

**Complementary neural representations for faces and words:  
A computational exploration**

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Running title: Complementary systems for faces and words

Acknowledgements: This work was funded by NSF grant BCS0923763 to Behrmann and Plaut and by NSF grant #SBE-0542013 to the Temporal Dynamics of Learning Center, an NSF Science of Learning Center.

### Abstract

A key issue that continues to generate controversy concerns the nature of the psychological, computational and neural mechanisms that support the visual recognition of objects such as faces and words. While some researchers claim that visual recognition is accomplished by category-specific modules dedicated to processing distinct object classes, other researchers have argued for a more distributed system with only partially specialized cortical regions. Considerable evidence from both functional neuroimaging and neuropsychology would seem to favor the modular view, and yet close examination of those data reveal rather graded patterns of specialization that support a more distributed account. This paper explores a theoretical middle ground in which the functional specialization of brain regions arises from general principles and constraints on neural representation and learning that operate throughout cortex but that nonetheless have distinct implications for different classes of stimuli. The account is supported by a computational simulation, in the form of an artificial neural network, that illustrates how cooperative and competitive interactions in the formation of neural representations for faces and words account for both their shared and distinctive properties. We set out a series of empirical predictions, which are also examined, and consider the further implications of this account.

### INTRODUCTION

Two opposing theoretical perspectives have been offered to explain the manner by which biological structures, such as the ventral visual cortical regions, come to be functionally optimized for visual object recognition. The first approach argues that there are distinct cortical modules or subsystems, which mediate particular behavioral processes, such as face, word, and object recognition, in a domain-specific manner (for recent reviews, see Kanwisher, 2010; McKone & Robbins, in press).<sup>1</sup> Consistent with this approach is the finding that different regions in extrastriate visual cortex respond selectively to domain-specific categories of visual stimuli: many recent functional neuroimaging studies have shown, for example, that the fusiform face area (FFA) is activated in response to faces (e.g., Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Gore, & McCarthy, 1995), the parahippocampal place area (PPA) to scenes (e.g., Epstein, Harris, Stanley, & Kanwisher, 1999; Epstein & Kanwisher, 1998; Swards, 2011), the extrastriate body area (EBA) and fusiform body area (FBA) to human bodies and body parts

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1 We use the terms “module” and “modular” not in the strict senses in which Fodor (1983) defined them, but to denote a general class of theoretical commitments in which domain-specific cognitive processes, such as face recognition, are each carried out by a neuroanatomically identifiable cortical area, such as the FFA. To the extent that multiple cortical areas are involved in a given cognitive process, it would mitigate against a modular account of that process but might still be consistent with modular accounts of localized subprocesses.

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3 (e.g., Downing, Jiang, Shuman, & Kanwisher, 2001; Peelen & Downing, 2005; Schwarzlose,  
4 Baker, & Kanwisher, 2005; Taylor, Wiggett, Downing, 2010; Willems, Peelen, & Hagoort, 2010)  
5 and the visual word form area to orthographic inputs (e.g., Dehaene & Cohen, 2011). Indeed, in  
6 each of these regions, the cortical response for the preferred category is about twice that for the  
7 non-preferred category and this category-selectivity can be consistently observed in most  
8 normal individuals, even across a range of very different experimental paradigms. All of this  
9 attests to the robustness of the evidence that these regions are specialized for, and perhaps  
10 even dedicated to, the recognition of particular object classes (Kanwisher, 2010; McKone &  
11 Robbins, 2011).

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23 The second approach recognizes the apparent selectivity of neural systems for certain  
24 visual classes but argues that this selectivity need not implicate very specialized or dedicated  
25 modules per se. This theoretical account entails one or both of two possible brain-behavior  
26 organizations: rather than a single region alone subserving processing of a particular input type  
27 (e.g., faces), multiple regions mediate the recognition of a particular object type and/or an  
28 individual region mediates the neural representations of multiple object types. The claim, then,  
29 is that, under either of these scenarios, specialization is more graded and regions may be  
30 optimized for, but not necessarily dedicated to, a particular cognitive function. Consistent with  
31 this alternative perspective, in addition to the FFA, multiple other cortical regions evince face-  
32 selectivity, including the occipital face area (OFA, Gauthier et al., 2000), the posterior superior  
33 temporal sulcus (Hoffman & Haxby, 2000) and the anterior temporal lobe (Kriegeskorte et al.,  
34 2007; Rajimehr et al., 2009) and, indeed, multiple regions have sufficient neural information to  
35 discriminate between individual face exemplars (Nestor, Plaut, & Behrmann, 2011) (for more  
36 extended review, see Avidan & Behrmann, 2009; Haxby et al., 2000; Ishai, 2008). Furthermore,  
37 it is not simply that the distributed network is domain-specific as there are now many fMRI  
38 studies showing that even highly selective single regions, such as the FFA, evince a BOLD  
39 response to different object classes, albeit with lesser degrees of activation than, for example, to  
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3 faces (e.g., Grill-Spector, Sayres, & Ress, 2006; Hanson & Schmidt, 2011; Haxby et al., 2001;  
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5 Haxby, Petit, Ungerleider, & Courtney, 2000; Ishai, Schmidt, & Boesiger, 2005; Nestor et al.,  
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7 2011; Norman, Polyn, Detre, & Haxby, 2006) and the same is true for the vWFA (Nestor,  
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9 Behrmann, & Plaut, submitted; Price & Devlin, 2011).

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12 In this paper, we compare and contrast the more modular and more distributed accounts  
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14 with specific reference to two visual classes—faces and words. We choose these two classes  
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16 not only because, intuitively, they appear to be diametrically opposed but also because they  
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18 differ obviously along many other dimensions. Words and faces share little in common in their  
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20 overt geometry and so their image statistics share minimal, if any, overlap. Additionally,  
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22 whereas face representations are acquired naturally over the course of experience, word  
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24 recognition typically requires explicit instruction. Also, whereas faces are probably the most  
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26 ecologically relevant visual stimuli, orthographies have only been around for a few thousand  
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28 years and so the evolutionary trajectories of these two visual classes differ greatly.  
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32 We start by reviewing the clear evidence for the separability of the underlying systems  
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34 for words and faces. Thereafter, we present a proposal in which we argue that common  
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36 principles may account for both the similarities and differences in the mechanisms underlying  
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38 words and faces. We support this proposal with a computational simulation in which a common  
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40 underlying mechanism, constrained by a putative set of computational principles, mediates both  
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42 face and word recognition and demonstrates the types of functional specialization observed  
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44 empirically. Although we address the correspondences between brain and behavior in these two  
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46 particular domains, the argument has applicability to other aspects of cognition and its neural  
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48 correlates, as well, provided that these other cognitive behaviors place the same computational  
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50 demands on the visual recognition system. We also return to this point in the final discussion.  
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### 53 54 55 **Evidence for separability of word and face processing systems**

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57 On a modular account of brain-behavior organization, words and faces engage separate  
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3 psychological and neural mechanisms and are, essentially, unrelated and independent. Support  
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5 for this view is substantial and gleaned from functional imaging investigations, as well as from  
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7 neuropsychological studies (Kleinschmidt & Cohen, 2006)..  
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### 10 11 12 *The Visual Word Form Area*

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14 Numerous functional imaging studies have demonstrated that the word module or 'visual  
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16 word form area' (VWFA) (e.g., Cohen et al., 2000; Cohen et al., 2003; Dehaene, Cohen,  
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18 Sigman, & Vinckier, 2005; Dehaene & Cohen, 2011) responds selectively to visually presented  
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20 words and letter strings (e.g., Fiez, Balota, Raichle, & Petersen, 1999; Mechelli, Gorno-Tempini,  
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22 & Price, 2003; Petersen, Fox, Snyder, & Raichle, 1990; Petersen & Fiez, 1993; Turkeltaub,  
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24 Eden, Jones, & Zeffiro, 2002) to a greater degree than digits (Polk et al., 2002) or pseudo-letters  
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26 (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Cohen & Dehaene, 2004), but not to spoken  
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28 words (Cohen & Dehaene, 2004). The VWFA activation is located in left extrastriate cortex  
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30 (Talairach coordinates: x=-43, y=-54, z=-12), is identifiable in single subjects (Puce, Allison,  
31  
32 Asgari, Gore, & McCarthy, 1996) and is sensitive to the individual's experience – Hebrew  
33  
34 readers show greater activation of this region for Hebrew than English words and vice versa  
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36 (Baker et al., 2007), and activation in this area is correlated with literacy (Dehaene et al., 2007,  
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38 2010; Dehaene & Cohen, 2011). The VWFA is situated anterior to retinotopic cortex and,  
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40 consistent with this, activation is relatively insensitive to retinal position and to the font, size or  
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42 case of the input (Polk & Farah, 2002). Activation of VWFA, as measured in ERPs, is rapid,  
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44 emerging around 150-200ms after stimulus onset (McCandliss, Cohen, & Dehaene, 2003). In  
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46 normal readers, the minimal increase in reaction time (RT) as a function of word length (Lavidor,  
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48 Ellis, Shillcock, & Bland, 2001; Weekes, 1997) is attributed to the parallel processing of multiple  
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50 letters (to the limits of foveal acuity, i.e., around 9 letters) and this parallel processing is ascribed  
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52 to the functionality of the VWFA.  
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57 Further support for the circumscribed functionality of the VWFA comes from studies of  
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3 premorbidly literate individuals with 'pure alexia' (for review of cases, see Montant & Behrmann,  
4 2000; Starrfelt & Behrmann, 2011). The lesion site in these cases is typically in the left  
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6 2000; Starrfelt & Behrmann, 2011). The lesion site in these cases is typically in the left  
7 occipitotemporal area along the fusiform and adjacent lingual gyrus, with possible incursion to  
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9 the inferior longitudinal fasciculus (Cohen, Henry et al., 2004; Cohen et al., 2003; Feinberg,  
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11 Schindler, Ochoa, Kwan, & Farah, 1994; Salvan et al., 2004) and overlaps the region of the  
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13 VWFA activation reported above (Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Petersen  
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15 et al., 1990; Puce et al., 1996). The characteristic profile of pure alexia is a linear increase in RT  
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17 as a function of the number of letters in the input (giving rise to the label 'letter-by-letter reading')  
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19 and this is assumed to reflect the breakdown of parallel processing in the VWFA and the  
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21 subsequent reliance on a serial, laborious left-right letter spelling strategy (McCandliss et al.,  
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23 2003; Warrington & Shallice, 1980). The patients are not aphasic, typically showing intact  
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25 production and comprehension of spoken language along with normal writing, all of which  
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27 supports the circumscribed nature of the problem as a specific difficulty in processing visual  
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29 word forms (but see Starrfelt & Behrmann, 2011, for discussion of high association with an  
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31 impairment of number processing as well).  
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### 38 *The Fusiform Face Area*

