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Common and distinct neural correlates of trial-by-trial expectancies for feature-based as compared to spatial attention

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Vorwort

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List of Abbreviations

AAL	Automated Anatomical labeling
ANOVA	Analysis of variance
BIS	Barratt Impulsiveness Scale
BOLD	Blood oxygen level dependent
contra	Contralateral
CV	Cue validity
DCM	Dynamic causal modeling
EPI	Echo-planar imaging
FEF	Frontal eye fields
fMRI	Functional magnetic resonance imaging
GLM	General linear model
HRF	Hemodynamic response function
HZ	Hertz
IFC	Inferior frontal cortex
IFG	Inferior frontal gyrus
inval	Invalid
ipsi	Ipsilateral
IPS	Intraparietal sulcus
IPL	Inferior parietal lobe
min	Minutes
mm	Millimeter
MNI	Montreal Neurological Institute
MOG	Middle occipital gyrus
MRI	Magnetic resonance imaging
ms	Milliseconds
MT	Middle temporal area
n	Number
ROI	Region of interest
RS	Response speed
RT	Response times
rTPJ	Right temporoparietal junction
sec	Second
SEM	Standard error of the mean
SFG	Superior frontal gyrus
SMG	Supramarginal gyrus
SOA	Stimulus onset asynchrony
SPL	Superior parietal lobe
SPM	Statistical parametric mapping
T	Tesla
val	Valid

0. Abstract

Since our brain can only process a small amount of sensory information at a time, attention systems select specific aspects for prioritized processing – such as features or locations – that are expected to be most relevant in a given context. The present thesis investigated responses of visual attention systems to expected and unexpected sensory events during uncertainty, when the probability of sensory events needs to be inferred from environmental observations. In the spatial attention domain these processes have already been described with the help of computational models and the underlying neural mechanisms have been explored with functional neuroimaging. However, it is not known whether other attentional subsystems such as feature-based attention behave similarly during uncertainty.

The core aim of this thesis was to characterize the modulation of attentional deployment by inferred probabilities during feature-based as compared to spatial attention. This was realized using a Posner-cueing paradigm in which feature and spatial cues were presented. Classically these cues predict the color or the location of an upcoming target with a fixed high probability, so that participants expect the cues to be valid and respond slower and less accurate when attention needs to be reoriented to invalidly cued targets. In the present paradigm, this probability was varied by changing the percentage cue validity (%CV) unpredictably over time.

In a behavioral experiment (Experiment 1) three different color cues were used to identify cue-related factors which influence the effects of probabilistic inference on feature-based attention and to establish an experimental paradigm for the comparison of feature-based and spatial attention systems. It was observed that all color cues affected attentional deployment. However, probability-dependent effects differed depending on the level of cue abstraction: More automatically processed cues required more observations of cue-target outcomes to establish probabilistic learning than abstract cues.

Experiment 2 employed functional magnetic resonance imaging (fMRI) to investigate the computational and neural mechanisms that modulate probabilistic inference using the experimental paradigm from Experiment 1 with abstract feature and spatial cues. The results indicated that probabilistic inference follows similar principles for both attention systems. However, their neural implementations seemed to be confined to domain-specific subsystems: The right temporoparietal junction (TPJ) was particularly involved in spatial attention, while the left intraparietal sulcus (IPS) was most crucial for feature-based attention. However, the left anterior IPS showed an effect of probability-dependent attention in both attention systems. These findings provide novel insights into the generality and specificity of the functional basis of visual attention, suggesting that probabilistic inference can distinctively affect each attentional subsystem, but that the left anterior IPS may establish probabilistic inference in a domain general manner.

Taken together our findings speak against a unitary visual attention network. Rather, we propose that depending on the nature of the selected aspects different attentional subsystems are activated following expectancy violations and these processes can even differ within one single domain such as feature-based attention.

1. Theoretical section

1.1 Attentional control in human visual perception

Attention is a core faculty of cognition that has concerned psychologists, philosophers and neuroscientists from history to the present. Despite divergence in theories about the causes and effects of attention, they all agree upon the assumption that our percept not only depends on the information we receive through our senses, but also on the state of our minds at any moment in time. William James emphasized this by stating that “my experience is what I agree to attend to” (James, 1890, p.402). In cognitive psychology, the term attention describes both the preparedness for and the selection of sensory events that our environment provides us with (Raz & Buhle, 2006). The preparatory aspect of attention comprises alertness, sustained attention and vigilance and describes activation states that unselectively modulate (enhance) the processing of incoming stimuli (Sturm, 2005). However, at any given moment, our environment presents far more sensory information than our brain is able to process simultaneously. Therefore, another function of attention is to select certain aspects from sensory inputs for prioritized processing, while ignoring others. This process of information selection is accomplished by focused attention and allows us to quickly adapt to environmental changes and modulate behavior accordingly (Sturm, 2005). In a visual scene, for example, we can attend to a particular region in space to enhance the processing of stimuli that are presented at this selected location. Alternatively, we can attend to a specific stimulus feature such as shape, color, or direction of motion to enhance the processing of stimuli which express the selected feature, independent from their spatial location. Or, we can attend to an entire object that is defined by many different features and prioritize it at the cost of processing of other objects (Carrasco, 2011).

The control of attentional selection can be guided voluntarily by *internal*, or endogenous, *top-down processes* on the basis of behavioral relevance, prior knowledge and expectations, or it can be guided automatically by *external*, or exogenous, *bottom-up processes* that are related to stimulus factors such as sensory salience or unexpectedness (Corbetta & Shulman, 2002; Itti & Koch, 2001; Jonides & Irwin, 1981). While these opponent processes have been described as separate systems with distinct anatomical substrates in the brain, they must flexibly interact to produce dynamic attentional control in a constantly changing environment. Psychological models have been put forward that aim at explaining how the interaction between bottom-up and top-down signals operates during attentional deployment. Amongst different approaches, a dominant idea of current theories of visual attention suggests that both factors are jointly reflected in a “priority map” that governs the distribution of attentional deployment and determines which features, objects or locations are selected in a visual scene (or "saliency map"; Ptak, 2012; Treue, 2003). However, there is little evidence for a unitary neural correlate for such a “priority map”. Rather, distributed frontoparietal and visual regions display enhanced responses to both bottom-up as well as top-down factors during attentional deployment (Ptak, 2012). Therefore, the question of how these brain regions functionally interact during attentional deployment remains a central question in cognitive neuroscience.

An influential framework has been proposed by Corbetta and Shulman (2002) suggesting that visual attention is controlled by two distinct neural networks (see Fig. 1): a dorsal frontoparietal network comprising the intraparietal sulcus (IPS) and the frontal eye fields (FEF) that controls the voluntary *orienting* of attention, and a right lateralized ventral frontoparietal network including the temporoparietal junction (rTPJ) and inferior frontal gyrus (IFG), which activates when *reorienting* of attention to unexpected or unattended stimuli is required. Nevertheless, the strict dichotomy between dorsal and ventral neural networks has been challenged in the recent past. There is growing evidence suggesting that dorsal and ventral systems work in collaboration to establish adaptive control of orienting and reorienting of attention and this interplay has been shown to crucially depend on current task demands (Macaluso & Doricchi, 2013; see Vossel, Geng, & Fink, 2014b for a review).

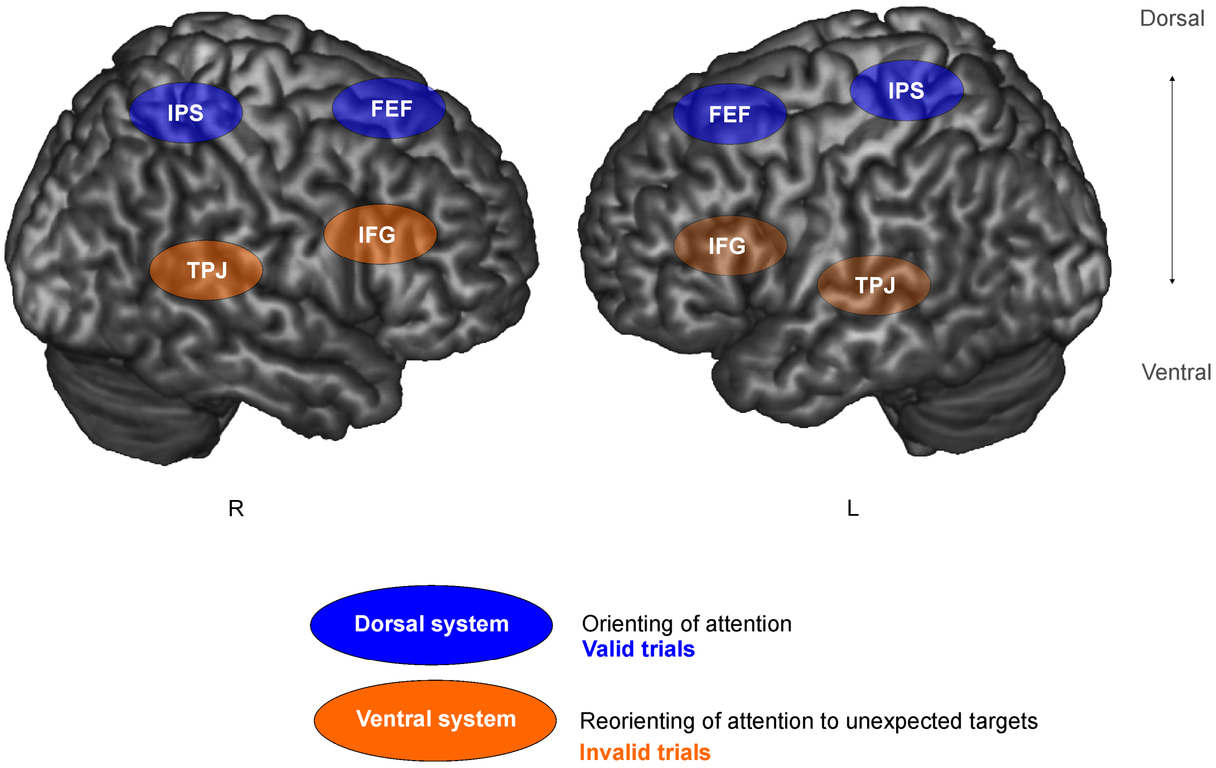


Figure 1 Dorsal and ventral attention networks as proposed by Corbetta and Shulman (2002).

The experimental paradigm which is most commonly applied to investigate these orienting and reorienting processes was introduced by Posner in 1980. In this paradigm, subjects are asked to respond to the occurrence of a target (detection task) or a specific target characteristic (discrimination task). Prior to target presentation, they are provided with a cue that informs them about the most likely location of the target (spatial cue; e.g. an arrow pointing to the left or right hemifield).

In a small proportion of trials (e.g. 20%) the cue is invalid and incorrectly predicts the location of the target. Since the subjects expect the cue to be correct in most of the trials they respond faster and more accurate on valid trials as compared to invalid and neutral trials during which uninformative cues are provided (Posner, 1980; see Fig. 2). The difference in response times (RT) between valid and invalid trials is referred to as “validity effect” and is used to quantify the attentional costs that occur when attention needs to be reoriented to invalidly cued targets.

Since the classical Posner paradigm employs spatial cues to study directed spatial attention, space-based orienting, reorienting and their neural correlates have been extensively investigated. One can, however, also present cues that inform subjects about the most likely feature of a target – such as its color – to study directed feature-based attention (feature-based cue; e.g. a color display specifying the target’s color). Feature-based versions of the Posner paradigm have already been applied to examine the neural mechanisms of orienting of attention to a target feature following a valid cue (Egner et al., 2008). However, the neural mechanisms of feature-based reorienting to invalid cues have not been explored so far.

For spatial as well as feature-based attention the validity effect scales with the proportion of valid trials, so that reaction time differences between valid and invalid trials increase when valid trials occur more frequently (see Fig. 2B; Egner et al., 2008; Eriksen & Yeh, 1985; Madden, 1992). A theoretical approach that conceptualizes how cue validity potentially modulates attentional deployment assumes that it is gradually aligned with the relevance for attentional allocation ("gradient model"; Madden, 1992). In other words, with a higher benefit of attentional deployment, more resources are employed following the cue and hence stronger reorienting is required during invalid trials.

Recently, it has been shown for the spatial attention system that explicitly signaled as well as unsignalled changes in the percentage of cue validity (%CV) induce increases or decreases in the validity effect and this modulation is accompanied by increased or decreased activation of space-based reorienting networks (Vossel, Mathys, Stephan, & Friston, 2015; Vossel, Thiel, & Fink, 2006). These effects have not been investigated for feature-based reorienting as yet.

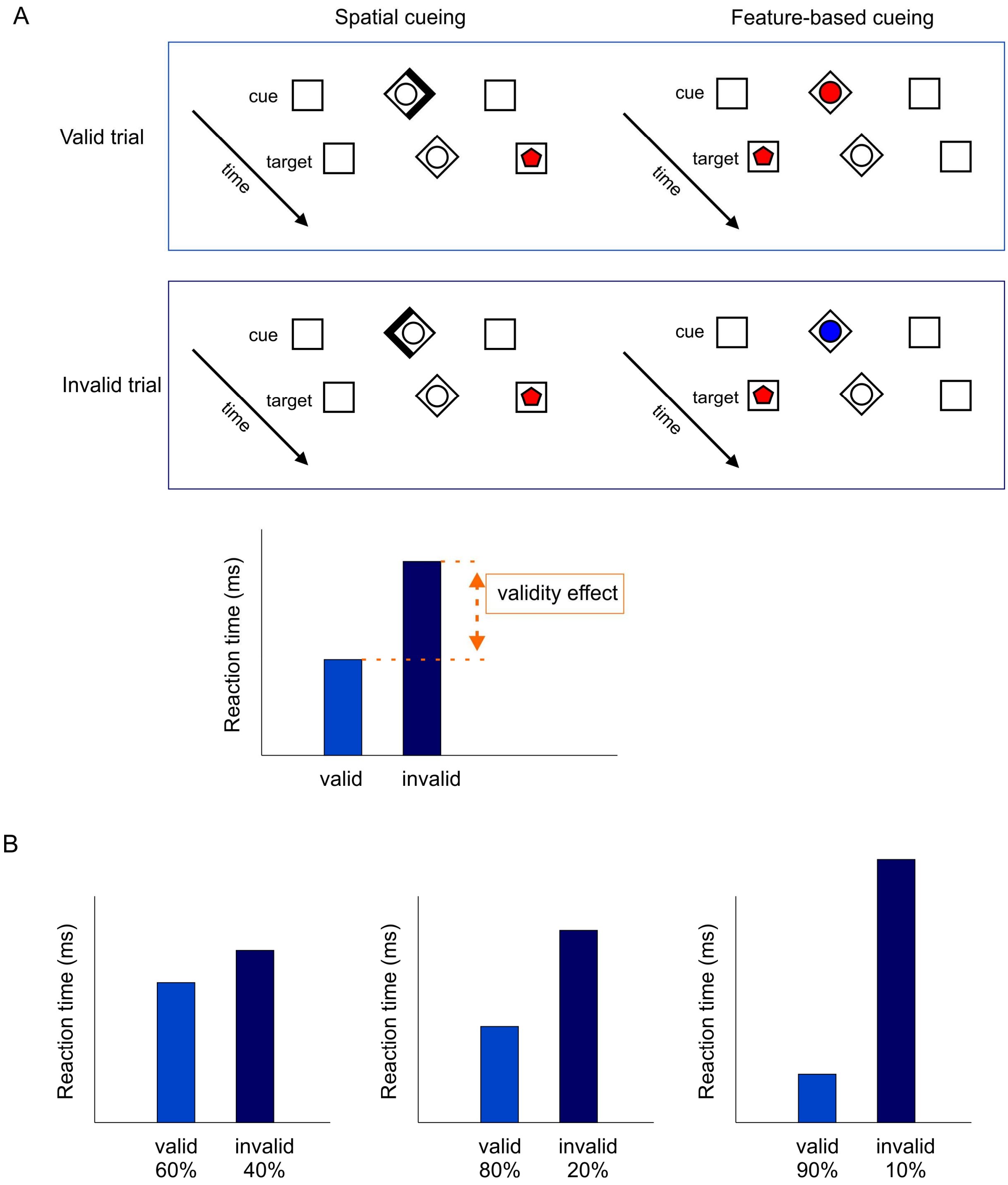


Figure 2 Illustration of the Posner-cueing paradigm with feature-based and spatial cues.

A Posner-cueing paradigm with feature-based and spatial cues and the corresponding reaction time pattern illustrating the validity effect.

B Prototypical illustration of validity effects that scale with the proportion of valid trials.

1.2 Spatial attention

We can covertly orient attention in space without directing eye gazes to a specific location. Covert orienting of spatial attention increases responses in extrastriate cortex neurons whose receptive fields overlap with the attended location and therefore facilitates the processing of stimuli that are presented at this location (Luck, Hillyard, Mouloua, & Hawkins, 1996; Moran & Desimone, 1985). These facilitatory effects of attentional deployment can be measured behaviorally with RTs (see section 1.1).

Models of spatial attention systems in the human brain have been informed by observations of stroke patients with attentional deficits. For instance, patients suffering from unilateral brain lesions show impaired spatial orienting to the visual field opposite to the damage, referred to as the contralesional hemifield. These impairments are strongest when attention needs to be reoriented from the intact ipsilesional hemifield to the contralesional hemifield (Mesulam, 1999). Since these patients tend to ignore one side in visual space, their neurological syndrome is called spatial neglect (Stone, Halligan, & Greenwood, 1993). Most spatial neglect patients have lesions in the right parietal lobe such as the angular gyrus and inferior parietal cortex (Mort et al., 2003). Based on these observations it has traditionally been assumed that spatial attention is controlled by the parietal cortex of the right hemisphere. Although less frequently, spatial neglect symptoms can however also be induced by damage to the left hemisphere and lesions to frontal and subcortical regions (see Husain & Rorden, 2003 for a review). Therefore, it was proposed that spatial neglect underlies dysfunctional interactions between both dorsal and ventral frontoparietal networks (see Bartolomeo, Thiebaut de Schotten, & Chica, 2012 for a review).

Consistently, neuroimaging studies in healthy subjects have shown that the IPS and FEF of the dorsal network contain representations of spatial coordinates in a visual scene that compose topographic maps (see Silver & Kastner, 2009 for a review). Thus, these regions comprise spatial information that could potentially be used for biasing responses in visual areas. The extent to which this spatial information is lateralized during spatial attentional orienting is still a matter of debate. Some studies have reported that responses in IPS and FEF are stronger during spatial attention shifts to the contralateral hemifield (Szczepanski & Kastner, 2013; Szczepanski, Konen, & Kastner, 2010), while others have observed bilateral activity during spatial attention shifts to either hemifield (Hopfinger, Buonocore, & Mangun, 2000; Shomstein & Yantis, 2006). The ventral network displays a well described right hemisphere lateralization. However, it does not contain topographic maps of space (Corbetta & Shulman, 2011). In particular, the rTPJ is thought to induce attentional reorienting to unexpected or infrequent stimuli occurring in either hemifield (Corbetta & Shulman, 2011). It has originally been proposed that the rTPJ acts as a “circuit breaker” to the dorsal network that signals the required reorienting of attention following expectancy violations (see section 1.1). However, some studies have shown that dorsal network responses precede rTPJ activity during sensory processing (see Geng & Vossel, 2013 for a review). This indicates that rTPJ activity occurs later during the evaluation of sensory information rather than solely during early stages of attentional reorienting. Based on these findings, other theories on the role of the rTPJ in spatial attention have emerged. Amongst these, the “contextual updating hypothesis” has been proposed, suggesting that the rTPJ integrates incoming sensory information with internal models of contextual information and updates these models when violations occur (Geng & Vossel, 2013).

While it is well recognized that dynamic interactions between dorsal and ventral networks provide flexible control of spatial attention, it remains to be clarified whether these networks similarly respond to other domains of visual attention, such as feature-based attention, or whether they are selective to the spatial system.

1.3 Feature- based attention

Since to this point most research on attentional control systems in the human brain has been focused on spatial attention, much less is known about feature-based attention. Some of the few neuroimaging studies investigating feature-based mechanisms with cueing paradigms have indicated that the dorsal network associated with spatial attention also maintains feature-based information (Egner et al., 2008; Giesbrecht, Woldorff, Song, & Mangun, 2003; Wojciulik & Kanwisher, 1999; also see Corbetta & Shulman, 2002). For instance, similar brain regions including superior parietal lobe (SPL), IPS and FEF have been shown to engage when attention is directed to a specific motion direction or a stimulus color (Liu, Hospadaruk, Zhu, & Gardner, 2011; Liu & Hou, 2013). Although, based on these findings, it has been proposed that feature-based and spatial attention embody different forms of the same attentional control system, there still is some evidence pointing to differences between them. For example, transcranial magnetic stimulation (TMS) over the right supramarginal gyrus decreases spatial orienting, while leaving feature-based orienting unaffected (Schenkluhn, Ruff, Heinen, & Chambers, 2008). Likewise, the behavioral effects of feature and spatial cueing did not interact in a combined cueing task, indicating that they adhere to independent mechanisms (Egner et al., 2008). As distinguished from spatial attention, feature-based attention occurs independently from the spatial location of the attended stimuli since it globally enhances sensory processing throughout the visual field without topographic distribution (Maunsell & Treue, 2006; Saenz, Buracas, & Boynton, 2002). These modulatory effects are thought to increase neural responses in cortical sites that are sensitive to the attended feature, such as MT/V5 for motion processing and V4 for color processing (Beauchamp, Cox, & DeYoe, 1997; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991; Saenz, Buracas, & Boynton, 2003). Interestingly, signals in IPS and FEF also carry dimension-specific information differentiating between attending to motion and attending to color (Liu et al., 2011), suggesting that distinct neural populations within the dorsal network represent different stimulus features during attentional orienting.

