

**Dynamic reorganization of the middle fusiform gyrus: long-term bird  
expertise predicts decreased face selectivity**

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**Keywords:** FFA; perceptual expertise; whole-brain correlation; dynamic reorganization

**Running Head:** Dynamic reorganization of fusiform gyrus

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**Includes:** 6 pages, 14 references, 1574 words, supplemental methods, 3 supplemental figures

**What is the functional relationship between face-selective and expertise-predicated object-selective regions in the human middle fusiform gyrus? In two separate fMRI experiments, superior behaviorally-measured bird expertise predicts both *higher* middle fusiform gyrus selectivity for birds and, concomitantly, *lower* selectivity for faces. This finding suggests a long-term dynamic reorganization of the neural mechanisms underlying the visual recognition of faces and non-face.**

David Starr Jordan, an ichthyologist and president of Stanford, remarked that he wanted to learn the names of all of his students, but that every time he remembered a student, he forgot a fish. This anecdote suggests that although our ability to learn new categories continues throughout life, this plasticity may have consequences for our prior knowledge and, in particular, for the neural representation of faces. Category selectivity in human ventral-temporal cortex has been associated with both faces<sup>1-3</sup> and expertise in non-face homogeneous object categories<sup>4-6</sup>. Here we explore whether there is a tradeoff between the category-selective codes for faces and objects of expertise. If these two domains share some of the same finite neural resources, we predict that increasing expertise in a non-face domain may decrease the neural resources available for processing faces (independent of behavioral consequences). This tradeoff is evident during expertise acquisition<sup>4</sup> – increasing expertise with “Greebles” led to neural responses in the “fusiform face area” (FFA)<sup>1</sup> that increased for Greebles and, concurrently, decreased for faces<sup>(4, Fig. 2, pp. 569)</sup>. A visual agnostic trained to recognize Greebles showed a similar pattern<sup>7</sup>. Event-related potentials measured for laboratory-acquired<sup>8</sup> and extant expertise<sup>9</sup> also suggest competition between non-face expertise and face processing. In this study we investigate whether real-world experts – “birders” – show a similar tradeoff in their localized category-selective responses for faces and birds in the human middle fusiform gyrus (mFG).

New England bird experts and novices participated in two fMRI experiments (informed consent approved by the Brown University IRB). Experiment 1 included four stimulus categories: faces, objects, Rhode Island and Asian birds; in four tasks (order counterbalanced):

passive viewing (PV), 1-back identity (1bID), 1-back location (1bLO), and 2-back identity (2bID) (Fig. 1a). Experiment 2 included three categories (faces, objects, and Rhode Island birds) in a PV task (**Supplemental Methods**). Because our subjects showed a wide range of “birding” abilities, standard region-of-interest (ROI) methods are unlikely to find significant group effects in that they focus on positive face- or expertise-selective regions *a priori* (i.e., by definition, the FFA cannot be “face-unselective”<sup>1</sup>). Indeed, percent signal change within each subject’s functionally-defined FFA did not show any significant correlations with expertise across any of the four tasks (*r*’s from -.1 to .1). To better assess the relationship between expertise and neural responses, we used whole-brain correlation (WBC) in which each subject’s “expertise score”<sup>5</sup> for birds (*d*’) was correlated with *all* measured voxel responses for a given comparison. This correlation was run for two functional localizers: activity for birds as compared to objects,  $[\beta_{\text{RI\_birds}} - \beta_{\text{objects}}]$ , and activity for faces as compared to objects,  $[\beta_{\text{faces}} - \beta_{\text{objects}}]$ , both corrected for multiple correlations<sup>10</sup>. This analysis method differs from correlations within fixed ROIs<sup>5,3,6</sup>, in that it avoids the “face-selection” bias in which the ROI is defined as the voxel cluster that is maximally face *selective*. WBC makes no such *a priori* assumptions, identifying those voxels maximally *correlated* with each neural comparison – here faces or birds relative to objects.

