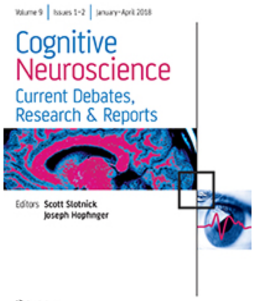

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AUTHOR RESPONSE

Does spatial attention modulate the C1 component? The jury continues to deliberate

Hannah M. Baumgartner[a], Christian J. Graulty[b], Steven A. Hillyard[c] and Michael A. Pitts[b]

[a]Department of Psychology, University of Michigan, Ann Arbor, MI, USA; [b]Department of Psychology, Reed College, Portland, OR, USA; [c]Department of Neurosciences, University of California San Diego, La Jolla, CA, USA

ABSTRACT
The thoughtful comments on our study (Baumgartner et al., this issue) that failed to replicate the C1 attention effect reported by a previous study roughly fall into three broad categories. First, the commentators identified specific differences between the two studies that may have contributed to the discrepant results. Second, they highlighted some of the theoretical and methodological problems that are encountered when trying to demonstrate attention effects on the initial evoked response in primary visual cortex. Third, they offered a number of proposals for optimizing experimental designs and analysis methods that may increase the likelihood of observing attention-related modulations of the C1. We consider each of these topics in turn.

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Experimental design differences

Several commentators (Ding, this issue; Klein, this issue; Pourtois et al., this issue) suggested that the diagonal stimulus configuration used by Kelly, Gomez-Ramirez, and Foxe (2008; K et al.) might have enabled greater attentional selectivity than the horizontally symmetrical configurations used by Baumgartner et al. (B et al.) Such increased selectivity might arise because of the larger spatial separation between the diagonally situated attended and unattended locations or because of their belonging to separate upper and lower visual quadrants. In terms of spatial separation, the stimuli used by K et al. were separated by 8° of visual angle, while in B et al., the stimuli were separated by either 4° (closer pair) or 6.92° (farther pair) depending on which locations elicited an optimal C1 during the probe session. When we restricted our analyses to include data only from subjects assigned the farther pair of locations (6.92° separation), a C1 attention effect was still not evident. While it can’t be ruled out that a 1.08° difference in stimulus separation or the diagonal vs. horizontal configuration difference had an influence on the observed C1 attention effects, if this were the case it would suggest that early V1 modulation is not a consistently engaged mechanism of visual spatial attention but rather is obtained only under a highly limited set of conditions.

Kelly and Mohr (this issue) identified another physical stimulus difference between K et al. and B et al. that may be consequential. Due to the use of updated/improved code for stimulus presentation in B et al. (kindly provided by K et al.), the non-target gratings contained only high spatial frequencies while the target rings embedded in these gratings contained a low spatial frequency component. In K et al., both the target and non-target stimuli contained low spatial frequency energy. Kelly and Mohr point out that such a difference might impact the way in which the target detection task was performed, and consequently, whether attention modulated processing of the non-target gratings. Kelly and Mohr also suggested that participants in K et al.’s study may have been more highly motivated to perform the task well due to experimenter encouragement. The potential importance of motivation and reward in modulating C1 was also pointed out by Slagter et al. (this issue). We agree that these are all important factors to consider, particularly if the C1 can only be modulated by attention under a narrow range of conditions.

Ding pointed out another design difference between the studies that may be important. In B

CONTACT Michael A. Pitts mpitts@reed.edu Department of Psychology, Reed College

et al., each subject completed two identical sessions of the attention experiment in which stimuli were positioned in upper or lower fields during different blocks. In K et al., each subject completed a single session of the attention experiment in which the stimuli remained fixed at two diagonally opposite locations. Ding suggested that this difference might have allowed a 'fast learning' of the stimulus configuration in K et al. that may have increased attentional selectivity. This proposal seems plausible and is readily testable in future experiments. However, Ding's suggestion that the C1 attention effect observed by K et al. may have been a long-latency, anticipatory response time-locked to the cue rather than a short-latency response elicited by the target seems less plausible. Even if participants' could learn to precisely estimate stimulus onset after a cue-target interval of 833 ms, any anticipatory ERP or oscillation would have to have opposite polarity for anticipated targets in upper and lower visual fields.

Inherent problems in studying C1/V1 attention effects

While numerous fMRI studies have demonstrated that spatial attention modulates neural activity in V1 (reviewed in DiRusso et al. 2003, 2012), the poor time resolution of hemodynamic measures does not allow a conclusion as to whether the initial feed-forward response of V1 is affected. As several commentators indicated, evaluations of V1 attention effects using non-invasive EEG or MEG techniques, which do have adequate time resolution, are nonetheless problematic. First, as Slagter et al. point out, modulations of cortical neurons by attention may or may not produce a surface manifestation that is detectable by EEG or MEG recordings. Second, Klein referred to the lively debate that has ensued about whether the surface-recorded C1 does in fact originate from primary visual cortex, and whether the classic polarity inversion of the C1 is diagnostic of a neural generator in V1 (Ales, Yates, & Norcia, 2013; vs. Kelly, Vanegas, Schroeder, & Lalor, 2013). In our view, the initial phase of C1 (~50–80 ms) is very likely to represent neural activity in V1, but other cortical areas may well become active during the middle and later phases of the C1 (~80–120 ms) and may contribute to any amplitude modulations that may occur. Third, and perhaps most problematic, is the enormous inter-individual variability in the gyral anatomy of V1 and consequently of the surface-recorded waveforms in the C1 latency range, as pointed out by Klein and Pourtois et al. Both K et al. and B. et al. attempted to mitigate this inconvenient fact by choosing stimulus positions that maximized C1 amplitude and its polarity inversion, but notable individual differences persisted. These differences make it very difficult to obtain group averages with high signal to noise ratios of attentional modulations of a common neural generator.