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40 Just as in the case of the VWFA, there is substantial evidence for face-processing  
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42 specificity gleaned from fMRI studies and from patient studies. Functional imaging studies have  
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44 provided evidence that the region that is functionally specialized for faces, the 'fusiform face  
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46 area' (FFA) ( $x=40, y=-55, z=-10$ ), is selectively activated by faces, especially upright faces,  
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48 over other non-face objects (Kanwisher, 2010; Puce et al., 1995; Yovel & Kanwisher, 2005) and  
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50 over animal or cartoon faces (e.g., Kanwisher, 2000; Kanwisher et al, 1997; Kanwisher, Woods,  
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52 Iacoboni, & Mazziotta, 1997; Sergent, Ohta, & MacDonald, 1992a, 1992b; Spiridon, Fischl, &  
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54 Kanwisher, 2006) and the magnitude of the activation is correlated with face identification ability  
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56 (Furl, Garrido, Dolan, Driver, & Duchaine, 2010; Yovel, Tambini, & Brandman, 2008). FFA  
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3 activation is situated anterior to retinotopic cortex and, consistent with this, activation is  
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5 relatively insensitive to retinal position and to size, color, format (drawing or photographs) and  
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7 viewpoint of input. The FFA is selectively activated for faces but abuts other cortical regions  
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9 that are specialized for other visual categories, such as scenes, animals and tools (e.g., Reddy  
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11 & Kanwisher, 2006; Spiridon & Kanwisher, 2002; also, Puce et al., 1995, 1996; Tranel,  
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13 Damasio, & Damasio, 1997).

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16 Correspondingly, lesions to the FFA (Bouvier & Engel, 2006; Damasio, Damasio, &  
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18 Tranel, 1986; Kleinschmidt & Cohen, 2006) result in prosopagnosia, a selective impairment in  
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20 face recognition. The lesion in prosopagnosia is often bilateral, affecting the temporo-occipital  
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22 cortex in the region of the FFA, but unilateral right hemisphere lesions to this same region may  
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24 suffice to give rise to this disorder (Barton, 2008; Bouvier & Engel, 2006), and prosopagnosia  
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26 can also be congenital or developmental in the absence of a frank lesion (Behrmann & Avidan,  
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28 2005). The difficulty in recognizing faces can be dramatic, including failures to recognize friends  
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30 or even close family members. Unlike normal observers, these individuals do not obviously  
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32 exhibit the advantage for upright over inverted faces (occasionally even showing an inversion  
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34 superiority effect; Farah, 1996; Farah, Tanaka, & Drain, 1995) and do not appear to process  
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36 faces configurally, thus failing to evince the benefit from the presence of the whole face over just  
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38 parts of the face (Barton, 2009; Barton, Cherkasova, Press, Intriligator, & O'Connor, 2004;  
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40 Busigny & Rossion, 2010; Tanaka & Farah, 1993).

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43 Taken together, these studies provide empirical support for the claim that there is  
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45 specialized processing of faces and words associated with two distinct cortical modules, the  
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47 FFA for faces and the VWFA, for words, and that these two systems are separable and  
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49 independent.  
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### 52 53 54 55 **Not only differences but also commonalities**

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57 Although there is general consensus that the FFA and VWFA are tuned to faces and words,  
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3 respectively, there are also intriguing empirical data that suggest that both their tuning and their  
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5 hemispheric specialization is relative or graded. For example, it appears that both the VWFA  
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7 and FFA can be activated by a wide range of stimuli, not just faces or words: the VWFA is  
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9 strongly activated in response to checkerboards, pictured objects, and verb naming to pictures  
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11 (Devlin et al., 2006; Murtha, Chertkow, Beauregard, & Evans, 1999; Price & Devlin, 2003, 2011)  
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13 and even to non-visual inputs such as Braille (Büchel, Price, Friston, 1998; Reich, Szwed,  
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15 Cohen, & Amedi, 2011), whereas the FFA is activated by a range of non-face stimuli, such as  
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17 houses and cars, but also novel objects such as Greebles (Gauthier et al., 1999) and chess  
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19 configurations (Bilalic et al., 2011), although the full extent of the selectivity is still controversial  
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21 (Gauthier et al., 1999; Grill-Spector et al., 2006; Haxby, 2006). Neither the FFA nor the VWFA,  
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23 however, appears to be as strongly activated by these other stimuli as is the case when shown  
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25 the 'preferred' input type, reflecting perhaps the graded nature of the underlying  
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27 representations. Recent imaging studies adopting multivariate methods applied to fMRI data of  
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29 ventral visual cortex have begun to uncover the co-mingling of patterns of activation associated  
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31 with different stimulus types (e.g., face and word representations) to an even greater degree  
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33 than was revealed in earlier studies employing univariate analyses (for an example of a recent  
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35 study using multi-voxel pattern analysis, see Nestor et al., 2011). In these multivariate studies, it  
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37 is not simply the magnitude of the activation that is crucial but the distribution of the neural  
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39 information in the patterns of voxel activation.  
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45 Also relevant to the similarities across classes is the observation that almost all fMRI  
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47 and ERP studies show bilateral activation for words and for faces, albeit with differential  
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49 hemispheric asymmetry and greater scalp potential for the preferred stimulus type in the  
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51 corresponding hemisphere – words on the left and faces on the right (e.g., see Hasson et al.,  
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53 2002; Kanwisher et al., 1997; Kronbichler et al., 2004; Price & Mechelli, 2005; Puce et al., 1996;  
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55 Sergent et al., 1992; Tagamets, Novick, Chalmers, & Friedman, 2000). Moreover, the peak  
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57 activation for words in vWFA and for faces in FFA (although coordinates differ a little across  
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3 different studies) are very comparable in the two hemispheres (for example, Talairach  
4 coordinates for peak for words  $x=-43$ ,  $y=-54$ ,  $z=-12$  and for faces  $x=40$ ,  $y=-55$ ,  $z=-10$ ). We also  
5 note that these coordinates roughly demarcate cortical sites that are anterior to retinotopic  
6 cortex but are situated in what would be the anterior extrapolation of the fovea (Levy et al.,  
7 2001; Hasson et al., 2002). The localization of the functional regions in this cortical location is  
8 consistent with the invariance of face and word activation over retinal position of the inputs, but  
9 also with the fact that reliance on fine-grained visual discrimination is a necessary component of  
10 both face and word recognition.  
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20 Somewhat surprisingly, there has not been a systematic examination of the word  
21 recognition of prosopagnosic individuals and the face recognition of pure alexic individuals.  
22 There are some hints, however, that each hemisphere may play a dual, albeit graded, role in  
23 both face and word recognition. For example, it has been reported that the face recognition  
24 impairment is more severe following bilateral than unilateral lesions (Damasio et al., 1985;  
25 Gainotti & Marra, 2011), implicating both hemispheres to some extent and that TMS of the RH  
26 even impairs reading in patients with LH lesions (Coslett & Monsul, 1994).  
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36 Additionally, in a few case studies in which both stimulus classes have been examined,  
37 some prosopagnosic individuals show increased word length effects in reading aloud single  
38 words: for example, the slope of the reaction time in single word reading was 104 ms and 241  
39 ms per additional letter for prosopagnosic patients SM and RN, respectively, compared with the  
40 normal slope of about 10 ms for words 3 through 8 letters in length (Behrmann & Kimchi, 2003).  
41 In a complementary fashion, there have only been a few reports of pure alexic individuals who  
42 have difficulties with face recognition (also see Farah 1991, 1992, 1999, for listing of co-  
43 occurrences of different forms of agnosia/alexia) although this is not always assessed in these  
44 cases. One recent relevant study documents a case with left occipital arteriovenous  
45 malformation in whom both pure alexia and prosopagnosia were evident (Liu et al., 2011). Many  
46 studies do report abnormalities in the recognition of non-orthographic stimuli in pure alexia even  
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3 after a unilateral lesion (Behrmann, Nelson & Sekuler, 1998; Starrfelt & Behrmann, 2011) and  
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5 so one might predict that a decrement in face recognition in these cases, as well. As evident,  
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7 closer scrutiny of the existing data, to the extent they are available, suggest that there may be  
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9 more overlap in face and word processing in the preeminent face (right FFA) and word (left  
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11 VWFA) regions than originally considered. To account for both the apparent differences and the  
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13 similarities, we propose an account that differs from the strictly modular or domain-specific view.  
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### 18 **An alternative proposal: Common constraints on faces and words**

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20 The theoretical proposal outlined in this paper adopts an alternative perspective with respect to  
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22 the key systems engaged in face and word processing. The central idea is that visual object  
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24 recognition (e.g., face and word recognition) is supported, not by highly specialized (or  
25  
26 dedicated) modules per se, but by a distributed and interactive network of brain regions with  
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28 similar computations but whose organization is strongly shaped and modified by experience.  
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30 This view then incorporates both the claim that multiple cortical regions are engaged and that  
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32 these nodes of this distributed network play a role in representing more than one stimulus type.  
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34 Importantly, on this view, the functional specialization of brain regions is graded rather than  
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36 absolute and reflects the consequences of a set of general principles and constraints on neural  
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38 computation that operate throughout cortex but that nonetheless have distinct implications for  
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40 different classes of stimuli. Note that, on this account, there is no appeal to pre-specified  
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42 modules and, rather than claiming de facto sensitivity to different visual classes, the origin and  
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44 emergence of these graded mechanisms is captured too. The novelty of this approach is not the  
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46 principles themselves (see both Dehaene & Cohen, 2011, and Price & Devlin, 2011, for similar  
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48 notions about the VWFA) but their integrated application to derive common consequences for  
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50 cortical organization and behavior for words and faces.  
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55 This alternative proposal takes as its starting assumptions three general principles of  
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57 neural computation, that the neural system for face/word recognition is distributed, that  
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3 knowledge is represented in this system by cooperation and competition between the  
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5 processing units, and that the organization of the system is constrained by topographical  
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7 considerations, pressure for proximity and the division of labor between the two hemispheres of  
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9 the brain. We expand on these assumptions here.  
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#### 11 12 13 14 *Distributed representation and knowledge* 15

