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Spatial frequency processing in scene-selective cortical regions

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ABSTRACT

Visual analysis begins with the parallel extraction of different attributes at different spatial frequencies. Low spatial frequencies (LSF) convey coarse information and are characterized by high luminance contrast, while high spatial frequencies (HSF) convey fine details and are characterized by low luminance contrast. In the present fMRI study, we examined how scene-selective regions—the parahippocampal place area (PPA), the retrosplenial cortex (RSC) and the occipital place area (OPA)—responded to spatial frequencies when contrast was either equalized or not equalized across spatial frequencies. Participants performed a categorization task on LSF, HSF and non-filtered scenes belonging to two different categories (indoors and outdoors). We either left contrast across scenes untouched, or equalized it using a root-mean-square contrast normalization. We found that when contrast remained unmodified, LSF and NF scenes elicited greater activation than HSF scenes in the PPA. However, when contrast was equalized across spatial frequencies, the PPA was selective to HSF. This suggests that PPA activity relies on an interaction between spatial frequency and contrast in scenes. In the RSC, LSF and NF elicited greater response than HSF scenes when contrast was not modified, while no effect of spatial frequencies appeared when contrast was equalized across filtered scenes, suggesting that the RSC is sensitive to high-contrast information. Finally, we observed selective activation of the OPA in response to HSF, irrespective of contrast manipulation. These results provide new insights into how scene-selective areas operate during scene processing.

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Introduction

Over the past 20 years, there has been mounting scientific excitement about the perception of scenes containing more realistic and complex stimuli than simple objects or drawings. It is now widely agreed that visual recognition of scenes is a fast, automatic and reliable process. In the case of signal representation, a scene can be expressed in the Fourier domain, in terms of both amplitude and phase spectra (Field, 1987; Ginsburg, 1986; Hughes et al., 1996; Tolhurst et al., 1992). The amplitude spectrum refers to the luminance contrast distribution across spatial frequencies and orientations. Contrast refers here to the magnitude of luminance variation in a stimulus relative to the mean luminance (Shapley & Enroth-Cugell, 1984). On a neurobiological level, it has been established that the cells of the primary visual cortex respond to contrast, spatial frequency and orientation (Boynton, 2005; De Valois et al., 1982a, 1982b; Poggio, 1972; Shams & von der Malsburg, 2002; Shapley & Lam, 1993). According to influential models of visual perception (Bar & Aminoff, 2003; Bullier, 2001; Hegdé, 2008; Kauffmann et al.,

2014; Schyns & Oliva, 1994), visual analysis begins with the parallel extraction of different attributes at different spatial frequencies and follows a predominantly “coarse-to-fine” default processing sequence. Low spatial frequencies (LSF) in a scene, conveyed by fast magnocellular visual channels, are thought to activate visual pathways and subsequently access the occipital cortex and high-order areas in the dorsal cortical stream (parietal and frontal) more rapidly than high spatial frequencies (HSF). This permits an initial coarse parsing of visual inputs, prior to their complete propagation along the ventral (inferotemporal) cortical stream, which ultimately mediates object recognition. This initial low-pass visual analysis is believed to guide the subsequent finer analysis of HSF, conveyed more slowly by parvocellular visual channels to the ventral cortical stream.

Interestingly, the ventral cortical stream contains a mosaic of different areas that respond selectively to different categories of visual stimuli (Haxby et al., 2001; Lerner et al., 2001). Three occipito-temporal regions have been shown to be scene-selective (Dilks et al., 2013; Epstein et al., 2007; Epstein & Kanwisher, 1998): the parahippocampal place area (PPA), the retrosplenial cortex (RSC), and the occipital place area (OPA). These regions have been linked to high-order functions during scene perception, such as navigation (Epstein et al., 2007; Vass & Epstein, 2013), spatial layout processing and scene recognition (Dilks

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et al., 2013; Epstein, 2005, 2008; Epstein et al., 1999, 2003; Epstein & Higgins, 2007; Epstein & Kanwisher, 1998; Epstein & Ward, 2010), and contextual association (Aminoff et al., 2007; Bar, 2004, 2007; Bar & Aminoff, 2003; Bar et al., 2008a; Bar et al., 2008b). Interestingly, some studies have shown that scene-selective regions are also sensitive to low-level visual features in scenes, such as statistical regularities in the amplitude spectrum of visual stimuli (Andrews et al., 2010; Watson et al., 2014), dominant cardinal orientations (Nasr & Tootell, 2012), and spatial frequencies (Rajimehr et al., 2011).

The aim of the present study was, therefore, to further investigate the neural bases of spatial frequency processing during scene categorization, by examining how scene-selective regions of the ventral cortical stream analyze spatial frequencies. The involvement of scene-selective regions has not, as yet, been systematically investigated in this theoretical context. It is however a key issue for the development of current neurally-grounded models of visual perception and for obtaining a better understanding of the role played by spatial frequency at high-level stages of visual processing. In a recent study, Rajimehr et al. (2011) examined the PPA's response to spatial frequencies in scenes and showed that this region was more strongly activated by HSF than by LSF. These authors suggested that during spatial perception and navigation, the PPA relies predominantly on HSF information in order to detect details and the borders of objects. However, other studies have come up with divergent results. In a functional magnetic resonance imaging (fMRI) study, Peyrin et al. (2004) showed greater activation in the right PPA and a number of other regions for the categorization of LSF than of HSF scenes. Similarly, in an event-related brain potential (ERPs) study, Schettino et al. (2011) observed strong activation in the parahippocampal cortex (PHC), including the PPA, during the categorization of LSF scenes. This activation decreased when HSF information was progressively added to LSF scenes, suggesting that the PHC is more sensitive to LSF information. Overall, these results indicated that the PPA is involved in the spatial frequency processing of scenes. Whether or not it responds selectively to a particular spatial frequency content remains unclear. Furthermore, very little evidence is available on spatial frequency processing in the RSC and the OPA.

