Neuropsychologia 92 (2016) 90–106

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Retinotopic information interacts with category selectivity in human ventral cortex

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ARTICLE INFO

Article history:
Received 6 December 2015
Received in revised form
7 April 2016
Accepted 20 May 2016
Available online 27 May 2016

Keywords:
Retinotopy
Category selectivity
Face processing
fMRI
Scene processing
Functional connectivity

ABSTRACT

Until recently, the general consensus with respect to the organization of ventral visual cortex is that early, retinotopic regions are sensitive to the spatial position of the input stimuli whereas later, higher-order regions are sensitive to the category of the input stimuli. Growing recognition of the bidirectional connectivity of the visual system has challenged this view and recent empirical evidence suggests a more interactive and graded system. Here, based on findings from functional MRI in adult observers, in which meridians and category selective regions are localized and their activation sampled, we support this latter perspective by showing that category effects are present in retinotopic cortical areas and spatial position effects are present in higher-order regions. Furthermore, the results indicate that the retinotopic and later areas are functionally connected suggesting a possible mechanism by which these seemingly disparate effects come to be intermixed in both early and later regions of the visual system.

1. Introduction

Until fairly recently, there has been a general consensus that more posterior, earlier, parts of the visual cortical hierarchy are governed by principles of topography, retaining an isomorphic relationship between the location of the stimulus in the world and the activation of a particular region of early visual cortex. In contrast, the more anterior, later, cortical regions are tuned to respond to particular categories of objects (for example, faces or houses), abstracted away from spatial location of the input stimuli. These two principles, 'spatial specificity' and 'category specificity', are thought to guide the transition from positional specificity instantiated in the progression from smaller to larger receptive field sizes as one moves caudally to rostrally in the visual cortex to position independence and the ability to generalize across higher-order changes, including viewing angle, pose and size (Desimone and Gross, 1979; Kobatake and Tanaka, 1994). Thus, the standard view has been that the goal of the computation of the ventral visual cortex is to derive stable and invariant properties of the perceptual input by gradually abstracting away low-level properties of the input through the derivation of more conceptual representations. Similar arguments have been made with respect to the dorsal system, as well (Roth and Zohary, 2015).

There has, however, been growing recognition that this strict division into retinotopic versus non-retinotopic cortex may not hold in this binary fashion. Accumulating evidence has led to an alternative conceptualization of ventral visual cortex which posits that, in a fully connected bidirectional network (Felleman and Van Essen, 1991), even more anterior, higher-order regions, standardly associated with the representation of more complex patterns, might reflect some of the topographic constraints of the area from which signals are received. And, by the same token, the activation profile of early visual areas which are considered primarily driven by and responsive to the input topography, perhaps on a purely feedforward basis, might reflect some of the properties of higher-order (even category-selective) areas perhaps by virtue of receiving feedback signals from these more anterior regions (for recent discussion of this point, see Furl, (2015)).

Support for the idea of an interactive and more graded system that results in a mixture of positional and category specificity in the visual system has been gleaned from various studies (for comprehensive review, see Kravitz et al., (2013)). As we review below, some of these investigations have argued for positional and retinotopic influences in later parts of the visual system and some have provided evidence of category-selective effects in earlier spatially-organized parts of the visual system. To our knowledge, however, there has been no consideration of the functional connectivity between earlier and later parts of the visual system that would permit and facilitate the bidirectional influence of retinotopic properties and category specificity. The focus of this manuscript, then, is, first, to characterize the influence of

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http://dx.doi.org/10.1016/j.neuropsychologia.2016.05.022
0028-3932/

positional (as well as category) specificity in high-level parts of the visual system and the influence of category (as well as positional) information in early parts of the visual system. Thereafter, we explore the functional connectivity between the low-level and high-level regions so as to elucidate the bidirectional influence of these principles.

1.1. Retinotopic effects in higher-level cortical regions

One way of exploring the influence of the spatial position of the stimulus is to examine whether the known low-level preference for contralateral over ipsilateral stimuli is also observed in high-level visual areas. Unsurprisingly, in one study aimed to explore this, participants who viewed faces, objects, scenes and scrambled images shown in the right or left visual fields evoked greater BOLD signal in primary visual cortex for contralateral stimuli. Of note, although this contralateral preference was greater in low-level regions, all regions examined (including Lateral Occipital (LO), Occipital Face Area (OFA), posterior fusiform and Fusiform Face Area (FFA)), revealed this preference, indicating that sensitivity to stimulus position is evident even in high-level ventral cortex (Hemond et al., 2007). This finding has now been replicated several times (McKyton and Zohary, 2007; Niemeier et al., 2005), and there are now many reports demonstrating location representations in anterior ventral areas (Arcaro et al., 2009; Kravitz et al., 2010; Schwarzlose et al., 2008; Strother et al., 2010). Interestingly, detailed scrutiny of positional and category specificity reveals their co-existence (and potentially even equal strength) in some high-level regions. Using fMRI and MVPA analyses exploring correlations between even and odd runs in LOC (Lateral Occipital Complex), FFA, EBA (Extrastriate Body Area) and PPA (Parahippocampal Place Area), Golomb and Kanwisher (2012) have shown that the highest correlations in all these regions were for the same category of image presented in the same combined location. The rank ordering of the remaining categories were as predicted, with weaker correlations when the stimuli were from the same category but in different locations or when location was preserved but category differed. The weakest correlation was observed for those comparisons when both category and location differed.