16 We assume that the neural system for visual object recognition consists of a set of  
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18 hierarchically organized cortical areas, ranging from local retinotopic information in V1 through  
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20 more global, object-based and semantic information in anterior temporal cortex (Grill-Spector &  
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22 Malach, 2004). At each level, the visual stimulus is represented by the activity of a large  
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24 number of neurons, and each neuron participates in coding a large number of stimuli.  
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26 Generally, stimuli that are similar with respect to the information coded by a particular region  
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28 evoke similar (overlapping) patterns of activity. The set of constraints on how activity at one  
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30 level produces activity at the next level—that is, the knowledge of how features combine to form  
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32 features at the next level—is encoded by the pattern of synaptic connections and strengths  
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34 between and within the regions. Learning involves modifying these synapses in a way that  
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36 alters the representations evoked by visual stimuli—typically in a way that captures the relevant  
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38 information in the domain better and that supports more effective behavioral outcomes. With  
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40 extended experience, expertise develops through the refinement, specialization, and elaboration  
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42 of representations, requiring the recruitment of additional neurons and a larger region of cortex  
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44 (Quartz & Sejnowski, 1997).  
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#### 51 *Representational cooperation and competition* 52

53 As illustrated by artificial neural networks (e.g., McClelland & Rumelhart, 1985), a single  
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55 pattern of synaptic connections can learn to encode the knowledge needed to represent many  
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57 stimuli, but its ability to do so depends on the degree to which the relevant knowledge is  
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3 consistent or systematic (i.e., similar representations at one level correspond to similar  
4 representations at another). In general, systematic domains benefit from highly overlapping  
5 neural representations that support generalization, whereas unsystematic, unrelated domains  
6 require largely non-overlapping representations to avoid interference. Thus, if a cortical region  
7 represents one type of information, it is ill-suited to represent another type of information that  
8 requires unrelated knowledge, and so, that information must be represented by a different  
9 region. On the other hand, effective cognitive processing requires the coordination of multiple  
10 levels of representation within a given domain, and often across multiple domains. Of course,  
11 representations can cooperate directly only to the extent they are connected—that is, there are  
12 synapses between the regions encoding the relevant knowledge of how they are related;  
13 otherwise, they must cooperate indirectly through mediating representations. In this way, the  
14 neural organization of cognitive processing is strongly constrained by available connectivity (see  
15 Mahon & Caramazza, 2011, for a similar argument regarding connectivity serving as an  
16 endogenous constraint on topographic organization in the ventral stream).  
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### 36 *Topography, proximity, and hemispheric organization*

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38 Brain organization must permit sufficient connectivity among neurons to carry out the  
39 necessary information processing, but the total axonal volume must fit within the confines of the  
40 skull (for similar discussion, see Cowey, 1979). This constraint is severe: if the brain's  $10^{11}$   
41 neurons were placed on a sphere and fully interconnected with 0.1 mm radius axons,  
42 accommodating the axon volume would require a sphere over 20 km in diameter (Nelson &  
43 Bower, 1990). If we think of brain organization as the result of a complex optimization process  
44 that minimizes “costs” associated with the degree to which various pressures or biases are  
45 violated, then clearly there is a strong pressure to keep connectivity as local as possible. Long-  
46 distance projections are certainly present in the brain but they are relatively rare and  
47 presumably play a sufficiently critical functional role to offset their cost in volume. In fact, the  
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3 organization of human neocortex as a folded sheet can be understood as a compromise  
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5 between the spherical shape that would minimize long-distance axon length and the need for  
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7 greater cortical area to support highly elaborated representations. The organization into two  
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9 hemispheres is also relevant here, as interhemispheric connectivity is largely restricted to  
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11 homologous areas and is thus vastly less dense than connectivity within each hemisphere.  
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13 Even at a local scale, the volume of connectivity within an area can be minimized by adopting a  
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15 topographic organization so that related information is represented in as close proximity as  
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17 possible (Jacobs & Jordan, 1992). This is seen most clearly in the retinotopic organization of  
18  
19 early visual areas, given that light falling on adjacent patches of the retina is highly likely to  
20  
21 contain related information. Note that the dimensions of this topography are not in the  
22  
23 Cartesian (x, y) coordinates that apply naturally to images, but something closer to polar (r,  $\theta$ )  
24  
25 coordinates, where eccentricity (central vs. peripheral) is coded along one axis and rotational  
26  
27 angle is coded along another (e.g., De Yoe et al., 1996; Grill-Spector & Malach, 2004; Sereno et  
28  
29 al., 1995; Tootell et al., 1997). The relevant dimensions of similarity for higher-level visual areas  
30  
31 are, of course, far less well understood, but the local connectivity constraint is no less pertinent  
32  
33 (Jacobs, 1997).  
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37  
38 Despite these commonalities, the principles rule out using the very same cortical region  
39  
40 to represent both faces and words because these stimuli require entirely distinct primitives to be  
41  
42 represented as visual objects, and typically have distinct consequences for cognition (faces  
43  
44 designate individuals, whereas—apart from proper names—words designate objects, actions,  
45  
46 properties, typically at a basic rather than individual level). Given the need for written words to  
47  
48 interact with aspects of language that are left lateralized in most individuals (Cai et al., 2008), it  
49  
50 follows from representational competition and cooperation that visual word representations  
51  
52 would be predominantly located in the dominant language hemisphere (Price & Devlin, 2011)  
53  
54 whereas face representations would be located in the homologous region in the RH. Indeed,  
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56 some data to support this competition/cooperation comes from the observation that, with  
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3 increasing literacy, there is a decrease in response to faces in the VWFA (Dehaene et al., 2010)  
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5 and that, in four-year olds, performance in identifying alphanumeric characters (digits and  
6  
7 letters) was correlated with a decrease in left fusiform activity (Cantlon et al., 2011). In both of  
8  
9 these studies, however, the competition appears to be restricted to the left hemisphere with the  
10  
11 trading relations between faces and words manifesting in the left fusiform region. The  
12  
13 hypothesis we propose, however, encompasses the left and the right hemispheres with the  
14  
15 competition and cooperation playing out for words and faces across both sides of cortex.  
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## 20 21 **SIMULATION**

22  
23 To date, the majority of computational work on face recognition has an applied focus with only  
24  
25 tangential relevance to the human cognitive and neural system—this includes approaches  
26  
27 based on Principal Components Analysis (e.g., Turk & Pentland, 1991), Independent  
28  
29 Components Analysis (e.g., Bartlett et al., 2002), Linear Discriminant Analysis (e.g., Etemad &  
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31 Chellapa, 1997), Kernel methods (e.g., Bach & Jordan, 2002; Yang, 2002), 3D morphable  
32  
33 models (e.g., Blanz & Vetter, 2003) and Bayesian inference (e.g., Moghaddam et al., 2000).  
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35 Modeling efforts that explicitly address psychological and neuropsychological issues (e.g.,  
36  
37 Burton et al., 1991; Farah et al., 1993) have tended to focus on the interaction of higher-level  
38  
39 knowledge with rather less consideration of low- and intermediate-level visual representation  
40  
41 and processing (although see Burton et al., 1999). More recently, Cottrell and colleagues  
42  
43 (Dailey & Cottrell, 1999; Dailey et al., 2002; Hsiao et al., 2008; Kanan & Cottrell, 2010; Tong et  
44  
45 al., 2008) have extended this work by coupling distributed network modeling with more realistic  
46  
47 assumptions about early visual processing.  
48  
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50  
51 A similar situation holds with regard to word recognition. Although some early cognitive  
52  
53 and neuropsychological modeling employed hierarchical visual representations of letters and  
54  
55 words (Mozer, 1991; Mozer & Behrmann, 1990; McClelland & Rumelhart, 1981), the vast  
56  
57 majority of more recent work has emphasized higher-level interactions of orthographic,  
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3 phonological, and semantic knowledge (e.g., Coltheart et al., 2001; Harm & Seidenberg, 1999,  
4 2004; Plaut et al., 1996; Perry et al., 2007; although see Plaut, 1999). Efforts to model  
5 orthographic representations per se (e.g., SOLAR, Davis, 1999; SERIOL, Whitney, 2001) have  
6 typically focused more narrowly on letter position effects in orthographic priming. One notable  
7 exception is the split-fovea model (Shillcock et al. 2000), which explicitly considers the  
8 representational implications of a divided visual field. Although this specific model runs into  
9 some empirical difficulties (see, e.g., Grainger et al., 2006), there is no doubt that the cortical  
10 representation of words is shaped in important ways by hemispheric organization and  
11 specialization (Cai et al., 2008).

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Given the apparent lack (to date) of any proposed relationship between face and word processing, it is not surprising that our computational work is the first to address these domains together within a single model. Although the current implementation does not extend to the higher-level knowledge involved in face and word recognition, the underlying principles are fully compatible with ongoing modeling work at these higher levels.

