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Still wanted: a reproducible demonstration of a genuine C1 attention effect

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DISCUSSION PAPER



The experimental parameters that affect attentional modulation of the ERP C1 component

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ABSTRACT

There is current debate as to whether spatial attention can modulate V1 activity during the initial wave of visual processing. Research on this topic has focused on the event-related potential (ERP) C1 component, which primarily reflects activity in V1. The purpose of the present selective review was to compare experimental parameters across spatial attention studies to determine whether certain stimulus, task, or analysis conditions were more likely to produce significant C1 attention effects. Specifically, C1 attention effects were evaluated as a function of visual field location, presence or absence of distractors, load (perceptual or attentional), cue type (endogenous or exogenous), and electrode location. As the C1 component has its peak magnitude at midline parietal-occipital electrodes, only studies that measured C1 attention effects at these electrode locations were considered. Furthermore, only studies that manipulated spatial attention, and no other factors, were considered. The current analysis indicated that to maximize sensitivity to C1 attention effects, stimuli should be in the upper visual field, there should be distractors, conditions should be high perceptual or attentional load, there should be exogenous cuing, and effects should be measured at midline parietal-occipital electrodes POz, Pz, and CPz.

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Spatial attention effects have been observed in extrastriate cortex, but there has been intense debate regarding whether and when spatial attention effects occur in V1 (Slotnick, 2013). The nature of the V1 spatial attention debate has evolved over time. It was initially thought that V1 was not modulated by attention, but after V1 attention effects were consistently observed, attentional modulation was proposed to occur relatively late in time (> 100 milliseconds after stimulus onset) via feedback from extrastriate cortex (Di Russo, Martínez, & Hillyard, 2003; Di Russo et al., 2012).

The answer to the current debate hinges on whether or not spatial attention can modulate V1 activity early in time (< 100 milliseconds after stimulus onset) during the initial wave of visual processing in this region. Research on this topic has focused on the event-related potential (ERP) C1 component, which, as discussed in the next section, primarily reflects activity in V1. Some studies have observed that spatial attention can significantly modulate the C1 component, while other studies have not reported C1 attention effects. The purpose of the present paper was to compare experimental parameters across spatial

attention studies to determine whether there are certain stimulus, task, or analysis conditions that are more likely to produce significant C1 attention effects.

Polarity, timing, topography, and cortical source of the C1 component

V1 is retinotopically organized with the upper visual field mapped onto the lower bank of the calcarine sulcus, the lower visual field mapped onto the upper bank of the calcarine sulcus, the right visual field mapped onto the left hemisphere, and the left visual field mapped onto the right hemisphere. Figure 1(a), right, illustrates the mapping of the upper visual field and the lower visual field onto the lower bank of the calcarine sulcus and the upper bank of the calcarine sulcus, respectively (adapted from Figure 1 in Rauss, Schwartz, & Pourtois, 2011). Activity within the calcarine sulcus is well modeled by a dipole (separated positive and negative charge) current source that produces activity that can be measured on the scalp using electrodes (Nunez & Srinivasan, 2006). Figure 1(a), left, illustrates the activation time-courses corresponding to stimuli in the upper visual field (in blue) and the lower visual field stimulation (in red). Because the banks of the calcarine sulcus are