Strategies for inducing C1/V1 attention effects

Commentators offered a number of proposals for experimental designs that might reveal C1/V1 attention effects. Several experimental factors that may be conducive to eliciting C1 attention effects were proposed by Fu (this issue), Pourtois et al., and Slagter et al.: (1) Use stimuli specifically tuned to activate V1 neurons and thereby elicit large C1 components, but not so large as to create a ceiling effect for attention, (2) Use stimulus configurations that include distractors to increase perceptual load, (3) Use tasks that require high motivational engagement. These are all good suggestions.

In addition to these factors, Fu advocates for the use of peripheral cueing of exogenous attention rather than central cueing of endogenous attention in order to elicit detectable C1 attention modulations. Indeed three previous studies that combined high perceptual load stimuli with exogenous cueing of attention reported C1 modulations for validly versus invalidly cued targets (Dassanayake, Michie, & Fulham, 2016; Fu, Fedota, Greenwood, & Parasuraman, 2010; Fu et al., 2009). In all of these studies, the measured C1 enlargement took the form of a protracted negativity that was superimposed on both the C1 and subsequent midline P1. Based on this waveform, Dassanayake et al. suggested that the most parsimonious interpretation was that the attention effect observed in these exogenous cueing studies was most likely not a modulation of the C1, but rather a third component that overlapped the C1-P1 in time. Indeed, in the study by Fu et al. (2010) the enhanced negativity on valid trials had its onset well before the C1 and was largest at the CPZ site, while the C1 itself was largest more posteriorly, at the POZ site, and did not show an enhanced negativity on valid trials at this site. Without a thorough analysis of the scalp topography and neural sources of the attentional modulation in relation to those of the C1 itself, we remain unconvinced that the reported attention effects on the measured C1 actually represent a modulation of the initial evoked response in striate cortex. Indeed, the C1 modulation reported by Fu et al. (2009, 2010) appears to have a more anterior scalp topography than those reported for the C1 itself (e.g., Clark, Fan, & Hillyard, 1994, 2003; Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Di Russo et al., 2012).

While exogenous cueing creates potential stimulus confounds due to overlap between the cue and target evoked ERPs at short SOAs, these previous studies (Dassanayake et al., 2016; Fu et al., 2009, 2010) attempted to circumvent this issue by including cue-only or long SOA trials followed by an initial subtraction of cue-locked ERPs prior to C1 analysis. A further complication in studies using exogenous cues, however, is that sensory interactions between the cue and target may differ when they are presented at the same versus different locations. These interactions typically result in refractory effects on target ERPs that are greater for valid trials when the cue and target occur at the same location. In the studies under consideration here, such a refractory effect might account for the apparent C1 enhancement on valid trials if the amplitude of the temporally overlapping midline P1 was reduced due to a refractory interaction with the cue. That is, for stimuli in the upper visual field, a reduced P1 amplitude on valid trials would produce less cancellation of the overlapping portion of the C1 waveform and thus could result in a larger (more negative) measured C1 amplitude. Consistent with this interpretation, the reported C1 enhancements on valid trials (which were only reported for upper field stimuli) were associated with reduced midline P1 amplitudes in all the above-mentioned exogenous cueing studies. With exogenous cueing of attention there is always the possibility that validity effects on the target ERP may be influenced by sensory interactions as well as by shifts of attention. For these reasons, it is important to restrict analyses of potential C1 attention effects to the leading edge of the C1 peak (~50–80 ms) at occipital-parietal electrode sites, and to demonstrate C1 amplitude modulations for both upper and lower visual field stimuli.

In addition to improved experimental designs, several commentators (Klein, Pourtois et al. & Slagter et al.) recommended the use of more advanced multivariate and Bayesian analysis techniques to detect C1/V1 modulations within the morass of individual variability. This is an important point, because the primitive mean-amplitude-at-a-few-electrodes measures that we have been making over the years may not capture more subtle patterns of neural modulation that may be occurring in V1.

Finally, Klein proposed an intriguing experiment that combines SSVEPs and fMRI with the aim of identifying a V1 source of attentional modulation with greater precision. If an SSVEP source specific to V1 could be isolated from concurrent SSVEPs in other areas, this approach could be fruitful. Such an experiment would be a methodological tour de force, but it might be the case that attention could modulate the V1 response to steady-state, continuously present stimuli in a different way from its effect on transient stimuli.

In summary, as standard bearers of the 'majority view' our conclusion is that the C1 component may well be modulated by spatial attention under some circumstances, but consistent and reproducible effects localized to the primary visual cortex have yet to be demonstrated. We look forward to further experiments that will surely be forthcoming to illuminate this potentially important mechanism of visual selective attention.

Disclosure statement

No potential conflict of interest was reported by the authors.

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