The neural signatures of feature-based shifts of attention as required during attentional reorienting have so far only been investigated using task-switching paradigms with changing feature dimensions. In particular, it has been shown that a left rather than a right lateralized network including the left precentral gyrus, precuneus and left IPS transiently activates when task-relevant feature dimensions change, for instance, from motion to color and vice versa (Liu, Slotnick, Serences, & Yantis, 2003; Shulman, d'Avossa, Tansy, & Corbetta, 2002; Weidner, Krummenacher, Reimann, Muller, & Fink, 2009). While this indicates that distinct networks are involved in feature-based reorienting as compared to spatial reorienting, the two mechanisms have so far not been systematically compared. Moreover, evidence from cueing paradigms with invalid feature cues is missing.

1.4 Expectations, predictions and probabilistic inference

Since in everyday life sensory inputs carry a high level of uncertainty, the brain needs to implicitly predict which sensory inputs to expect from the environment. On account of this, computational approaches claim that the brain acts as a prediction machine (Clark, 2013; Friston, 2005). More precisely, predictive coding frameworks suggest that the brain maps the sensory inputs it receives from the environment with predictions that it has formed based on prior knowledge. Following this approach, it is assumed that predictions are obtained by generative models, which represent internal models of environmental states based on evidence from observations. The brain continuously keeps track of the mismatch between these predicted states and the actual observed states and in return updates its internal model based on this mismatch or prediction error signal (Daunizeau et al., 2010b; Friston & Kiebel, 2009).

Principles of probability theory can describe this inference process. These principles rest upon *Bayesian statistics*, which suggest that beliefs about uncertain sensory inputs are represented in terms of probability distributions (Pouget, Beck, Ma, & Latham, 2013). The aim is to obtain probability distributions over a variable of interest (s) given sensory measurements (I) and prior knowledge $p(s)$ according to Bayes' rule:

$$p(s|I) = \frac{p(I|s)p(s)}{p(I)}$$

Here, the posterior distribution $p(s|I)$ is computed by multiplying the prior distribution $p(s)$ with the likelihood function $p(I|s)$, and dividing it by the term $p(I)$ which ensures that the posterior integrates to 1. Table 1 lists examples of these terms for the inference of the direction of a moving stimulus on the basis of the activity of neurons in the motion-sensitive area MT.

Table 1. Definitions of the terms used in the formula of Bayes' rule (Pouget et al., 2013)

Form	Term	Example
$p(s\|I)$	posterior	Inferring the direction of a moving stimulus s given patterns of neural activity of neuron in area MT.
$p(I\|s)$	likelihood	Probability of an observed pattern of neural activity of MT neurons given a moving stimulus *s.*
$p(s)$	prior	Prior probability over the direction of motion before observing neural activity in MT.
$p(I)$	denominator	How probable is our data given all possible models?

The goal of this Bayesian inference process is to decrease prediction errors about sensory inputs and to increase the posterior probability by updating predictions whenever new sensory inputs are observed (Friston & Kiebel, 2009).

One account proposes that the reduction of future prediction errors minimizes the "free-energy" in the exchange between the observer and the environment (Friston, Kilner, & Harrison, 2006; see Box 1) and thereby reduces the "surprise" about sensory inputs.

Indeed, computational models that rely on Bayesian principles have been applied to different domains of cognition and there is increasing evidence that these models explain human behavior better than normative theories (Behrens, Woolrich, Walton, & Rushworth, 2007; den Ouden, Daunizeau, Roiser, Friston, & Stephan, 2010; Kording & Wolpert, 2004).

Box 1. The free-energy principle

The free-energy principle

The concept of free-energy is derived from thermodynamics and suggests that free energy represents the amount of energy within a physical system that can be transformed into work. It has been used to explain how biological systems – such as the brain – maintain their functioning (Clark, 2013; Friston, 2010a). It states that “any self-organizing system that is at equilibrium with its environment must minimize its free energy. The principle is essentially a mathematical formulation of how adaptive systems (that is, biological agents, like animals or brains) resist a natural tendency to disorder.” (Friston, 2010a, p.127).

For instance, in the domain of attention, it has been shown that the behavioral effects of valid and invalid spatial cues in the Posner cueing paradigm can be explained by Bayesian principles (Feldman & Friston, 2010). More precisely, it has been proposed that spatial attention increases the *precision* of the sensory inputs so that reactions to attended stimuli (valid trials) are faster than to unattended stimuli (invalid trials). In this context, precision refers to the *confidence* or *inverse uncertainty*.

Bayesian models can also be employed to explain the effects of variable %CV (see section 1.1) when the predictive value of the cue varies over the course of the experiment (see Fig. 2B). In these volatile situations the belief about the %CV at a given trial must be inferred based on observations of previous cue-target outcomes. Following new observations, the belief about the %CV requires to be updated to decrease prediction errors in subsequent trials. Thus, in this particular context probabilistic inference can be understood as trial-by-trial learning of cue-target outcomes.

Most Bayesian learning models assume that human behavior can be described as "Bayes-optimal", yet there are clearly differences between individuals in the capacity for learning (Daunizeau et al., 2010a). Recently, Mathys et al. (2011) developed a hierarchical Bayesian learning model, which allows quantifying the influence of volatile situations on behavior of individual subjects (see Fig. 3). Hence, this model contains fixed parameters, which can vary between individuals to account for individualized (Bayes-optimal) learning. The model incorporates analytical update equations describing updating of beliefs about the environmental state that are used to form sensory predictions. It comprises hierarchical states with superordinate levels governing subordinate levels. Applying this hierarchical Bayesian learning scheme to empirical data provides trial-by-trial estimates of prediction errors and their precision for the different levels in the hierarchy.

The model of Mathys et al. (2011) has been applied to response speed (RS) data in an adapted version of the Posner paradigm with spatial cues and block-wise changing cue validities (Vossel et al., 2014a; Vossel et al., 2014c; Vossel et al., 2015). In this specific case, the hierarchical model consisted of three hierarchical levels: The lowest level represented the presence of a valid or an invalid trial at a given observation, whereas the next higher level represented changes in cue validity over time. The highest level represented the estimation of the volatility of these changes appreciating that there were periods with faster and slower changing cue validity. Here, the individual learning parameters could be interpreted as the individuals' susceptibility to updating trial-by-trial estimates about cue validity and estimates about their volatility (see Fig. 3).

By inverting the model on the basis of RS data, precision-based attentional weights were derived for each trial, which were interpreted as the proportion of attentional allocation to the cued location (Vossel et al., 2014c). This framework offers an elegant way to identify how attentional systems behave during uncertainty. The following section will describe how these computational modelling approaches can be incorporated in the analysis of fMRI data.

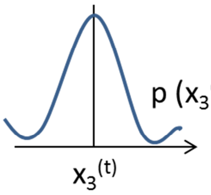
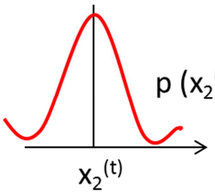
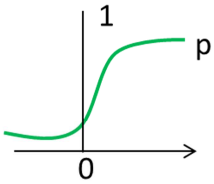
Level	**State of the world**	**Generative model**	**Example:** **Cueing paradigm with changes in cue validity**
x_3	Log-volatility of tendency	 $p(x_3^{(t)}) \sim N(x_3^{(t-1)}, \vartheta)$	**Volatility of cue validity changes**
x_2	Tendency towards category „1“	 $p(x_2^{(t)}) \sim N(x_2^{(t-1)}, e^{x_3+\omega})$	**Tendency towards valid trials**
x_1	Stimulus category Binary values  „1“ „0“	 $p(x_1 = 1) = \frac{1}{1+e^{-x_2}}$	**Observation:** **valid / invalid trial**

Figure 3 Illustration of the hierarchical generative model by Mathys et al. (2011).

The posterior distribution at each level is determined by the quantities and parameters at the next highest level. These levels relate to each other by determining the step size (volatility or variance) of the change (Gaussian random walk). This model has been applied to empirical data in a spatial cueing paradigm, as illustrated in the right column (Vossel et al., 2014c; This figure is adapted from Mathys et al. (2011)).

1.5 Functional neuroimaging and computational modeling

Functional magnetic resonance imaging (fMRI) is a technique that is often used to characterize how cognitive processes may be represented in the human brain. It relies on the assumption that active neurons increase metabolic activity, causing a change of regional blood flow and blood oxygenation in the brain. This change in the ratio between oxygenated and deoxygenated blood can be measured on the basis of their differential magnetic properties. More specifically, the carrier of deoxygenated blood (deoxygenated hemoglobin) is paramagnetic and induces inhomogeneities in the MR signal, while oxygenated hemoglobin is diamagnetic and increases the MR signal. Hence, fMRI measures changes in blood oxygenation level dependent signals (or BOLD signals), providing an indirect measure of neuronal activation (Logothetis & Pfeuffer, 2004; Logothetis & Wandell, 2004). The change in BOLD contrast in response to a stimulus is termed hemodynamic response function (HRF; Ogawa, Lee, Kay, & Tank, 1990).

Consequently, the neural correlates of cognitive processes can be inferred using statistical analysis of the BOLD signal. This is done by isolating specific events of interest that are defined based on experimental manipulations. Variations of the BOLD signal over time are modelled time locked to the occurrence of particular events. Such events could for instance be valid as compared to invalid cues or spatial as compared to feature cues (see Fig. 4). Subsequently, a general linear model (GLM) is used to explain voxel-wise variation in BOLD signal, assuming that it represents a linear combination of the explanatory variables (experimental conditions, nuisance regressors) and an error term. As standard in linear regression models, the variation in BOLD signal that is explained by a particular experimental condition is expressed in beta weights (Holmes & Friston, 1997). These beta weights can be contrasted directly between experimental conditions (e.g., invalid > valid) or between experimental conditions and an implicit baseline (e.g., invalid ∩ valid > baseline). Importantly, factorial designs also allow for the investigation of interactions between experimental conditions in different contexts (e.g., spatial invalid > spatial valid vs. feature invalid > feature valid).

Furthermore, parametric modulation can be included in the fMRI design to additionally model variations in HRF amplitudes of a certain experimental condition with a parameter value of interest. These values are continuous variables and can, for instance, denote parameters derived from computational models. By applying this method, brain regions can be identified where the influence of experimental conditions on BOLD signal responses varies with increasing or decreasing parametric values (see Fig. 4). These fMRI designs are particularly interesting for investigating the neural mechanisms of adaptive behavior in uncertain situations when responses *within* an experimental condition vary across time, so that averaging all trials would abolish subtle trial-by-trial effects. An example for parametric values that can be incorporated in the analysis of fMRI data could be trial-by-trial estimates of cue validity.

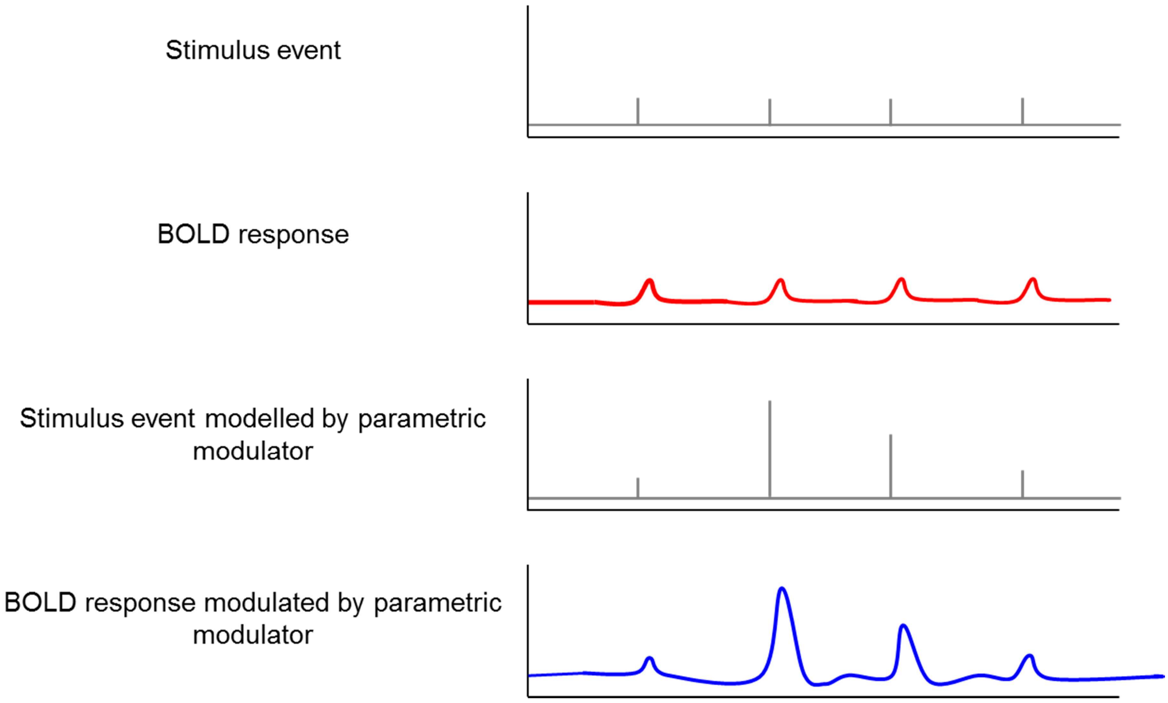


Figure 4 Illustration of the relation between stimulus onset and BOLD responses. The lower graph depicts how BOLD responses are modelled by parametric modulation.

2. Empirical section

2.1. Objectives of the thesis

The present thesis aimed at investigating the influence of inferred trial-by-trial expectancies on feature-based as compared to spatial attentional deployment and at elucidating the neural mechanisms of these processes. The empirical section will describe two experiments which have been conducted to address the following research questions:

1. Does the effect of probabilistic inference on feature-based attentional deployment depend on the level of feature cue abstraction (Experiment 1)?
2. Which brain areas are involved in feature-based reorienting of attention (Experiment 2)?
3. Are the physiological implementations of probabilistic inference universal across feature-based and spatial attention systems, or are they domain-specific with differential neural correlates for the two systems (Experiment 2)?

Declaration of Authorship

Both experiments were conducted in collaboration with co-authors. The author of the present thesis essentially contributed to the operationalization of the experiments, to the collection and analysis of the data, as well as writing of the papers.

2.2. Experiment 1: Psychophysical experiment

Dombert, PL., Fink, G.R., Vossel, S. (2016). The impact of probabilistic feature cueing depends on the level of cue abstraction. *Exp Brain Res*, 234, 685-694.

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The impact of probabilistic feature cueing depends on the level of cue abstraction

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Abstract

Allocation of attentional resources rests on predictions about the likelihood of events. While this effect has been extensively studied in the spatial attention domain where the location of a target stimulus is pre-cued, less is known about the cueing of stimulus features such as the color of a behaviorally relevant target. Moreover, there is disagreement about which types of color cues are effective for biasing attention. Here we investigated the effects of probabilistic context (percentage of cue validity, %CV) for different levels of cue abstraction to elucidate how feature-based search information is processed and used to direct attention. The color of a target was cued by presenting the perceptual color, the color word, or two-letter abbreviations. %CV, i.e., the probability that the cue indicated the color correctly, changed unpredictably between 50, 70 and 90%. Response times (RTs) for valid and invalid trials in each %CV condition were recorded in 60 datasets and analyzed with analyses of variance. The results showed that all cues were associated with comparable RT costs after invalid cueing. The modulation of RT costs by probabilities, however, depended upon level of cue abstraction and time on task: while a strong, immediate impact of %CV was found for two-letter cueing, the effect was solely observed in the second half of the experiment for perceptual and word cues. These results demonstrate that probabilistic feature-based information is processed differently for different levels of cue abstraction. Moreover, the modulatory effect of the environmental statistics differentially depends on the time-on-task for different feature cues.

Keywords: cue validity; color cueing; probabilistic context; time-on-task; visual attention.

Introduction

Probabilistic expectancies about upcoming sensory events guide attentional deployment and affect the speed with which we process behaviorally relevant stimuli. Attentional resources can be allocated to spatial locations (Posner, 1980), but also to stimulus features such as color or orientation. Experimentally, these processes can be studied with cueing paradigms, in which a cue indicates either the location or a feature of a behaviorally relevant target stimulus with a specific probability (percentage of cue validity, %CV) (e.g., Egner et al., 2008). For the allocation of spatial attention, it has already been shown that changes in probabilistic context affect the response time costs associated with invalid cueing, even when the subjects are not explicitly instructed about the underlying environmental statistics (Vossel et al., 2014a; Vossel et al., 2014c). Higher levels of %CV lead to higher validity effects (i.e., higher response time differences between trials with invalid and valid cues), since invalid trials are less expected. For the cueing of stimulus features (e.g., color), it has been shown that similar effects can be observed when the subjects are explicitly informed about the different levels of %CV (Egner et al., 2008). However, these effects have not been investigated in situations in which no explicit information about cue validity is provided.

Furthermore, no study has systematically compared the effect of different levels of abstraction of color cues. The color of a stimulus can, for example, be cued perceptually by presenting the most likely physical color of an upcoming target. Moreover, the target color can be cued by the presentation of the color word or by more abstract letters. Whether these different kinds of cues are equally effective for directing attention remains a matter of debate. While some studies have shown that verbal guidance, or knowledge of the feature dimension, can bias visual selection (Ansorge & Becker, 2012; Muller & Geyer, 2009; Muller et al., 2010; Soto, Rotshtein, Hodsoll, Mevorach, & Humphreys, 2012), others claim that perceptual priming by the physical color is needed (Theeuwes, 2013; Theeuwes & Van der Burg, 2007).

The present study investigates the contribution - and putative interaction - of different levels of feature cue abstraction and probabilistic context on attentional deployment. More specifically, we cued the color of a behaviorally relevant target stimulus perceptually (by presenting a colored disk) or verbally (by presenting either the whole color word or by presenting a two-letter abbreviation of the color word). Classical Stroop paradigms have illustrated the automatic nature of visual word recognition (Brown, Gore, & Carr, 2002; Ferrand & Augustinova, 2014; MacLeod, 1991; Neely, VerWys, & Kahan, 1998). Interestingly, however, the Stroop effect diminishes when a single target letter in a word is deviant from expected, e.g., presented in a unique color (Labuschagne & Besner, 2015). Hence, we employed the two-letter abbreviation to create a more abstract cueing condition with less automaticity of the retrieval of cue meaning than whole color words or the perceptual color, respectively. Additionally to the three different levels of cue abstraction, we varied %CV over the time of the experiment. This allowed us to test for main effects and interactions of different levels of cue abstraction and %CV on the cueing effects in response times (i.e., the validity effect as the difference in response time between invalid and valid trials). We aimed at disambiguating between the following competing hypotheses: If sensory priming is a prerequisite for attentional deployment in response to color cues, we should observe a main effect of the different feature cue conditions, such that significant response time costs in invalid trials (i.e., the validity effect) can only be found for the perceptual cues. If these perceptual priming processes are not purely automatic but susceptible to probabilistic information, these effects should furthermore be modulated by %CV, with higher cueing effects with higher %CV. Alternatively, if more abstract cues such as the color word or two-letter abbreviations are equally effective in biasing attentional deployment, the main effect of feature cue abstraction on the validity effect should not be significant. Equal or differential susceptibilities of the different feature cue types to probabilistic context would be reflected in the presence or absence of feature cue by %CV interaction effects, respectively. In addition, the effects of unsignalled changes of %CV may depend on the number of observations, i.e., the time-on-task. In other words, the number of observed cue-target outcomes or the exposure to volatile contingencies may affect the impact of the environmental statistics and the adaptation of behavior (Behrens et al., 2007). For this reason, we analyzed the first and second half of the trials separately to also test for a differential evolvement of the effects of probabilistic context and feature cues over the time of the experiment.

Materials and Methods

Subjects

Sixty datasets were acquired from 49 healthy subjects (30 females; mean age 24.3 years, ranging from 18 to 34 years) who gave written informed consent to participate in the current study. Eleven subjects participated in two experimental versions (intersession interval > one week; order randomized). Subjects were randomly allocated to three experimental versions, (i.e., perceptual cueing task: n=20, 10 female; mean age 23.9 years, range 18-31 years; word cueing task: n=20, 12 female; mean age 23.9 years, range 20-31 years; two-letter cueing task: n=20, 14 female; mean age 24.6 years, range 18-31 years). All subjects were right-handed, had normal or corrected to normal vision, and did not suffer from any neurological or psychiatric conditions. The ethics committee of the German Psychological Society had approved the study. The study was performed in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Stimuli and Experimental Paradigm

We used a feature-cueing paradigm with central cues (adapted from Egner et al., 2008). Stimuli were presented on a 19-inch monitor (spatial resolution 1024 × 768 pixels, refresh rate 60 Hz) with a viewing distance of 70 cm. A central diamond (0.8° eccentric in each visual field) served as a fixation point. On each trial, subjects were shown a cue stimulus followed by a search array consisting of four peripherally located diamond stimuli (6.7° eccentric in each visual field, see Fig. 1a). The diamond stimuli could be either blue or red and were placed in the corners of a virtual rectangle centered around the fixation diamond on a gray background. Each hemifield always contained a blue and a red diamond. The color and position of the red and blue stimuli was counterbalanced, resulting in an equal number of diagonal and horizontal arrangements of red and blue stimuli in the different %CV blocks and across valid and invalid trials (see Fig. 1a, diagonal arrangement). One of the diamonds was missing either its upper or lower corner. Subjects were asked to detect this target diamond and indicate via button press with the right index or middle finger whether the upper or lower corner of the diamond was missing. The search array was preceded by a feature cue appearing in the central fragment of the fixation diamond for 400 milliseconds (ms). After a 1000-ms stimulus onset asynchrony the target display was shown for 500 ms. Trials were separated by a response period of 1000 ms (see Fig. 1a).

