How early does attention modulate visual information processing? The importance of experimental protocol and data analysis approach

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reminded of the ultimate achievement of reaching the 11th level, which was celebrated on the rare occasions where it was achieved. Experimenters also monitored difficulty levels online and announced changes in level as they occurred. Whether this really means that subjects performed the detection task more keenly than in Baumgartner et al. is hard to verify because differences in the method of luminance decrement as well as the background brightness render the levels not directly comparable (See supplementary Figure 1b). The P1 modulation observed in Baumgartner et al. was significant and indicates that subjects did deploy spatial attention, but the effect sizes are smaller (Early P1: 0.58, late P1: 0.44) than in Kelly et al. (Early P1: 0.70, late P1: 0.61). Whether subjects go the extra mile in honing their feature as well as spatial selectivity to optimize accuracy may depend on their level of motivation, and it is possible that this was a factor in the present discrepancy.

In sum, the present findings highlight the fact that we are far from a good understanding of the mechanistic principles governing spatially-selective attention in V1, while at the same time illuminating promising avenues for future investigations towards this goal.

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How early does attention modulate visual information processing? The importance of experimental protocol and data analysis approach

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ABSTRACT
Whether attention can influence afferent information processing in primary visual cortex (V1) has long been topic of scientific debate. Findings from a recent study by Baumgarter et al. (this issue) add to this debate by providing a null replication of an influential study that reported that spatial attention can enhance feedforward information processing in human V1, as reflected in the amplitude of the C1 ERP component (Kelly, Gomez-Ramirez, & Foxe, 2008). Here we discuss several factors, including analytic approach, experimental design, and motivational factors, that, once scientifically tested, may help resolve discrepancies in the current literature.

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V1; spatial attention; EEG; ERP; C1; selective attention

Whether attention can influence afferent information processing in primary visual cortex (V1) has long been topic of scientific debate. Findings from a recent study by Baumgarter et al. (this issue) add to this debate by providing a null replication of an influential study that reported that spatial attention...
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Like Baumgartner, Graulty, Hillyard, & Pitts (this issue), most previous human ERP studies have failed to observe modulations of afferent input to V1 by spatial attention (Ding, Martinez, Qu, & Hillyard, 2014). This contrasts with results from single-unit recordings in non-human primates (Slotnick, 2013) and human fMRI studies, which have generally reported that spatial attention can induce changes in baseline activity and stimulus-evoked responses in V1 (Sylvester, Shulman, Jack, & Corbetta, 2009). Yet, these modulations are generally weaker than those in extra-striate cortex. For anatomical (e.g., large inter-individual variability in V1 anatomy and small receptive fields) and methodological (e.g., dependence of EEG signal on the co-activation of thousands or millions of parallel-oriented neurons) reasons, it may be difficult to reliably pick up on weak attentional modulations of V1 activity, if they exist, with scalp EEG. We list three factors that could enhance sensitivity.

First, multivariate analyses that take into account activity from many scalp electrodes, may be more sensitive in picking up weak attentional modulations than the analytic approach of only looking at the C1 peak electrode, as in Baumgarter et al. and Kelly et al. Importantly, this could also reveal attentional effects that are not reflected in activation strength, but in how information is represented in activity patterns, similar to attention-related sharpening of neural representations in V1 observed using BOLD fMRI (Jehee, Brady, & Tong, 2011).

Second, boosting the strength of stimulus-driven activation may increase the sensitivity in detecting weak attentional modulations. Certain stimuli elicit larger, i.e. less noisy, C1 components, than others. For example, in one study, texture displays elicited C1’s of −10/+7μV (Pourtois, Rauss, Vuilleumier, & Schwartz, 2008), compared to C1 amplitudes of −1.5/+2μV in the Baumgarter et al. and Kelly et al. studies.

Third, motivational factors and reward may be important to take into account in future studies. For instance, non-human primates are typically motivated by rewarding accurate task performance, whereas humans are usually not. Notably, a recent study in humans reported that spatial cues predicting reward during successful task performance enhanced the amplitude of the C1, while spatial attention did not (Bayer et al., 2017). This may suggest that motivation, but not spatial attention, facilitates early afferent processing. Yet, reward and attention have also been reported to engage strongly overlapping selection mechanisms in monkey V1 (Stănișor, Van Der Togt, Pennartz, & Roelfsema, 2013). It is hence possible that only under conditions of high motivation, attention is directed such that its effects are implemented already in V1 and/or strong enough to be measured with scalp EEG.

Future EEG studies should also disentangle effects of attention (stimulus relevance) and expectation (stimulus likelihood) on afferent information processing. fMRI research shows that both top-down influences can modulate V1 activity (Kok, Rahnev, Jehee, Lau, & De Lange, 2012). Yet, in probabilistic cuing tasks, like the one employed by Baumgarter et al., attended stimuli are also always predicted and unattended stimuli always unpredictable. To what extent attention and/or expectation can influence feedforward processing in V1 thus is an important question for future studies.

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References
Whether attention modulates the C1 component is controversial. I tend to agree that ‘until the specific conditions that enable such modulation of C1 can be identified and replicated, the “majority view”, which posits that the initial afferent processing stages in V1 are impenetrable by visual-spatial attention, seems to be the safer bet’ (Baumgartner, Graulty, Hillyard, & Pitts, this issue), but I am also open and cautious to see evidence supporting the ‘minority view’ that C1 can be modulated by spatial attention under certain experimental settings.

The elusiveness of attentional modulations on C1 has been demonstrated in our previous studies with different experimental settings—the C1 component is immune to attentional modulation (Fu, Caggiano, Greenwood, & Parasuraman, 2005a; Fu, Fan, Chen, & Zhuo, 2001; Fu, Fedota, Greenwood, & Parasuraman, 2010b; Fu, Greenwood, & Parasuraman, 2005b), is enhanced by attention (Fu, Fedota, Greenwood, & Parasuraman, 2010a; Fu et al., 2009), and even attenuated by attention (Fu et al., 2008). From these studies, we have tentatively proposed that factors such as V1-tuned stimuli with distractors, involuntary attention and high perceptual (but not attentional) load are important for eliciting the potential C1 attentional effect (Fu et al., 2010b; Fu, Fedota, Greenwood, & Parasuraman, 2012; Fu et al., 2009). This is because only two studies satisfying all the abovementioned conditions have demonstrated significant C1 attentional effects (Fu et al., 2010a, 2009), whereas our other studies using a sustained attention paradigm (Fu et al., 2008), manipulating attentional load (Fu et al., 2010b), or using peripheral cuing but presenting only a single stimulus without distractors or without applying high perceptual load (Fu et al., 2005a, 2001, 2005b) show no such C1 attentional effects. Notably, however, a recent study using similar V1-tuned stimuli with distractors and high perceptual load and applying a peripheral cuing paradigm basically replicated this attentional modulation on C1 (Dassanayake, Michie, & Fulham, 2016), consolidating the camp of the ‘minority view’. While both studies of the present debate (Kelly, Gomez-Ramirez, & Foxe, 2008; Baumgartner et al., this issue) used a voluntary attention paradigm, it seems to me that an involuntary attention paradigm (peripheral cuing) and its combination with other factors are probably more promising in eliciting potential C1 attentional effect because peripheral cuing is faster, more reflexive or automatic.