-selective regions were defined using functional localizer scans consisting of twelve runs of a block-design experiment in which images of faces, limbs, flowers, houses, cars, guitars, and scrambled objects were presented (Stigliani et al., 2015). We defined three face-selective regions—namely mid and posterior FFAs and OFA—based on their significantly higher response to faces compared to other stimuli. V1 was defined according to the Kastner probabilistic atlas (Wang et al., 2015).

MRI methods. Functional BOLD signals were measured using a 7T MR scanner (gradient-echo EPI sequence;

multiband: 2; iPAT: 3; 0.8-mm isotropic voxels; TR: 2.2s). Cortical depths were reconstructed using FreeSurfer on T1-weighted anatomical volumes (0.8-mm). Depths were defined using an equi-distant approach, whereby six surfaces are placed within the gray matter, ranging from 10% to 90% of the distance between the white/gray boundary and the pial surface in steps of 16%.

Analyses. We performed GLM analysis to estimate beta weights associated with the BOLD response amplitude of each voxel to each condition; this was done independently per task and run. Gender and identities were collapsed across phase coherence levels, resulting in nine stimulus conditions, each comprising forty trials (20 male and 20 female). Within each region of interest we computed the mean across all vertices; this was done independently per cortical depth. For V1 only (before averaging across the whole ROI), we selected vertices showing an average beta response > 0 across all stimulus conditions and tasks.

Results

Our data show that BOLD responses in both higher (OFA, FFAp, FFAm) and lower (V1) visual areas were modulated by task demands (Figure 1b). Moreover, as expected, we also observed larger BOLD responses in face areas to higher phase coherences (Figure 1a). Importantly, the data show that we can successfully distinguish the response profile of different layers in high-level cortices (Figure 1b). 95% bootstrap confidence interval (sampling with replacement the subjects) revealed that top-down attentional modulations to stimulus-relevant tasks are most prominent in the innermost layers in V1, FFAm and, to a lesser extent, OFA (Figure 1b). We also observed task effects to be largest in the FFAm, followed by FFAp, OFA and V1.

Conclusion

The complex computations underpinning face processing build upon both stimulus-driven feed-forward (FF) and top-down feed-back (FB) responses. As suggested by animal studies (e.g. Larkum, 2013), integration of FB and FF activity occurs within distinct compartments of individual pyramidal neurons residing in different layers. Understanding the functional role of different cortical layers therefore has the potential to significantly advance our knowledge of the neural computations of face processing.

We report that neural responses in two of the core face network regions are modulated by both stimulus properties and task demands (Figures 1a and 1b). Crucially, top-down task-related attention modulations are more pronounced in the innermost cortical depths (Figure 1b). These results suggest that response scaling induced by higher-level/decision-making areas, such as IPS (Kay and Yeatman, 2017), might arrive in inner layers of high-level visual areas (that are dominated by long-range FB connections) to then spread to other layers and lower-level visual areas. Future studies can exploit UHF fMRI to build quantitative models characterizing information flow at a layer-specific level.

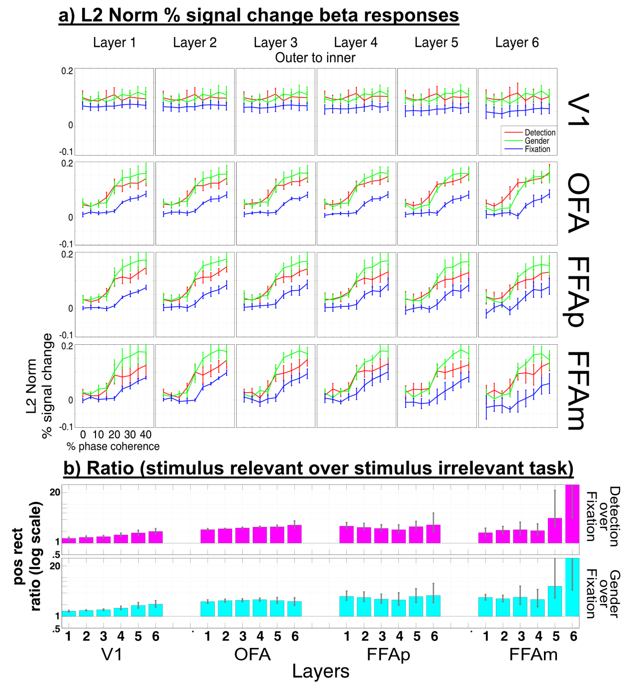

Figure 1. Panel a) shows the beta amplitude elicited by each task, condition, ROI and cortical depth. Panel b) shows the ratio of the two stimulus-relevant tasks over the fixation task. The ratio was computed as follows: we first calculated the mean across all conditions; we then positively rectified the beta responses, computed the ratio between the betas elicited by the two stimulus-relevant tasks and those elicited by the fixation task, and then performed log-transform.

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