In Experiment 1, regressing  $[\beta_{\text{RI\_birds}} - \beta_{\text{objects}}]$  against expertise scores reveals significant mFG clusters (Fig. 1b) in the PV, 1bLO, and 1bID tasks; similar to the expertise effect found using location-based<sup>5,6</sup> and identity tasks<sup>5</sup>. Surprisingly, regressing  $[\beta_{\text{faces}} - \beta_{\text{objects}}]$  against expertise scores also reveals significant mFG clusters across all four tasks (Fig. 1b). What is critical is the relative *direction* of these two effects, as well as the spatial overlap of the ROIs within the mFG. Consistent with expertise in a non-face domain impacting the neural coding of

faces, we observe *positive* correlations between bird expertise and  $[\beta_{\text{RI\_birds}} - \beta_{\text{objects}}]$ , but *negative* correlations between expertise and  $[\beta_{\text{faces}} - \beta_{\text{objects}}]$ .

As alternatives to neural reorganization in birders, we should consider three possibilities: (1) across-subject neuroanatomical differences might account for the tradeoff; (2) age, a covariate of expertise, could account for the reduction in face selectivity; (3) greater bird expertise could manifest as an on-line preference for birds over faces that would produce reduced neural responses to faces concurrently with hyper-activated neural responses to birds, particularly when bird and face stimuli are intermixed – as in Experiment 1.

To address alternative (1), we ran an additional whole-brain correlation following inter-subject hemispheric alignment, which minimizes the neuroanatomical sulci and gyri variation across subjects<sup>11</sup>. Though weaker, for  $[\beta_{\text{faces}} - \beta_{\text{objects}}]$ , we again observe four negative expertise-correlated mFG areas (**Fig. S1**), indicating that across-subject neuroanatomical differences cannot account for the tradeoff. To address alternative (2), we ran Experiment 2 (PV only) in which the mean ages of our bird experts (43 yrs) and novices (39 yrs) were roughly equivalent. If age alone, instead of bird expertise, predicts diminished face selectivity, we would expect to find a negatively correlated, age-predicated cluster in mFG for  $[\beta_{\text{faces}} - \beta_{\text{objects}}]$  irrespective of each individual's bird expertise. However, in Experiment 2 we again find an inverse correlation between bird expertise and  $[\beta_{\text{faces}} - \beta_{\text{objects}}]$  in the mFG (**Fig. 2**), but do not observe an age-predicated face-selective ROI. This finding both replicates Experiment 1 with additional subjects and indicates that age alone cannot explain our pattern of results. Finally, to address alternative (3), we selected three superior bird experts (expertise scores:  $d' = 2.06, 1.89, \text{ and } 1.72$ ) and ran an additional “pure” functional FFA localizer:  $[\beta_{\text{faces}} - \beta_{\text{objects}}]$ , including only faces and objects blocks in the 1bID task. We predicted that if the decreased face-selective responses in bird



experts' mFGs were due to the presence of bird blocks interleaved with face blocks, this reduction in face selectivity should dissipate in a face/object-only imaging session. However, although the overall difference between face and object selectivity was smaller in this control condition, there was no systematic shift in which face-related activity could be statistically or qualitatively differentiated from activity arising from objects (one expert showing no change, one expert showing a shift from faces greater than objects to no difference and one expert showing a shift from no difference to faces greater than objects; **Fig. S2**). Thus, the negative relationship between bird expertise and neural responses to faces does not appear to arise from temporary deactivation due to lateral inhibition or attentional factors.

Notably, in Experiment 1 the error rates and reaction times of novices and experts in the 1bLO, 1bID, and 2bID tasks were not significantly different from one another, nor did performance in these tasks correlate with bird expertise (all  $p > .05$ , **Fig. S3**). That is, our bird experts, with respect to both faces and birds appearing in the tasks used during fMRI scanning, were behaviorally equivalent to bird novices. It may be that the tasks we used during scanning were insufficiently sensitive to reveal the behavioral consequences of this neural tradeoff, or that this neural tradeoff does not have any behavioral consequences unless the visual recognition system is heavily taxed or resources are abnormally limited (i.e., due to brain injury<sup>7</sup>). Future studies could rely on more sensitive performance metrics to assess whether there is a change in advanced birder's facial recognition performance.