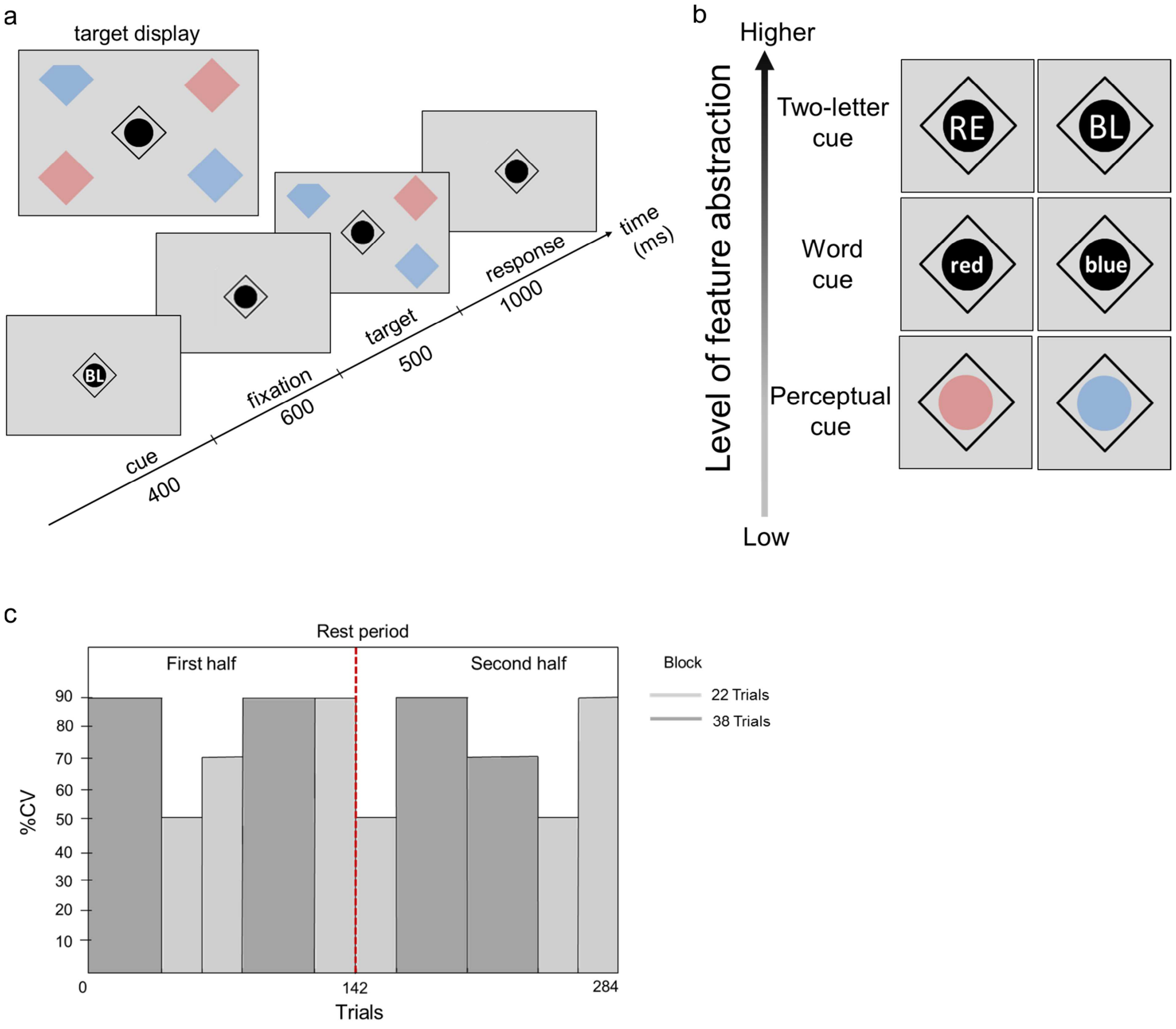

Figure 1 Illustration of the experimental task

a The example shows a valid trial of the two-letter cueing condition. Subjects were asked to detect the diamond with a missing corner and to indicate by button press whether the upper or lower corner was missing. Subjects were requested to maintain central fixation throughout the experiment.

b Illustration of the different cue stimuli for the three versions of the task as a function of level of feature processing.

c Manipulation of the percentage of cue validity (%CV) over the 284 trials.

Three different variants of the feature cues were used, realizing three different levels of cue abstraction. In the perceptual-cueing version, the most likely physical color of the target was presented. Word cues comprised the written word of the color (‘rot’ or ‘blau’; [i.e., ‘red’, ‘blue’ in German, respectively]). The abstract cueing consisted of a two-letter cue indicating the color (‘RO’ or ‘BL’; [i.e., ‘RE’, ‘BL’ in German, respectively] (see Fig. 1b). It is important to note, that the three tasks differed only in the cue stimuli that conveyed the feature-based information; target stimuli and trial sequences were identical between the different feature cue versions. The experiment consisted of 284 trials with blockwise changes in the percentage of cue validity (%CV) between ~50, ~70, and ~90%. Moreover, 84 “null trials”, during which only the baseline display (i.e., a fixation diamond) was shown, were included to jitter trial onsets. %CV could change after either 32 or 22 trials (see Fig. 1c). The overall rate of %CV amounted to 75% (78% in the first, and 72% in the second half, respectively), which is within the range that is commonly used in endogenous cueing paradigms (~75-80%) (Macaluso & Doricchi, 2013; Posner, 1980; Theeuwes & Van der Burg, 2007). A one-minute rest period was included after half of the trials, separating the experiment in two parts. Subjects were informed that there would be changes in %CV over the course of the experiment, but were not aware of the levels of those probabilities or the time when they would change. Importantly, subjects were instructed to use the cue according to how much they “trust” it in order to speed up reaction times. In accordance with standard procedures of studies investigating learning processes that require inferring conditional probabilities, the order of trials was identical for all subjects (Behrens et al., 2007; Daunizeau et al., 2010a; Daunizeau et al., 2010b; Vossel et al., 2014ca,b). Hence target inputs were identical between cue versions. Within each block of constant %CV, the color of the four diamonds, the location of the target diamond, and the position of the missing fragment were presented with equal probability and counterbalanced across valid and invalid trials. Each session started with a short practice version (four min) of the task with 98 trials (+ 28 “null trials”) and a constant %CV of 80%. In this training block, the subjects were explicitly informed about the percentage of cue validity. The training was used to familiarize the subjects with the task and to practice fixation and the manual responses to the targets. Data from the training session were not analyzed.

Data analysis

The main dependent variable of interest in the present study was the validity effect in the different experimental conditions, i.e., the difference in response times (RT) between invalid and valid trials. However, we also analyzed the accuracy (percentage of correct responses) in the different experimental conditions. Individual median RTs from correct trials in each condition were included in the RT analyses and trials with missing, incorrect or anticipated responses (RT<100 ms) were excluded from the RT analyses. The two halves of the experiment were analyzed separately. Since the number of trials in the different %CV levels differed between the first and second half, we did not test for interactions between *%CV* and *time*. However, since the trial sequence was identical for all subjects, we still tested for interaction effects of the experimental factors including *time* with the between-subject factor *feature cue*. Validity effects (RT costs) were calculated by subtracting median RTs of valid trials from median RTs of invalid trials in each %CV condition (50, 70, and 90%). These validity effects entered the group analyses with ANOVAs. In particular, validity effects were analyzed with a 3 (*%CV*: 50, 70, 90%) × 2 (*time*: 1st half, 2nd half) repeated measures ANOVA with the additional between-subject factor for the *feature cue* (perceptual cue, word cue, two-letter cue). The same analysis was performed on accuracy. A main effect of *feature cue* would reflect differential effectiveness of the different levels of cue abstraction for attentional deployment. An effect of probabilistic context would be reflected in a significant *%CV* main effect, with higher validity effects with higher %CV. A significant interaction effect of *%CV* × *feature cue* would reflect a differential susceptibility of the different feature cues to probabilistic context during the deployment of attention. In addition, we tested if these effects were modulated by the time-on-task.

To test for general effects of valid versus invalid cueing, we also included an analysis on median RTs in invalid and valid trials, where the factor *cueing* (valid, invalid) was added to the ANOVA described above. However, for reasons of simplicity, we report the effects of *%CV*, *feature cue*, and *time* from the ANOVA on the RT differences (validity effects) (note, that the p-values are identical for both analysis).

Previous research has investigated the influence of different cue-target contingencies in the spatial attention domain and has shown that the validity effect varies linearly with %CV (e.g., Giessing, Thiel, Rosler, & Fink, 2006; Riggio & Kirsner, 1997; Vossel et al., 2014a; Vossel et al., 2014c). Based on this, we predicted a linear effect of %CV on the deployment of attention in the feature domain. Such an effect has already been demonstrated for explicit probability manipulations with single letter color cues (Egner et al., 2008). In the present study, we tested if this probability modulation was likewise observed for an implicit manipulation of probabilistic context, and for different levels of cue abstraction. For this reason, we report within-subjects linear contrasts for the effects of *%CV*.

We additionally applied a distributional analysis fitting ex-Gauss distributions to RT data on the single-subject level using the DISTRIB toolbox (Lacouture & Cousineau, 2008). This procedure allows for a more comprehensive analysis of RTs and the central tendency measure. However, it requires many data points per participant and condition (Whelan, 2008). We were therefore only able to fit ex-Gauss functions to the data from the whole experiment, thereby ignoring time effects. Results from this analysis are reported in the Online Resource 1. Data Analyses were performed using MATLAB® (2012b, The MathWorks, Inc., Natick, Massachusetts, United States) and SPSS (IBM SPSS Statistics for Windows, Version 21.0. Armonk, NY: IBM Corp). Since we used a between-subject design in the current study, we repeated the 3 *(%CV*: 50, 70, 90%) × 2 (*time*: 1st half, 2nd half) × 3 (*feature cue*: perceptual, word, two-letter) ANOVA with inclusion of *age* and *gender* as covariates. Moreover, since it has been shown that the size of the validity effect can be related to trait impulsivity (Landau, Elwan, Holtz, & Prinzmetal, 2012), we added the subject-specific scores from the subscales of the Barratt Impulsiveness Scale 11 (BIS-11; Patton, Stanford, & Barratt, 1995) as a further covariate.

Eye Movement Recording and Analysis

We monitored movements of the right eye with an EyeLink® 1000 (SR Research) eye-tracking system with a sampling rate of 1000 Hz. At the start of the experiment, a 9-point eye-tracker calibration and validation was performed (validation error <1° of visual angle). Analysis of the data was performed using MATLAB (2012b, The MathWorks, Inc., Natick, Massachusetts, United States). The critical period analyzed for gaze deviations from the center was the time window between presentation of the cue and the target display (cue-target period). Saccades were identified when the eye velocity exceeded 30°/s. Gaze deviations from fixation >1.5° visual angle in the cue-target period were determined and expressed as a percentage score. Group differences in percentage fixation scores were analyzed by entering the percentage scores for each subject into an ANOVA with the within-subject factor *time* (first half, second half) and the between-subject factor *feature cue* (perceptual cue, word cue, two-letter cue).

Results

Behavioral results

Table 1. depicts median RTs based on which validity effects were calculated. The 3 (*%CV:* 50, 70, 90%) × 2 (*time:* 1^{st} half, 2^{nd} half) × 3 (*feature cue:* perceptual, word, two-letter) ANOVA on the validity effects revealed no significant main effect of feature cue ($F_{2,57}$= 0.47, p =.63), reflecting that the three different cues did not differ significantly in biasing attention. When median RTs for valid and invalid trials per subject entered the ANOVA instead of the RT difference (validity effect), the main effect of *cueing* was significant ($F_{1,57}$= 75.24, p<0.01), such that RTs for invalid trials were consistently slower than for valid trials. In the ANOVA on the validity effect, the main effect of *%CV* was significant (linear contrast: $F_{1,57}$= 6.08, p<0.05) indicating stronger cueing effects (i.e., higher RT costs after invalid cueing) with higher *%CV*. Moreover, we observed a significant interaction effect between *%CV* × *feature cue* (linear contrast: $F_{2,57}$= 3.85, p<0.05, See Fig.2). This effect was also observed when using a distributional analysis of RTs with ex-Gauss functions (See Online Resource 1).

Table 1 RT data

Average (± SEM) individual median RTs for valid and invalid trials in the three %CV conditions, calculated separately for first and second half of the experiment and feature cue.

		50 %CV		**70 %CV**		**90 %CV**	
		Valid	Invalid	Valid	Invalid	Valid	Invalid
Two-letter cue	1st half	617.8 (23.2)	681.9 (30.3)	601.8 (19.0)	693.5 (37.6)	608.4 (15.0)	756.4 (30.6)
	2nd half	587.5 (13.5)	649.8 (21.9)	597.3 (13.6)	661.2 (37.6)	593.4 (14.4)	689.1 (35.8)
Word cue	1st half	534.1 (29.9)	703.6 (46.4)	649.1 (32.4)	724.5 (39.9)	638.5 (31.1)	710.1 (36.0)
	2nd half	596.3 (27.5)	632.9 (22.9)	614.2 (30.4)	661.9 (31.1)	609.7 (28.6)	701.6 (34.7)
Perceptual cue	1st half	624.1 (30.6)	742.7 (44.6)	628.5 (30.4)	705.5 (32.9)	619.4 (24.9)	691.5 (29.1)
	2nd half	625.6 (23.3)	688.5 (22.3)	623.0 (23.5)	704.6 (33.9)	596.8 (19.2)	683.9 (28.1)

Adding the additional factor time, showed that this effect was additionally modulated by *time* (linear contrast: *%CV* × *feature cue* × *time* interaction effect: $F_{2,57}$= 3.19, p<0.05), suggesting a differential impact of probabilistic context on the validity effect in the three feature cueing versions in the first and the second half of the experiment. Figure 3 illustrates this 3-way interaction effect graphically by plotting the validity effects separately for the different feature cue versions and experimental conditions. Following up this 3-way interaction effect, the validity effects of the first and second half of the experiment were further analyzed by calculating separate ANOVAs with the factor *%CV* and *feature cue*. For the first half of the experiment the ANOVA revealed a significant interaction effect of *%CV* and *feature cue*, but no main effect of *%CV* (main effect of *%CV*: $F_{1,57}$= 0.66, p=.42; interaction effect *%CV* × *feature cue*: $F_{2,57}$= 5.46, p<.01). This significant interaction was further analyzed by performing separate ANOVAs for the three feature cues with the factor

%CV. The analyses revealed a significant effect of *%CV* for the two-letter cueing only (main effect of *%CV*: two-letter cueing: $F_{1,19}= 21.44$, $p<.001$; word cueing: $F_{1,19}= 0.004$, $p=.95$; perceptual cueing: $F_{1,19}= 2.22$, $p=.16$). Analysis of the second half of the experiment revealed a significant main effect of *%CV*, and no interaction between *%CV* and *feature cue* (main effect of *%CV*: $F_{1,57}= 8.26$, $p<.01$; interaction effect *%CV* × *feature cue*: $F_{2,57}= 0.49$, $p=.61$).

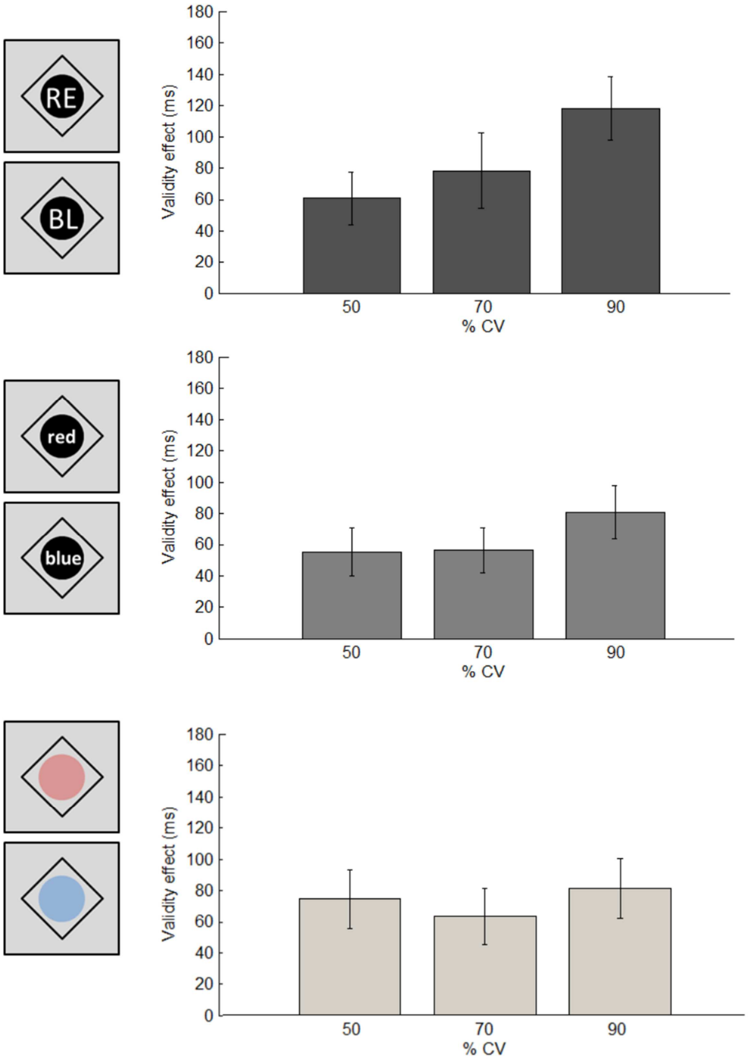

Figure 2. Response time results across the whole experiment

Illustration of the average validity effects (response time (RT) invalid minus RT valid) for the three %CV levels (across the whole experiment) separately for each feature cue. Darker bars represent more abstract and lighter bars less abstract processing. Mean validity effects and standard errors of the mean are reported in milliseconds (ms).

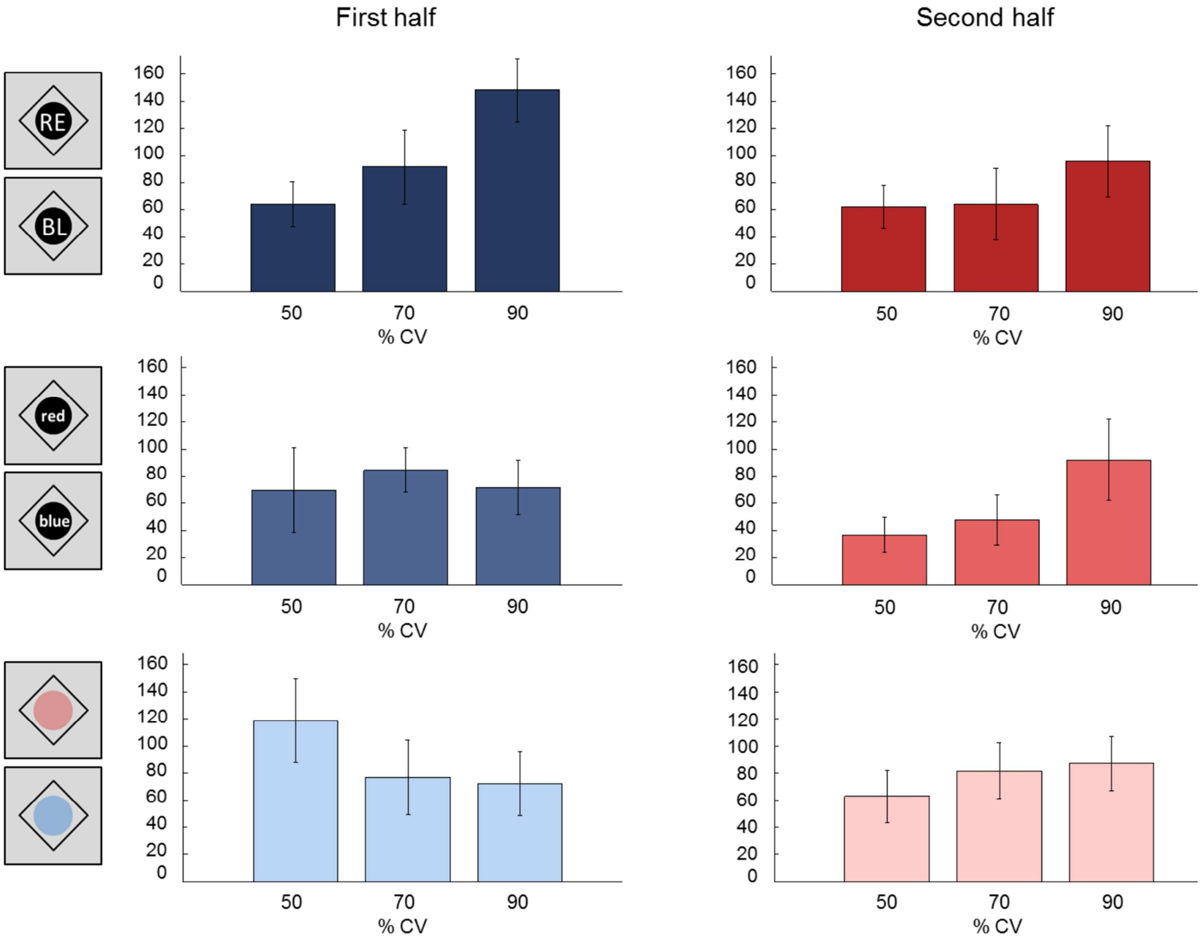

Figure 3. Response time results in the two halves of the experiment

Illustration of the average validity effects (response time (RT) invalid minus RT valid) for the three %CV levels as a function of time (first vs. second half of the experiment) and feature cue. Blue (left) bars depict validity effect data for the first half of the experiment; red (right) bars show validity effect data for the second half of the experiment; darker bars represent more abstract- and lighter bars less abstract processing. Mean validity effects and standard errors of the validity effects are reported in milliseconds (ms).

These additional analyses show that a modulation of the validity effect by *%CV* (higher validity effects with higher %CV) was in the first half only present in the two-letter cueing condition (*%CV* × *feature cue* interaction), while it was observed for all three cueing versions in the second half of the experiment (main effect of *%CV*, no interaction with *feature* *cue*). There was a marginal trend of the factor time ($F_{1,57}$= 3.12, p=.08), so that (irrespective of %CV) validity effects tended to be slightly lower in the second half of the experiment. However, there was no interaction of time and feature cue ($F_{2,57}$= .19, p=.83), and no other terms of the ANOVA reached significance. The present results showed that all three feature cues produced similar response time costs after invalid cueing and that the subjects were able to infer the probabilistic context from the observations (main effect of *%CV*). However, there was an interaction between the effect of probabilistic context and the level of abstraction of the feature cues, which was additionally modulated by *time*. We observed that in the first half of the experiment the expected impact of *%CV* on the validity effect (i.e., higher validity effects with higher %CV) was only present in the two-letter-cueing condition. In the other two conditions, probabilistic context affected validity effects with increasing time on task and the linear effect of %CV was only obvious in the second half of the experiment (see Fig. 3). The critical three-way interaction of *feature cue*, *%CV*, and *time* remained significant when *age*, *gender*, and scores from the BIS-11 impulsivity subscales entered the above ANOVA as covariates, while there was no significant effect of this interaction on any of the covariates.

