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Effect of temporal predictability on exogenous attentional modulation of feedforward processing in the striate cortex

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ABSTRACT

Non-informative peripheral visual cues facilitate extrastriate processing of targets [as indexed by enhanced amplitude of contralateral P1 event-related potential (ERP) component] presented at the cued location as opposed to those presented at uncued locations, at short cue-target stimulus onset asynchrony (SOA). Recently, two lines of research are emerging to suggest that the locus of attentional modulation is flexible and depends on 1) perceptual load and 2) temporal predictability of visual stimuli. We aimed to examine the effect of temporal predictability on attentional modulation of feed-forward activation of the striate cortex (as indexed by the C1 ERP component) by high-perceptual-load (HPL) stimuli. We conducted two ERP experiments where exogenously-cued HPL targets were presented under two temporal predictability conditions. In Experiment 1 [high-temporal-predictability (HTP) condition], 17 healthy subjects (age 18–26 years) performed a line-orientation discrimination task on HPL targets presented in the periphery of the left upper or diagonally opposite right lower visual field, validly or invalidly cued by peripheral cues. SOA was fixed at 160 ms. In Experiment 2 [low-temporal-predictability (LTP) condition], ($n = 10$, age 19–36 years) we retained HPL stimuli but randomly intermixed short-SOA trials with long-SOA (1000 ms) trials in the task-blocks. In Experiment 1 and the short-SOA condition of the Experiment 2, validly-cued targets elicited significantly faster reaction times and larger contralateral P1, consistent with previous literature. A significant attentional enhancement of C1 amplitude was also observed in the HTP, but not LTP condition. The findings suggest that exogenous visual attention can facilitate the earliest stage of cortical processing under HTP conditions.

1. Introduction

Abrupt changes in the periphery of the visual field attract attention even if they are non-informative and irrelevant to the behavioural goals at the time. Salient stimuli that immediately follow at this cued location elicit faster reaction times than those presented at uncued locations. This stimulus-driven attentional deployment is termed exogenous visuospatial attention (Posner, 1980). It is synonymous with the reflexive (Hopfinger and Mangun, 1998), automatic (Jonides, 1981) or involuntary (Fu et al., 2005) attention described elsewhere in the visual attention literature.

Hopfinger and Mangun (1998) showed that exogenous attention could facilitate early extrastriate processing, as indexed by enhancement of contralateral P1 (P1cl) event-related potential (ERP[1]) component over lateral parieto-occipital region over 90–140 ms post-stimulus latency range. This effect has been replicated in many subsequent ERP studies (Fu et al., 2001, 2005; Hopfinger and Mangun, 2001; Hopfinger and West, 2006). However the C1 ERP component (a negative peak around 80 ms post-stimulus) arising from initial feed-forward processing in the striate cortex (V1) was not modulated by attention in any of these studies, suggesting that initial striate processing is not amenable to attentional modulation. Single-cell recordings in monkeys (Motter, 1993) and fMRI studies in humans (Gandhi et al., 1999; Martinez et al., 1999) show that attention can modulate striate processing, but concurrent EEG recording indicates that that this differential activation represents feedback activation from V1 rather than modulation of initial afferent impulses (Martinez et al., 1999).

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[1] Abbreviations: ERP, event-related potential; MEG, magnetoencephalopgraphy; HPL, high perceptual load; LPL, low perceptual load; UVF, upper visual field; LVF, lower visual field; SOA, cue-target stimulus onset asynchrony; EOG, electrooculogram; ANOVA, analysis of variance

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In contrast, some recent ERP and magnetoencephalography (MEG) studies indicate that the feedforward activation of the striate cortex could be facilitated by attention under certain experimental conditions. These include endogenous visuospatial attentional paradigms (Kelly et al., 2008), object-based exogenous attentional paradigms (Khoe et al., 2005), and exogenous visuospatial attention paradigms which directly (Fu et al., 2010a, 2009; Poghosyan and Ioannides, 2008) or indirectly (Rauss et al., 2009) manipulated attention to peripheral stimuli. In a recent review, Rauss et al. (2011) propose heterogeneity of experimental paradigms as a cause for presence or absence of C1 attentional effects in different studies (Rauss et al., 2011). The authors point out that when exploring the C1 attentional effects, the stimulus properties and the task demands should exploit the functional characteristics of V1 (e.g. contrast sensitivity and retinotopic organisation), so that V1 can substantially contribute to the task, thus enabling any top-down effects to modulate the degree of contribution by V1 in turn modulating C1 amplitude.