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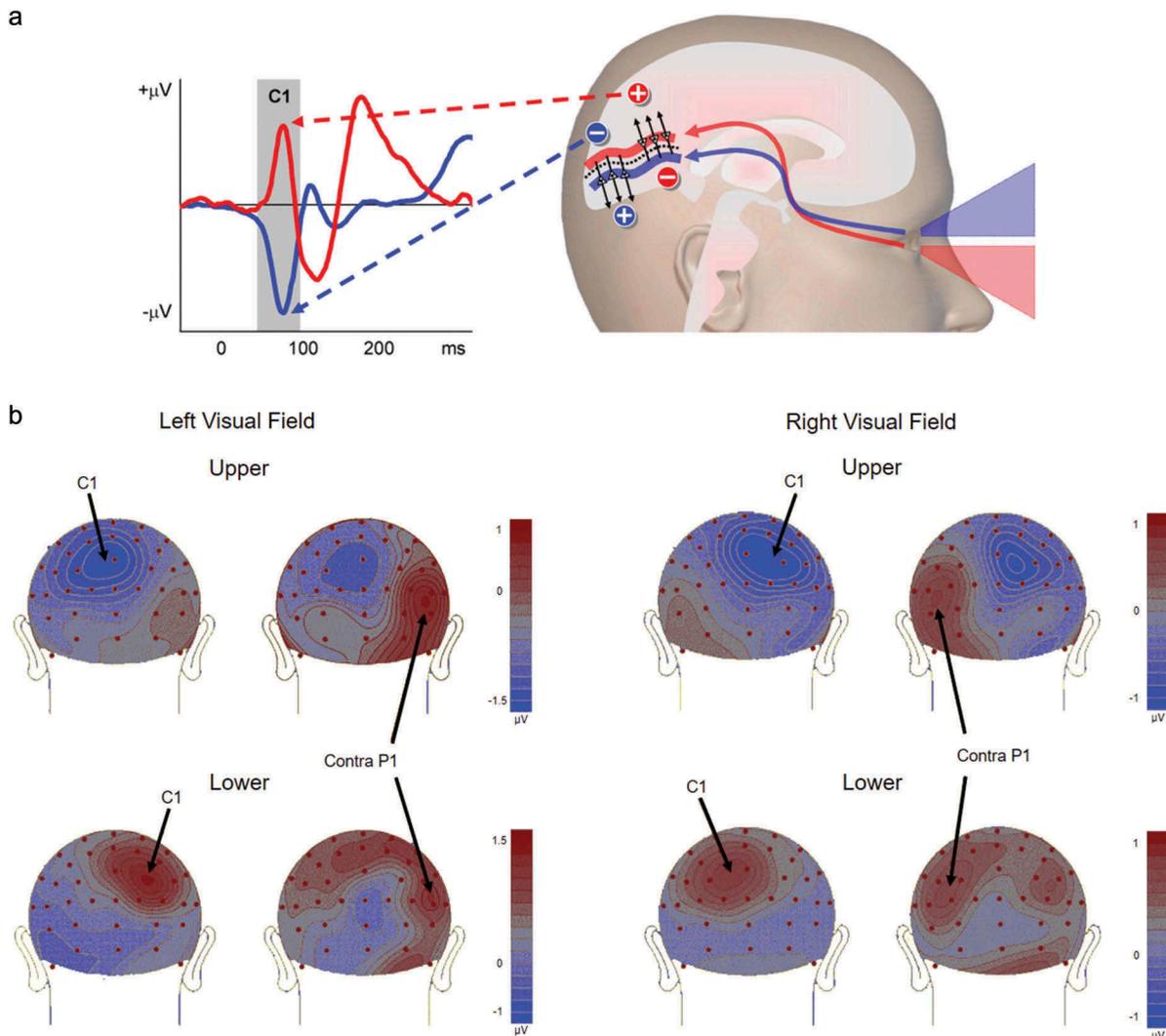


Figure 1. C1 activation timecourses produced by upper visual field stimuli and lower visual field stimuli. (a) Right, the upper visual field maps onto the lower bank of the calcarine sulcus (in blue) and the lower visual field maps onto the upper bank of the calcarine sulcus (in red). Left, activation timecourses (microvolts x milliseconds) for an upper visual field dipole source (in blue) and a lower visual field dipole source (in red). The C1 activation period is shown in gray. Reprinted from *Neuroscience and Biobehavioral Reviews*, 35/5, Karsten Rauss, Sophie Schwartz, and Gilles Pourtois, Top-down effects on early visual processing in humans: A predictive coding framework, 1237–1253, 2011, with permission from Elsevier. (b) C1 and early P1 topographic maps associated with each quadrant of the visual field. Left, left visual field topographic maps (posterior views, electrode locations in red; keys, in microvolts, to the right of each panel). Right, right visual field topographic maps. Reprinted from *Human Brain Mapping*, Volume 15, Francesco Di Russo, Antígona Martínez, Martin I. Sereno, Sabrina Pitzalis, and Steven A. Hillyard, Cortical sources of the early components of the visual evoked potential, Pages 95–111, Copyright (Di Russo et al., 2002), with permission from John Wiley and Sons.