Overall accuracy amounted to 91.5 ± 1.1%, 88.3 ± 1.7%, and 93.2 ± 1.2% (mean ± SEM) in the perceptual, word, and two-letter feature cue version, respectively. Figure 4 depicts differences in accuracy between invalid and valid trials in the different experimental conditions. The 3 (*%CV:* 50, 70, 90%) × 2 (*time:* 1st half, 2nd half) × 3 (*feature cue:* perceptual, word, two-letter) ANOVA on accuracies revealed a significant main effect of *%CV*, reflecting higher accuracy costs for invalid cueing with higher %CV (linear contrast: $F_{1,57}$= 6.01, p<0.05). Moreover, there was a significant main effect of *time* indicating that accuracy differences between valid and invalid cueing were higher in the first part of the experiment ($F_{1,57}$= 11.04, p<0.05). There was no significant interaction of *feature cue* with any other factor.

Eye-movement data

Eye-movements were recorded to control for central fixation during the cue-target period. Valid eye-movement recordings could be obtained in 14 subjects in the perceptual-cueing task, 20 subjects in the word-cueing task, and 16 subjects in the two-letter-cueing task. In the remaining subjects, eye-movements were monitored on-line by the experimenter. During the cue-target period, subjects maintained fixation in 99.1 ± 0.3% of the perceptual-cueing trials, 99.3 ± 0.2% of the word-cueing trials, and in 98.8 ± 0.4% of the two-letter-cueing trials (mean ± SEM). The percentage of fixation trials did not differ significantly between the three groups ($F_{2,47}$= 0.99, p=.38). Furthermore, there was no difference in fixation performance between the first and second half of the experiment (main effect *time*: $F_{2,47}$= 0.6, p=0.44), nor an interaction effect of *time* and *feature cue* (interaction effect *time* × *feature cue*: $F_{2,47}$= 1.88, p=0.16).

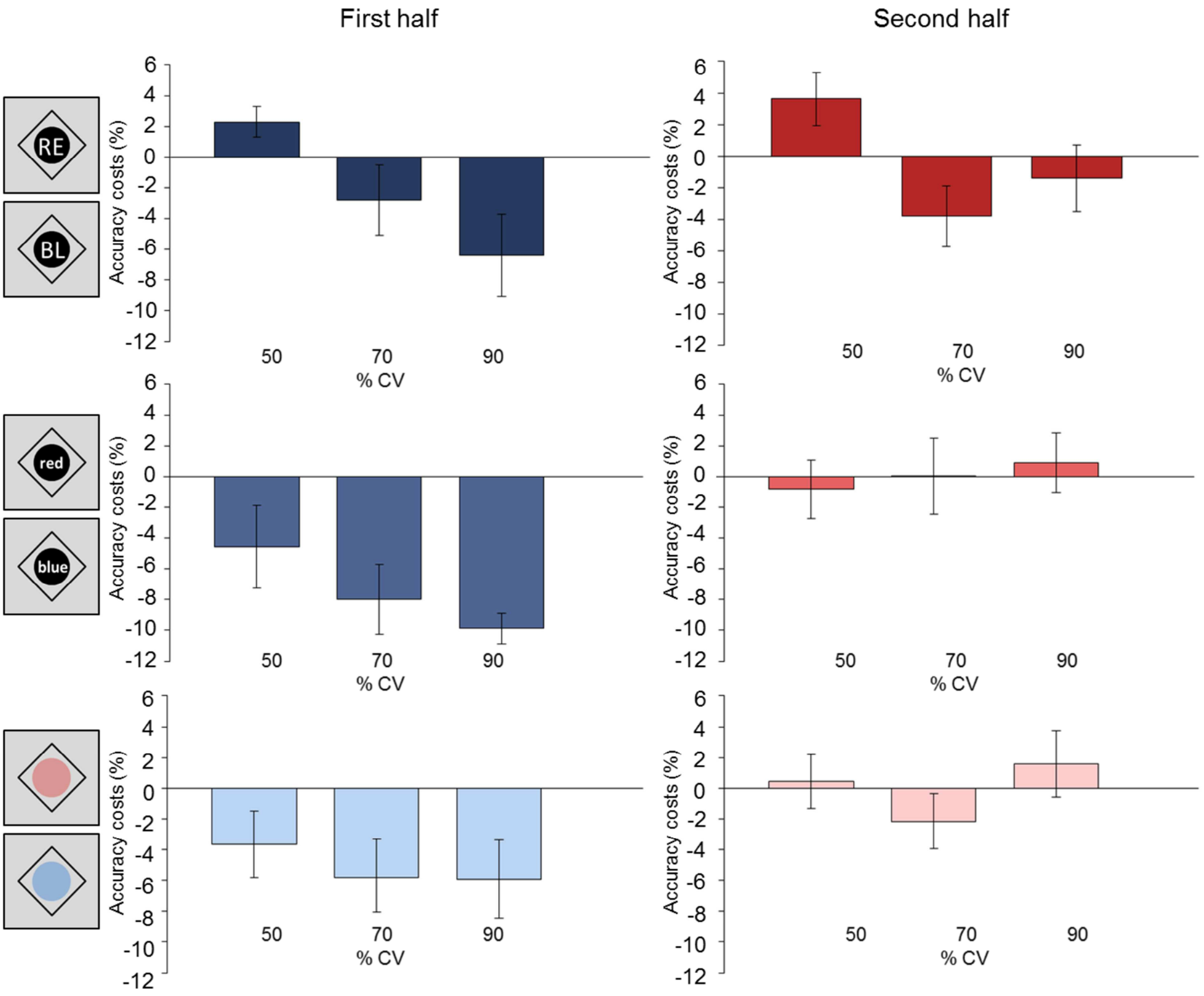

Figure 4. Accuracy results

Average accuracy costs (accuracy invalid minus accuracy valid) are depicted for the three %CV levels as a function of time (first vs. second half of the experiment) and feature cue. Blue (left) bars depict accuracy cost data for the first half of the experiment; red (right) bars show accuracy cost data for the second half of the experiment; darker bars represent more abstract- and lighter bars less abstract processing. Mean accuracy costs and standard errors of the accuracy costs are reported in percentages.

Discussion

The present study investigated attentional modulation by color cues as a function of different levels of cue abstraction and probabilistic context (cue validity). The color of a behaviorally relevant target stimulus was cued by presenting the perceptual color, the color word, or two-letter abbreviation and %CV was varied over the time of the experiment. The results showed that all three feature cues elicited validity effects (i.e., response time costs after invalid as compared to valid cueing) to a similar extent. Moreover, probabilistic context significantly affected attentional deployment, with higher validity effects associated with higher %CV. This modulation, however, depended on the type of feature cue and on the time on task: the type of feature cue determined the effects of probabilistic context, i.e., the adaptation of attentional deployment to statistical regularities in the course of the experiment.

All three feature cues elicited cueing effects in our experimental task, such that response times were slower after invalid as compared to valid cues. There were no general differences in the magnitude of these cueing effects between the different levels of cue abstraction. These results support the notion that priming by the physical presentation of the color is *not* a necessary prerequisite for biasing attentional selection, i.e., that perceptual priming of color-sensitive neurons cannot be the *only* mechanism causing attentional effects in the feature-based domain (Ansorge & Becker, 2012; Muller et al., 2010; Rangelov, Muller, & Zehetleitner, 2011a; Soto et al., 2012). Still, we observed differences in the effects of the different feature cues in our paradigm with unsignalled changes in the percentage of cue validity over time. The modulation of these cueing effects by probabilistic context (%CV) was initially (i.e., in the first half of the experiment) only present in the two-letter cueing condition. Only in this condition did we observe the predicted linear increase of the validity effect with higher %CV as reported in visuospatial cueing paradigms (Geng & Behrmann, 2005; Macaluso & Doricchi, 2013; Stankevich & Geng, 2014; Vossel et al., 2014aa,b). Which mechanism could underlie this differential modulation by percentage of cue validity in the three feature cue conditions? Our data suggest that when cue processing is more automatic (i.e., in the case of the perceptual cues and word cues) and hence evokes less explicit cognitive effort to encode the meaning of the cues (as in the case of the two-letter cues), it may take more time to add a top-down guided attentional modulation by probabilistic information. However, with an increasing amount of observations and exposure to volatile contingencies, these probability-dependent effects can still be initiated, as suggested by the observation that the modulation by %CV depended on the time on task. This type of behavior (initial resistance to probabilistic context with evolvement of the effect over time) was observed for both the perceptual color and the word cues. For the latter, classical Stroop paradigms have illustrated the automatic nature of visual word recognition (Brown et al., 2002; Ferrand & Augustinova, 2014; MacLeod, 1991; Neely et al., 1998). Consistently, the data suggest that with the word cue – similar to the perceptual color cue – processing was automatic and the modulatory influence by inferred probabilities could only evolve with increasing time on task. In contrast, new observations changed probability estimates more rapidly in the case of the more abstract two-letter cues which required more active processing to encode the meaning of the cues.

It should be noted that we used identical cue-target intervals for all three cueing versions in the present study. In the spatial domain, exogenous, automatic orienting triggered by briefly presented peripheral cues shows a different time course than endogenous, voluntary orienting of attention after centrally presented symbolic cues such as arrows (Muller & Rabbitt, 1989). We cannot rule out that the time course of feature-based orienting differs between the feature cues (requiring different levels of processing or automaticity to retrieve cue meaning). In other words, different cue-target intervals may have increased or decreased the reported effects. Nonetheless, our finding has important implications for the study of feature-based attention effects and particularly for the comparison with space-based mechanisms.

Neuroimaging studies on the neural mechanisms underlying cueing effects in the spatial and feature-based domain differ in the types of feature cues they employed. While some studies used the direct physical color as cues (Vandenberghe, Gitelman, Parrish, & Mesulam, 2001b), others used color word abbreviations (Giesbrecht et al., 2003). Our results suggest that the attentional mechanisms triggered by the different color cues may not be identical and this may affect the comparison with spatial cues. Support for this assumption can be derived from a TMS study which showed that TMS of the right supramarginal gyrus impaired spatial attention (manipulated by central arrows) but not feature-based attention (manipulated by *perceptual* color cueing) (Schenkluhn et al., 2008). This finding suggests that more automatic perceptual cueing of the target color does not rely on the supramarginal gyrus. A novel hypothesis from our present findings would be that this differential TMS effect may disappear, when the symbolic spatial cues are compared with more abstract color cues.

The present study employed a between-subject design for comparing the effect of different feature cues. This was done to avoid carry-over effects caused by the repeated exposure to the identical %CV sequence or interaction effects of the cueing versions with the order of administration (so-called asymmetrical transfer, Millar, 1983). However, the use of a between-subjects design has also disadvantages: individual participant characteristics can differ from one group to another and these differences may potentially confound the group comparison. Our additional analysis with age, gender, and BIS-11 impulsivity subscale scores suggested that these variables did not affect the observed pattern of results, but we cannot rule out that the three groups differed in other unknown variables which may have contributed to the observed differences.

In sum, our findings show that the role of the level of cue abstraction for attentional control in color cueing paradigms is highly complex and depends on contextual factors. The findings contribute to the debate on the relative influence of stimulus-related and goal-directed factors in attentional control in two ways: First, we show that all three feature cues lead to a similar biasing of attentional settings, but that attentional allocation by expectancies depends on the level of cue abstraction. Second, we demonstrate the dynamic nature of this interaction: depending on the time on task (first versus second half of the experiment), the susceptibility to probabilistic context could be observed for all feature cue types.

Conflict of Interest

The authors declare that they have no conflict of interest.

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2.3. Experiment 2: Computational modelling and fMRI experiment

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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 modelling 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 fronto-parietal 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.

Key words: visual attention networks; Bayesian inference; belief updating; cue validity; fMRI.

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 & 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, Patel, & Shulman, 2008; Corbetta & 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, Carr, Mayer, & Rao, 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, Fink, & Vossel, 2015; Egner et al., 2008; Vossel et al., 2006; Vossel, Weidner, Driver, Friston, & Fink, 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 unsignalled 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, Daunizeau, Friston, & Stephan, 2011; Vossel et al., 2014c). Though the update equations of this Bayesian model bear structural similarity to reinforcement learning models such as the Rescorla-Wagner rule (Rescorla & 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 trialwise 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., 2014c). Another advantage of the current modelling 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 modelling 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 modelling - 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 & 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 (milliseconds). 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).

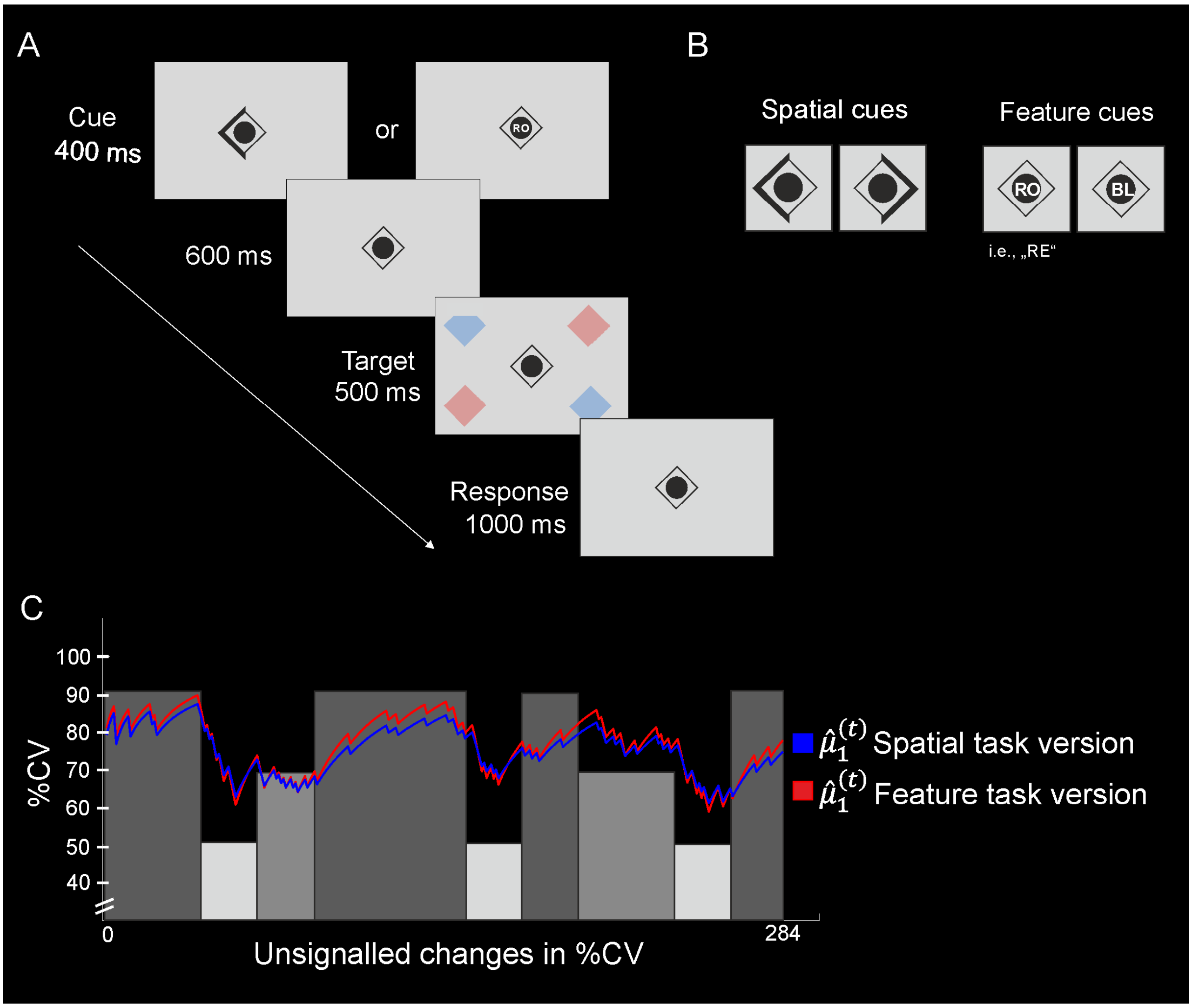

Figure 1 Illustration of the experimental paradigm

A) The example shows the experimental paradigm consisting of two runs during which either feature or spatial cues were presented. Subjects were asked to detect the diamond with a missing corner and to indicate by button press whether the upper or lower corner was missing. Central fixation needed to be maintained throughout the experiment.

B) Illustration of the cue stimuli for the spatial and feature task version of the experimental paradigm.

C) Trial-by-trial changes in probability-dependent attention $\hat{\mu}_1^{(t)}$ reflecting the subject's belief that the cue is valid in relation to the experimentally manipulated percentage of cue validity (%CV) over the 284 trials, for spatial- and feature cueing, respectively. For this graph, $\hat{\mu}_1^{(t)}$ was calculated on the basis of the average parameter estimates over all subjects. Note that individual values were used as parametric regressors in the fMRI analyses.

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 modelled 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 speed up response times to the target. Additionally, 84 "nulltrials" (i.e., baseline fixation) were randomly intermixed with the experimental trials to jitter trial onsets. Furthermore, a one-minute rest period during which the word "pause" was shown on the display was implemented after half of the trials in each run. The total duration of the fMRI experiment (both runs) amounted to 34 minutes.

In order to familiarize the subjects with the task, fixation, and the manual responses, we included a practice session in the experiment. This practice took place at the same or the previous day of the fMRI session and consisted of a block with a constant %CV of 80% and a block with changes in %CV. We aimed at a direct comparison between feature and space-based cueing effects using the same search task, stimuli, and methods in a within-subjects design. It should be noted, however, that the visual search task always contained a spatial component, also in the feature-based task. The cue-induced spatial shift was crucial and of interest for the spatial task (one spatial shift in validly cued trials versus two spatial shifts in invalidly cued trials). In the feature task, spatial shifts should occur in invalid as well as valid trials, since in each trial two stimuli in the cued color (one in each hemifield) were presented. Hence, this effect should presumably cancel out in the contrast of invalid and valid trials in the feature task. If this was not the case (i.e., if there still was a stronger spatial component in invalid trials in the feature task), this should lead to similar activation patterns for the invalid versus valid contrast for both tasks. In contrast, our test for interaction effects between cue type and validity (see below) cannot be explained by a common spatial component and should hence reflect differential functional mechanisms of spatial versus feature-based reorienting. Moreover, the parametric effects of probability-dependent processing should not be affected by this.

Functional localizer experiment

We included a functional localizer to identify regions-of-interest (ROIs) in visual cortex that were activated in response to visual stimulation at the four stimulus locations of the target display. Participants were asked to passively view checkerboard stimuli presented at the same eccentricity and in the same size as the targets, while maintaining gaze on the central fixation cross. All stimuli were presented on a black background (see Supplementary Fig. S2). Checkerboard stimuli induced a flickering sensation by alternating color between white and the uniform black background at a frequency of 4 Hz. The experiment consisted of

8 stimulus blocks (2 for each display position) of 16 secs length, which were presented in pseudorandom order and separated by intervals of 16 secs of fixation-only blocks. The functional localizer took about 5 minutes and was presented to the participants after the main fMRI experiment.

Eye movement recording and analysis

Eye movements were recorded during the main experiment from the right eye with an EyeLink® 1000 MR-compatible eye-tracker (SR Research Ltd.) with a sampling rate of 500 Hz. A 9 or 5-point eye-tracker calibration and validation were performed at the start of the experiment. Data analysis was performed using MATLAB (2012b, The MathWorks, Inc., Natick, Massachusetts, United States) and ILAB (Gitelman, 2002). Gaze deviations that exceeded 1.5° visual angle from the center were analyzed. The amount of time spent within the central fixation zone was determined and expressed as percentage score. Gaze deviations in the time interval between cue and target presentation were compared between spatial and feature cues with a paired t-test. The amount of time spent within the central fixation zone was determined and expressed as percentage score. Gaze deviations in the time interval between target presentation and response were analyzed with a 2 (*validity*: valid, invalid) × 2 (*cue type*: spatial, feature) within-subject ANOVA.

MRI data acquisition

Using a 3T MRI System (Trio; Siemens), T2* weighted EPI images with BOLD contrast were acquired with a repetition time of 2.2 secs and an echo time of 30 ms. A total of three functional runs was acquired: 458 EPI volumes for each run of the main experiment (i.e., for each task version), and 128 EPI volumes for the functional localizer task. Each volume consisted of 36 axial slices with interleaved slice acquisition. The field of view was 200 mm, using a 64 × 64 image matrix, which resulted in a voxel size of $3.1 \times 3.1 \times 3.3$ mm^3. The first five volumes were discarded from the analysis to allow for T1 equilibration effects.

The remaining volumes (main experiment: 2 × 453; functional localizer: 123) were analyzed using the Statistical Parametric Mapping software SPM12 (Wellcome Department of Imaging Neuroscience, London; Friston et al., 1995; http://www.fil.ion.ucl.ac.uk/spm). Images were bias-corrected. Slice acquisition time differences were corrected using sinc interpolation to the middle slice. During spatial realignment, a mean EPI image was computed for each subject and spatially normalized to the MNI template using the segmentation function. Subsequently, the obtained transformation was applied to the individual EPI volumes to translate the images into standard MNI space and resample them into 2 x 2 x 2 mm^3 voxels. Finally, the normalized images were spatially smoothed using an 8 mm full-width half-maximum Gaussian kernel.

