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Interrelation of attention and prediction in visual processing: Effects of task-relevance and stimulus probability

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ABSTRACT

The potentially interactive influence of attention and prediction was investigated by measuring event-related potentials (ERPs) in a spatial cueing task with attention (task-relevant) and prediction (probabilistic) cues. We identified distinct processing stages of this interactive influence. Firstly, in line with the attentional gain hypothesis, a larger amplitude response of the contralateral N1, and Nd1 for attended gratings was observed. Secondly, conforming to the attenuation-by-prediction hypothesis, a smaller negativity in the time window directly following the peak of the N1 component for predicted compared to unpredicted gratings was observed. In line with the hypothesis that attention and prediction interface, unpredicted/unattended stimuli elicited a larger negativity at central-parietal sites, presumably reflecting an increased prediction error signal. Thirdly, larger P3 responses to unpredicted stimuli pointed to the updating of an internal model. Attention and prediction can be considered as differentiated mechanisms that may interact at different processing stages to optimise perception.

1. Introduction

The brain needs to process multiple incoming sensory stimuli selectively. To do so effectively, it may exploit statistical regularities in the environment to predict what happens next, and thereby minimise surprise. Consequently, several influential theories of perception consider that the brain forms predictions about incoming sensory information based on Bayesian inferential principles (Friston, 2005, 2009; Lee & Mumford, 2003). Predictions, also referred to as perceptual expectations, are defined as top-down signals that facilitate perception by utilising information about prior probability (Schröger, Marzecová, & SanMiguel, 2015; Summerfield & de Lange, 2014). Predictions are compared to incoming sensory input, and an observed difference is expressed in the prediction error, a signal that is passed upwards in the sensory hierarchy to update and refine the current model. Within this predictive coding framework, perception can be described as an inferential process of minimising prediction errors through the integration of bottom-up sensory input with the top-down modulation effected by prediction. Attention, defined as a mechanism that prioritises processing of sensory information that is relevant for current goals (Summerfield & Egner, 2009), constitutes another source of top-down influence. While the neural responses to attended vs. unattended, and predicted vs. unpredicted stimuli have been widely studied, the interactive influence of these two factors has rarely been considered, and studies conducted so far show a seemingly inconsistent pattern of findings (for reviews see Schröger et al., 2015; Summerfield & de Lange, 2014).

Att ending to goal-relevant stimuli facilitates their detectability and the behavioural response to them. On the neuronal level, the attentional effect is reflected in increased and less variable neuronal responses to attended stimuli (Carrasco, 2011). The effects of spatial attention on event-related potentials (ERP) have mainly been studied in spatial cueing tasks, in which cues direct spatial atten-

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tion to the most likely location of an upcoming lateralised target in either a sustained or a transient manner. In these paradigms, attended stimuli usually evoke enhanced early responses, namely the parieto-occipital P1–a positive deflection with a latency of 80–130 ms – and the N1–a negative deflection with a latency of 120–200 ms (for reviews see Herrmann & Knight, 2001; Hillyard & Anllo-Vento, 1998; Luck, Woodman, & Vogel, 2000). The effects of attention have been observed mostly for electrode-sites contralateral to the stimulus, and the enhancements have been attributed to the mechanism of sensory gain (Hillyard, Vogel, & Luck, 1998). However, an enhancement of the ipsilateral P1 component has also been reported. This enhancement presumably reflects the inhibition of potentially competing information processing in the task-irrelevant visual field (for a review see Klimesch, 2011, 2012). In studies in which the effects of attention have been tested by means of transient probabilistic cues (for ERP studies see e.g., Eimer, 1994; Hillyard, Luck, & Mangun, 1994; Mangun & Hillyard, 1991), an additional negative component, specific to trial-by-trial manipulations of attention, has been reported at midline parietal electrodes ("Nd1", Eimer, 1994; Schröger & Eimer, 1993). Nd1 is thought to reflect spatially selective and modality unspecific activity within the posterior parietal cortex occurring with transient – visual and auditory – spatial attention (for reviews see Eimer, 1998; Näätänen, Alho, & Schröger, 2002). In spatial cueing studies, effects of attentional orienting are observed already in the prestimulus period (e.g., Dale, Simpson, Foxe, Luks, & Worden, 2008; Simpson et al., 2011; Yamaguchi, Tsuchiya, & Kobayashi, 1995). Attention cues elicit lateralised activity that is manifested in several cue-related ERP components (Harter, Miller, Price, Lalonde, & Keyes, 1989; Nobre, Sebestyen, & Miniussi, 2000; van der Lubbe, Neggers, Verleger, & Kenemans, 2006; van der Lubbe & Utzerath, 2013; Velzen & Eimer, 2003). The earliest of these is a posterior component between 150 and 350 ms, known as the early directing attention negativity (EDAN). The EDAN likely reflects attentional selection of the relevant parts of the cue (Talsma et al., 2007; Talsma, Mulckhuyse, Slagter, & Theeuwes, 2007; van der Lubbe et al., 2006; Velzen & Eimer, 2003). The EDAN is usually followed by the anterior directing attention negativity (ADAN, ∼400 ms) and the late directing attention positivity (LDAP, ∼500–650 ms) at posterior sites.