oriented in opposite directions, the activation timecourses corresponding to upper visual field stimuli and lower visual field stimuli in the 50 to 100 millisecond time range (highlighted in gray) are of opposite polarity at midline parietal-occipital electrodes, which is the C1 ERP component. Figure 1(b) illustrates scalp topographies of C1 components (which reflect V1 sources) and early P1 components (which reflect extrastriate sources) corresponding to stimuli in each quadrant of the visual field (adapted from

Figures 5 and 6 in Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002). The C1 component is maximal over midline parietal-occipital electrodes and reverses in polarity for upper visual field stimuli and lower visual field stimuli, while the early P1 component is maximal over contralateral occipital electrodes and is always positive in magnitude. The C1 component onsets at approximately 55 milliseconds with a peak latency of 90–92 milliseconds, while the early P1 component onsets at approximately 72–80

milliseconds with a peak latency of 98–110 milliseconds (Di Russo et al., 2002). Thus, these components have substantial temporal overlap but are topographically separable.

There has been recent debate regarding whether the C1 component reflects activity in V1 or might reflect activity in extrastriate regions V2 and V3. Ales, Yates, and Norcia (2010) conducted simulations and showed that V2 and V3 sources reversed in polarity for upper visual field versus lower visual field stimulation. Kelly, Schroeder, and Lalor (2013a) responded by pointing out the simulations were limited because of the quadrant-sized stimuli employed. In response, Ales, Yates, and Norcia (2013) conducted additional simulations using much smaller stimuli, including a small circle (1° of visual angle in radius), and found that upper visual field stimulation and lower visual field stimulation produced polarity inversion for V1, V2, and V3 sources. These findings illustrate that polarity inversion alone cannot be used to differentiate between these regions. However, as pointed out in a final reply by Kelly, Vanegas, Schroeder, and Lalor (2013b), at midline parietal-occipital locations, simulated V1 sources produced negative activity for upper visual field stimuli and positive activity for lower visual field stimuli, whereas simulated V2 and V3 sources produced positive activity for upper visual field stimuli and negative activity for lower visual field stimuli. As empirically measured C1 responses match the predicted V1 source activation profile (see Figure 1) and is in direct opposition to the predicted V2 and V3 source activation profiles, it can be concluded that the C1 component primarily reflects V1 activity (see Kelly et al., 2013b, for additional simulations supporting this conclusion). It should be noted that some studies have employed dipole source localization in an attempt to isolate the cortical generator of the C1 component.

However, the spatial resolution of dipole source localization is about 1 centimeter at best (Slotnick, 2004), which is too low to differentiate between V1 and early extrastriate regions; thus, source localization results are not considered in the present paper. Of importance, since the C1 component primarily reflects activity in V1, the magnitude of this component can be measured to assess whether spatial attention modulates V1 activity.

Experimental parameters that affect attentional modulation of C1

Across spatial attention studies, the magnitude of the C1 component has been evaluated as a function of many key experimental parameters including visual field location, presence or absence of distractors, load, cue type (endogenous or exogenous), and electrode location. The term load refers to the processing demands of a particular stimulus or task (Lavie, 1995) and can be dissected into perceptual load and attentional load. Higher perceptual load may lead to greater attentional allocation to targets in a smaller region of the visual field, whereas higher attentional load (e.g., in the central visual field) may lead to lesser attentional allocation to distractors at other visual field locations. Perceptual load and attentional load are considered separately in this section, as these are unique constructs and it has been debated whether attentional load, in particular, is crucial for eliciting C1 attention effects (Rauss, Pourtois, Vuilleumier, & Schwarz, 2012b; Fu, Fedota, Greenwood, & Parasuraman, 2012). As the C1 component has its peak magnitude at midline parietal-occipital electrodes, only studies that measured C1 attention effects at these electrode locations are considered in this section. Furthermore, only studies that manipulated spatial attention, and no other factors, are considered in this section (other studies are

Table 1. Spatial attention study parameters and C1 significance.