Data analysis

Behavioral data analysis

Classical inference was first performed to investigate whether probabilistic context significantly affected response times. Incorrect trials, misses, anticipations, and responses deviating more than 2 standard deviations from the individual subject's mean RT were excluded from the analysis. Mean RTs from valid and invalid trials for each subject, %CV condition, and cue type entered a 2 (*validity*: valid, invalid) × 3 (*%CV*: 50%, 70%, 90%) × 2 (*cue type*: feature, spatial) within-subject ANOVA. RT differences between valid and invalid trials would be reflected in a significant main effect of *validity*. An impact of probabilistic context onto the deployment of attention would result in a significant interaction effect of *validity* × *%CV*, with enhanced differences between invalid and valid trials (i.e., validity effects) with higher *%CV*. Based on increasing evidence for a linear relationship between validity effects and *%CV* (Dombert et al., 2015), we report within-subject linear contrasts for the effects of *%CV*. To test for an effect of administration order of the spatial and feature task versions, we performed an additional analysis with *order of task administration* as between-subject factor. Equivalent analyses were performed on accuracy data (% correct responses), although, based on previous results, we expected most pronounced effects of probabilistic context on RTs. All results are reported at a significance level of $p<0.05$ after Greenhouse–Geisser correction.

In a second step, the effects of changes in %CV were modelled in terms of trial-wise Bayesian belief updating. Single-trial RTs were used to estimate parameters from a hierarchical, approximately Bayes-optimal learning scheme (Mathys et al., 2011). This model allows for a formal characterization of individual learning processes on the basis of recent cue-target outcomes in volatile environments. Hierarchically coupled Gaussian random walks enable a flexible control of updating of the beliefs about cue validity in each trial, in relation to beliefs about volatility and subject-specific parameters. As explained in previous work (Mathys et al., 2011; Vossel et al., 2014a; Vossel et al., 2014c), this computational model consists of a *perceptual model* that explains updating of beliefs based on (hidden) causes of experimental inputs (here: cue-target outcomes) and a *response model* that derives responses (i.e., RTs) based on these beliefs (see Fig. 2). Details about the derivation of the equations of the perceptual model are provided in Mathys et al. (2011). In what follows, we will describe the model parameters as relevant for the present study. The perceptual model comprises three states denoted by x (see Fig. 2).

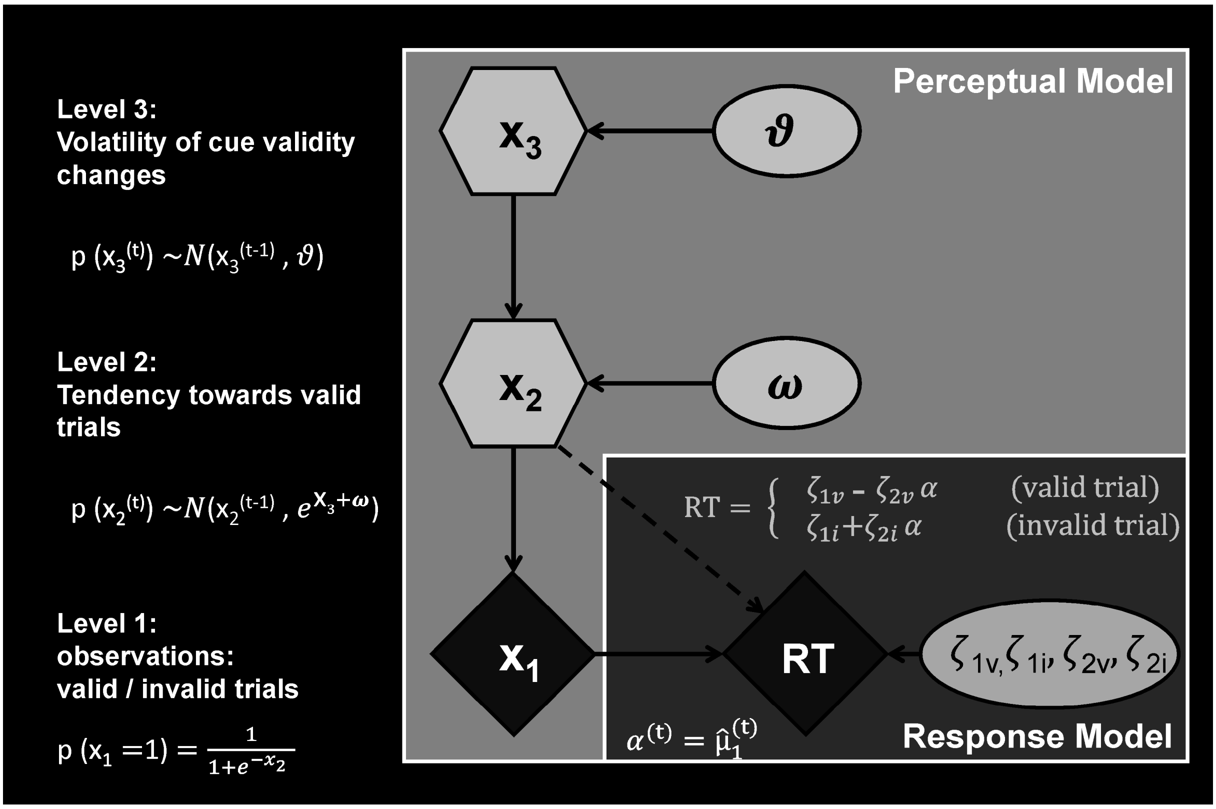

Figure 2. Illustration of the perceptual model and response model of the hierarchical Bayesian learning scheme

The perceptual model comprises a hierarchy of states x_1, x_2, and x_3. The model parameters ω and ϑ express how fast subjects update their beliefs about state x and are estimated from the individual subject's RTs. Circles represent constants, diamonds represent quantities that change in time, while hexagons represent quantities that change in time but additionally depend on their previous states in a Markovian fashion.

The state $x_1^{(t)}$ represents the environmental state of each trial, which, in the present paradigm, consisted of either a validly or invalidly cued target (with $x_1^{(t)}$= 1 for valid and $x_1^{(t)}$ = 0 for invalid trials). The probability distribution of $x_1^{(t)}$ = 1 is a Bernoulli distribution governed by a sigmoidal transformation of the next higher state $x_2^{(t)}$, which in turn changes over time as a Gaussian random walk. The volatility of $x_2^{(t)}$ (i.e., how fast $x_2^{(t)}$ changes after new observations) is determined by two quantities: $x_3^{(t)}$ (the state of the next upper level of the hierarchy) and a subject-specific updating parameter ω. The third state $x_3^{(t)}$ also changes as a Gaussian random walk, with the dispersion of the random walk being determined by a second subject-specific parameter ϑ. The values of the subject-specific parameters ω and ϑ were estimated from the individual RT data (see below).

To infer the probabilistic representations of the subject from environmental states, the perceptual model needs to be inverted; this yields the posterior densities of the three hidden states $x^{(t)}$. In the following, the sufficient statistics of the subject's posterior belief will be denoted by $\mu^{(t)}$ (mean) and $\sigma^{(t)}$ (variance) or $\pi^{(t)} = \frac{1}{\sigma^{(t)}}$ (precision). We use the hat symbol (^) to denote predictions before the observation of $x_1^{(t)}$ on a given trial t. As described in detail in Mathys et al. (2011), variational model inversion under a mean field approximation yields simple analytical update equations – where belief updating rests on precision-weighted prediction errors. These update equations provide approximately Bayes-optimal rules for the trial-by-trial updating of the beliefs. In this experiment, they provide us with the subject's estimate of the probability that the target appears at the cued location or in the cued color on a particular trial (note that this is an individualized approximate Bayes-optimality, in reference to the subject-specific values for the updating parameters ω and ϑ).

A response model was used to map the derived posterior beliefs to the observed RTs. In previous work using a saccadic response task with spatial cueing, RTs could most plausibly be explained by the trial-wise precision of the prediction at the first level of the perceptual model (Vossel et al., 2014a; Vossel et al., 2014c). However, since we employed a novel paradigm with manual responses in this study, we again compared the three alternative response models considered in the previous work. All models describe trial-wise RTs as a linear function of the attentional factor $\alpha^{(t)}$, which represents the proportion of total attentional resources that is allocated following the cue, as follows:

$$RT^{(t)} = \begin{cases} \zeta_{1v} - \zeta_{2v}\alpha^{(t)} & \text{for } x_1^{(t)}=1 \text{ (i.e., valid trial)} \\ \zeta_{1i} + \zeta_{2i}\alpha^{(t)} & \text{for } x_1^{(t)}=0 \text{ (i.e., invalid trial)} \end{cases}$$

Variational Bayesian estimation was used to derive the model parameters based on RTs, as implemented in the HGF toolbox (http://www.translationalneuromodeling.org/tapas/) running on MATLAB® (2012b, The MathWorks, Inc., Natick, Massachusetts, United States). The relative plausibility of the three models was compared using a random effects Bayesian model selection (Penny et al., 2010; Stephan, Penny, Daunizeau, Moran, & Friston, 2009). This analysis revealed that the model in which RTs were governed by the trial-wise probability estimate that the cue will be valid $\alpha^{(t)} = \hat{\mu}_1^{(t)}$ described the data most plausibly. In the following, this quantity will be termed probability-dependent attention.

FMRI data analysis

Main experiment

At the single-subject level, the spatial and feature task versions were included as separate sessions in a general linear model (GLM) of the BOLD responses. For each session, regressors of interest for left and right valid and invalid trials were defined at the individual subject level. Orienting and reorienting effects were investigated using two separate GLMs with event time locked to *cue* onset for *orienting*, and to *target* onset for *reorienting*, respectively. For each task regressor, probability-dependent attention $\hat{\mu}_1^{(t)}$ as derived from the single-subject computational modelling was included as parametric modulator. The volatility estimate from the third level of the model $\mu_3^{(t)}$ was additionally added to the design matrices. Error trials (anticipations, misses, and incorrect responses) and outliers (RTs above or below 2 standard deviations from the subject's mean) were discarded from the effects of interest and modelled separately (on average 13.5% of the feature trials and 12.5% of the spatial trials). Events were modelled using the canonical hemodynamic response function and its time derivative. Additionally, the rest period and twelve movement parameters of the (rigid body) realignment (6 motion parameters and their power of two, (Friston, Williams, Howard, Frackowiak, & Turner, 1996)) were included in the design matrices as nuisance regressors. The data were high-pass filtered at 1/128 Hz.

For the analysis of orienting and reorienting effects at the group level, and their modulation by probability-dependent attention $\hat{\mu}_1^{(t)}$, we combined a whole-brain with a region of interest (ROI)-based approach. In particular, we identified brain areas involved in orienting or reorienting in each task version by whole-brain contrasts in a second-level within-subject ANOVA (thresholded at $p<0.05$ family-wise error corrected at the cluster-level with a voxel-level cut-off of $p<0.001$). Subsequently, the parameter estimates from the peak voxels of these contrasts were extracted for each subject and tested for interaction effects with task version, as well as for condition-specific effects of the parametric modulator for probability-dependent attention $\hat{\mu}_1^{(t)}$. Note that the interaction and parametric effects are orthogonal to the contrast with which the regions were identified.

Orienting. We first identified brain regions related to attentional orienting in response to feature and spatial cues by contrasting both left and right valid trials against the implicit baseline by means of planned t-contrasts in a second-level within-subject ANOVA. Note that this contrast also captures the activity related to target detection and the motor response, since the present paradigm was not designed to separately investigate the cue and target phase. Still, this contrast allows for the identification of ROIs to compare spatial and feature-based orienting, and contralateral versus ipsilateral processing. To investigate topographical (i.e., lateralized) effects of attentional orienting, we extracted beta estimates for valid feature and valid spatial trials from the respective peaks of bilateral ROIs, and contrasted the locus of activation (hemisphere) with the locus of target presentation (ipsilateral vs. contralateral hemifield, cf. Egner et al., 2008) using 2 (*target hemifield:* ipsilateral, contralateral) × 2 (*cue type:* spatial, feature) within-subject ANOVAs. The same analysis was repeated for the parameter estimates of the parametric regressor for probability-dependent attention $\hat{\mu}_1^{(t)}$ to test whether the orienting response or its lateralisation is modulated by trial-wise beliefs about cue validity. Moreover, these analyses were performed for early visual areas identified by the functional localizer task.

Reorienting. In a second-level within-subject ANOVA, planned t-contrasts were used to test for enhanced activity for invalid as compared to valid trials in both attentional systems. Subsequently, we extracted the parameter estimates from the peak voxels of these contrasts and tested for interaction effects of *validity* (valid, invalid) and *cue type* (feature, spatial).

To test for a modulation of the activity in areas of the reorienting network by the trial-wise probability-dependent attention $\hat{\mu}_1^{(t)}$, beta estimates were extracted for this parametric regressor for valid and invalid trials for both task versions and tested with a 2 (*validity*: valid, invalid) × 2 (*cue type*: feature, spatial) within-subject second-level ANOVA. Note that here negative parametric effects of probability-dependent attention would be expected for valid trials (reflecting a decrease in activity with higher anticipated cue validity in a given trial), while positive parametric effects would be expected for invalid trials (reflecting an increased response to an invalid target when estimated cue validity in a given trial was high). To compare the present results with those reported by Vossel et al. (2015) from a location-cueing paradigm with saccadic responses, we additionally tested beta estimates from the peak activation foci from this previous study in the right FEF, putamen, and the right TPJ.

Brain regions were defined anatomically by using the SPM Anatomy Toolbox (Eickhoff et al., 2005) for those regions that have been cytoarchitectonically mapped, and the Automated Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002) for the remaining regions.

Functional localizer experiment

BOLD responses from the functional localizer task were analyzed using a GLM with separate regressors for each of the four checkerboard positions at the individual subject level. Blocks were defined time locked to visual stimulation onset and modelled with a duration of 16 secs using the canonical hemodynamic response function and its time derivative. Parameters of the (rigid body) realignment were included in the design matrix as nuisance regressors. High-pass band filtering at 1/128 Hz was applied to the images. Contrast images corresponding to the position of visual stimulation were created for each subject and analyzed using a within-subject second-level ANOVA with the factor position. Differential contrasts were calculated by testing one particular position against the remaining three positions. All contrasts were thresholded at $p<0.001$ at the voxel-level (uncorrected).

Results

Behavioral results

The 2 (*validity*: valid, invalid) × 3 (*%CV*: 50%, 70%, 90%) × 2 (*cue type*: feature, spatial) within-subject ANOVA on mean RTs revealed a significant main effect of validity ($F_{1,23}= 13.59$, $p<0.001$), reflecting faster RTs to validly than to invalidly cued targets (see Table 1). Moreover, we observed a significant *validity* × *%CV* interaction effect (linear contrast: $F_{1,23}= 20.94$, $p<0.0001$), indicating higher differences between valid and invalid trials with higher *%CV* (see Fig. 3A). There was no significant main effect of *cue type* ($F_{1,23}= 0.59$, $p=0.45$), i.e., the overall level of response times was similar for the spatial and feature task versions. Moreover, the interaction between *validity*, *%CV,* and *cue type* was not significant ($F_{1,23}= 0.66$, $p=0.43$), suggesting that in both attention systems RTs were equally susceptible to contextual variations of probability (experimentally manipulated changes in %CV). To additionally test for the effect of the order of task administration, the factor *order* entered the above ANOVA as a between-subject factor. There was neither a significant main effect of *order* nor an interaction of *order* with any of the experimental factors. Importantly, the interaction between *validity* and *%CV* remained significant.

Table 1. RT data. Average (± SEM) individual mean RTs for valid and invalid trials in the three %CV conditions for feature and spatial cueing.

		%CV		
Cue type	**Validity**	**50%**	**70%**	**90%**
Spatial	Valid	599.5 (±18.6)	600.5 (±18.1)	592.7 (±15.9)
	Invalid	612.6 (±18.4)	614.6 (±19.9)	621.5 (±17.2)
Feature	Valid	591.6 (±18.9)	595.9 (±19.7)	587.7 (±18.9)
	Invalid	605.7 (±19.1)	611.7 (±20.4)	628.2 (±17.4)

The equivalent ANOVA on accuracy, not considering outlier responses, revealed a significant main effect of *cue type* ($F_{1,23}$= 5.03, $p<0.05$), indicating overall higher accuracy in the spatial version than in the feature version (91.5+/-1.27% versus 89.8+/-1.48%). However, accuracy was not significantly affected by *validity* or *%CV* and there were no significant interaction effects among the factors and no interaction effects with *order*.

In a next step, trial-wise estimates of probability-dependent attention $\hat{\mu}_1^{(t)}$ were derived from our Bayesian model. These estimates are influenced by the subject-specific parameters governing the step size of the random walks at the second (ω) and third level (ϑ). Comparing these parameters between both task versions revealed no significant differences in any of the parameters. Also, the response model parameters $\zeta_{1\mathrm{v}}$, $\zeta_{1\mathrm{i}}$, and $\zeta_{2\mathrm{v}}$, $\zeta_{2\mathrm{i}}$, quantifying the absolute level of RTs and the strength of the dependency on $\hat{\mu}_1^{(t)}$, respectively, did not significantly differ between the two task versions. The subject-specific values for the updating parameter ω were significantly correlated between the two task versions (r= 0.44, p<0.05; see Fig. 3B). This indicates that updating behavior was similar for spatial and feature-based attention for a given subject. In other words, subjects who rapidly or slowly updated their belief about cue validity in one task also showed rapid or slow updating in the other task.

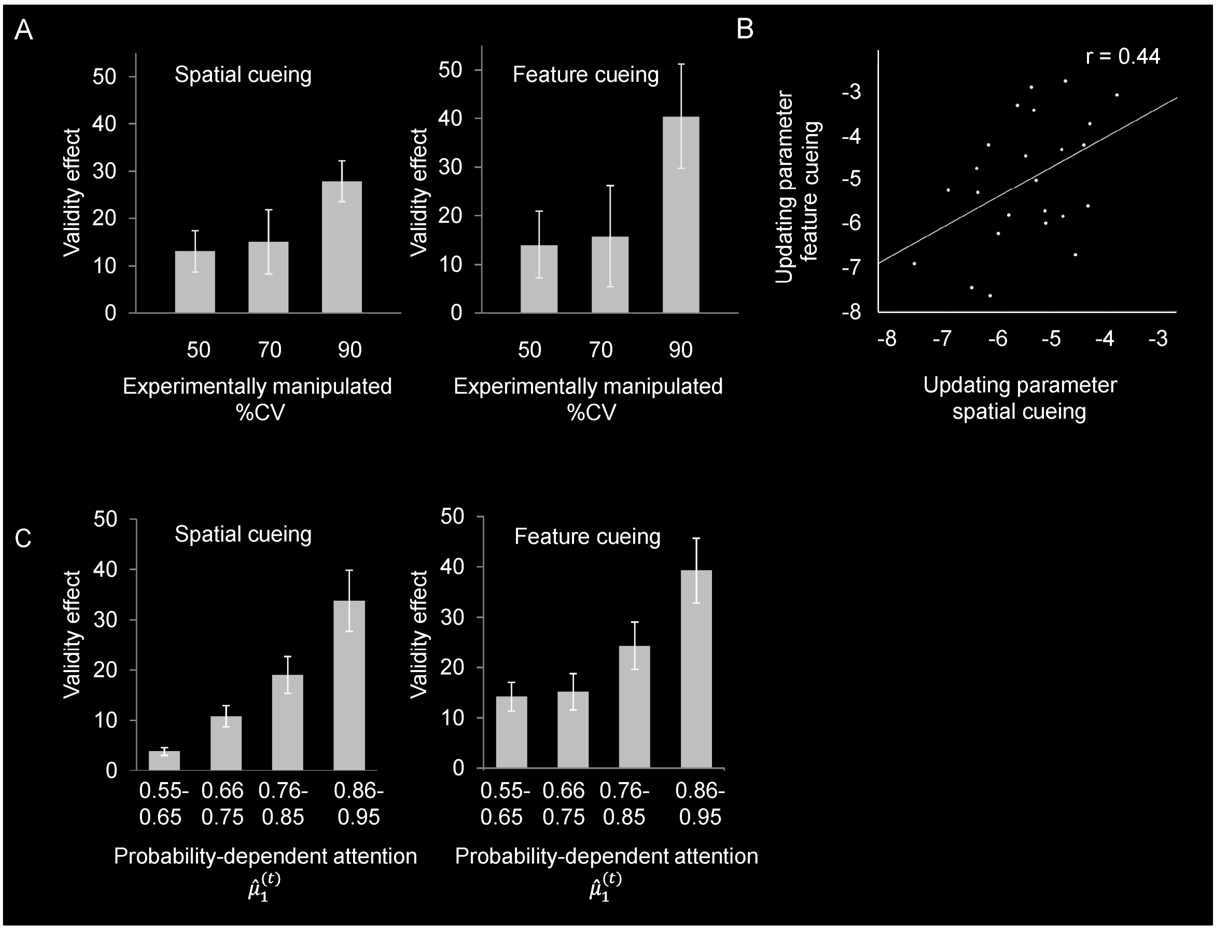

Figure 3 Behavioral results

A) RT costs after invalid cueing (validity effects) as a function of true (unknown) percentage of cue validity %CV, for spatial- and feature cueing, respectively. Mean RT costs and standard error of the mean are reported in milliseconds (ms).

B) Scatterplot of the subject-specific volatility estimates ω as derived from the Bayesian model in the spatial and feature-based task version.

C) Validity effects as a function of trial-wise probability-dependent attention $\hat{\mu}_1^{(t)}$, for spatial- and feature cueing, respectively. Mean RT costs and standard error of the mean (SEM) are reported in milliseconds (ms).

To illustrate the modulation of RTs by probability-dependent attention, $\hat{\mu}_1^{(t)}$ was calculated on the basis of the average parameter estimates over all subjects and RTs were binned in relation to $\hat{\mu}_1^{(t)}$ (bin$_1$: 0.55-0.65; bin$_2$: 0.66-0.75; bin$_3$: 0.76-0.85; bin$_4$: 0.86-0.95) for each version of the task (see Fig. 3C). A 2 × 4 × 2 repeated-measures ANOVA with the factors *validity* (valid, invalid), *probability-dependent attention* (0.55-0.65; 0.66-0.75; 0.76-0.85; 0.86-0.95), and *cue type* (feature, spatial) revealed a significant main effect of *validity* ($F_{1,23}$= 20.17, p <0.01), again indicating faster responses to validly than invalidly cued targets. There was a significant interaction of *validity* with *probability-dependent attention* (linear contrast: $F_{1,23}$= 4.68, p <0.05), indicating an increase in cueing effects with higher estimated probability that the cue will be valid. We did not observe any interaction of the factor *cue type* with *validity* or *trial-wise probability-dependent attention*, suggesting that Bayesian belief updating and its impact on RTs were comparable between both task versions.

