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Functional mechanisms of probabilistic inference in feature- and space-based attentional systems

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ABSTRACT

Humans flexibly attend to features or locations and these processes are influenced by the probability of sensory events. We combined computational modeling of response times with fMRI to compare the functional correlates of (re-)orienting, and the modulation by probabilistic inference in spatial and feature-based attention systems. Twenty-four volunteers performed two task versions with spatial or color cues. Percentage of cue validity changed unpredictably. A hierarchical Bayesian model was used to derive trial-wise estimates of probability-dependent attention, entering the fMRI analysis as parametric regressors. Attentional orienting activated a dorsal frontoparietal network in both tasks, without significant parametric modulation. Spatially invalid trials activated a bilateral frontoparietal network and the precuneus, while invalid feature trials activated the left intraparietal sulcus (IPS). Probability-dependent attention modulated activity in the precuneus, left posterior IPS, middle occipital gyrus, and right temporoparietal junction for spatial attention, and in the left anterior IPS for feature-based and spatial attention. These findings provide novel insights into the generality and specificity of the functional basis of attentional control. They suggest that probabilistic inference can distinctively affect each attentional subsystem, but that there is an overlap in the left IPS, which responds to both spatial and feature-based expectancy violations.

Introduction

Prior information about the location or features of a stimulus facilitates its detection and speeds up response times (RTs). Conversely, violations of spatial or feature-based expectancies result in RT costs. These effects, as well as their neural underpinnings, can be investigated with probabilistic cueing paradigms in which a spatial or feature cue is presented prior to a behaviorally relevant target (Posner, 1980).

Orienting of attention in response to spatial or feature cues engages a shared frontoparietal network including the bilateral frontal eye fields (FEF), intraparietal sulcus (IPS), and inferior frontal cortex (IFC) (Egner et al., 2008; Giesbrecht et al., 2003; Liu et al., 2003; Schenkluhn et al., 2008; Slagter et al., 2007; Vandenberghe et al., 2001b; Wojciulik and Kanwisher, 1999). However, only spatial cues lead to a lateralized biasing of activity of visual areas (Egner et al., 2008).

Reorienting of attention to unexpected events in cueing paradigms is investigated by contrasting invalidly with validly cued targets. Spatially invalidly cued targets increase activity in ventral frontoparietal regions such as the temporoparietal junction (TPJ) and IFC, but also in dorsal frontoparietal regions such as the FEF and IPS (Corbetta et al., 2008; Corbetta and Shulman, 2011). Reorienting of attention to invalidity cued targets in the feature-based domain has rarely been investigated as yet, but one study has reported that activation in the left supramarginal gyrus (SMG), bilateral inferior frontal gyrus (IFG), medial frontal areas, and the cerebellum is enhanced during dimensional reorienting, i.e., when the target-defining dimension (orientation or color) in a visual search task is invalidly cued (Weidner et al., 2009). Additionally, it has been shown that shifts from color to motion, or vice versa, activate the left IPS, left precentral gyrus, the precuneus, and visual areas (Liu et al., 2003). A left hemispheric dominance has also been reported for object-based as compared to location-based spatial attention orienting (Arrington et al., 2000). However, the functional correlates of spatial and feature-based reorienting have so far not been directly compared within the same paradigm.

Importantly, the behavioral effects of orienting and reorienting in both attentional systems scale with the percentage of cue validity (%CV), i.e., the probability that the information provided by the cue is correct (Dombert et al., 2015; Egner et al., 2008; Vossel et al.,

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2006, 2012). More specifically, response time differences between invalidly and validly cued targets increase with higher %CV. Most studies explicitly informed the subjects about the %CV; however, more recent work has shown that even without this explicit information, RTs are highly sensitive to unsignaled changes in %CV, suggesting that the subjects continuously infer the probability of the cue-target outcome in a given trial on the basis of observations in prior trials. This inference process can plausibly be described by approximate Bayes-optimal learning rules (Mathys et al., 2011; Vossel et al., 2014a). Though the update equations of this Bayesian model bear structural similarity to reinforcement learning models such as the Rescorla–Wagner rule (Rescorla and Wagner, 1972) in that the update of the probability estimate is the product of a learning rate and a prediction error, the learning rate in the Bayesian model is not fixed but governed by higher hierarchical levels. In our specific case, the update of the probability that the cue will be valid in a given trial depends on the trial-wise belief about the stability/volatility of the environment (highest hierarchical level) and on a subject-specific parameter. In other words, updating will be faster if the subject has learned that the environment is not stable. Such flexible models have been shown to provide a more plausible account of behavior than the Rescorla–Wagner rule, particularly in volatile environments where a fixed learning rate is suboptimal (Behrens et al., 2007; den Ouden et al., 2010; Vossel et al., 2014a). Another advantage of the current modeling approach is that it represents an individualized Bayes-optimality, allowing for a quantification and comparison of updating behavior in the two attentional systems. These parameters can be estimated on the basis of trial-wise RTs. This computational modeling of behavioral responses has been combined with functional magnetic resonance imaging (fMRI) (Vossel et al., 2015). It was observed that activity in the right FEF, TPJ, and the putamen during reorienting responses in a spatial cueing paradigm with saccadic responses to the targets was modulated by the trial-wise belief about cue validity. No significant effect of the belief about cue validity was found for orienting of attention.