Study	VF	Distractors	Load	Cue	Electrode(s)	C1 significance
Di Russo et al. (2003)	LUVF/RUVF/LLVF/RLVF	No	Low per/att	End	POz	LVF marginally sig
Hopfinger and West (2006)	LUVF/RUVF	No	Low per/att	End/Exo	Pz/POz	Not sig
Fu et al. (2009)	LUVF/RUVF	Yes	Low/Med/High per	Exo	POz/Pz/CPz	High load sig Pz
Rauss et al. (2009)	UVF/LVF	Yes	Low/High att	End	CP1/CPz/CP2/P1/Pz/P2	UVF low vs. high load sig
Fu et al. (2010a)	LUVF/RUVF	Yes	Low/High per	Exo	POz/Pz/CPz	High load sig Pz/CPz
Di Russo et al. (2012)	LUVF/RUVF/LLVF/RLVF	No	Low per/att	End	PO1/PO2/P1/P2	Marginally sig
Rauss et al. (2012a)	UVF	Yes	Low/High att	End	CP1/CPz/CP2/P1/Pz/P2	High vs. low load sig
Ding et al. (2014)	UVF/LVF	Yes	Low/High att	End	POz	Not sig
Dassanayake et al. (2016)	LUVF/RLVF	Yes	High per	Exo	Oz/POz/Pz	UVF sig at POz

L = left, R = right, UVF = upper visual field, LVF = lower visual field, Per = perceptual, Att = attentional, End = endogenous, Exo = exogenous, Sig = significant. Significant, marginally significant, and non-significant effects are shown in darker gray, lighter gray, and white, respectively. Only low/med/high load and low/high load studies manipulated load. Low perceptual/attentional load studies were classified as such because there were no distractors and the tasks were simple target detection.

considered in the following section). The goal of this selective review is to focus on studies that found a C1 spatial attention effect to identify the parameters that are critical for observing this sometimes subtle effect.

Table 1 shows the experimental parameters and C1 attentional modulation significance for nine studies (Dassanayake, Michie, & Fulham, 2016; Ding, Martinez, Qu, & Hillyard, 2014; Di Russo et al., 2003, 2012; Fu, Fedota, Greenwood, & Parasuraman, 2010a; Fu et al., 2009; Hopfinger & West, 2006; Rauss, Pourtois, Vuilleumier, & Schwartz, 2009, 2012a). Five of these studies (shown in darker gray) reported significant attentional modulation of the C1 component. For each of these studies, significant C1 attention modulation was observed for a particular parameter and/or electrode location. Fu et al. (2009) only observed significant attentional modulation (i.e., a greater magnitude of activity for valid than invalid trials) in the high perceptual load condition at electrode Pz, even though effects were also measured at electrodes POz and CPz. Similarly, Fu et al. (2010a) measured attention effects at the same electrodes and observed significant C1 modulation in the high perceptual load condition at electrodes Pz and CPz. These findings illustrate that C1 attention effects can be maximal at electrode locations near to but other than POz. Dassanayake et al. (2016) used a very similar

paradigm as Fu et al. (2009), with only a high perceptual load condition, and reported significant C1 modulation at electrode POz. Rauss et al. (2009) observed significant attentional modulation for only upper visual field stimuli, which corresponded to a low versus high attentional load central visual field task (where central and peripheral stimuli were temporally distinct). Rauss et al. (2012a) employed a similar paradigm, but with temporally synchronous central and peripheral stimuli, and also observed significant attentional modulation for only upper visual field stimuli; however, this corresponded to the reverse high versus low attentional load central visual field task. It is notable that the opposite effects in Rauss et al. (2009) and Rauss et al. (2012a) indicate that they were not simply due to greater arousal in the high attentional load condition. Of primary importance, both of the studies by Rauss et al. showed attentional modulation of the C1 component. The findings above indicate that either high perceptual load conditions (Dassanayake et al., 2016; Fu et al., 2010a, 2009) or high attentional load conditions (Rauss et al., 2009, 2012a) can produce significant C1 attention effects.

Although two of the studies (shown in lighter gray in Table 1) reported non-significant attention modulation of the C1 component, there is evidence for some degree of attentional modulation in these studies. Di Russo et al.

