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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-Raminez, & 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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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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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.

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 (Stănişor, 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 unpredicted. To what extent attention and/or expectation can influence feedforward processing in V1 thus is an important question for future studies.

Disclosure statement

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