Perhaps the least familiar of our computational principles concerns the impact of local connectivity on learning. Thus, as an initial exploration of the impact of topographically constrained learning on cortical organization, we carried out a simulation in which an artificial neural network was trained to take retinotopic visual information as input and to map these via hemisphere-specific intermediate representations (corresponding to left and right occipitotemporal cortex) to recognize faces, words, and—as a commonly used contrasting category—houses. The topographic bias on learning, combined with the demands for high-acuity information for faces and word recognition, should lead to these stimuli being represented in intermediate (fusiform) regions near central vision. The need for representational cooperation between words and language-related information, in conjunction with representational competition between faces and words (given their incompatibility as visual objects) is predicted to give rise to left-hemisphere specialization for words and right-hemisphere specialization for

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3 faces. Due to the graded nature of the learning constraints, this specialization should be only  
4  
5 partial, with both regions participating in processing both types of stimuli to a certain degree.  
6  
7 Houses are expected to be represented by more peripheral regions in fusiform cortex,  
8  
9 analogous to the “parahippocampal place area” (PPA; Epstein & Kanwisher, 1998; Levy et al.,  
10  
11 2001).  
12

13  
14 All simulations were developed within the Light Efficient Network Simulator (Lens;  
15  
16 version 2.63), developed by Doug Rohde and available for download at [tedlab.mit.edu/~dr/Lens](http://tedlab.mit.edu/~dr/Lens).  
17  
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## 19 20 21 **Methods**

22  
23 *Stimuli.* As the goals of the current work are to explore and illustrate the implications of  
24  
25 a set of putative computational principles rather than to build a realistic model of visual face and  
26  
27 word perception, the task and network architecture employed in the simulation were kept as  
28  
29 simple as possible. The stimuli used in the simulation were derived from 32x32 bit schematic  
30  
31 line drawings of faces, houses and words that embodied critical differences in the demands of  
32  
33 recognition of these classes of stimuli (see Figure 1). Each of 34 faces differed in terms of small  
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35 changes in the positions or shapes of central features (e.g., separation and height of eyes,  
36  
37 length of nose, height and width of mouth). Each of 40 3-letter (CVC) words were created from  
38  
39 combinations of 5 possible letters for each position and, like faces, differed from each other only  
40  
41 in terms of features within central vision. By contrast, each of 9 houses differed in terms of  
42  
43 properties that varied across the entire visual field (e.g., size of windows, number of eaves,  
44  
45 presence of porch, size of base). Note that these rather small differences place high demands  
46  
47 on fine visual acuity to ensure accurate discrimination between exemplars.  
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51 Insert Figure 1 approximately here

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53 Each item was presented at nine different scales, ranging from 1.0 to 0.6 in steps of 0.05, for a  
54  
55 total of 747 input patterns. For each pattern, retinotopic input activation was generated by  
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57 smoothing the original bit patterns by convolving them with a Gaussian (sd=0.5) and then  
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3 transforming the resulting values into polar coordinates  $(r, \theta)$ , such that eccentricity  $r$  varied  
4 along the horizontal axis (with central information on the left and peripheral information on the  
5 right), and visual angle  $\theta$  varied along the vertical axis (see Figure 2 for examples).  
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10 Insert Figure 2 approximately here

11  
12 As the current work is concerned only with the nature of the visual representations of  
13 various stimulus classes, no attempt was made to approximate the structure of higher-level  
14 information that such representations provide access to, beyond the need to identify  
15 (individuate) each unique face, word, and house (despite changes in scale). Accordingly, the  
16 output representations used in the simulation consisted of individual “localist” units for each of  
17 the 34 faces, 40 words, and 9 houses. We recognize, of course, that this is unlikely to be the  
18 veridical output of the system.  
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29 *Network architecture.* The network architecture is depicted in Figure 3. In the model,  
30 32x32 retinotopic visual input to each hemisphere (in polar coordinates) is mapped via 64  
31 (32x2) intermediate units in each hemisphere (corresponding to fusiform cortex) onto a set of 83  
32 “Identity” units (one for each unique word, face and house). In addition, to approximate the  
33 influence of a left-hemisphere specialization for language, word inputs were also trained to  
34 activate one of a set of 40 “Language” units that receive input solely from the left-hemisphere  
35 intermediate units. Finally, the input-to-intermediate connections were subject to strong  
36 topographic bias during learning. Although this bias is assumed to be enforced in the brain by  
37 the relative density of synapses as a function of distance, the small scale of the simulation made  
38 it more appropriate to implement this bias slightly differently. Specifically, the input units were  
39 fully connected to the intermediate units, but the efficacy of learning decreased as a Gaussian  
40 function ( $sd=3.0$ ) of the distance between the connected units (Plaut, 2002). As we were  
41 primarily concerned with the impact of eccentricity on learning, this metric considered only  
42 horizontal distance in the simulation (i.e., all units in the same column in Figure 2 were  
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3 considered to have the equivalent functional position). Thus, in practical terms, learning was  
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5 effective on connections from inputs directly “below” a given intermediate unit, but increasingly  
6  
7 ineffective on connections from units with progressively different horizontal positions. For similar  
8  
9 reasons, although we would claim that all connectivity in the brain is subject to a topographic  
10  
11 bias, we did not apply this bias to any of the intermediate-to-output connections because we  
12  
13 had no hypothesis concerning the relative proximity of semantic or identity information (beyond  
14  
15 the left-lateralization of language information). The important consequence of this is that the  
16  
17 Identity units for faces, words and houses are equivalent in their connectivity with the  
18  
19 intermediate units, and thus any distinction in the specialization of the intermediate units must  
20  
21 arise solely from properties of the inputs. Finally, the simulation employed a feed-forward  
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23 architecture, without lateral (within-layer) or top-down connections, solely for computational  
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25 convenience.  
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30 Insert Figure 3 approximately here  
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34 *Training and Testing.* When presented with a scaled version of each face, word or  
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36 house, the network was trained to activate the correct Identity unit (and, for words, the correct  
37  
38 “Language” unit). Back-propagation (Rumelhart et al., 1986) was used to calculate how to  
39  
40 change each connection weight in the network to reduce the discrepancy between the output  
41  
42 activation pattern generated by the network and the correct pattern. Although not biologically  
43  
44 plausible in literal form, back-propagation is functionally equivalent to more plausible procedures  
45  
46 such as contrastive Hebbian learning (see, e.g., O'Reilly, 1996). The topographic bias on  
47  
48 learning at the intermediate layer was implemented by scaling these weight changes by a  
49  
50 decreasing (Gaussian) function of the horizontal distance between the connected input and  
51  
52 intermediate units. Following training, the network was considered to be correct if, for a given  
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54 input, the correct Identity unit was more active than any other.  
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57 The primary basis for establishing specialization in the network was its performance  
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3 following lesions restricted to spatially contiguous areas of either the left or right intermediate  
4 (fusiform) layer. Lesions were administered by removing three adjacent columns (6 units in  
5 total) from one of these layers and evaluating the performance of the damaged network for each  
6 of the 747 input patterns (83 identities x 9 scales). The horizontal position of these lesions were  
7 varied systematically in order to evaluate the relative specialization of each intermediate layer  
8 for each stimulus class as a function of visual eccentricity.  
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### 19 **Results and Discussion**

20 After 1000 training presentations of each pattern, the network is fully accurate at recognizing  
21 instances of each face, word and house (see Figure 4). Over the course of acquisition,  
22 performance on houses is better than on the other stimulus classes because there are fewer of  
23 them to differentiate. Performance on words is better than on faces in part because the latter  
24 involve more subtle featural distinctions and, in part, because the extra demands of activating  
25 “Language” information for words provides additional error (and therefore learning). By the end  
26 of training, however, performance on all three classes is equivalent and at ceiling.  
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36 Insert Figure 4 approximately here  
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40 To illustrate the effects of the topographic bias on learning in the network, Figure 5  
41 shows examples of the “receptive” and “projective” fields learned by two intermediate units. The  
42 left display is for a unit that has a receptive field in central vision (i.e., toward the left of the  
43 retinotopic input) and has output that is largely selective for faces (third and fourth rows in the  
44 top group of units). By contrast, the right display is for a unit that has a more peripheral  
45 receptive field (i.e., toward the center or right of the input) and is largely selective for houses  
46 (last row in the top group). These weight diagrams illustrate the impact of the topographic  
47 constraint on learning, and provide indirect evidence for learned category specificity of  
48 intermediate units as a function of their eccentricity.  
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Insert Figure 5 approximately here

More direct evidence for topographic specialization comes from the effects of localized lesions to the network. Figure 6 shows the performance of the network for each category of stimuli as a function of the horizontal position of lesions to three adjacent columns of units in either the left or right intermediate (fusiform) layer. Left-hemisphere lesions to the region of the fusiform near central visual information (analogous to the VWFA) produce a marked impairment in word recognition, but also a milder impairment in face recognition (relative to house recognition). By contrast, lesions to the corresponding region in the right hemisphere, (analogous to the FFA) impair face recognition most, but also word recognition to a lesser extent. Finally, lesions to the right fusiform adjacent to more peripheral visual information (analogous to the PPA) produce the greatest impairment on houses and a milder impairment on faces (relative to words). These findings are in qualitative agreement with existing observations (Epstein et al., 2001) and our derived predictions for graded functional specialization.<sup>2</sup>

Insert Figure 6 approximately here

This small-scale simulation provides a simple but clear demonstration of the impact of a topographic constraint on learning on the organization of representations mediating face, word and house recognition. The reliance of face and word recognition on central, high-acuity information leads to selectivity in the intermediate (fusiform) units closest to this information (Hasson et al., 2002; Levy et al., 2001, 2004). Competition between inconsistent information (and cooperation between word representations and language-related information) lead to substantial but still graded hemispheric specialization, with words represented primarily on the left and faces primarily on the right.

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<sup>2</sup> Although not reported here in detail, these qualitative results are stable over changes to non-essential aspects of the network architecture and training methods, including variations (within reasonable limits) in random initial weights, learning parameters, and numbers of hidden units.

## GENERAL DISCUSSION

This paper takes at its starting point a debate about the manner in which the brain is organized in the service of behavior. One longstanding view is that different parts of the brain are specialized, and perhaps even dedicated, for different cognitive functions. An alternative account is one in which there is no unique, one-function one-region correspondence; rather, a single region subserves many different tasks and/or a single task is mediated by many different regions. We have explored this latter, distributed perspective in the context of the ventral visual cortex and its organizational structure, taking as a model the case of face and word recognition. This is a particularly good domain in which to explore these different theoretical accounts as there are considerable empirical data on both the psychological and neural mechanisms involved in these functions, derived primarily from neuroimaging and neuropsychological investigations. We note, however, that the theoretical proposal is more general and applies to other visual domains that have the same computational demands as do words and faces.

