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Motion responses in scene-selective regions

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ABSTRACT

The vast majority of studies on scene processing were conducted using stationary scenes. However, during natural vision, scene views change dynamically due to self-induced eye-, head-, and body-motion, and these dynamic changes are crucial for other higher-level functions such as navigation, self-motion perception, and spatial updating. Yet, we do not know whether or how scene selective regions are modulated by visual motion and to which degree their motion response depends on scene content. In this study, we used fMRI to examine both questions using a 2 × 2 factorial design with the factors 2D planar motion (motion versus static) and scene content (natural scenes versus their Fourier scrambles). We found that among independently localized scene-responsive regions, parahippocampal place area (PPA) and transverse occipital sulcus (TOS), also referred to as occipital place area (OPA), were significantly motion responsive, whereas retrosplenial cortex (RSC) was not. Additionally, PPA showed an interaction between motion and scene in that it responded more to motion in context of scenes than scramble, with similar trends in TOS and RSC. These results provide a novel functional dissociation between motion-responsive PPA and TOS/OPA versus motion-unresponsive RSC and suggest a strong role for PPA in integrating motion and scene content.

Introduction

Scene perception and processing is one of the everyday functions of the human visual system. Its neural processing has therefore been studied in great detail, identifying scene selective responses in the parahippocampal place area (PPA) (Aguirre et al., 1998; Epstein and Kanwisher, 1998) as well as in comparably less studied regions such as the retrosplenial cortex (RSC) (Maguire, 2001) and the transverse occipital sulcus (TOS) (Grill-Spector, 2003; Hasson et al., 2003; Nakamura et al., 2000) that has also been referred to as "occipital place area" (OPA) due to its causal contribution to scene perception (Dilks et al., 2013). In the past, scene processing regions have almost exclusively been studied using static snapshots of scenes. However, scene perception is not only important on its own, but also crucial for other higher-level functions such as navigation, self-motion perception, and spatial updating. During natural vision, scene views change dynamically due to self-induced eye, head, and body motion. A subset of this dynamics, that of instant view changes such as induced by saccades, has been investigated by several prior previous studies, using static snapshots created by dividing larger panoramic scenes into partially overlapping subsections (Epstein et al., 2005; Golomb et al., 2011; Park and Chun, 2009; Park et al., 2010). These studies found viewpoint specific responses in PPA (Epstein et al., 2003, 2005, 2007a,b, 2008; Park and Chun, 2009; Park et al., 2010; Vass and Epstein, 2013), and in TOS/OPA (Epstein et al., 2005, 2007a). RSC was reported to be viewpoint independent for the same scene, and to distinguish between different scenes (Park and Chun, 2009; Vass and Epstein, 2013), or to be partly viewpoint independent while viewpoint dependent under some conditions (Park et al., 2010). One more recent study found viewpoint invariance in PPA but viewpoint sensitivity in TOS/OPA (Dilks et al., 2011). These discrepancies illustrate that these regions exhibit distinct functional properties that have not been fully understood yet. In particular, the response to motion or to scene motion of scene-selective regions has not been addressed at all until now. Given the importance and abundance of scene motion in real-life conditions, this seems an important question worth addressing in a systematic way.

Hence, in this fMRI study, we examined two main questions: are scene-responsive regions in the human brain modulated by motion during viewing of natural and scrambled scenes, and if they are, do their responses show any interaction between scene content and motion? We investigated these questions by using scene and non-scene stimuli that were shown either statically or in horizontal linear motion. This led to a two-by-two factorial design allowing for full factorial control over main effects and their interaction. The factorial design also ensured that every contrast was fully balanced in terms of low-level stimulus properties. The scene images were gray-scale photographs of landscapes and cityscapes. For non-scene stimuli, we used phase-scrambled images of the scenes matched in luminance, contrast, and

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frequency spectra to the gray-scale scene images. We chose horizontal motion as it is among the most abundant motion types in natural scenes and as our visual system has a tuning bias to cardinal motion directions (see, e.g.,Bartels et al., 2008; Gros et al., 1998). We found that scene-responsive regions showed differential responses to motion, with TOS/OPA showing highest, PPA intermediate, and RSC lacking motion responses. TOS/OPA could be differentiated from PPA and RSC in their motion responses. Moreover, PPA showed a significant interaction between scene content and motion, with similar (non-significant) trends apparent in RSC and TOS/OPA.

Materials and methods

Subjects

17 healthy subjects (9 female, 1 left handed, age between 20 and 36 (mean = 27.8)) participated in this study. All subjects had normal or corrected to normal vision and gave written informed consent before the experiments. The study was approved by the local ethics committee of the University Hospital of Tübingen.

