Spotlight

Heterogeneity of FFA responses or multiplexing?

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Recent work using cluster analysis of brain activity during movies revealed distinct clusters that respond to faces and different non-face categories in the fusiform face area (FFA). Because of the limited heterogeneity observed, these results could mean that the FFA contains one population of cells capable of representing multiple categories.

The FFA is a functionally defined region of the temporal lobe with greater response to faces than other objects. On the one hand, it has been argued that the FFA is a domain-specific module for face recognition [1–3]. On the other hand, its apparent selectivity for faces has made it central to domain-general, expertise-based accounts [4], which argue that the FFA is engaged by expert individuation more generally.

Recently, Çukur *et al.* [5] investigated whether ostensibly face-selective voxels within the FFA might be selective for other categories of object. Çukur *et al.* measured the response of the FFA as participants watched video footage that included 1705 labeled semantic categories. Fitting regression models with a unique parameter for each semantic category, they characterized the selectivity of each voxel individually. They then investigated the predictive value of the non-face regressors, asking whether the face regressors alone could explain as much variance as the full model. Testing on an independent dataset suggested that approximately 18% of the variance in FFA responses was attributable to non-face objects.

Next, the authors used clustering analysis to reduce the various response profiles across FFA voxels, embodied by the 1705 regression weights. Although the fitted regression model does impose some *a priori* assumptions based on the semantic structure, the possible groupings are multifarious. The large number of object categories coupled with the clustering analysis allowed the authors to assess the heterogeneity of the FFA, asking whether all FFA voxels are essentially face selective [3] or whether this provisory conclusion stemmed from the paucity of stimuli that researchers thus far were including in experiments.

Çukur *et al.* propose that their results support heterogeneity in the FFA. The voxels, classified as face-selective based on a standard localizer, were found to separate reliably into three distinct clusters: the first cluster included voxels whose response was enhanced by humans and animals and weakly enhanced by vehicles, the second cluster included voxels whose response was strongly enhanced by humans and animals and weakly enhanced by communication actions and body parts, and the third cluster included voxels whose response was strongly enhanced by humans and weakly enhanced by communication actions and body parts but suppressed by manmade artifacts and buildings. The authors suggest that the differential tuning of FFA voxels to non-face objects may provide contextual information for face recognition, with different subregions tuned for different environments in which faces are typically encountered.

However, we would argue that Çukur *et al.*'s findings are also in line with a different account, whereby FFA voxels are functionally homogeneous but become heterogeneous as a function of experience. From this perspective the most striking aspect of these results is that, despite the large range of semantic categories going into the analysis, FFA voxel responses seem to map on patterns of selectivity obtained in prior studies that used many fewer categories. Recent work suggests that two FFAs can be reliably defined in most subjects and separated by a body-selective region located between the two [6]. Overlap between selectivity for human faces and animals has also been reported [4] – indeed, selectivity for faces and animals is not doubly dissociated even at high resolution [4,7]. Moreover, although prior work failed to find reliable selectivity for cars or planes in high-resolution FFA voxels when not taking subjects' experience with these categories into account, the reliability of such responses to vehicles increases with expertise [4]. Çukur *et al.* did not measure their subjects' expertise, although we know that men show more interest and higher performance with vehicles [4,8], so it is possible that Çukur *et al.*'s sample of four men and one woman led to more car selectivity (and that testing more women could have led to selectivity for other categories [8]). Whatever the reason for vehicles emerging here as a category eliciting FFA responses, it is interesting that neither here nor in high-resolution functional MRI (fMRI) work was the response to faces and vehicles doubly dissociated: those voxels that showed selectivity for vehicles were also responsive to faces.

Çukur *et al.*'s results contrast with studies concluding that there is only face selectivity in the FFA [2]. As we briefly reviewed, this face-only view is inconsistent with much research showing substantial responses in the FFA to non-face objects, with those responses growing with expertise for categories as diverse as cars, birds, chess displays, and radiographs. However, in the context of neurophysiological recordings in fMRI-defined face-selective patches in the monkey, which have been reported to contain as much as 97% face-selective cells [3], this new study, because it had better odds of finding more

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heterogeneity than prior work and did not, might instead provide support for considerable homogeneity in the FFA. Çukur *et al.*'s three clusters, one of which appears highly similar in response and location to the body-selective area situated between FFA1 and FFA2 [6] and which is typically not considered FFA, are consistent with a model in which all FFA voxels contain one homogeneous population of neurons: neurons that become tuned to features of objects we learn to individuate, with more neurons developing selectivity as the degree of experience increases. The size of face-selective areas in any one subject would be determined by how many of these neurons in the lateral fusiform gyrus have developed selectivity for faces. Subsets of this population (clusters) would emerge, because face-selective neurons also develop selectivity for other categories the subjects may individuate but for which experience levels rarely match that for faces. In other words, clusters may result from differences in expertise between categories, but functionally all neurons in this area may be *a priori* capable of responding to many categories. Such multiplexing is observed in earlier visual areas [9]. Neurons that can participate in the representation of faces and other objects of expertise, as part of neural ensembles, which may not be able optimally to represent objects from distinct categories simultaneously, is one way to account for competition observed between faces and cars in car experts [10].

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