The computational account we propose puts forward the theoretical claim that the representations of faces and words, albeit so apparently different in their surface characteristics and their underlying neural substrate, are the product of the same computational principles. Specifically, the visual recognition system has at its core three general principles, all of which have profound implications for both the commonalities and differences in the neural organization and functionality of face/word processing. The key principles include

1. *distributed representation and knowledge*: visual objects are represented by distributed patterns of neural activity within a hierarchically organized system, where learning involves modifying the pattern of synaptic connectivity between neurons within and between regions on the basis of experience;
2. *representational cooperation and competition*: effective cognitive processing requires the coordination of related information across multiple levels of representation, whereas unrelated or incompatible information must be

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3 represented over separate regions to avoid interference; and

- 4  
5 3. *topography, proximity, and hemispheric organization*: representational  
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7 cooperation must be accomplished with largely local connectivity between  
8  
9 topographically organized brain regions, and with limited connectivity between  
10  
11 hemispheres, so that total axonal volume fits within the confines of the skull.  
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14 These constraints have a fundamental impact on how faces and words are represented  
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16 and processed within the visual system.  
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18 Here, we show that a small-scale simulation that is trained to recognize faces, words  
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20 and houses in a manner consistent with these principles illustrates how a topographic constraint  
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22 on learning can give rise to learned category specificity of intermediate units as a function of  
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24 their eccentricity. This topographic constraint is further anchored by the reliance on fine-grained  
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26 visual processing for discriminating subtle visual differences among words and among faces.  
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28 Specifically, left-hemisphere lesions to the region of the intermediate layer near central visual  
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30 information (analogous to the VWFA) produce a marked impairment in word recognition, but  
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32 also a milder impairment in face recognition (relative to house recognition). By contrast, lesions  
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34 to the corresponding region in the right hemisphere (analogous to the FFA) impair face  
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36 recognition most, but also word recognition to a lesser extent. These findings are in qualitative  
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38 agreement with existing observations and our derived predictions for graded functional  
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40 specialization.  
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44 The results of the simulation provide an existence proof of a system in which face and  
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46 word recognition are subject to the same computational constraints but in which relative  
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48 specialization, by virtue of other competing pressures (to restrict connection length specifically  
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50 with language areas, see Cai et al., 2008; Price & Devlin, 2011) also demonstrates some  
51  
52 functional specialization. The idea that there are both many similarities as well as differences  
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54 among the mechanisms supporting face and word recognition is endorsed by the existing  
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56 neuroimaging studies (many or even most of which reflect bilateral activation for faces and  
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3 words) and some neuropsychological studies, which show dual impairment following a unilateral  
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5 hemispheric lesion.  
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### 8 9 10 **Converging evidence**

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12 There are some additional considerations, which favor a common-mechanism perspective. Both  
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14 face and word recognition are domains with which most individuals have extensive experience  
15  
16 and expertise. Both classes place demands on high-acuity information to encode subtle but  
17  
18 critical visual information and thus, the fact that the cortical regions that are selective for face  
19  
20 and word processing are located adjacent to the central visual information within the highest  
21  
22 level of retinotopic representation (Hasson et al., 2002; Levy et al., 2001) can be understood as  
23  
24 a natural consequence of topography and the constraint on local connectivity. Furthermore, the  
25  
26 cortical regions selective for these stimuli come to be located adjacent to retinotopic regions  
27  
28 coding foveal information, but in different hemispheres, with words in the left to permit  
29  
30 coordination with other language-related knowledge. Additionally, the VWFA and FFA are both  
31  
32 insensitive to low-level input variations (e.g. letter font; viewpoint for faces) suggesting that both  
33  
34 regions reflect functional specialization of higher-order visual cortex.  
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38 A further commonality is that lesions to each region renders the individual reliant on a  
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40 more piecemeal or segmental approach rather than one in which the configural or whole is  
41  
42 accessible. Just as vWFA lesions result in a laborious letter-by-letter sequential decoding of the  
43  
44 individual letters, lesions resulting in prosopagnosia give rise to a similar sequential process  
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46 with greater reliance on some features of the face (e.g. mouth, see example in Bukach et al,  
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48 2008) and a laborious encoding of the features as reflected in eye movement patterns (e.g., see  
49  
50 Stephan & Caine, 2009). Also, just as VWFA activation is affected by experience (Baker et al.,  
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52 2007; Wong et al., 2005), so adult-like face processing in the FFA also emerges with age and  
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54 experience and both regions evince a protracted developmental trajectory with signs of  
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56 specificity emerging roughly when children are in elementary school (Brem et al., 2005; Cohen  
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3 Kadosh & Johnson, 2007; Golarai et al., 2009, 2010; Joseph, Gathers & Bhatt, 2011; Scherf et  
4  
5 al. 2007)<sup>3</sup>. Finally, both regions are rather plastic: the VWFA can be acquired in the RH after left  
6  
7 occipital resection in childhood (Cohen, Lehericy et al., 2004) and there may also be a shift to  
8  
9 the right in patients following acquired LH lesions (Cohen, Lehericy et al., 2004; Cohen et al.,  
10  
11 2003). Relatedly, there are no apparent differences in the face recognition deficits of individuals  
12  
13 with unilateral lesions in infancy that impacted either the LH or RH (de Schonen et al., 2005).  
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16  
17 One apparent challenge to our emphasis on the role of visual experience in shaping the  
18  
19 cortical organization of face and word processing is the recent observation by Reich et al.  
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21 (2011) that the VWFA, as localized in sighted individuals, is also the location of peak activation  
22  
23 in congenitally blind individuals reading Braille words (compared to nonsense Braille control  
24  
25 stimuli). It should be noted, however, that Reich et al. found reliable differences in the entire left  
26  
27 ventral occipitotemporal cortex all the way to V1, consistent with earlier findings by Noppeney,  
28  
29 Friston, & Price (2003) that were attributed to recruitment of these areas for semantic  
30  
31 processing. Reich et al.'s only evidence for (tactile) word-form representations per se was that  
32  
33 activation differences were larger for Braille reading compared with auditory verb generation,  
34  
35 but this comparison is possibly dubious as it involves separate and unrelated control tasks.  
36  
37 Moreover, the fact that activation differences peaked in the same location in blind and sighted  
38  
39 individuals may arise because of intrinsic patterns of connectivity between early visual cortex  
40  
41 and parietal structures involved in spatial attention (Greenberg et al., submitted manuscript) and  
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43 this inherent white matter arrangement biases where activation peaks are likely to be observed  
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45 in functional imaging studies.  
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### 51 **Where do hemispheric differences come from?**

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53 3 The exact nature of the change over developmental time remains somewhat controversial with some  
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55 studies showing changes in the volume of activation for one category over another and others showing  
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57 a change in functional/effective connectivity over the course of development. The studies are also not  
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59 entirely consistent with each other (see Cantlon et al., 2010, showing adult-like activation to faces as  
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well as sensitivity to alphanumeric symbols in four year olds although volume/cluster size was not  
evaluated in this study). These empirical discrepancies remain to be resolved.

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3 Our account presupposes that the hemispheric differences and asymmetries emerge  
4 over the course of experience, during which time the connectivity and topography constraints  
5 play out. There are, however, other theoretical stances, which interpret the emergent  
6 hemispheric differences as arising from a different origin. One such account is that the left  
7 hemisphere (LH) processes input in an analytical or part-based way (hence its role with words)  
8 whereas the right hemisphere (RH) processes input more holistically (hence its role with faces)  
9 (see also Farah 1991, 1992). A second view attributes the word/face distinction to the distinction  
10 between linguistic (LH) and spatial (RH) processing. Yet a further view is that the face/word  
11 difference arises from differential frequency sensitivity (Robertson & Ivry, 2000) with the RH and  
12 LH responding to relatively low and high spatial frequency information, respectively, and the  
13 former critical for faces (RH), and the latter for words (LH). A final possibility is that the  
14 face/word differences arise from the differential predisposition to process inputs categorically  
15 (LH words) versus by coordinate relations (RH faces) (Kosslyn et al., 1989). These accounts all  
16 suggest that it is the fundamental (perhaps even hard-wired or innately specified) properties of  
17 the two hemispheres that play a role in shaping the underlying computational differences  
18 between words and faces, but how and to what extent this is so remains to be determined.

19  
20 Our approach is not mutually exclusive with these process-based accounts but it  
21 emphasizes the importance of expertise in shaping cortical organization and function (Gauthier  
22 & Bukach, 2007; Gauthier & Nelson, 2001), although expertise alone cannot explain why the  
23 FFA and VWFA are located where they are, nor why other types of expertise (namely, those not  
24 demanding high-acuity visual information) do not engage these areas. It also shares the  
25 fundamental assumption of Malach and colleagues (Levy, Hasson, Hendler, & Malach, 2001;  
26 Levy, Hasson, & Malach, 2004) regarding pressure for foveal acuity and cortical topography, but  
27 goes beyond this by implementing the ideas in explicit simulations, enabling the testing of  
28 specific predictions concerning the relationship of face and word processing. There remain of  
29 course, complex questions about why the left hemisphere is language-dominant in the majority  
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3 of the population and the source of this organizational pattern. Such issues are beyond the  
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5 scope of this paper but are intriguing and remain to be addressed, too.  
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### 9 10 **Predictions**