In sum, we find an inverse relationship between bird and face selectivity in the mFG that is modulated by an individual's expertise with birds. Our findings are also consistent with other studies of experience-dependent neural plasticity: Braille reading impacting the primary visual cortex of blind subjects<sup>12</sup>, route knowledge affecting the hippocampi of London taxi drivers<sup>13</sup>,

and extensive finger training producing changes in primary motor cortex<sup>14</sup>. Beyond the implications of our results with regard to neural coding and potential capacity limits within human inferior temporal cortex, they also support the theory that category selectivity arises, at least in part, as a consequence of our everyday experiences, and that some components of the ventral pathway are subject to dynamic reorganization throughout our life span.

#### ACKNOWLEDGEMENTS

*Thanks to Isabel Gauthier for her comments. Funding provided by the Perceptual Expertise Network (#15573-S6), a collaborative award from James S. McDonnell Foundation; NSF award to MJT: #BCS-0094491; and the Ittleson Family Foundation to Brown University.*

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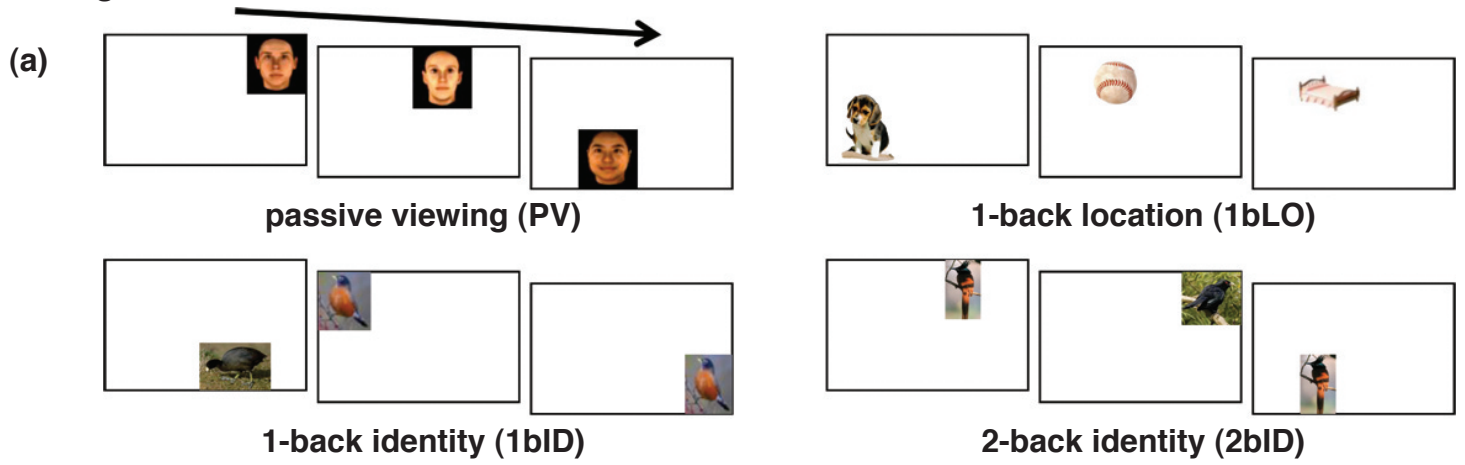
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## Figure Captions