In probabilistic spatial cueing tasks, attention is directed to the expected and more probable location or feature predicted by the cue, and the attention-related enhancement of the N1 component is usually observed (e.g., Doherty, Rao, Mesulam, & Nobre, 2005; Eimer, 1997). However, an opposite pattern, namely a larger amplitude response to invalidly cued events, has also been observed ('an inverse N1 effect'; Eimer, 1993, Experiment 1a). This pattern has been attributed to the confounding effects of prediction (Eimer, 1993; Lange, 2013). Predictions are formed based on stimulus probability and are induced in a spatial cueing task through probabilistic manipulations of attention (Summerfield & de Lange, 2014; Summerfield & Egner, 2009, 2014). Predictions facilitate the interpretation of sensory data, and lead to more efficient behavioural responses in a similar fashion as attentional selection (see e.g. Kok, Jehee, & de Lange, 2012, for review see Summerfield & de Lange, 2014). However, task-relevance, that drives attentional selection, and signal probability that leads to sensory predictions may constitute potentially orthogonal sources of information flow (Summerfield & Egner, 2009; Summerfield & de Lange, 2014). The underlying neural signatures of prediction appear to differ from the markers of attentional selection. Diverse evidence indicates that while attended as compared to unattended input increases neural responses predicted input usually elicits reduced ERP responses as compared to unpredicted input (for review see Schröger et al., 2015; see also Summerfield & de Lange, 2014; Summerfield & Egner, 2009). For example, in a number of oddball studies, low-probability unexpected stimuli (i.e., deviants) elicited larger responses than high-probability expected stimuli (i.e., standards). In ERPs, this differential response is indicated by the mismatch negativity (MMN; auditory MMN: Näätänen, Gaillard, & Mäntysalo, 1978; visual MMN: Czigler, Balázs, & Winkler, 2002). Within a predictive coding framework, this effect is explained as a reduction of prediction error responses to sensory input that matches predictions generated by an internal model (see e.g. Garrido, Kilner, Stephan, & Friston, 2009). The phenomenon of repetition suppression (RS; for a review see Grill-Spector, Henson, & Martin, 2006), namely an "experience-related" adaptation, or attenuation, of the N1 component in response to repeated stimuli is considered to partially contribute to the MMN response (see e.g. Horváth et al., 2008; Stefanics, Kremláček, & Czigler, 2014). Furthermore, a suppression of the auditory N1 component for stimuli predicted based on one's own action (for reviews see Horváth, 2015; Hughes, Desantis, & Waszak, 2012; Schröger et al., 2015) has also been interpreted as a reduction of sensory consequences to a stimulus that is predicted, and thus explained by an internal model. Consequently, this effect has been considered to reflect a reduction of prediction error signal (for review see Schröger et al., 2015). The attenuation effect was also observed for the visual N1 component (see e.g. Gentsch & Schütz-Bosbach, 2011; Roussel, Hughes, & Waszak, 2014). Based on the evidence from the diverse research lines reviewed above, it appears that ERPs in the time window of the N1 component are sensitive to both attention (i.e., increased for attended stimuli) and prediction (i.e., suppressed for predicted stimuli).

Taking a predictive coding perspective, attention and prediction can also be considered as interdependent mechanisms. Recent studies (Brown & Friston, 2013; Feldman & Friston, 2010) have proposed that attention can be understood as a top-down gain control mechanism that optimises the precision of prediction errors through synaptic gain modulation (see also Bastos et al., 2012). The effects of prediction, reflected in the amplitude of the prediction error, would therefore be dependent on the degree of attentional precision. Evidence for an interface between prediction and attention comes from an fMRI study employing a modified spatial cueing task. Kok, Rahnev, Jehee, Lau, and de Lange (2012) manipulated selective endogenous attention and prediction independently through two types of cues: probabilistic ('prediction') cues and task-relevant cues. Probabilistic cues presented at the beginning of each block indicated the likely location of visual stimuli in the subsequent block of trials. Across blocks, stimuli appeared either with higher probability (75%) on one side of the fixation (predicted condition) than on the other (unpredicted condition), or with equal probability on either side (no prediction blocks). Task-relevant cues that preceded the stimulus on every trial indicated which side to attend and respond to. The results showed interactive effects of attention and prediction on the Blood Oxygenation Level Dependent (BOLD) response in primary visual cortex (V1). Response suppression to predicted compared to unpredicted input was observed for the unattended (i.e., task-irrelevant) visual stimuli. However, consistent with the hypothesis that the prediction error is scaled by attentional precision, the prediction effect was reversed when stimuli were attended to (i.e., task-relevant), and an enhanced BOLD response to predicted compared unpredicted gratings was observed. In ERP studies, markers of attentional and predictive processing have largely been studied separately, in attentional cueing and oddball studies, respectively. However, the degree of interdependence between prediction-related and attentional processes is under debate (Kimura, 2012; Stefanics, Kremláček, & Czigler, 2014).

In the current study, we utilised the ERP method to investigate the time course of attentional selection, prediction, and their possible interaction in the context of a spatial cueing task. Analysing the time-course of these possible interactive effects seems important