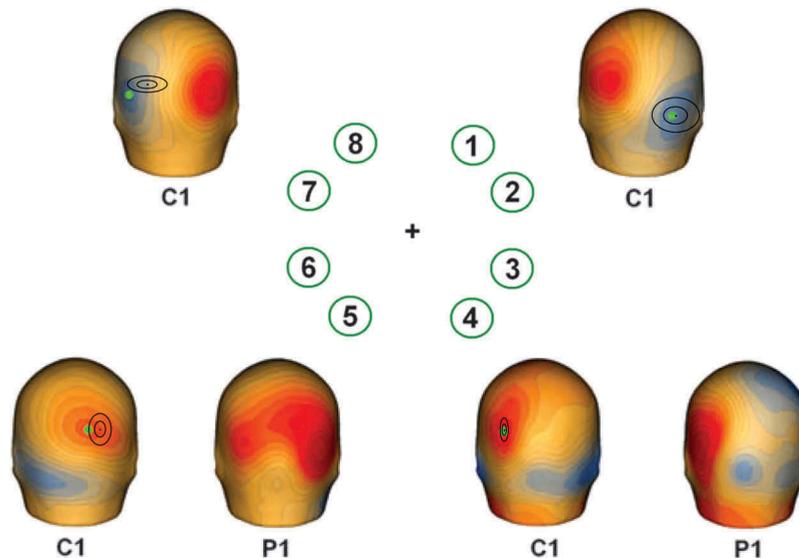


Figure 2. Electrode locations used to measure 'C1' attention effects in Kelly et al. (2008). For each quadrant, peripheral stimulus locations (1 and 2 in upper right, 3 and 4 in lower right, 5 and 6 in lower left, and 7 and 8 in upper left) and mean electrode location (center of each bullseye \pm 1 and 2 standard errors) used to measure 'C1' attention effects. Electrode locations are projected onto representative individual participant 'C1' topographic maps for each quadrant (posterior views, positive and negative voltages in red and blue, respectively; individual participant electrode locations in green). 'C1' topographic maps and, for lower visual field stimuli, P1 topographic maps were measured at 80 and 100 milliseconds after stimulus onset, respectively. Simon P. Kelly, Manuel Gomez-Ramirez, and John J. Foxe, Spatial attention modulates initial afferent activity in human primary visual cortex, *Cerebral Cortex*, 2008, 18(11), 2629–2636, by permission of Oxford University Press.

(2003) measured the peak C1 amplitude of activity associated with attended and unattended stimuli in each quadrant at electrode POz. For lower visual field stimuli, collapsed over quadrant, the magnitude of the C1 component for attended stimuli versus unattended stimuli was marginally significant ($p < .10$; see their Table 1). Inspection of their Figure 2 shows that the left lower visual field stimulus had close to zero attentional modulation, while their Figure 3 shows that the right lower visual field stimulus had marked attentional modulation (which presumably drove the marginal significance). As such, it is likely that Di Russo et al.'s right lower visual field C1 attention effect would have been significant if tested alone. Di Russo et al. (2012) similarly measured the peak C1 amplitude of activity associated with attended stimuli and unattended stimuli in each quadrant just lateral to electrodes POz and Pz. In all four quadrants, the magnitude of activity associated with attended stimuli was numerically greater than the magnitude of activity associated with unattended stimuli, which corresponds to a marginally significant attentional modulation of the C1 component ($p < .10$; one-tailed binomial test). As the results of Fu et al. (2009, 2010a) showed that C1 attentional modulation may occur at other electrode sites other than POz (i.e., Pz and CPz), it is also possible that the electrode sites evaluated by Di Russo et al. (2003, 2012) were not optimal for detecting attention effects.