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12 A full assessment of the tractability of our account remains to be undertaken and, in particular,  
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14 there are a number of predictions that can be tested. Much of our work, thus far, has focused on  
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16 the need for representational cooperation between words and the language-related output, as  
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18 the key pressure that drives the left hemisphere specialization. But this cooperation occurs in  
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20 conjunction with representational competition between faces and words (given their  
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22 incompatibility as visual objects) and this competition, too, motivates the hemispheric  
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24 distinctions with left and right biased for words and faces, respectively. A prediction of this  
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26 trading relations view is that individuals who have greater asymmetries for faces (e.g. relative to  
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28 baseline, greater performance advantage for faces presented to left than right visual field or  
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30 greater activation in the right hemisphere in imaging) should show the converse for words on an  
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32 individual-by-individual basis, depending on how the cooperation and competition play out  
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34 during the course of development and experience. We also anticipate that some individuals will  
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36 have more bilaterally graded representation and that there will be a large range of individual  
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38 differences across the population. This prediction is eminently testable through half-field  
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40 studies, as well as functional imaging investigation, and we are currently undertaking such  
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42 explorations including examining hemispheric asymmetries for faces and words within individual  
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44 and across groups of young children, adolescents and young adults.  
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49 A further rather obvious prediction is that individuals with damage to the left VWFA and  
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51 presenting with pure alexia might also be impaired at face recognition, relative to normal  
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53 participants, albeit to a lesser extent than individuals with prosopagnosia following a lesion to  
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55 the right FFA. The converse is also predicted: individuals with a lesion to the right FFA and  
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57 presenting with prosopagnosia might also be impaired at word recognition, relative to controls,  
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3 albeit to a lesser extent than individuals with pure alexia following a lesion to the left VWFA. We  
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5 have examined these predictions in a small group of individuals, all of whom were pre-morbidly  
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7 normal and have acquired unilateral ventral cortex lesions (Behrmann & Plaut, in preparation).  
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9 In this study, we used the same series of face and of word experiments to evaluate the  
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11 performance of three adults with circumscribed unilateral right hemisphere lesions and  
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13 prosopagnosia and four pure alexic adults with circumscribed unilateral left hemisphere lesions.  
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15 Control participants matched to the two groups were also tested. In addition to the expected  
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17 impairment in face recognition, the prosopagnosic individuals showed abnormal word  
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19 recognition relative to the controls albeit not as marked as in the pure alexics and, in  
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21 complementary fashion, the pure alexic individuals showed abnormal face recognition relative to  
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23 the controls albeit to a lesser extent than in the prosopagnosics (for related findings, see  
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25 Buxbaum, Glosser, & Coslett, 1996, 1999). These empirical findings anchor a key prediction of  
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27 our account which is that hemispheric asymmetries for face and word recognition are graded  
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29 and not fully and independently segregated.  
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### 36 **Limitations and extensions**

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38 The computational simulation presented here was intentionally kept as simple as possible in  
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40 order to provide the clearest illustration of the consequences of our putative computational  
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42 principles for graded specialization of the neural representations of faces and words (and, to a  
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44 more limited extent, houses). The most obvious limitations of the simulation are that it used a  
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46 small set of highly schematized stimuli, a strictly feedforward network architecture without lateral  
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48 and top-down interactions within or between hemispheres, a lack of separate excitatory and  
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50 inhibitory unit populations, and a biologically implausible learning procedure. Although we claim  
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52 that the core findings regarding learned functional specialization do not depend critically on any  
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54 of these simplifications, it is important to validate these findings in more realistic follow-up  
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56 simulations. Such follow-up versions should use realistic stimuli, employ a more biologically  
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3 plausible learning procedure (e.g., contrastive Hebbian learning; see O'Reilly, 1996), and permit  
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5 only excitatory connections between layers by using a separate population of local inhibitory  
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7 units within each layer. We do not anticipate that these elaborations will alter the basic  
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9 operation of the model but they will bring it into much closer alignment with the operation of real  
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11 neural systems.  
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## 13 14 15 16 **Conclusion**

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18 Our central hypothesis is that the commonalities in the neural mechanisms of face and word  
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20 processing are not merely coincidental, as modular theories are left to conclude, but rather, are  
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22 the signature consequences of a set of general principles and constraints on neural computation  
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24 that operate throughout cortex. We note that these principles themselves are not intended to be  
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26 novel; in fact, we take them to be largely non-controversial. Instead, the novelty derives from  
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28 their common consequences for cortical organization and behavior in two seemingly unrelated  
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30 domains, specifically, in the context of words and faces,  
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34 Critically, when instantiated in explicit computational terms, these principles provide  
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36 insight into why each of these properties is partial rather than absolute. This is because the  
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38 principles and constraints are inherently graded—adherence to the forces of cooperation,  
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40 competition, and proximity in the process of learning cortical representations is a matter of  
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42 degree as these constraints trade off against each other, and thus the consequences for neural  
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44 and behavioral specialization is also graded. As a result, the implications of graded constraints  
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46 go beyond explaining why neither pure alexia nor prosopagnosia is entirely 'pure', and why,  
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48 across a host of imaging studies, the FFA and VWFA show substantial responses to stimuli  
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50 other than faces and words, respectively. They also imply that the functional and anatomical  
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52 division between face and word recognition should be graded—despite the clear differences  
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54 between the two domains, the FFA should be partially involved in word recognition and the  
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56 VWFA should be partially involved in face recognition. In this way, our theoretical perspective  
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3 leads to important and otherwise unexpected predictions concerning the partial co-mingling of  
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5 face and word processing, including face recognition impairments in pure alexia, word  
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7 recognition impairments in prosopagnosia, graded participation of the FFA and VWFA in  
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9 face/word recognition in normal observers, and a number of other implications that remain to be  
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11 tested.  
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## Figure legends

Figure 1. The full set of face, word, and house stimuli used to create inputs to the simulation. Each picture defines a unique identity; the actual inputs to the network were generated by smoothing and transforming into polar coordinates (see Figure 2 for examples).

Figure 2. Example face, house, word stimuli after Gaussian smoothing. For each stimulus class, the left three panels show stimuli in x-y coordinates; the corresponding right panel shows the same stimulus in polar co-ordinates—the form actually presented to the network as input. Also, for each class, the top two rows differ in identity; the bottom two rows differ only in scale.

Figure 3. The network architecture used in the simulation. Each square corresponds to a particular processing unit. Activations for a particular example input are depicted by the grey-scale value of the square (black=0.0; white=1.0). Sets of connections are depicted by lines/arrows but are not shown in detail. For each of the two retinotopic input layers, activations toward the left encode central visual information whereas activations toward the right encode more peripheral information. The projections from the two input layers to the left and right intermediate (fusiform) layers are subject to a horizontal topographic bias favoring short connections.

Figure 4. Correct performance of the network in identifying faces, words, and houses as a function of the number of presentations of the entire set of 747 example patterns received by the network during training.

Figure 5. Example receptive (input-to-intermediate) and projective (intermediate-to-output) fields for two units in the right-hemisphere intermediate layer. (Units in the left-hemisphere intermediate layer show essentially the same patterns of receptive and projective fields as those shown here.) Each square in the receptive and projective fields shows the value of the weight (red for positive weights; blue for negative weights) from that unit either into or out of the depicted unit in the intermediate layer (outlined in yellow). The top group of units are output units; the first two rows are for words, the next two rows are for faces, and the last row is for houses.

Figure 6. Correct performance on faces, words, and houses following focal lesions to either the left or right intermediate (fusiform) layer in the network, as a function of the horizontal position of the lesion (ranging from central to peripheral moving left to right within each hemisphere).

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Figure 1a

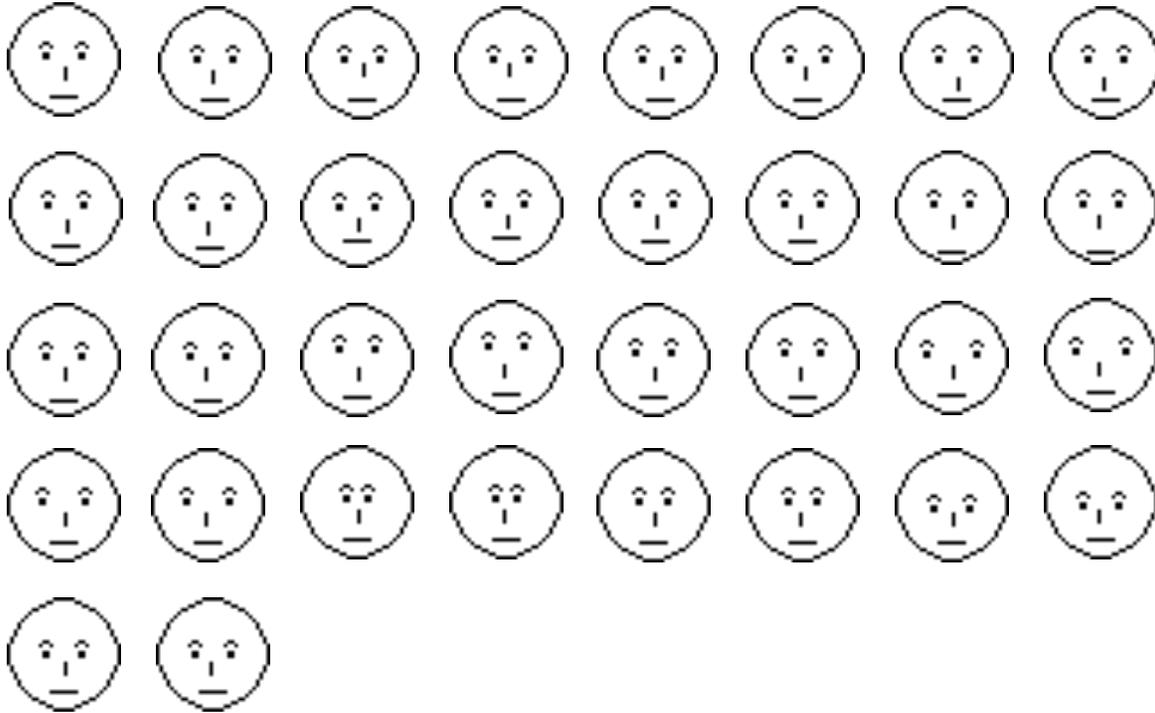


Figure 1b

BAG	BED	BEG	BET	BID	BIG	BIT	BUD
BUT	DAD	DID	DIG	DIP	DOG	DOT	DUG
MUD	MET	MEN	MAT	MAP	MAN	MAD	PAD
PAN	PEN	PET	PIG	PIP	POP	POT	PUT
TAG	TAN	TAP	TEN	TIN	TIP	TON	TOP