A number of methodological aspects also need to be taken into consideration when investigating spatial frequency processing. LSF and HSF stimuli are created by using low and high pass filters which attenuate signals for frequencies which are higher and lower, respectively, than the cut-off frequencies applied when filtering. However luminance contrast in scenes decreases as spatial frequency increases, following a $1/f$ function (Field, 1987). This means that luminance contrast is higher for LSF than for HSF. Importantly, differences in contrast were found to influence cerebral activation. Several fMRI studies have shown, for example, that as the contrast level of stimuli increased, so did activation in the primary visual cortex (Boynton et al., 1996; Goodyear & Menon, 1998; Olman et al., 2004; Rieger et al., 2013). In the studies described previously, differences in contrast may, therefore, partially account for variations in brain activation related to the different spatial frequencies. In order to avoid any confusion between spatial frequency content and luminance contrast in scenes, recent studies have equalized the contrast of filtered stimuli used (see for example, Goffaux et al., 2011; Kauffmann et al., 2015; Mu & Li, 2013; Vlamings et al., 2009). RMS contrast (root mean square) is the most frequently-used normalization. RMS contrast corresponds to the standard deviation of luminance values and has been shown to be the most reliable indicator of the visibility of broadband filtered images (Bex & Makous, 2002). In their ERP study, Vlamings et al. (2009) used, LSF and HSF filtered faces either with or without contrast equalization between spatial frequencies. On a behavioral level, they found that LSF faces were categorized more rapidly than HSF faces when contrast was not modified. This difference decreased significantly when contrast was equalized across LSF and HSF faces. These results suggest that contrast normalization plays a crucial role in highlighting differences in LSF and HSF processing. However, the effects of equalizing contrast between LSF and HSF have never

been directly investigated at neurobiological level in the context of natural scene perception.

The present fMRI study aimed to investigate spatial frequency processing during scene categorization in scene-selective regions, by examining how the PPA, and for the first time the RSC and OPA, process spatial frequency information. Our study also aimed to address methodological issues, by examining the effects of contrast normalization on spatial frequency processing within these regions. In order to do so, we used a categorization task of scenes from two categories (indoors and outdoors) filtered in LSF and HSF, and non-filtered (NF) scenes. In one experimental condition, mean luminance in each scene was equalized to a fixed value and the contrast level was not modified (LUM experimental condition). In another experimental condition, mean luminance in each scene was again equalized, but this time contrast was also equalized using the RMS contrast normalization (RMS experimental condition). We also examined the possible existence of a relationship between spatial frequency processing in scene-selective regions and the spatial frequency cut-off used to filter scenes. We used a block-design fMRI paradigm in which scenes from each spatial frequency content (3 LSF cut-offs, 3 HSF cut-offs, and NF) and contrast condition (LUM and RMS) were displayed in separate experimental blocks.

We began by identifying scene-selective regions in both hemispheres in each participant using a localizer adapted from previous studies (Bar et al., 2008a, 2008b; Epstein et al., 2003; Epstein & Kanwisher, 1998; Musel et al., 2014; Walther et al., 2009). Participants were shown gray-scale pictures of scenes, faces, and common objects. The contrast between scenes and other categories was used to localize the regions specifically involved in scene processing. Once localized, we compared the activation elicited by the different spatial frequency and contrast conditions in the areas defined as the PPA, RSC, and OPA. Based on influential models of visual perception which show that scenes are processed in terms of spatial frequencies (Bar, 2003; Kauffmann et al., 2014; Peyrin et al., 2010; Schyns & Oliva, 1994), and on previous studies showing a sensitivity of scene-selective areas to low-level visual features (Andrews et al., 2010; Nasr & Tootell, 2012; Rajimehr et al., 2011; Watson et al., 2014), we hypothesized that these regions respond to spatial frequencies, and we expected to observe different responses to LSF, HSF, and NF scenes in each of these regions. Furthermore, given that these three scene-selective areas have been seen to support different functions during scene perception (e.g., Bar et al., 2008b; Dilks et al., 2013; Epstein & Higgins, 2007), we also hypothesized that response to spatial frequencies would vary in the three regions. We therefore expected to observe different patterns of response to spatial frequency information in the regions concerned. Finally, we hypothesized that spatial frequency processing in these regions would be influenced by luminance contrast equalization. We therefore expected to observe different responses to spatial frequencies in each region depending on the contrast condition.

Method

Participants

Sixteen right-handed participants (nine males; 23 ± 2 years) with normal or corrected-to-normal vision and no history of neurological disorders were included in this experiment. All participants gave their informed written consent before participating in the study, which was approved by the local ethics committee. All participants were included in two experiments: the Spatial Frequency experiment and the Localizer experiment.

Stimuli and procedure in the spatial frequency experiment

Stimuli consisted of 20 black and white photographs (256-level gray-scales, 1042×768 pixels) of scenes classified into two distinct

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