Eye-movement data

Valid eye-movement recordings could be obtained in 10 subjects. In the remaining subjects, no reliable eye position data could be recorded due to technical problems within the MR environment. In these subjects, eye-movements were still monitored on-line on the camera image displayed on a video screen by the experimenter. Analysis of the eye movement data revealed that subjects maintained fixation in (mean +/- SEM) 87.5 ± 2.9% and 89.5 ± 2.4% of the time during the cue-target period and in 90.8 ± 2.4% and 92.6 ± 2.1% of the time during the target-response period of feature and spatial task trials, respectively. Mean fixation time did not differ between spatial and feature trials in the cue-target period (t_9=-0.9, p=0.39). The 2 (*validity*: valid, invalid) × 2 (*cue type*: spatial, feature) ANOVA of the eye movement data in the target-response period revealed neither a significant effect of *validity*, nor an interaction of *validity* with *cue type* (main effect *cue type*: $F_{1,10}$= 0.87, p=0.37; main effect *validity*: $F_{1,10}$= 0.001, p=0.98; interaction effect *validity* × *cue type*: $F_{1,10}$= 0.57, p=0.47).

fMRI results

Orienting. To identify brain areas involved in orienting of attention, valid trials were contrasted against the implicit baseline, separately for the two task versions (see Fig. 4A and Supplementary Table S1 for MNI-coordinates and cluster sizes). Spatial orienting was associated with enhanced activation in bilateral frontoparietal areas comprising the superior parietal lobe (SPL), intraparietal sulcus (IPS), superior frontal lobes, including an area located at the junction of superior frontal and precentral sulci that has been previously defined as the human equivalent of the frontal eye fields (FEF; Vernet, Quentin, Chanes, Mitsumasu, & Valero-Cabre, 2014), as well as the putamen, cerebellum, and occipital regions. Attentional orienting after feature cues enhanced activation in a similar network, comprising the SPL and IPS, superior frontal lobes, the FEF, the putamen, cerebellum, occipital cortex, and additionally the left frontal operculum.

To test for interaction effects between feature and spatial orienting, we contrasted valid feature with valid spatial trials. In line with Egner et al. (2008), this analysis identified no differential activations at the whole-brain level, suggesting a close overlap between both attentional orienting networks.

To further investigate potentially differential functional mechanisms of attentional orienting, topographical effects were compared between the two task versions by means of an ROI approach. Beta estimates were extracted from the peak voxels of bilateral SPL, IPS, and FEF and averaged with respect to locus of activation (hemisphere) and target hemifield (ipsilateral versus contralateral presentation of the target, cf. Egner et al. (2008)). Results from these analyses are depicted in Table 2 and Figure 4B.

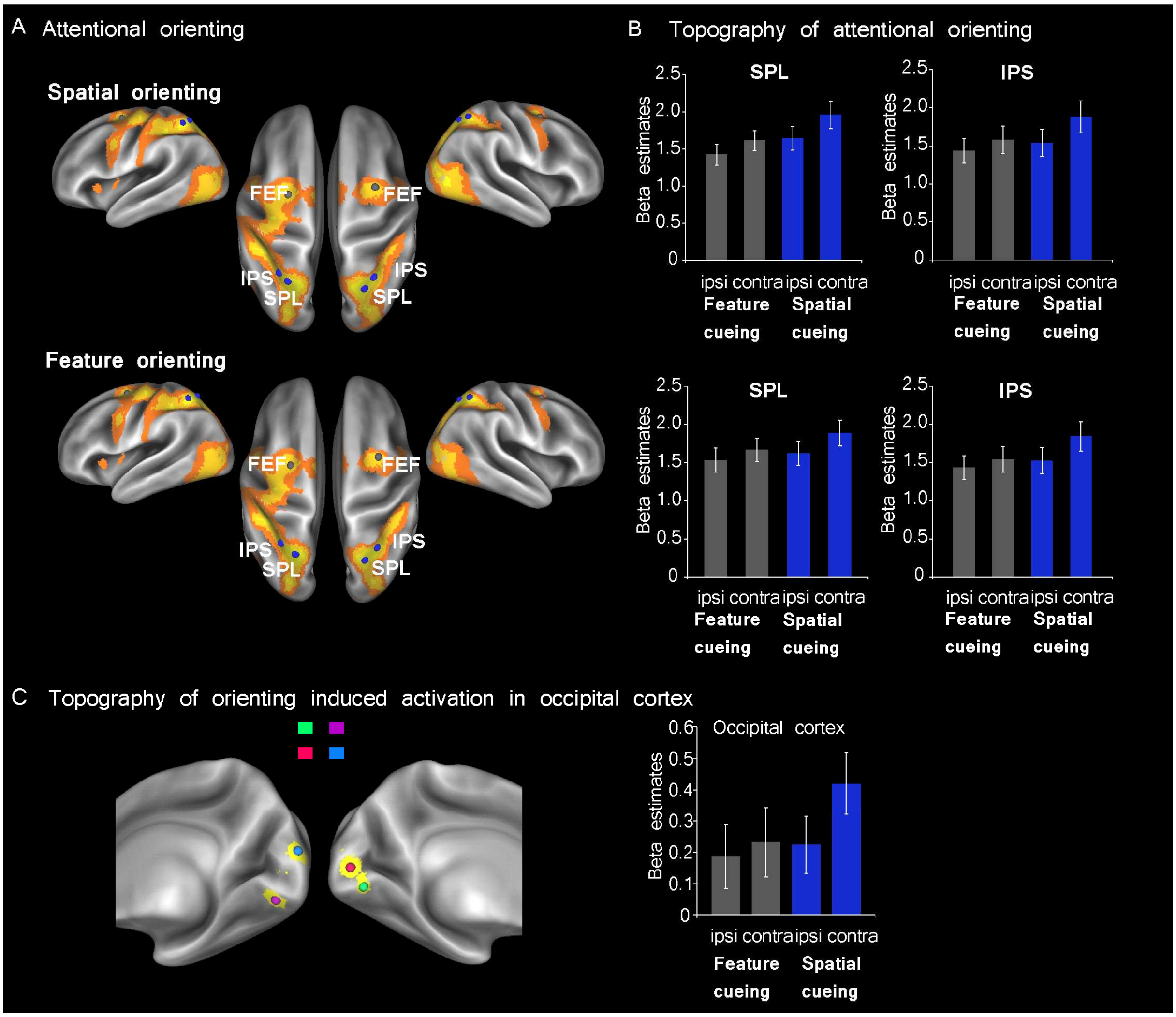

Figure 4 Attentional orienting

A) Results from the GLM analysis of valid trials for spatial cueing and feature cueing.

B) Topography of attentional orienting. Bar graphs depict mean beta estimates (and SEM) in the SPL and IPS, and occipital ROIs from the functional localizer (please see C). In all areas the lateralization of activity was more pronounced in the spatial task version.

C) Illustration of the peak activation foci (depicted with 8mm spheres) in occipital cortex as derived from the visual localizer task.

Table 2. fMRI data. Topography of orienting. Results of the *cue type* (spatial, feature) x *target hemifield* (ipsilateral, contralateral) ANOVA on the parameter estimates from the contrast of valid trials against the implicit baseline.

Region	Main effect cue type	Main effect target hemifield	Interaction effect cue type × target hemifield
Spatial orienting			
FEF/SFG	p=0.361	p=0.685	p=0.462
IPL/IPS (hIP3)	p=0.265	***p<0.001***	***p=0.001***
SPL (7A)	p=0.153	***p<0.001***	***p=0.025***
Feature orienting			
FEF/SFG	p=0.383	p=0.083	p=0.922
IPL/IPS (hIP3)	p=0.271	***p<0.001***	***p<0.001***
SPL (7A)	p=0.212	***p<0.001***	***p=0.029***
Visual localizer			
Lingual gyrus (hOc3v/hOc1)	p=0.321	***p<0.001***	***p=0.002***

Brain regions were defined anatomically using the Automated Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002) and the SPM Anatomy Toolbox (Eickhoff et al., 2005). Where available, labels of the cytoarchitectonic subregions from the Anatomy toolbox are provided in parentheses.
FEF: frontal eye fields, *SFG:* superior frontal gyrus, *SPL:* superior parietal lobe, *IPL:* inferior parietal lobe, *IPS:* intraparietal sulcus.

BOLD activity in the SPL and IPS was enhanced for targets in the contralateral hemifield, with this lateralization effect being more pronounced in the spatial than in the feature task version. The same significant *hemifield* × *cue type* interaction effects were observed for the early visual areas as identified by the functional localizer for the 4 target locations (see Fig. 4B (lower panel) and C; MNI-coordinates [16, -92, 14], [-10, -94, 4], [14, -82, -10], [-6, -84, -8]). No significant hemifield effects were observed in the FEF.

In a second step, we analyzed the effect of trial-wise probability-dependent attention on attentional orienting. Beta estimates from the parametric regressors for valid spatial and valid feature trials were not significantly different from zero and there was no effect of probability-dependent attention on the lateralization of activity within the orienting networks.

Reorienting. To characterize brain areas involved in attentional reorienting, we looked for brain regions showing enhanced activity during invalid as compared to valid trials in the two task versions (see Table 3 and Fig. 5).

Reorienting of spatial attention activated a bilateral frontoparietal network including the precuneus/SPL, bilateral inferior parietal lobe (IPL) as well as the right inferior frontal gyrus (IFG) and the FEF/SFG (see Fig. 5A). Reorienting after an invalid feature cue activated a cluster along the left IPS extending into the middle occipital gyrus (MOG) and IPL (see Fig. 5A). At the whole brain level, target hemifield modulated spatial reorienting activity in the IFG and occipital cortex of the right hemisphere, with higher activity in left compared to right spatial trials. No other significant effects of target hemifield were observed. Analysis of the beta estimates in the peak voxels of these contrasts (see Table 3 and Supplementary Fig. S3) revealed that all areas exhibiting reorienting-related activity in the spatial task version showed *validity* × *cue type* interaction effects with higher differences between invalid and valid trials for spatial than for feature-based reorienting. The cluster along the left parietal cortex activated by feature-based reorienting showed a main effect of *validity* across both tasks in the MOG and in the posterior subpeak of the IPS (cytoarchitectonic area hIP3 according to the Juelich atlas). In the anterior subpeak of the IPS (cytoarchitectonic area hIP1/hIP2 of the Juelich atlas) there was a significant *validity* × *cue type* interaction effect with higher reorienting-related activity for feature-based than for spatial reorienting.

Modulation of attentional reorienting by trial-wise probability-dependent attention $\hat{\mu}_1^{(t)}$ was investigated by means of *validity* × *cue type* within-subject ANOVAs on the beta estimates from the parametric regressors (see Table 3). This analysis revealed that the bilateral precuneus expressed a modulation of reorienting-related activity by probability-dependent attention only for spatial cueing (see Fig. 5B). We found no significant parametric effects in the remaining nodes in the IFG, SMG, and FEF, neither for spatial nor feature reorienting. In the left parietal cluster related to feature-based reorienting, there was a significant main effect of *validity* in the anterior subpeak of the IPS. There was no significant interaction with the factor *cue type*, suggesting an involvement in probability-dependent attention for both feature and spatial reorienting. Conversely, the more posterior subpeak of the cluster as well as the MOG expressed a significant interaction of *validity* and *cue type,* in that a differential modulation by probability-dependent attention in valid and invalid trials was only observed for spatial reorienting (see Fig. 5B). Previously, modulation of spatial reorienting by inferred probability has been observed in the right FEF [42, 4, 42], TPJ [46, -46, 6], and the putamen [22, 16, 4] when subjects responded with saccades to left and right targets (Vossel et al. 2015). We found a probability-dependent modulation of BOLD responses specifically for spatial reorienting in our paradigm in the right TPJ (interaction effect *validity* × *cue type*: $F_{1,23}= 5.45$, $p<0.05$). There were no probability-dependent effects for feature-based reorienting in any of these regions. For the multiple regions showing probability-dependent effects in the spatial version, a 2 (*validity*: valid/invalid) × 6 (*region:* left/right precuneus, left anterior/posterior IPS, left MOC, right TPJ) ANOVA revealed no significant interaction between the two factors, indicating that the effects of probability-dependent attention were not significantly different in the different regions ($F_{1,3.5}= 0.27$, $p=0.93$).

Table 3. fMRI data. Reorienting and its modulation by probability-dependent attention. Results of the *cue type* (spatial, feature) x *validity* (valid, invalid) ANOVA on the parameter estimates from the contrast of invalid versus valid trials for the main HRF regressor and the parametric regressor for probability-dependent attention $\hat{\mu}_1^{(t)}$.

		MNI Coordinates					**HRF regressor**		**Parametric regressor $\hat{\mu}_1^{(t)}$**	
Region	**Side**	**x**	**y**	**z**	**Voxels**	**z-score**	**validity effect**	**validity × cue type**	**validity effect**	**validity × cue type**
Spatial reorienting: invalid > valid										
FEF/SFG	R	24	6	56	294	4.19	***p=0.002***	***p=0.031***	p=0.418	p=0.340
IFG	R	38	18	20	219	4.10	***p<0.001***	***p=0.038***	p=0.132	p=0.170
IPL (PFt)	L	-58	-20	34	251	4.29	***p=0.003***	***p=0.003***	p=0.633	p=0.754
Precuneus/ SPL (5L/5M)	R	10	-52	58	3260	4.80	***p<0.001***	***p=0.012***	p=0.390	***p=0.010***
Precuneus	L	-10	-60	58	*s.c.*	4.62	***p<0.001***	***p=0.033***	p=0.425	***p=0.014***
IPL (PFt)	R	60	-20	34	*s.c.*	4.52	***p=0.003***	***p=0.006***	p=0.538	p=0.430
Feature reorienting: invalid > valid										
IPS (hIP3)	L	-26	-62	36	439	4.10	***p<0.001***	p=0.161	p=0.218	***p=0.050***
IPS (hIP1/hIP2)	L	-32	-42	34	*s.c.*	3.59	***p=0.001***	***p=0.028***	***p=0.049***	p=0.304
MOG	L	-28	-72	26	*s.c.*	3.92	***p<0.001***	p=0.244	p=0.951	***p=0.028***

s.c.: same contiguous cluster. Brain regions were defined anatomically using the Automated Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002) and the SPM Anatomy Toolbox (Eickhoff et al., 2005). Where available, labels of the cytoarchitectonic subregions from the Anatomy toolbox are provided in parentheses. *FEF:* frontal eye fields, *SFG:* superior frontal gyrus, *SPL:* superior parietal lobe, *IPL:* inferior parietal lobe, *IPS:* intraparietal sulcus.

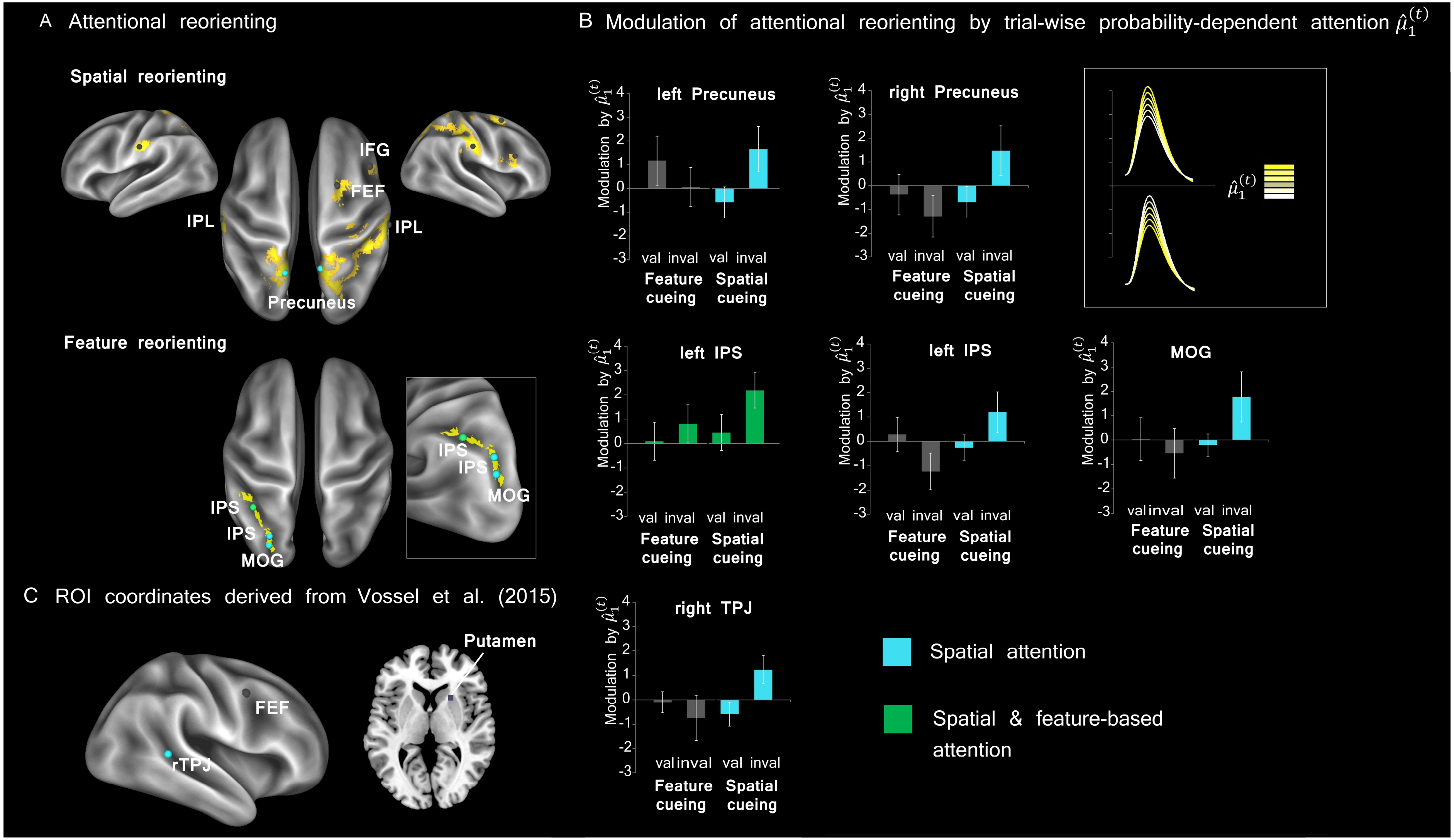

Figure 5 Attentional reorienting

Figure 5 Attentional reorienting

A) Results from the GLM analysis of reorienting networks as revealed by a t-contrast for invalid>valid trials for spatial cueing and feature cueing and illustration of the ROIs for the analysis of probability-dependent effects. Brain regions in which the ROI analysis did not reveal any significant effects are shown with *grey* spheres. *Green* spheres denote brain regions with a significant probability-dependent modulation by $\hat{\mu}_1^{(t)}$of spatial- and feature reorienting. *Light blue* colour refers to brain regions that displayed a probability-dependent modulation of spatial reorienting only.

B) Bar graphs depict mean beta estimates (and SEM) for the parametric regressors of probability-dependent estimates for valid and invalid trials in regions with significant effects. The illustration in the right box shows the effect of positive and negative beta estimates of the parametric modulation with $\hat{\mu}_1^{(t)}$ on BOLD amplitudes. While positive beta estimates reflect higher BOLD amplitudes with higher estimated cue validity, negative beta estimates indicate smaller BOLD amplitudes with higher values of $\hat{\mu}_1^{(t)}$.

Discussion

The present study combined computational modelling of response times with fMRI to characterize the functional correlates of attentional orienting, reorienting, and their modulation by probabilistic inference in spatial and feature-based attention systems in the human brain. The novel aspect of the present study with regard to previous work was to consider not only average condition-specific effects, but to investigate trial-by-trial effects of Bayesian probabilistic inference about the most likely cue-target outcome as a critical factor influencing performance and BOLD activity in the brain regions underlying the processes involved. Manual response times in two probabilistic cueing task versions were affected by unsignalled changes in the validity of a cue that indicated either the location or the color of a target stimulus. The analysis of the functional correlates of attentional orienting replicated previous results. Reorienting attention in invalid trials activated the precuneus, bilateral IPL, as well as right inferior and superior frontal gyri in the spatial attention task, while feature-based reorienting enhanced activity along the left IPS. While orienting-related activity was not modulated by probability-dependent attention as derived from our computational model, a probability-dependent modulation of reorienting-related activity was observed in the bilateral precuneus, the left IPS, MOG, and the right TPJ in the spatial domain. A modulation of feature-based and spatial reorienting by probability-dependent attention was observed in the anterior part of the left IPS.

Behaviour

Our modified paradigm was designed to directly compare the processing of valid and invalid a priori spatial and feature-based information. Behaviorally, there were no RT differences between the two task versions, neither in the absolute level of RTs, nor in their modulation by valid/invalid cues and true or inferred probabilistic context. Most interestingly, the subject-specific parameter ω of the Bayesian model - which quantifies the magnitude of trial-by-trial changes in the belief that the cue will be valid - was significantly correlated between both task versions. This finding points to overlaps of the mechanisms for the trial-wise inference about cue validity in both systems. While the characterization of inter-individual differences merits further investigation, the present study focused on the within-subject comparison of spatial and feature-based attentional mechanisms and their modulation by inferred cue validity. The identification of a region exhibiting probability-dependent effects in both domains in the left IPS (please see discussion below) fits well with the correlation of the updating parameters at the behavioral level.

Probability-independent BOLD effects in spatial and feature-based systems

For the orienting systems, our fMRI results of the average (probability-independent) activity are in line with previous research that has identified a common network for preparatory spatial and feature-based attention (Egner et al., 2008; Giesbrecht et al., 2003; Liu et al., 2003; Slagter et al., 2007; Vandenberghe et al., 2001b). We also replicated existing work by Egner et al. (2008) showing a directional modulation of BOLD activity in contralateral SPL, IPS, and visual areas (but not FEF) during spatial- but not feature orienting.