Perceptual load (Lavie, 1995) and *temporal predictability* (Nobre et al., 2007) seem to be two independent modulators of the magnitude and the locus of top-down attentional effects. Lavie's load theory of attention proposes that the stage of attentional filtering is flexible depending on the 'perceptual load' of visual stimuli (Lavie, 1995; Lavie et al., 2004; Lavie and Tsal, 1994): the higher the perceptual load, the earlier attention interacts with visual processing. The original concept of perceptual load has been refined in to two distinct operational definitions in more recent work: 1) *attentional load* which refers to 'the differences in processing demands in the absence of physical stimulus differences' (Ding et al., 2014; Fu et al., 2012; Rauss et al., 2012, 2009) and 2) *perceptual load* which refers to 'the amount of stimulus information that need to be processed to perform a given task' (Fu et al., 2010a, 2009; Rauss et al., 2012). In the present study, we use the term 'perceptual load' in this latter sense. The effect of attentional load on C1 modulation shows inconsistent results. These contrasting findings are debated with regards to the optimal method of attentional-load manipulation that enables C1 modulation (Fu et al., 2012, 2010b; Rauss et al., 2012, 2009) and the source localisation of the attentional effect (Ding et al., 2014; Rauss et al., 2009). These last two studies indirectly manipulated the exogenous attentional load allocated to peripheral stimuli by modulating the attentional load allocated to an attentional task at fixation (Ding et al., 2014; Rauss et al., 2009). In contrast, perceptual-load studies by Fu et al employed a line-orientation choice-reaction task under direct exogenous cueing (Fu et al., 2010a, 2009). In these studies, the degree of target-distracter overlap and/or the relative orientation of target vs. distracter array determine the discriminability of the target from concurrent distracters, consequently modulating the perceptual load on a trial-by-trial basis. Their results in general, comply with Lavie's load theory, showing an attentional facilitation of C1 amplitude elicited by high-perceptual-load (HPL) but not low-perceptual-load (LPL) stimuli. Interestingly, the attentional facilitation of C1 for HPL stimuli was observed only when they were intermixed with LPL stimuli within a task block (Fu et al., 2009).

Neuroimaging (Coull and Nobre, 2008; Coull et al., 2000; Coull and Nobre, 1998) and EEG/ERP (Doherty et al., 2005; Miniussi et al., 1999; Praamstra et al., 2006; Rohenkohl and Nobre, 2011) evidence in humans and single cell recordings in monkeys (Ghose and Maunsell, 2002) show that attentional circuitry of the brain can be tuned to predict not only the location of visual stimuli but also their timing. Doherty et al. (2005) examined the combined effect of spatial and temporal predictability of on visual ERPs in an exogenous attention task. The target was a circle moving across the screen in steps and then disappearing beneath a band of occlusion. When it appeared on the other side the subjects had to respond only if the circle contained a dot in the middle. The researchers modulated the trajectory and regularity of initial movement of the circle thus modulating the spatial and temporal expectancy of its appearance beyond the occlusion. As expected, the targets that moved in a linear trajectory (i.e. high spatial orienting) and reappeared in predictable locations beyond the occlusion elicited larger P1 components. More importantly, this P1 facilitation was further augmented when the target circle moved at regular time intervals (i.e. high temporal predictability). These results have been replicated by Rohenkohl and Nobre (2011). Collectively, the studies on temporal orienting suggest that high temporal predictability (HTP) of target stimuli help to pace top-down attentional systems to facilitate their processing.

Even though a large body of literature has addressed the significance of stimulus characteristics and perceptual/attentional load in attentional modulation of early visual processing, the role of temporal predictability of stimuli on C1 attentional effects has not been methodically examined. The aim of the present study was to determine the role of temporal predictability on attentional modulation of feedforward visual processing at V1. To maximize the contribution of V1 we administered an exogenously-cued, HPL, line-orientation discrimination task. We hypothesised that HPL and HTP should be the optimal combination to move the locus of attentional modulation as far downstream as possible and to facilitate initial stages of V1 processing of visual stimuli. If HPL is sufficient and HTP is not essential for attentional facilitation of V1 processing, we expected an attentional modulation of C1 to be present even when the SOA is variable. To examine these hypotheses, we examined the attentional effect on C1 ERP component by modulating the temporal predictability in two separate exogenous visuospatial attention experiments. In the first experiment we maintained a HTP of targets by employing a fixed SOA, whereas the second had a low temporal predictability (LTP) produced by a variable SOA.

2. Experiment 1

2.1. Materials and methods

2.1.1. Participants

Twenty-three healthy university undergraduates participated in this study. All were right handed and had normal or corrected-to-normal vision. None of the participants had significant neurological/psychiatric illnesses or used psychoactive drugs. The study was approved by the Human Research Ethics Committee of The University of Newcastle, Australia and was conducted in accordance with the standards laid down in the Declaration of Helsinki (1964). Informed written consent was obtained from all participants.

Data from six subjects were excluded: three due to low (<70%) accuracy rates, two due to excessive alpha activity in EEG recordings and one due to absence of an identifiable C1. Had we averaged more trials to generate ERP waveforms, exclusion due to last two causes could also have been mitigated, but at the cost of possible fatigue due to prolonged testing. Data are reported from the remaining 17 participants (15 women) aged between 18 and 26 years (mean = 20.5, SD = 2.6).

2.1.2. Stimuli and procedure

The task was a modified version of the Fu et al., 2009 experimental paradigm (Fu et al., 2009). Presentation (Neurobehavioral Systems, CA, USA) software was used to generate visual stimuli. The participants performed a visual stimulus discrimination task under an exogenous cuing paradigm. They maintained gaze on a $0.33° \times 0.33°$ black central fixation cross in a white background from a distance of 70 cm throughout each experimental block. The peripheral cue, a Kanizsa box ($4.73° \times 4.73°$) (Fig. 1a) flashed for a duration of 50 ms, randomly in either the left upper visual field (UVF) or diagonally opposite right lower visual field (LVF) at an eccentricity of 7.4° from fixation. The centre of each cued location formed a 23.7° polar angle with the horizontal meridian. Each cue was followed by a target array (duration 100 ms, $2.74° \times 2.74°$) that randomly appeared at the cued location (in 50% of the trials viz. valid trials) or the diagonally opposite location (in other 50% of the trials viz. invalid trials). The target was either a forward diagonal ("/" requiring left index finger response, 50% probability) or backward diagonal ("\" requiring right index finger response, 50%

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