The two remaining studies (unshaded in Table 1) found non-significant attention modulation of the C1 component. Although the C1 attentional modulation of Hopfinger and West (2006) was non-significant for both exogenous and endogenous cueing conditions (collapsed over visual field), in both instances the magnitude of activity associated with the attended stimuli was greater than the magnitude of activity associated with the unattended stimuli (similar to Di Russo et al., 2012). Ding et al. (2014) used a similar experimental protocol to Rauss et al. (2009), but did not observe significant C1 attentional modulation of upper visual field stimuli. One substantive difference between these studies was the primary stimulus. Rauss et al. employed a colored upright or inverted T-shape in the central visual field (less than 2° of visual angle), while Ding et al. employed a grid of twelve horizontal or vertical lines in the central visual field and the peripheral visual field (greater than 5° of visual angle). Ding et al.'s larger central/peripheral visual field stimulus, or some other difference between these studies, presumably eliminated the C1 attentional modulation of the upper

visual field stimulus observed by Rauss et al. The null findings of Ding et al. indicate that C1 attentional modulation is stimulus specific, but they do not question the validity of Rauss et al.'s significant results.

Comparisons across studies can provide insight into the parameters that give rise to more significant C1 attention effects. Rauss et al. (2009) observed significant C1 attentional modulation for upper visual field stimuli but not lower visual field stimuli. However, many studies that observed significant effects only tested upper visual field stimulus locations (Dassanayake et al., 2016; Fu et al., 2010a; Rauss et al., 2009, 2012a) and there was evidence of marginal significance for lower visual field stimuli in one study (Di Russo et al., 2003). These findings indicate that C1 attention effects can occur for upper visual field stimuli, while there is limited evidence regarding lower visual field stimuli. All of the studies that reported significant C1 attention effects had distractors and the majority of the non-significant or marginally significant studies did not have distractors, which indicates that distractors increase the magnitude of attention effects. Cue type was variable for the studies that reported significant C1 attention effects; however, the majority of non-significant or marginally significant studies employed endogenous cueing. This suggests that exogenous cueing is more likely to elicit C1 attentional modulation. In the studies that employed exogenous cueing, the stimulus onset asynchrony (SOA) between the cue and the target was either variable (68–268 in Hopfinger & West, 2006, and 100–300 milliseconds in Fu et al., 2010a) or fixed (150 milliseconds in Fu et al., 2009, and 160 milliseconds in Dassanayake et al., 2016). The lower range of SOAs in Hopfinger and West (2006) were somewhat shorter than in the other studies; however, it is unlikely this contributed to the differential findings, as the mean SOA was similar between studies. To isolate target activity from cue activity, the studies that employed a variable SOA used Adjar (Woldorff, 1993) and the studies that employed a fixed SOA subtracted cue-only activity from cue-target activity. As significant C1 attention effects were observed for both SOA types and component correction methods, these do not appear to be important factors for the present analysis. Across all studies, the electrodes at which significant attention effects occurred varied and included Pz (also measured at POz and CPz), CP1/CPz/CP2/P1/Pz/P2, Pz/CPz (also measured at POz), and POz (also measured at Oz and Pz). The electrodes at which non-significant or marginally significant attention effects occurred were

measured at one electrode location (POz), two electrode locations (Pz and POz), or off-midline electrode locations (PO1/PO2/P1/P2). As the most sensitive electrode can vary across studies, C1 attention effects should be measured at midline electrodes POz, Pz, and CPz (e.g., measuring effects separately at each electrode, Bonferroni corrected for multiple comparisons; Fu et al., 2009, 2010a; Dassanayake et al., 2016; entering all three electrodes in a repeated-measures test may be less sensitive due to optimal electrode variability). With regard to ideal study parameters to maximize sensitivity to C1 attention effects, stimuli should be in the upper visual field, there should be distractors, conditions should be high perceptual or attentional load, there should be exogenous cuing, and effects should be measured at electrodes POz, Pz, and CPz.

Other spatial attention studies

Many other studies have measured C1 spatial attention effects; however, the results of these studies are unclear for a variety of reasons. As described above, the C1 component is maximal at midline electrode locations at or just anterior to POz, the early P1 component is maximal at contralateral occipital electrodes, and these components temporally overlap. As detailed in Table 2, some studies evaluated attention effects at lateral occipital electrodes (Martínez et al., 1999; Kelly, Gomez-Ramirez, & Foxe, 2008; Mangun et al., 2001; Proverbio, Del Zotto, & Zani, 2007; Zani & Proverbio, 2012). However, lateral occipital activity primarily reflects the P1 component rather than the C1 component. Most of these studies measured attention effects at locations that clearly included lateral occipital electrodes (Martínez et al., 1999; see their Figure 3a) or were restricted to lateral occipital electrodes (Mangun et al., 2001; Proverbio et al., 2007; Zani & Proverbio, 2012). Significant attention effects in these studies, if observed, may have reflected some degree of P1 attentional modulation rather than only C1 attentional modulation.