While dorsal frontoparietal regions were recruited regardless of whether attention was biased to location or color, the re-calibration of these attentional weights (i.e., reorienting) involved differential activation patterns (despite no significant differences in RT costs at the behavioral level). For spatial reorienting, activity was enhanced in dorsal areas such as the SPL and FEF, as well as in more ventral regions in the bilateral IPL and the right IFG (Corbetta et al., 2008; Corbetta & Shulman, 2011). Such co-activation of dorsal and ventral frontoparietal regions after spatial reorienting has been described before and potentially reflects interaction of both systems to establish flexible attentional control (for a review see, e.g., Vossel et al., 2014b). Interestingly, however, these regions exhibited validity × cue type interaction effects, i.e., they responded more strongly to spatially invalid targets. In contrast, a region in the anterior part of the left IPS showed the reverse effect, with stronger reorienting effects when color was invalidly cued. These findings - together with the results for probability-dependent attention described below - argue against the idea of a universal right-hemispheric ventral ‘circuit-breaking’ system (Corbetta & Shulman, 2002). They rather suggest that depending on the type of expectancy violation or type of task, different subsystems may be engaged with the same behavioral outcome.

The involvement of left rather than right-hemispheric brain regions for feature reorienting resonates with previous studies that reported enhanced left parietal and frontal activations during non-spatial attention shifts of the relevant feature dimension (Weidner et al., 2009; Weidner, Pollmann, Muller, & von Cramon, 2002). Also, the left IPS has been shown to transiently activate when attention needs to be shifted between color and motion (Liu et al., 2003), and more so, distinct patterns of BOLD activity in the left and right IPS could differentiate between attending to one of these two feature dimensions (Liu et al., 2011).

Modulations of BOLD-activity by probability-dependent attention in spatial and feature-based systems

Orienting

The main focus of this study was to investigate how BOLD amplitudes in valid and invalid trials are modulated by trial-wise probability estimates of cue validity for the two cue types as derived from our Bayesian model. As in a previous study on saccadic responses (Vossel et al., 2015), we did not observe a significant modulation of orienting-related activity (or its lateralization) by trial-wise probability-dependent attention. From a conceptual point of view, one could have expected a stronger modulation of cortical responses by high expectations that the cue will be valid, and Egner et al. (2008) demonstrated parametric effects of different %CV-levels in the orienting networks. However, important differences in the task design between this and our study may explain this discrepancy. First, the subjects in Egner et al. (2008) were explicitly informed about the cue-target contingencies. They were hence not required to infer cue validity on a trial-wise basis and were less uncertain about the probabilistic context than the subjects who participated in our study. Second, the task design aimed at characterizing cue-related activity and accordingly used longer and variable cue-target SOAs (jittered between 4-8 secs, as opposed to 1 sec in the present study). In contrast, with short and constant SOAs as in the present study, the signal may be predominantly driven by target-related responses so that the paradigm may be more suited to detect differences between invalidly and validly cued targets, which was also of main interest here. Our finding of a stronger probability-dependent modulation of BOLD responses in invalid than valid trials is consistent with previous data, which suggest that variation of cue probability has higher effects on attentional reorienting costs than on attentional orienting benefits in a spatial attention task (Lasaponara, Chica, Lecce, Lupianez, & Doricchi, 2011).

Reorienting

A modulation of reorienting-related activity by probability-dependent attention $\hat{\mu}_1^{(t)}$ in the spatial task version was observed in the bilateral precuneus, left IPS and MOG, as well as the right TPJ. Beta estimates of the parametric regressor were positive for invalid trials, reflecting increased BOLD responses with higher expected probability that the cue will be valid. In valid trials, the beta estimates were around zero or negative, reflecting either no modulation, or decreased activity with higher values of probability-dependent attention $\hat{\mu}_1^{(t)}$. This pattern is in line with the predictive coding perspective, since it reflects higher reorienting-related activity with increased unexpectedness of the target location or an attention shift, respectively.

Activation in the bilateral precuneus extended into the medial part of the SPL, a region that has often been implicated in spatial attention shifts (Brignani, Lepsien, Rushworth, & Nobre, 2009; Molenberghs, Mesulam, Peeters, & Vandenberghe, 2007; Vandenberghe et al., 2001b; Vandenberghe, Molenberghs, & Gillebert, 2012; Yantis et al., 2002). Activity in these regions has been shown to scale with the spatial extent of the attentional shift (Vandenberghe, Gitelman, Parrish, & Mesulam, 2001a), irrespective of shifting direction and visual hemifield (Brignani et al., 2009; Capotosto, Corbetta, Romani, & Babiloni, 2012). Our data suggest that BOLD activity in these regions does not only scale with the spatial extent, but also with the unexpectedness of the attentional shift. Unexpectedness also modulated reorienting-related activity in the right TPJ. These parametric effects may weaken the average differences between invalid and valid trials; so that TPJ activity was not significant at the whole-brain level in the global reorienting contrast. Our finding is consistent with previous studies that have reported a modulation of the right TPJ response by explicit and also by inferred cue-target contingencies (Vossel et al., 2015; Vossel et al., 2006; Vossel et al., 2012). The present study extends these previous results and suggests the right TPJ may be particularly sensitive to violations of spatial expectancies, as probability-dependent effects were confined to the spatial attention system in the employed paradigm. This interpretation may help to explain observations from patients with right-hemispheric brain damage who show disrupted repetition priming for spatial locations, but not for features (Shaqiri & Anderson, 2012, 2013): It could be speculated that the left-hemispheric regions in the present study receive their input from right TPJ in the spatial task, while feature-based reorienting and its probability-dependent modulation is predominantly mediated by left parietal structures.

The left IPS exhibited significant probability-dependent effects in the current study. Interestingly, neurophysiological studies linked neurons in the lateral intraparietal area to evidence accumulation during perceptual decision making (for a review see, e.g., Gold & Shadlen, 2007) since the neuronal firing rates followed predictions from diffusion/race models. In other words, these neurons show a steeper increase in firing rates with less uncertainty (i.e., faster perceptual convergence) and a more prolonged response with higher uncertainty. With regard to our paradigm, one could therefore assume faster and more transient responses to more expected stimuli (less uncertainty) and slower and prolonged responses to unexpected stimuli (higher uncertainty), which may lead to the observed probability-dependent effects on BOLD-amplitudes.

Depending on the subregion along the intraparietal sulcus, the probability dependent effects were observed for the spatial or both task versions. A common effect was observed in the hIP1/hIP2 subdivision (see Choi et al., 2006; Scheperjans et al., 2008 for the definition of the parietal subdivisons). The three cytoarchitectonically distinct subdivisions hIP1 to hIP3 are characterized by distinct functional and structural connectivity profiles (Bray, Arnold, Iaria, & MacQueen, 2013; Szczepanski, Pinsk, Douglas, Kastner, & Saalmann, 2013; Uddin et al., 2010). The more anterior (hIP1/2) subdivisions are structurally and functionally connected with frontal regions comprising prefrontal cortex, inferior frontal and middle frontal gyri, while the posterior IPS (hIP3) seems to preferentially connect with visual cortices (Bray et al., 2013; Lauritzen, D'Esposito, Heeger, & Silver, 2009; Uddin et al., 2010). This divergence between the roles of the anterior and posterior IPS is consistent with our observation. Due to its connectivity with topographically organized visual cortices, the posterior parietal cortex might be especially relevant when probabilistic information about the location of a visual stimulus is processed. On the contrary, the anterior IPS plays a central role in the integration of multisensory information (Grefkes & Fink, 2005; Grefkes, Weiss, Zilles, & Fink, 2002) and as it displayed probability-dependent effects in the spatial and the feature-based task, one could speculate that this role is not confined to different sensory modalities, but extends to distinct visual domains.

In conclusion, our findings provide novel insights into the generality and specificity of the functional and computational mechanisms underlying the flexible control in different attention subsystems. The present results can be interpreted in the context of contemporary theories proposing that the brain maintains probabilistic models of the world to minimize surprise about sensory inputs (see e.g., Friston, 2009, 2010b) and shed light on the physiological implementation of these processes by showing links - but also peculiarities - of two different attentional systems. Our data, together with the findings from Vossel et al.

(2015), suggest that probabilistic inference can distinctively affect different attentional subsystems, but that there is a potential link between the spatial and feature-based attentional system in the left anterior IPS. As such, this region may contribute to the significant correlation of the parameters governing probabilistic inference in the two attentional domains.

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3. General discussion section

Attention influences visual perception substantially by enhancing the processing of specific environmental aspects that are expected to be most relevant in a given context. While most research investigated spatial attention as a prototype for attentional systems, little is known about other types of attention such as feature-based attention. Yet, it is important to understand whether visual attention relies on a unitary neural system that directs attention irrespective of the selected aspect (e.g. space or features) or whether there are different subsystems that are specialized for specific aspects.

It is well known that expectancies about statistical regularities in the environment influence attentional selection processes. In everyday life these expectancies need to be formed based on probabilistic inference and this process most likely follows Bayesian principles. It remains to be established whether probabilistic inference is performed in distinct brain regions for different types of visual attention, or whether there is a common and domain general system for visual attention that computes predictions based on experiences. The present thesis investigated these questions by means of a psychophysical and a functional neuroimaging experiment. The following section will discuss the obtained results in light of the current literature and in relation to a third experiment that was conducted as a coauthor (Mengotti, Dombert, Fink, & Vossel, 2017).

3.1 Experiment 1

The influence of cue-related factors on feature-based attention and the effect of probabilistic inference

Two questions were addressed in Experiment 1. First, it aimed at investigating cue-related factors that influence how prior information about a target feature is used to direct attention. Second, it was performed to investigate whether feature cues can elicit probability-dependent effects on attention to establish an experimental paradigm for Experiment 2, in which feature and spatial cues were to be compared. For this purpose, three different color cues were used in an adapted version of the Posner cueing task with blockwise changes in probabilistic context, i.e. the percentage of cue validity (%CV). The color cues differed in their perceptual properties allowing for different levels of cue abstraction with color being presented either perceptually, as a written word or as a two-letter abbreviation of the color word. It was observed that all color cues produced similar validity effects. However, the effect of probabilistic context on validity effects differed between the three color cues and this differential effect depended on the time on task: The type of color cue affected how much time was required to adapt attentional deployment to changes in the percentage of cue validity. The probability-dependent effects on attention were initially present in the two-letter cue condition, and only emerged over the course of the experiment in the perceptual and word cue condition. This indicates that experience-based learning of statistical regularities in the environment greatly depends on the properties of the provided feature cues.

Regarding the first research question, our findings contribute to the ongoing discussion about how different types of feature cues are effective in biasing attention. It has been claimed that feature-based attention requires perceptual priming of color-sensitive neurons, meaning that bottom-up priming is needed to engage attention (Theeuwes, 2013; Theeuwes & Van der Burg, 2007). Nevertheless, others have proposed that, similar to spatial cues, mere feature-based information can also be used to direct attention (Ansorge & Becker, 2012; Muller et al., 2010; Rangelov, Muller, & Zehetleitner, 2011b; Soto et al., 2012).

Since we could demonstrate that perceptual as well as word and abstract (i.e., two-letter abbreviation) cue information can affect attentional deployment per se, perceptual priming cannot be the *only* mechanism causing feature-based attention effects.

We assume that processing of perceptual cues and word cues was automatic and evoked less cognitive effort to be encoded than abstract cues. This is suggested by findings from Stroop paradigms that have shown that word cues require fewer processing demands than abstract cues whose meaning is less intuitive (Brown et al., 2002; Ferrand & Augustinova, 2014; MacLeod, 1991; Neely et al., 1998). By comparing cueing effects between word and abstract cues, we could also elucidate the effect of cognitive effort on feature-based attention. Since there was *no* difference in (*probability-independent)* validity effects averaged over all trials, feature-based attention appears to be engaged via mechanisms that encode feature-based information independent from the level of cue abstraction. As we employed purely behavioral methods in Experiment 1, we cannot draw any conclusions on the neural mechanisms underlying these common effects. Moreover, despite similar behavioral effects, perceptual color cues might have engaged visual neurons mostly via (perceptual) mechanisms that are different from the neural mechanisms of word and abstract cues. This could indeed be the case because, although all cues engaged feature-based attention, we identified differences in *probability-dependent* effects on attentional deployment between cue types.

We observed that probability-dependent effects on attention in response to perceptual and word cues required more time-on-task as compared to abstract cues. In terms of the predictive coding framework, this reflects that with intuitive cue types trial-by-trial probabilistic inference required more observations of cue-target outcomes to establish changes in probabilistic estimates. A potential explanation is that the brain has acquired stronger (prior) probability estimates for well-recognized cues that need more time to adapt, while representations of newly learned cues can be updated faster and more flexibly. Since probability-dependent effects were observed with constant sensory inputs, they are assumed to reflect top-down attentional processes. Some authors differentiate between goal-directed factors and trial history effects (e.g., Awh, Belopolsky, & Theeuwes, 2012). However, in our present paradigm, goal-direction and trial history are two sides of the same coin: Trial history effects are related to the current goals as well as to probabilistic inference and the probability-dependent effects are essential for the current task. The finding that top-down attentional mechanisms depend on the perceptual qualities of the cues that are used to convey feature-based information has crucial implication for the study of feature-based attention and in particular for the comparison with spatial attention. Typically, spatial cueing paradigms involve symbolic cues consisting of central arrows that point to the left or right side in space. For feature-based paradigms there is less consistency in the cues used. While some studies provided perceptual color cues (Vandenberghe et al., 2001b), others used color word abbreviations (Giesbrecht et al., 2003). Our results suggest that heterogeneous findings from neuroimaging studies comparing attentional mechanisms between feature-based and spatial systems might be triggered by dissimilar color cues that were used to manipulate feature-based attention. Therefore, these findings from Experiment 1 were essential for the preparation of Experiment 2 that directly compared the neural correlates of spatial and feature-based cueing and their probability-dependent modulation.

3.1.1 Limitations

There are some limitations to Experiment 1 that will be discussed in the following section. First, we employed a between-subject design for the comparison of the different feature cues. Differences associated with the different individuals in the three groups might have confounded group comparisons. While an additional analysis including age, gender, and BIS-11 impulsivity subscale scores as covariates revealed that these known variables did not explain the reported results, we cannot rule out that there were other unknown variables, which might have contributed to the observed effects. Second, although only feature-based information was relevant in Experiment 1, we employed a search task that also contained a spatial component. This is because it was designed to establish the task paradigm for Experiment 2 that aimed at comparing feature and spatial cueing effects. However, this spatial component was present in invalid as well as valid trials, since in each trial two stimuli in the cued color (one in each hemifield) were provided. Therefore, any effects of spatial search should cancel out in the differential comparison of RT between invalid and valid trials. Moreover, differential feature cue effects should not contain effects of spatial search because they were present in all types of feature cues. Still, to exclude any spatial component in feature-based paradigms, one could use target stimuli that are presented superimposed to each other at a single location. Third, we used identical cue-target intervals for the three cue versions even though abstract cues might have involved a different time courses of attentional deployment than the automatic cues. We did, however, not find any effect of feature cue type on RTs or accuracy. This speaks against systematic differences in the time needed to deploy attention. It is however possible, that different cue-target intervals might have increased or decreased the reported effects. Finally, it would have been of great interest to investigate trial-by-trial learning for the different cue types using the computational modeling approach that was applied in Experiment 2. More precisely, comparing trial-by-trial learning parameters derived from the hierarchical Bayesian learning scheme between the first and second half of the experiment would have provided valuable information about the effect of time-on-task on individual updating behavior. However, in order to reliably estimate these model parameters separately for the two halves of the experiment, one would need to include a higher number of trials than provided in the present task paradigm.

3.2 Experiment 2:

A systematic comparison of the functional mechanisms of probabilistic inference of feature-based and spatial attentional deployment

Three main issues were addressed in Experiment 2. First, the neural mechanisms of feature-based attentional deployment were investigated with special emphasis on the neural system that engages during reorienting of feature-based attention after invalid cues. Second, we investigated probabilistic inference as a critical factor that influences behavioral performance, and compared whether it similarly affects spatial and feature-based attentional deployment. Third, Experiment 2 aimed at defining how probability-dependent modulation of attention is implemented in the brain to elucidate whether these implementations are domain general or whether they are domain specific with differential neural correlates for the two systems.

In order to investigate these questions, a combination of computational modeling of RTs and fMRI was applied to two different versions of the probabilistic cueing task that was introduced in Experiment 1. One version contained spatial cues and the other version contained feature cues. For the feature cues, abstract color cues consisting of two-letter abbreviations of the color word were presented. These have been found to produce immediate probability-dependent attention effects in Experiment 1.

The results of Experiment 2 showed that unsignalled changes in the percentage of cue validity similarly affected RTs in the two task versions with higher validity effects when there was a higher probability of the cue to be correct. No behavioral differences between spatial and feature cues were found. The following section will first discuss the neural results for *probability-independent* attentional deployment for the two task versions. The subsequent section will then consider the results from the computational modeling of RTs and the functional correlates of *probability-dependent* attention.

3.2.1 Probability-independent attention in feature-based and spatial systems

In line with previous findings, orienting of attention after valid cues engaged a *common* frontoparietal network for feature-based and spatial attention, indicating that similar neural systems are involved in both types of attention (Egner et al., 2008; Giesbrecht et al., 2003). However, when further exploring the neural mechanisms for both orienting systems, we found directional modulation of BOLD responses in contralateral SPL, IPS and visual areas during spatial but not feature-based orienting. These results suggest that despite similar brain structures, there are differential neural mechanisms for orienting of attention to features and orienting of attention to locations. Still, the main focus of the present work was to identify the neural systems that engage during reorienting of feature-based attention in comparison to the well-known spatial reorienting system. Feature-based reorienting engaged a cluster in the left hemisphere located along the IPS. On the other hand, spatial reorienting activated bilateral IPS, the precuneus, as well as right inferior and superior frontal gyri. Subsequent ROI analyses revealed stronger responses to spatially invalid trials within these areas, whereas the reversed pattern was observed for the anterior part of the IPS with stronger responses when color was invalidly cued. This indicates that despite similar behavioral effects, i.e., similar RT costs, the neural systems involved in feature-based reorienting and spatial reorienting differ substantially. The involvement of left rather than right lateralized network for feature-based reorienting is consistent with previous work that reported enhanced activity during shifting *between feature dimensions* in left parietal regions including IPS (Liu et al., 2003; Weidner et al., 2009). Our novel findings reveal that the left IPS also responds during reorienting *within a feature dimension* (see Fig. 5). Moreover, the finding that the anterior part of the IPS responds more strongly to feature-based as compared to spatial reorienting indicates considerable domain specificity in the neural basis of feature-based attention. To accomplish a more comprehensive picture of feature-based mechanisms it would be interesting to investigate whether the different color cues from Experiment 1 activate the same neural system, or whether depending on their different levels of processing, distinct reorienting systems respond to the different types of invalid color cues. Furthermore, future studies should explore whether the reported findings for the color dimension also extent to other feature dimensions such as motion.

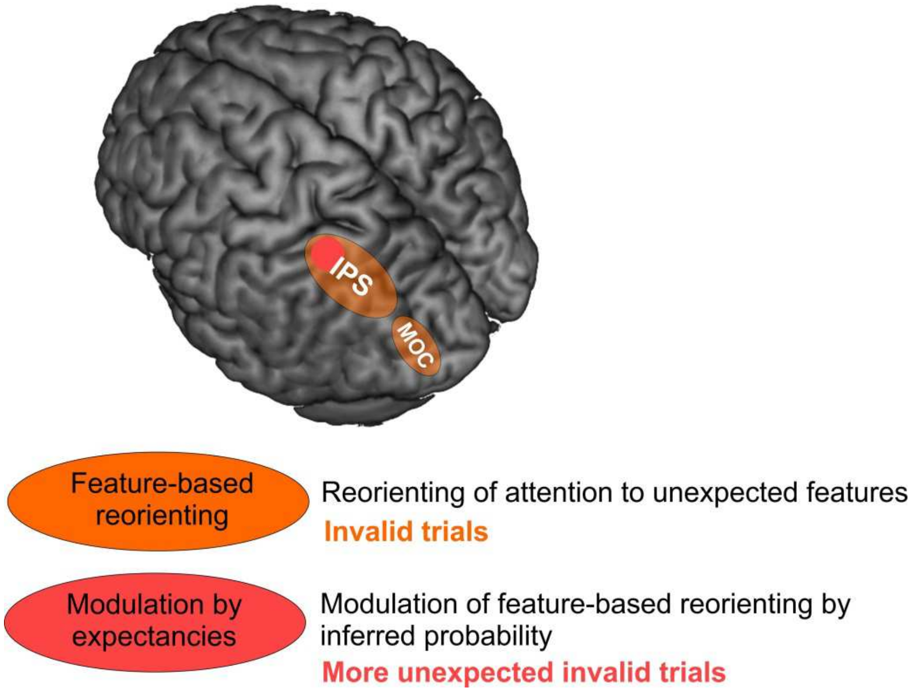

Figure 5 Feature-based reorienting network.

3.2.2 Probability-dependent attention in feature-based and spatial systems

Behaviorally there were no RT differences between feature and spatial systems neither in the absolute level of RTs nor in their modulation by probability-dependent attention. This indicates that probabilistic inference follows similar principles for both feature-based and space-based visual attention. Importantly, the subject-specific individual learning parameter ω, which quantifies the susceptibility to updating trial-by-trial estimates about cue validity, was significantly correlated between both task versions. This finding points to overlapping mechanisms for probabilistic inference between both attentional systems. Moreover, it shows that there are considerable inter-individual differences that persist across visual attention domains (i.e., higher ω in task version A predicts higher ω in task version B, and vice versa). This finding of consistent inter-individual differences is not trivial. Understanding which characteristics determine behavior under uncertainty could be crucial to comprehend essential aspects of brain function and disease (see Fig.6). For example, individual differences in probabilistic learning may be explained by variability in basic physiological mechanisms (Thiel, Huston, & Schwarting, 1998), which may also affect behavioral traits that are comorbid with maladaptive behavior (e.g., compulsive behavior). For the spatial attention system, it has been shown that subject-specific updating profiles can be modulated by cholinergic pharmacological intervention (Vossel, Bauer, et al., 2014), so that it is possible that genetic variations affecting cholinergic neurotransmission are linked to individual differences in probabilistic learning.