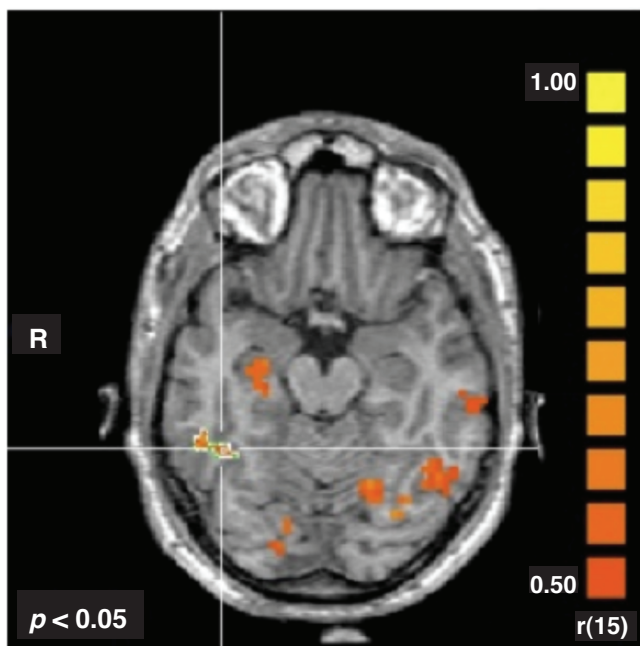
**Figure 1. Design, stimuli, and results from Experiment 1.** (a) Design and the stimulus examples in Experiment 1. Note that all of the stimuli were presented in every task, and the task orders were counter-balanced across subjects; (b) The bird-selective ( $[\beta_{RI\_birds} - \beta_{objects}]$ ) and face-selective ( $[\beta_{faces} - \beta_{objects}]$ ) expertise-correlated regions across participants in 1bID task ( $n=17$ ,  $p < .05$ ); (c) We find positive expertise-correlated (between behaviorally-measured bird expertise and  $[\beta_{RI\_birds} - \beta_{objects}]$ ) mFG regions in three tasks: in PV: Talairach coordinates: (43, -51, -13), 244 mm<sup>3</sup>; in 1bLO: TAL: (24, -52, -14), 121 mm<sup>3</sup>; in 1bID: TAL: (40, -47, -13), 312 mm<sup>3</sup>. We also find negative expertise-correlated (between behaviorally-measured bird expertise and  $[\beta_{faces} - \beta_{objects}]$ ) mFG regions across all four tasks: in PV, TAL: (38, -45, -18), 176 mm<sup>3</sup>; in 1bLO, TAL: (37, -44, -20), 889 mm<sup>3</sup>; in 1bID, TAL: (37, -44, -22), 284 mm<sup>3</sup>; and in 2bID, TAL: (40, -44, -20), 82 mm<sup>3</sup>. \*  $p < .05$ ; \*\*  $p < .01$ ; \*\*\*  $p < .001$ .

**Figure 2. Design, stimuli, and results from Experiment 2.** (a) Sample stimuli from Experiment 2 which exclusively used the passive viewing (PV) task ( $n=16$ ). The mean age difference between bird experts and novices was roughly matched (43.8 vs. 39.0 yrs) in Experiment 2 and there are a wider range of bird expertise ( $d'$  from  $\sim 0.5$  to  $\sim 3$ ); (b) The positive bird-selective ( $[\beta_{RI\_birds} - \beta_{objects}]$ ) expertise-correlated region is localized at TAL: (42, -43, -13), 170 mm<sup>3</sup>; and the negative face-selective as ( $[\beta_{faces} - \beta_{objects}]$ ) expertise-correlated region is localized at TAL: (30, -43, -17), 54 mm<sup>3</sup>; \*  $p < .05$ ; \*\*  $p < .01$ .

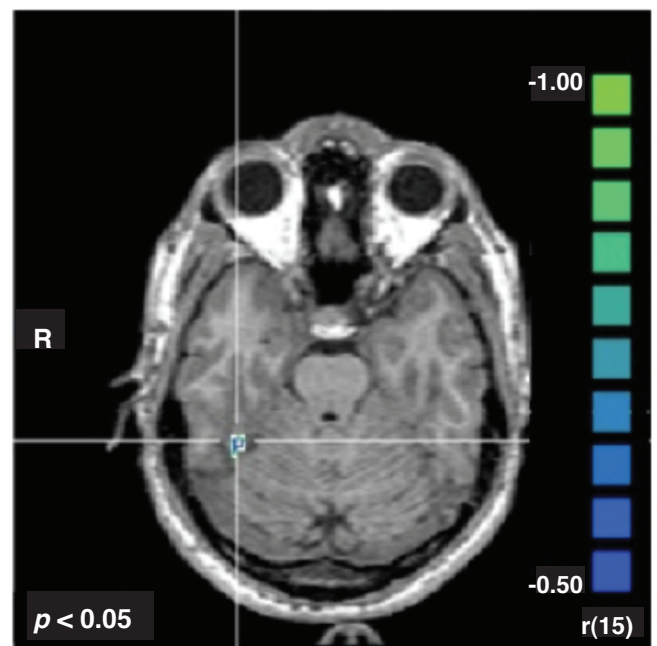
Tarr - Figure 1



(b) RI Birds – Objects



Faces – Objects



(c)