Figure 1c



Figure 2

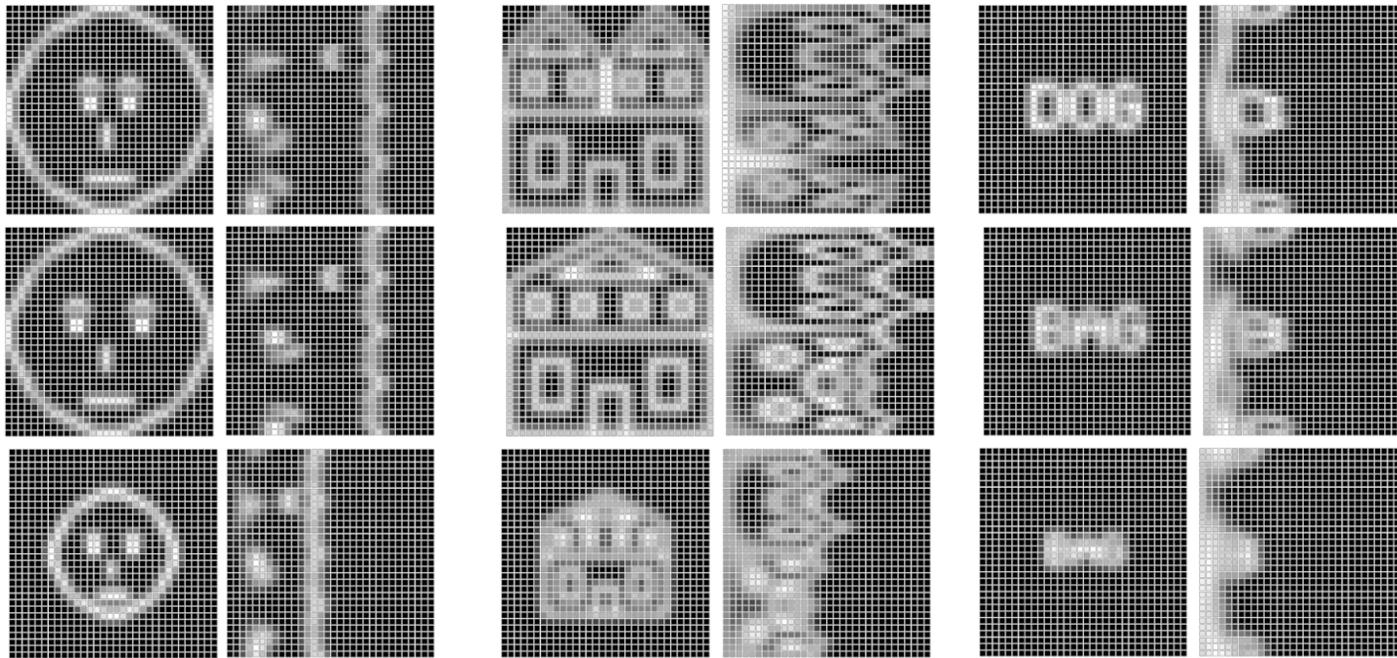


Figure 3

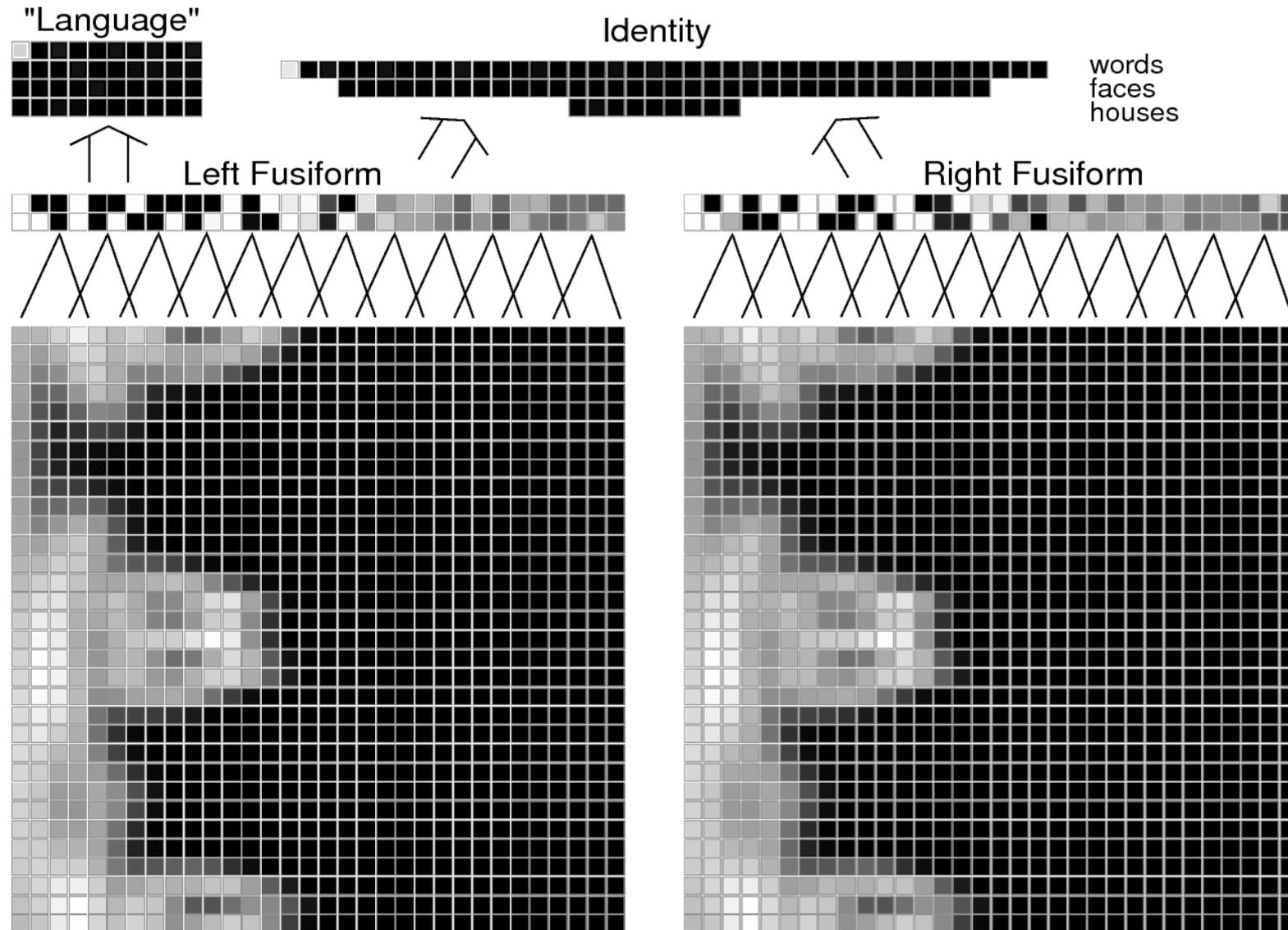
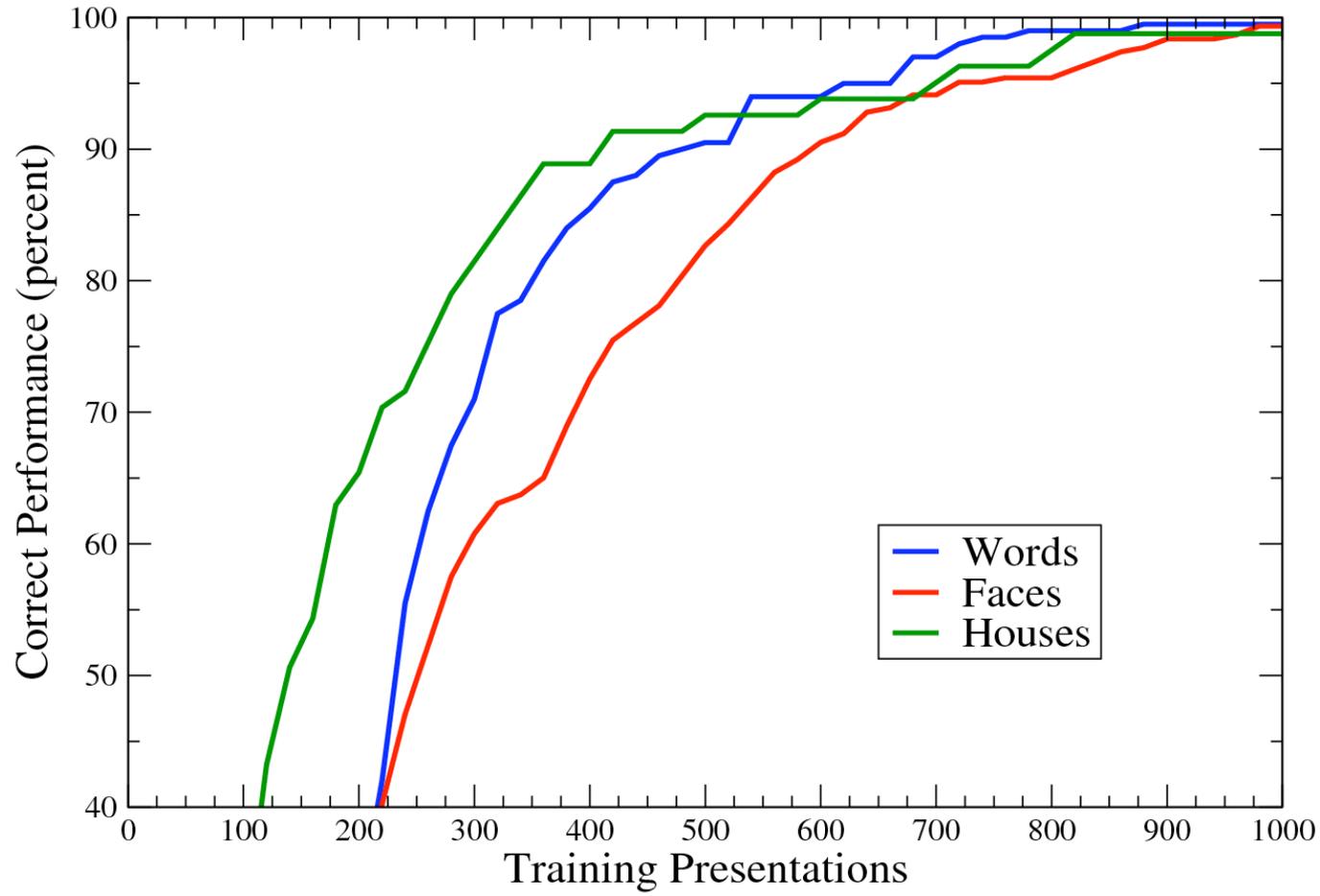
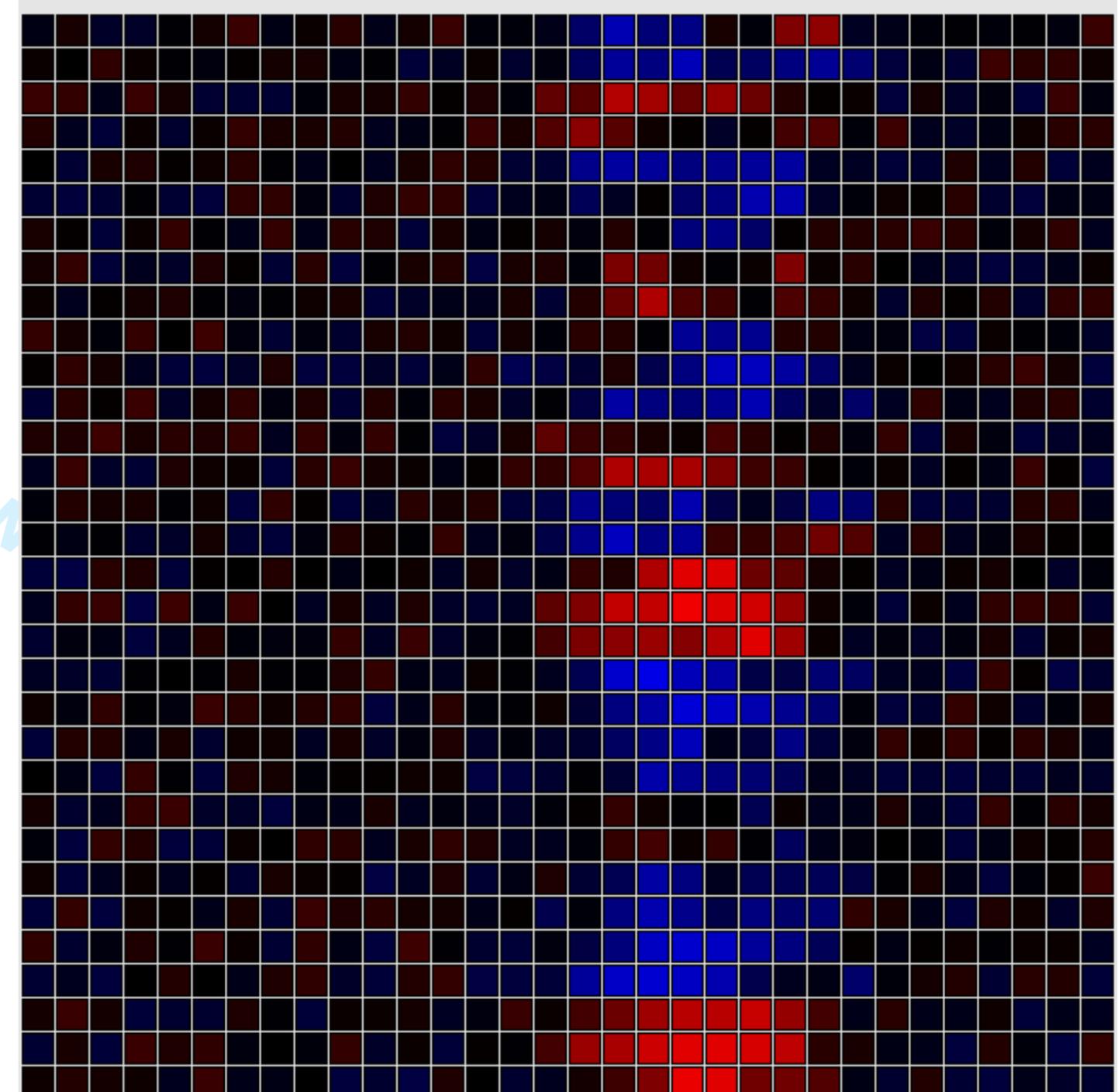