Moreover, computational modeling approaches offer a unique way to infer mechanisms that generate behavioral malfunctions in neurological or psychiatric patients. This is especially relevant for spectrum diseases that require differential diagnosis and individual treatment plans. Computational modelling has for instance been applied in patients suffering from schizophrenia (Moutoussis, Bentall, El-Deredy, & Dayan, 2011; Stephan, Baldeweg, & Friston, 2006). Here, it has been suggested that impaired probabilistic inference may prompt erroneous beliefs, which induce aberrant attribution of salience to irrelevant events ("aberrant salience"; Jardri & Deneve, 2013) and the formation of delusions (see Stephan & Mathys, 2014 for a review). Similarly, there is evidence that autism spectrum disorder patients display overly low precision of predictions about sensory inputs, which causes predominantly detail-driven perception and difficulties in extracting the global meaning of environmental information (see Haker, Schneebeli, & Stephan, 2016 for a review). The extent to which “computational profiles” deviate from the healthy population could be used as indicator of disease severity and diagnoses in individual patients (see Stephan, Iglesias, Heinzle, & Diaconescu, 2015 for a review).

An example for the domain of attention would be potentially impaired expectancy formation in stroke-induced (spatial) neglect syndrome (Shaqiri & Anderson, 2012, 2013). Here, applying our computational model could provide a useful tool to formally describe impaired behavior of spatial neglect patients and to identify the selectivity of their impairment with respect to other attention systems. Moreover, our method may be more sensitive to assess rehabilitation status following treatment.

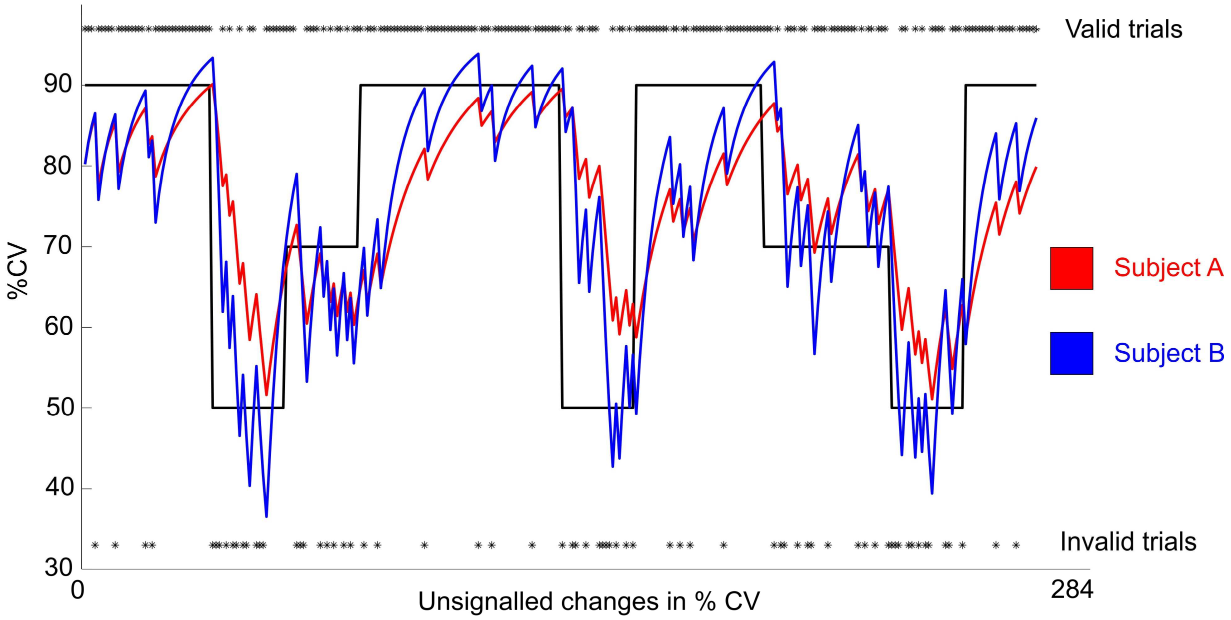

Figure 6 Illustration of individual differences in trial-by-trial changes in probability-dependent attention $\hat{\mu}_1^{(t)}$.

The example shows trial-by-trial changes in probability-dependent attention $\hat{\mu}_1^{(t)}$ of two different subjects, reflecting their updating of beliefs that the cue is valid in relation to the experimentally manipulated percentage of cue validity (%CV). Subject B (*blue*) displays faster updating after new observations than subject A (*red*), as indicated by faster changes in probability-dependent attention $\hat{\mu}_1^{(t)}$.

In a second step, the neural correlates of probabilistic inference were investigated. Trial-by-trial estimates about cue validity derived from the computational model were included as parametric regressors to the fMRI design. This approach allows examining the effects of probability-dependent attention on BOLD amplitudes in valid and invalid trials of the two task versions. We did not observe probability-dependent modulation of orienting responses. This (null)-finding could result from the employed task design: Short and constant SOAs were used, which does not allow differentiating between cue and target- related responses. The signal might have been mostly driven by target-related responses, which are usually stronger than cue-related responses. Thus, this task design was well suited to detect differences between invalidly and validly cued targets, which were of main interest in Experiment 2. On the other hand, this finding may also be a true finding, rather than a limitation of the task design, since it is consistent with previous data that showed higher probability-dependent effects on reorienting costs than on orienting benefits in a spatial attention task (Lasaponara et al., 2011). Future studies should employ task designs with varying SOAs to investigate whether our finding concerning cue-related activity is true, or whether the present task paradigm was simply not well suited to investigate this question.

With regard to attentional reorienting, we observed probability-dependent effects on feature-based as well as spatial attention. These effects were reflected in increased BOLD responses for invalid trials when the expected probability for valid cues was higher. On the other hand, BOLD responses for valid trials with higher expected probability for the occurrence of a valid trial were decreased. This different pattern of BOLD responses for valid and invalid trials mirrors the probability-dependent decrease or increase of validity effects that was reported in the analysis of RTs. For spatial attention these effects were present in the precuneus, left posterior IPS, middle occipital gyrus, and right temporoparietal junction. In the left anterior IPS these effects were present for feature-based as well as spatial attention. No regions were selectively modulated by feature-based attention. The following section will discuss the results for spatial attention with a special emphasis on a TMS experiment that was conducted as a co-author. Next, the novelty of the findings of common effect for spatial and feature-based attention will be discussed.

Consistent with previous work and in line with the contextual updating hypothesis (Geng & Vossel, 2013), we found probability-dependent effects on spatial attention in the rTPJ (Vossel et al., 2015; Vossel et al., 2006). This finding fits nicely with the results obtained from Vossel et al (2015) which investigated probability-dependent changes in cortical connectivity within the spatial reorienting system using dynamic causal modeling (DCM). In this study, functional data were acquired while participants performed a probabilistic cueing paradigm with saccadic responses to the targets. The analysis revealed that probability-dependent effects on spatial reorienting-activity were established via directional influences from rTPJ to other regions that were involved in the employed task paradigm (FEF, putamen). One can hypothesize that the finding of probability-dependent effects on spatial attention in the precuneus, left IPS and MOG in the present task paradigm may also be initiated by influences from the rTPJ.

Based on these findings a TMS Experiment investigating the role of the rTPJ in belief updating that was conducted as a co-author (Mengotti et al., 2017). The research questions that were addressed in this study concerned the causal involvement of the rTPJ in belief updating and the characterization of the timing of this process. To investigate these questions, participants performed a modified spatial cueing task, during which false explicit information about the %CV was provided in half of the experimental blocks. When false prior information was provided, participants needed to update their prior belief about %CV over the course of the block. Online double-pulse TMS was applied in two different runs – 300 ms or 50 ms after target appearance – in order to disrupt rTPJ activity at these time points. The results revealed that disrupting rTPJ activity 300 ms after target appearance selectively decreased participants' updating of false prior beliefs concerning %CV as indicated by a decreased learning rate (here: Rescorla-Wagner learning rate α) and by altered explicit beliefs concerning the validity of the cue. However, no such effects were found for disruption after 50 ms. These findings provide direct evidence for the causal involvement of rTPJ in the updating of prior beliefs. Our results from Experiment 2 extend the results from Mengotti et al. (2017) and Vossel et al. (2015) by showing that the involvement of rTPJ in probability-dependent attention may be confined to the spatial system, since we did not observe any effects for feature-based reorienting within this region.

Interestingly, activity in the left anterior IPS displayed probability-dependent effects on spatial as well as feature-based reorienting. The common effect within this region is a remarkable result because it indicates that even though probabilistic inference distinctively affects each of the two attentional subsystems, there may be domain general neural mechanisms. Moreover, the finding fits well with the correlation of the updating parameters at the behavioral level and suggests a potential link between probabilistic inference in both attention systems.

Interestingly, the involvement of the left anterior IPS resonates with its central role in the integration of multisensory information and one could speculate that this role is not confined to different sensory modalities but extends to distinct visual domains. Some evidence for the sensitivity of IPS to perceptual uncertainty can be derived from neurophysiological studies that link activity in lateral intraparietal area with evidence accumulation processes during (uncertain) decisions: Neurons in this area show increased firing rates with less uncertainty and prolonged responses with higher uncertainty (Gold & Shadlen, 2007). This provides a nice analogy with the parametric effects of probability-dependent attention in the present paradigm, i.e., increased responses to unexpected stimuli (invalid trials) and decreased responses to more expected stimuli (valid trials). As opposed to the common effects in the left anterior IPS, the posterior IPS did only show probability-dependent effects on spatial reorienting. The specific involvement of the posterior IPS in spatial processes can be explained by its dense connectivity with topographically organized visual cortex. As such, the posterior IPS may be especially involved when information about spatial locations is processed. On the contrary, we did not find regions that selectively displayed probability-dependent effects on feature-based attention. This finding does not imply that probabilistic inference is less relevant for the feature-based system. Rather, it suggests that probability-dependent effects were locally represented in the left anterior IPS. Together with the finding from the global reorienting contrast that revealed stronger responses within this region to feature-based as compared to spatial reorienting of attention, we suggest that the left anterior IPS plays a central role in feature-based attentional processes.

3.2.3 Limitations

The following section will discuss limitations of Experiment 2 focusing on the design and the fMRI analysis. Since we aimed at a direct comparison between feature and spatial cueing effects, a within subject design with the same search task, stimuli, and methods was used. As outlined in the discussion of Experiment 1, the search task always contained a spatial component, in both, the spatial and the feature cueing task.

In the spatial cueing task, the spatial cues induce an attention shift to the expected location. On invalid trails, an additional spatial shift to the uncued location occurs. This spatial shift was the aspect of interest for the spatial task version. In the feature-based cueing task, we expected the cues to cause preferential processing of the two stimuli in the cued color. On invalid trials, there was an additional shift in processing towards the stimuli in the uncued color. This attentional shift in preferential processing is the aspect of interest for the feature task version. Due to the nature of the search display, the feature task potentially also contained a spatial component. However, this effect presumably cancels out in the feature task when directly contrasting invalid and valid trials since this spatial component is present to the same degree in valid as well as invalid trials. If there had been a stronger spatial component in invalid trials in the feature task, we should have observed similar activation patterns for the invalid versus valid contrast for both tasks. In contrast, the reported interaction effects between cue type and validity revealed that (most) regions responded more in the spatial cueing than in the feature cueing task or vice versa. This speaks against a common (spatial) component to both task versions.

A second limitation of Experiment 2 is that we did not investigate *probability-dependent effects* on attention outside the attentional networks. It may be that there are other networks involved in probability dependent effects that have been overlooked in analyses focusing on attentional networks. It should be noted that the probabilistic effects are subtle and were only detectable using ROI analyses. Moreover, whole-brain analysis on the contrast images of the probability-dependent attention did not reveal any significant parametric effects at corrected thresholds. However, even this null finding does not prove that there are no probability-dependent effects outside attentional networks and future studies are needed that provide higher numbers of participants to increase statistical power. Likewise, potentially connectivity analyses would be helpful to answer the question of shared versus distinct mechanisms concerning the observed common effect in the left IPS for spatial and feature-based probability-dependent attention.

3.3 Conclusions and implications

The core research question of the present thesis concerns how the human brain forms expectancies during sensory uncertainty when information about probabilities is not available but needs to be inferred from observations. It was investigated whether this probabilistic inference process governs the deployment of feature-based and spatial attention in a similar way. This was accomplished by identifying which factors influence probabilistic inference in feature-based attention (Experiment 1), and by comparing the computational and neural mechanisms that modulate probabilistic inference in feature-based and spatial attention (Experiment 2). Identifying commonalities or distinctions between these two attention systems has implications for the study of visual attention and helps to understand whether the neural computations of probabilistic inference are implemented within a domain-general system that is responsible for predicting sensory inputs or whether there are several domain-specific systems that are localized in confined networks.

Our results show that behaviorally probabilistic inference similarly modulates feature-based and spatial attention systems. Hence, in the framework of predictive coding this supports the idea that the brain forms attentional predictions that influence the processing of sensory inputs. The speed with which new observations induce the updating of feature-based attentional predictions depends on the level of abstraction of the cues that are provided prior to the sensory inputs (Experiment 1). When through experiences in everyday life prior predictions have already been formed –for instance for automatically processed or well-learned cues– the updating of these predictions requires more time than for newly learned and more abstract cues. The susceptibility to updating trial-by-trial estimates about cue validity is correlated for abstract feature-based cues and spatial cues. This indicates that probabilistic inference represents a trait-dependent variable influencing domain general attentional deployment. However, the neural implementations for probabilistic inference seem to be dedicated to domain specific subsystems. The rTPJ seems to be particularly involved in probability-dependent spatial attention. For probability-dependent feature-based attention the anterior left IPS seems to be most crucial. However, the left anterior IPS also shows an effect of probability-dependent attention in the spatial system, which suggests that this region may establish probabilistic inference in a domain general manner.

Combining the results from Experiment 2 and (Mengotti et al., 2017) indicates however that the probability-dependent attention effects in the spatial system causally depend on the processing of rTPJ and cannot be taken over by the left anterior IPS. This is especially relevant when considering findings from patients with right-hemispheric brain damage that reveal preserved feature-based learning of environmental statistics (here: priming) *and* selectively impaired spatial learning (Shaqiri & Anderson, 2013). We hypothesize that spatial neglect patients lack modulation of right parietal cortex –comprising the rTPJ– for the updating of spatial predictions, while the left anterior IPS still establishes these processes for the feature-based domain. A deficit in the processing of probabilities could result spatial neglect symptoms in stroke patients because they may lack the ability to learn from previous experiences and to adapt their spatial attentional systems accordingly. As such, this deficit could perpetuate the symptomatology. Likewise, it would be interesting to test whether patients with damage to the left anterior IPS also show impaired updating of probabilities for feature-based systems.

With regard to visual attention our findings speak against a global unitary network which has been suggested by the influential framework from Corbetta and Shulman (2002). Rather, we propose that depending on to be selected aspects different attentional subsystems are activated controlling the reorienting of attention following expectancy violations. Depending on the task at hand, attentional processes can even differ within one single attentional domain such as the selection of features. In conclusion, understanding the influence of probabilistic inference on attentional processes offers a unifying way to describe flexible attentional deployment as required in everyday life situations.

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5. CURRICULUM VITAE

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Ausbildung

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10. 2013 - heute	**Promotionsstudium** Humanwissenschaftliche Fakultät der Universität zu Köln
09.2011 - 08. 2013	**M.Sc. in kognitiven und klinischen Neurowissenschaften** Schwerpunkt: Neuropsychologie Universität Maastricht, Niederlande Masterarbeit (Note: 9.5/10 entspricht 1,0 (sehr gut)[1]): “Attentional Control Networks, Alpha Oscillations and Resting State Functional Connectivity in Patients with Focal Brain Lesions: “Power and Synchrony of Pulsed Inhibition”. D’ Esposito laboratory, University of California at Berkeley, USA.
09.2008 - 08.2011	**B.Sc. in Psychologie** Universität Maastricht, Niederlande Bachelorarbeit (Note: 8.5/10 entspricht 1.3 (sehr gut) [1]): “Impulsivity and Cue-Reactivity in Alcohol Dependent People”. Universität Maastricht und U-Center Epen, Niederlande
2011	**Auslandssemester** Bond University, Australien
2009 - 2011	**Honors Programm** der Fakultät für Psychologie und Neurowissenschaften, Universität Maastricht, Niederlande
06.2007	**Allgemeine Hochschulreife** (Note 2,1) Anne-Frank-Gymnasium, Aachen, Deutschland

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[1] Offizielle Umwandlungsformel https://www.uni-frankfurt.de/44139376/noten_ausland

Forschungstätigkeiten

10. 2013 - heute	**Wissenschaftliche Mitarbeiterin (Doktorandin)** Forschungszentrum Jülich, Institut für Neurowissenschaften und Medizin. Arbeitsgruppe: Kognitive Neurowissenschaften (INM-3) Prof. Gereon R. Fink. (Betreuung: Jun.-Prof. Simone Vossel)
11.2012 - 07.2013	**Wissenschaftliche Hilfskraft** Helen Wills Neuroscience Institute, University of California in Berkeley. Arbeitsgruppe: Kognitive Neurowissenschaften Prof. Mark D'Esposito. (Betreuung: Sepideh Friberg Sadaghiani, Ph.D.)
08.2012 - 10.2012	**Wissenschaftliche Hilfskraft** Netherlands Institute for Neuroscience, Royal Academy of Sciences in Amsterdam. Arbeitsgruppe: Neuroimaging & Neuromodeling Prof. Rainer Goebel. (Betreuung: Judith Peters, Ph.D.)
06.2012 - 08.2012	**Wissenschaftliche Hilfskraft** Fakultät für Psychologie und Neurowissenschaften, Universität Maastricht. Arbeitsgruppe: Computational architecture of visual processing streams and Computational Brain Connectivity Prof. Rainer Goebel. (Betreuung: Judith Peters, Ph.D. und Joel Reithler, Ph.D.)
06.2012 - 09.2012	**Wissenschaftliche Hilfskraft** Fakultät für Psychologie und Neurowissenschaften, Universität Maastricht. Arbeitsgruppe: Learning and Memory Prof. Arjan Blokland. (Betreuung: Anke Sambeth, Ph.D.)
08.2010 - 12.2010	**Forschungspraktikum** U-Center Epen, Klinik für Suchterkrankungen. (Betreuung: Harilaos Papachristuo, Ph.D.und Chantale Nederkoorn, Ph.D.)

Andere Tätigkeiten

03.2008- 08.2012	**Studentische Hilfskraft** Alexianer Krankenhaus Aachen GmbH, Fachkrankenhaus für Psychiatrie, Psychotherapie und Psychosomatik

Extrakurrikulare Aktivitäten

2014	**SPM-Kurs** Institut für Systemische Neurowissenschaften, Universitätsklinikum- Hamburg Eppendorf. Prof. Christian Büchel.
2013	**Kurs zur Analyse von funktioneller Magnet Resonanz Tomographie** University of California in Berkeley Baptiste Poline, Ph.D. und Matthew Brett, Ph.D.
2012	**7th annual M-BIC fMRI workshop** Universität Maastricht, Niederlande

Publikationen

2017	Mengotti, P., **Dombert, PL**., Fink, GR., Vossel, S. (2017). Disruption of the right temporoparietal junction impairs probabilistic belief updating. *Journal of Neuroscience*, 37, 5419-5428.
2017	Kuhns, A., **Dombert, PL**., Mengotti, P., Fink, GR., Vossel, S. (2017). Spatial attention, motor intention, and Bayesian cue predictability in the human brain. *Journal of Neuroscience*, 37, 5334-5344.
2016	**Dombert, PL**., Kuhns, A., Mengotti, P., Fink, G.R., Vossel, S. (2016). Functional mechanisms of probabilistic inference in feature-and space-based attentional systems. *Neuroimage*, 142, 553-564.
2016	**Dombert, PL**., Fink, G.R., Vossel, S. (2016). The impact of probabilistic feature cueing depends on the level of cue abstraction. *Experimental Brain Research*, 234, 685-94.

Poster Präsentationen

2016	**Dombert, PL**., Kuhns, A., Mengotti, P., Fink, G.R., Vossel, S. (2016). Functional mechanisms of probabilistic inference in feature-and space-based attentional systems. Annual Meeting of the Organization for Human Brain Mapping 2016, 26.-31. Juni in Genf, Schweiz.
2015	**Dombert, PL**., Kuhns, A., Mengotti, P., Fink, G.R., Vossel, S. (2015). Statistical context and sensory stimulus abstraction dynamically interact during feature-based

	attentional control. Tagung Psychologie und Gehirn 2015, 4.-6, Juni in Frankfurt am Main, Deutschland.
2013	**Dombert, PL.**, Sadaghiani, S., Lovstad M., Funderud, I., Knight, RT., Solbakk, AK., D'Esposito. M., (2013). Lesion to the fronto-parietal adaptive control network impacts alpha-band phase synchrony. Annual Meeting of the Society for Neuroscience 2013, 9.-13. November in San Diego, CA, USA.

Auszeichnungen

2011	**Top 3% Award**, Akademisches Jahr 2010-2011, Universität Maastricht, Niederlande
2011	**First in class award**, Bond University, Australien
2010	**Top 3% Award**, Akademisches Jahr 2009-2010, Universität Maastricht, Niederlande

Erworbene Qualifikationen

Software Programme	SPSS, BrainvoyagerQX, SPM, MS Word, MS Excel, Presentation (Neurobehavioral Systems), Brainsight TMS Navigation (Rouge Research), Matlab.
Sprachen	Deutsch (Muttersprache) Niederländisch (Staatsexamen, B2) Englisch (fließend in Schrift und Sprache) Französisch (Grundkenntnisse)

Köln, den