A similar pattern of the co-existence of position and category specificity has also been obtained in neural recordings in non-human primates. For example, using high-resolution fMRI, Rajimehr et al. (2014) showed that distinct subregions within face-selective patches showed a coarse retinotopic map of both eccentricity and polar angle. Other patches revealed a retinotopic bias just to a specific location of the visual field and yet others showed no retinotopic selectivity. Retinotopic selectivity has even been documented in the anterior inferotemporal cortex (AIT) in a study in which both behavioral and neural responses were recorded in response to visual forms whose retinal position was varied. Unsurprisingly, AIT neurons were highly selective for the forms. The counterintuitive, and more relevant, result for the current purpose was the sensitivity to retinal position with an approximately 60% response decrease between positions within ± 1.5 degrees of the center of gaze (DiCarlo and Maunsell, 2003). In a related investigation using a large set of naturalistic visual images containing a range of real world objects that varied along object position, size, and pose variables, recordings obtained in IT and V4 also revealed that information about these so-called ‘low-level variables’ is explicitly coded in both V4 and IT, albeit to a lesser extent in the latter than former (Hong et al., 2016). Moreover, a convolutional neural network optimized for performance on a categorization task, accounted well for their empirical data, leading to the conclusion that the role of pooling in the ventral stream is not to discount object transformations as one progresses to more anterior regions, but, rather, to preserve some of this information.

Last, Hung et al. (2005) used a biologically plausible, classifier-based readout technique to investigate the neural coding of selectivity and invariance at the IT population level and revealed robust information about both object "identity" and "category" that was invariant over a range of object positions and scales in IT. Of relevance here, as in Hong et al. (2016), coarse information about position and scale could be read out from the very same neuronal population.

1.2. Category-specific effects in earlier visual cortex

As is clear from the evidence cited above, many studies, using a host of different methods, provide support for the view that later, higher-order regions of the ventral visual cortex retain information about low-level stimulus dimensions (location, size, pose). In complementary fashion, there are some (although admittedly, fewer) studies showing that early areas of visual cortex demonstrate some category-selectivity. One possible reason for the relative paucity of evidence is that category differences that manifest in retinotopic areas may result from differences in fundamental stimulus properties (for example, houses may contain more high-frequency information than faces) or any of a host of other image-based differences. Under controlled conditions, separability of category information is generally not observed in V1 or V2 (Grill-Spector and Weiner, 2014) although it has been shown that PPA exhibits a significantly greater response magnitude to upper visual field images compared to lower field images. In contrast, the FFA, EBA and LO exhibited opposite effects and greater response magnitudes to lower field images compared with upper field images (Sayres and Grill-Spector, 2008; Schwarzlose et al., 2008).

One relevant finding, however, that provides some evidence for category-selectivity in early visual cortex comes from a recent investigation using intracranial recording in children. This study demonstrated preferential neural activation to an upright versus inverted face, as reflected by roughly 23% augmentation of high-gamma activity at 80–150 Hz in lower-order visual cortex, roughly corresponding to V1 and V2, within the first 100 ms post-stimulus presentation (Matsuzaki et al., 2015). This very early activation profile is compatible with findings from magnetoencephalography (MEG) showing that face and house stimuli activate V1 around 40ms post stimulus onset, with the amplitude elicited by face stimuli significantly larger than that elicited by house stimuli (Shigihara and Zeki, 2014). Although in some cases, this apparent category difference may be a function of differences in some low-level properties of the stimuli, the amplitude enhancement for faces may also reflect some category-selectivity as in the case of upright versus inverted faces (where low-level image properties are matched). Moreover, the category-selectivity might reflect tuning of neurons as a function of retinal position at which faces and houses are typically observed in daily life and thus be a product of real-world statistics and experience (Levy et al., 2001b; Wang et al., 2013). The nature and extent of category effects in retinotopic cortex remains to be systematically evaluated and, here, we provide some evidence consistent with the suggestion (and some existing empirical evidence) that there is category tuning in early visual cortex.

1.3. Relationship between retinotopic and category-selective cortical regions

That we see mixing of category and spatial position (location) effects seems incontrovertible, especially at higher levels of the visual system and probably at lower levels as well. The question, then, is how does this topography of intermixing arise. One obvious possibility is that this occurs as a result of the coupling and connectivity pattern between earlier and higher-order areas in a