Two studies used a probe task where, for each participant, eight visual field locations were stimulated in an effort to identify the electrode site of maximal C1 amplitude (50–80 milliseconds after stimulus onset) corresponding to one upper visual field stimulus and one lower visual field stimulus (Baumgartner et al., this issue; Kelly et al., 2008). In a subsequent spatial attention task, those stimulus locations and electrode sites

were used for each participant, and then attention effects were evaluated separately for upper visual field stimuli and lower visual field stimuli across participants. The potential issue with this probe procedure is that it may have identified electrodes corresponding to the early P1 component rather than the C1 component, as these components are temporally overlapping. To assess whether this was the case, I computed the mean electrode location across participants corresponding to each quadrant of the visual field from Kelly et al. (taken from their Figure 4). Figure 2 (adapted from Figure 4 in Kelly et al., 2008) shows that, for each stimulus quadrant, attention effects were measured at lateral occipital electrodes (the mean electrode location is shown at the center of the bullseye above each 'C1' topographic map). In both lower visual field quadrants (Figure 2, bottom), the electrode locations were contralateral to the stimulus locations, which occurred for all but one (10/11) of the participants. Moreover, the topography of the lower visual field 'C1' component was similar to the topography of the P1 component in the large majority (8/11) of the participants (see Kelly et al.'s Figure 4). This provides evidence that the 'C1' component corresponding to lower visual field locations may have reflected the contralateral early P1 component to some degree. In both upper visual field quadrants (Figure 2, top), the electrode locations were ipsilateral to the stimulus locations, which occurred for all but one of the participants, and, in the same participants, the 'C1' topography showed a contralateral positivity that likely reflected the contralateral early P1 (see Kelly et al.'s Figure 4). Thus, rather than reflecting the negative polarity C1 component (which would be expected to be maximal over midline parietal-occipital regions), the upper visual field electrode locations appear to have been primarily locked onto the ipsilateral voltage sink that was associated with the contralateral early P1 voltage source. To evaluate the electrode locations of Baumgartner et al. (this issue), I computed the mean electrode location across participants corresponding to each quadrant of the visual field (taken from their Figure 7) and linearly scaled these values (in the x and y dimensions) to match the head size of Kelly et al. such that the electrode locations could be compared between studies. The pattern of electrode locations in Baumgartner et al. were identical to those in Kelly et al., with upper visual field stimuli corresponding to ipsilateral occipital electrodes and lower visual field stimuli corresponding to contralateral occipital electrodes. A

statistical comparison revealed that the electrode locations between the studies did not significantly differ for the lower visual field stimuli (weighted ANOVA; lower left quadrant, $F_x(1,11) < 1$, $F_y(1,11) < 1$; lower right quadrant, $F_x(1,13) = 4.00$, $p = .067$, $F_y(1,13) < 1$). For upper left quadrant stimuli, there was no difference in the x dimension ($F_x(1,14) < 1$), while the Baumgartner et al. electrode location was significantly inferior to the Kelly et al. electrode location ($F_y(1,14) = 8.71$, $p < .05$). For upper right quadrant stimuli, the Baumgartner et al. electrode location was significantly more medial ($F_x(1,10) = 5.13$, $p < .05$) and superior ($F_y(1,10) = 30.80$, $p < .001$) to the Kelly et al. electrode location. Critically, the 'C1' attention effects in both Kelly et al. and Baumgartner et al. were measured at lateral occipital electrodes, which are more lateral and inferior than the electrode locations that are most sensitive to the C1 component. As such, the findings of these studies may have reflected some degree of P1 attentional modulation rather than only C1 attention modulation. Although the present results suggests the significant attention effects in Kelly et al. may not have reflected only C1 attentional modulation, their ingenious strategy of using a probe session to identify the optimal electrodes to measure C1 on an individual participant basis opens up a new line of promising research. For instance, as the analysis in the previous section indicated that C1 attention effects should be measured at midline electrodes POz, Pz, and CPz, data from a probe session could be used to identify the best single electrode within this set to measure C1 on an individual participant basis. An alternative more advanced technique would be to employ data from each individual participant's probe session to compare the C1 topographic map and the P1 topographic map, and electrodes could be selected from the entire set that reflected

only the C1 component to subsequently measure attention effects.