Experimental paradigm and setup

Two functional experiments were carried out: a functional scene region localizer and the main experiment, plus a structural scan. The functional localizer was used to localize scene-responsive regions PPA, RSC, and TOS/OPA.

Visual stimuli were gamma corrected and projected via a projector outside the scanner room onto a screen behind the participants' head yielding a visual field of view subtending 19 × 15 visual degrees. The experiment was programmed using Psychtoolbox-3 (Brainard 1997; Kleiner, Brainard et al. 2007) on MATLAB 7.10.0 (The Mathworks, Natick, MA, 2010) and presented using a Windows PC.

Main experiment

Paradigm

The main experiment was designed as a 2 × 2 factorial design with the factors scene (on/off) and motion (on/off), resulting in four conditions: moving scenes, moving scramble, still scenes, and still scramble (Fig. 1).

Each condition was presented 4 times per run in a block design, with a total of 16 blocks per run. The condition sequence was pseudorandomized such that each condition preceded all conditions equally frequently. Each block lasted 12 s. In order to additionally counterbalance initial conditions, one additional block was added to the beginning of each run.

Each run started with 6.9 s of gray screen (luminance: 144 cd/m^2) with fixation and ended with 10 s of gray screen with fixation. Throughout the full duration of the experiment, participants fixated on a gray fixation disk (width: 0.74 deg, luminance: 282 cd/m^2) and performed the fixation task described below to ensure matched attentional demands across conditions. There were a total of 4 runs per participant.

Stimuli

Stimuli consisted of 32 gray scale images of outdoor scenes, namely, landscapes and cityscapes, and of their phase-scrambled versions. Half of these images were left–right flipped duplicates to balance potential horizontal differences in spatial frequency. We equated luminance and contrast across images (luminance: 144 cd/m^2, contrast: 32.4 cd/m^2 root-mean-square (RMS) contrast, leading to an average Michelson contrast of 0.9004 ± 0.0925). Image selection was randomized for

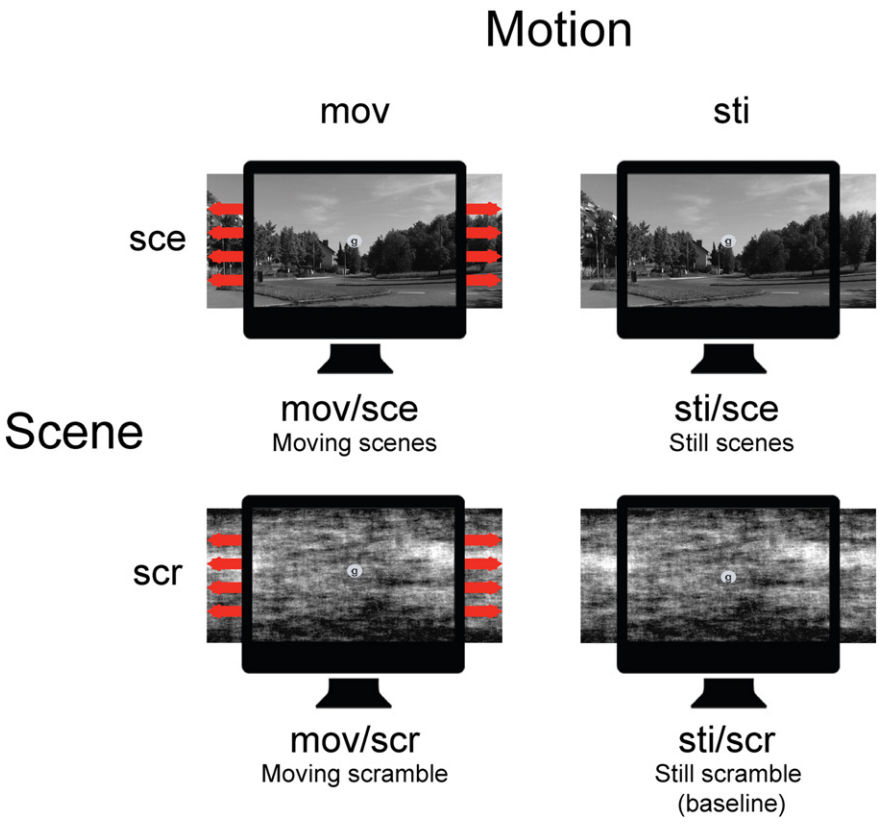

Fig. 1. Illustration of the four stimulus conditions used in the main experiment. The conditions formed a 2 × 2 factorial design with the factors "scene" (scene/scramble) and "motion" (moving/still). There was a gray fixation disk present at all times, with a one-back matching character task. Motion was horizontal with a sinusoidal left–right velocity profile. The four conditions were as follows: mov/sce: moving scene, sti/sce: still scene, mov/scr: moving scramble, sti/scr: still scramble.