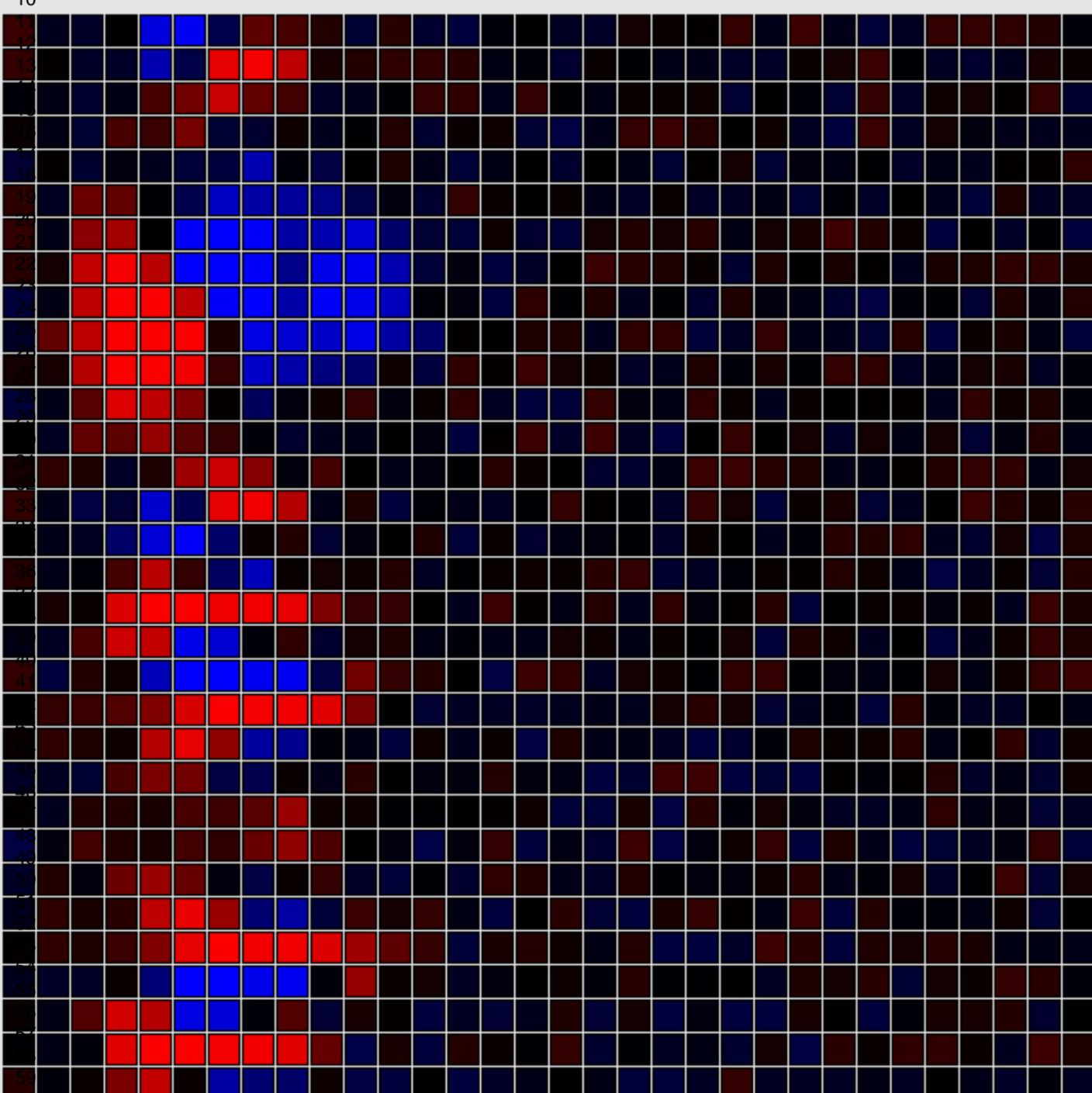
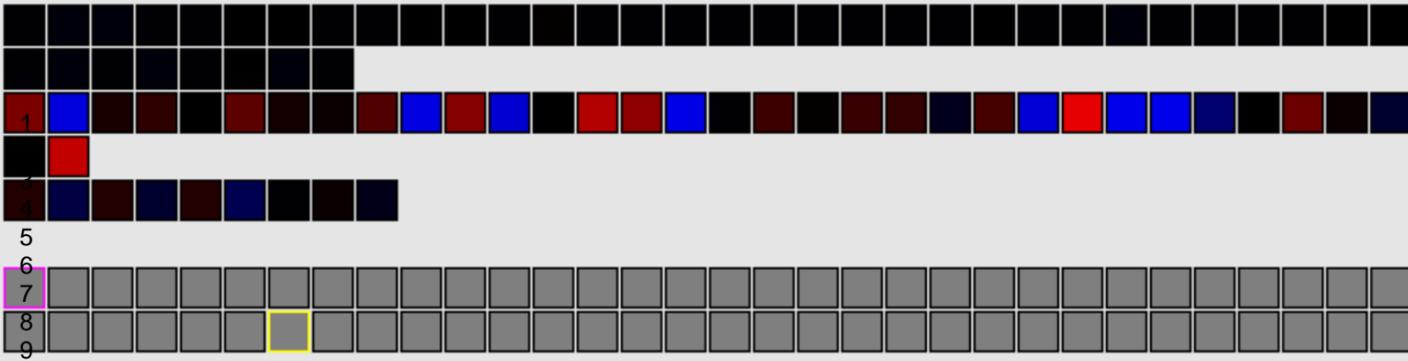


Figure 4





Peer Review

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Figure 6