Taken together, the functional mechanisms of orienting and reorienting of attention and the modulation of attentional deployment by inferred percentage of cue validity are well-characterized in the spatial attention system, but have so far not been studied for the cueing of target features such as color. Hence, it remains to be established whether reorienting, probabilistic inference, and their physiological implementations are universal across the two visual attentional systems—or whether they are domain-specific with differential functional correlates for spatial and feature-based attention. First behavioral observations from patients with right-hemispheric brain damage may point to differential functional mechanisms of the processing of statistical regularities (repetition priming) for locations and features: Shaqiri and Anderson (2012) reported that the speeding of RTs to the repeated presentation of a stimulus at the same location is disrupted after right-hemispheric stroke, while the RT benefit is still present for the repetition of stimulus color in these patients.

To address these outstanding issues, we applied the combined computational modeling—fMRI approach outlined above to two different versions of a probabilistic cueing task with spatial or color cues. While we also aimed at replicating the effects of attentional orienting in both domains with our modified paradigm, our specific emphasis was the characterization of reorienting after invalid cues, as well as its modulation by probability-dependent attention in the two systems. Based on Weidner et al. (2009) and Liu et al. (2003), we expected a stronger involvement of left parietal areas in feature-based reorienting. Due to the differential effects of spatial and non-spatial statistical regularities in stroke patients (Shaqiri and Anderson, 2012) and the results by Vossel et al. (2015), we hypothesized that attentional deployment by probabilistic inference involves right-hemispheric frontoparietal structures in the spatial attentional domain.

Materials and methods

Participants

Twenty-eight healthy participants gave written informed consent to take part in the study. Four subjects were excluded from the analyses due to extensive head movement in the scanner (>3 mm, $n = 1$), lack of central fixation in all trials ($n = 1$), physical discomfort during MR scanning ($n = 1$), and discontinuation of the task because of fatigue ($n = 1$). Therefore, data from twenty-four subjects were analyzed (14 females; mean age 27 years, ranging from 18 to 36 years). All subjects were right-handed as measured with the Edinburgh Handedness Inventory (Oldfield, 1971), had normal or corrected to normal vision, and did not suffer from any neurological or psychiatric conditions. The study had been approved by the ethics committee of the German Psychological Society and was performed in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Stimuli and experimental paradigm

Main experiment

Two versions of a central cueing paradigm with either spatial or feature cues (adapted from Egner et al., 2008) were presented on a TFT screen at the back of the magnet bore. The screen was presented to the subjects via a mirror system attached to the head coil. A central diamond was displayed on a grey background, serving as fixation point. At the beginning of each trial, a spatial or feature cue stimulus was shown for 400 ms. After a 1000 ms stimulus onset asynchrony (SOA), the target search array appeared for 500 ms, consisting of four peripherally located diamond stimuli that were arranged in the corners of an imaginary rectangle centered on the fixation diamond (4.8° eccentric in each visual field, see Fig. 1A). Each hemifield always contained one red and one blue diamond with counterbalanced positions across %CV blocks and valid and invalid trials, resulting in an equal number of diagonally and horizontally arranged trials (see Fig. 1A, diagonal arrangement).

The target diamond was missing its upper or lower corner. Subjects were asked to press a button with the right index or middle finger to indicate whether the upper or lower corner of the target diamond was missing. The response mapping was counterbalanced across subjects. They needed to respond to the target within a period of 1500 ms from target onset (see Fig. 1A). The task versions with feature or spatial cues were presented in two different runs, with counterbalanced order between subjects. Feature cues indicated the target's color by presenting a two-letter abbreviation of the color word ('RO' or 'BL'; [i.e., 'RE', 'BL', in German, respectively]) in the central part of the fixation diamond (see Fig. 1B). This type of color cue has been shown to elicit highest effects of probabilistic context (Dombert et al., 2015). For spatial cueing, a triangle appeared behind the fixation diamond creating an arrowhead pointing to the left or right side to indicate the hemifield in which the target would appear (see Fig. 1B). The experiment consisted of 284 trials that were presented in blocks of ~50, ~70, and ~90% cue validity. %CV changed after blocks of 32 or 22 trials, respectively (see Fig. 1C). This block length was chosen to enable learning of the statistical context by the participants and it should be noted that these hidden blocks were not modeled as blocks in the fMRI analysis. Instead, the trial-wise probability estimate of cue validity (which changes with a higher frequency and was expected to have differential effects in valid and invalid trials) was entered as a parametric regressor in an event-related analysis (please see below). In accordance with standard procedures in computational studies of trial-wise inference, target displays and trial sequence were identical between all participants and task versions. Participants were unaware of the different levels of %CV or when they would change, they were only informed that variations in %CV would occur over the course of the experiment. Subjects were instructed to use the cues according to how much they "trust" them to