Table 2 also illustrates that a few studies presented stimuli along the horizontal meridian (as did Martínez et al., 2001), extending into the upper visual field and the lower visual field. As upper visual field stimuli and lower visual field stimuli produce C1 activity of opposite polarity (see Figure 1), stimuli presented along the horizontal meridian would be expected to largely cancel out and produce a muted C1 response that would limit the sensitivity of detecting attentional modulation. Other studies measured C1 attention effects at electrodes that were distant from POz, including Cz (Martínez et al., 2001) and P3/P4 (Fu, Greenwood, & Parasuraman, 2005), or very near to the reference electrode (CPz with reference at Cz; Fu et al., 2008), which would be expected to produce null C1 attention effects (Fu et al., 2005; Martínez et al., 2001) or inverted C1 attention effects (Fu et al., 2008). One study evaluated C1 attention effects by comparing attend left and attend right conditions (Noesselt et al., 2002), rather than comparing attended and unattended conditions for the same stimulus type, as is commonly done (e.g., Di Russo et al., 2003, 2012; Martínez et al., 1999). As attention was constant in both conditions of Noesselt et al. (2002), no differential C1 activity would be expected. There are also studies that aimed to investigate C1 attentional modulation (Schuller & Rossion, 2005; Zani & Proverbio, 2009); however, the expected polarity reversal did not occur. Finally, there have been a number of studies that manipulated arousal (directly, Fu, Fedota, Greenwood, & Parasuraman, 2010b; or indirectly, Woldorff et al., 2002; Karns & Knight, 2009), prediction (Herde, Rossi, Pourtois, & Rauss, this issue), motivation (Bayer et al., 2017), emotional processing (Pourtois,

Table 2. Spatial attention study parameters and significance at lateral occipital electrodes.

Study	VF	Distractors	Load	Cue	Electrode(s)	Significance
Martínez et al. (1999)	HM	Yes	High per/low att	End	TO1+	Marg sig
Mangun et al. (2001)	LUVF/RUVF	No	Low per/att	End	O1/O2	Not sig
Proverbio et al. (2007)	HM	No	Low per/high att	End	Lateral occ	Sig
Kelly et al. (2008)	LUVF/RUVF/LLVF/RLVF	No	Low per/att	End	Lateral occ	Sig
Zani and Proverbio (2012)	HM	No	Low per/att	End	Lateral occ	Sig
Baumgartner et al. (this issue)	LUVF/RUVF/LLVF/RLVF	No	Low per/att	End	Lateral occ	Not sig

L = left, R = right, UVF = upper visual field, LVF = lower visual field, HM = horizontal meridian, Per = perceptual, Att = attentional, End = endogenous, Sig = significant. Significant, marginally significant, and non-significant effects are shown in darker gray, lighter gray, and white, respectively. None of these studies manipulated load. Low perceptual/attentional load studies were classified as such because there were no distractors and the tasks were simple target detection. Martínez et al. (1999) was classified as high perceptual load as the target shared features with many distractors. Proverbio et al. (2007) was classified as high attentional load as the task required conjunction identification of shape and location.

Grandjean, Sander, & Vuilleumier, 2004; Santesso et al., 2008), or mood (Vanlessen, Rossi, De Raedt, & Pourtois, 2013, 2014), where C1 effects were considered from a spatial attention perspective. Many of these studies presumably employed conditions with a relatively high degree of ecological validity in an effort to increase the magnitude of attention effects; however, it is uncertain whether the effects reflected differential spatial attention or other factors that were manipulated. The studies that investigated C1 effects with manipulations other than spatial attention may be important to understanding disparate results. If not sufficiently controlled for, these factors could produce C1 effects in experiments that aim to manipulate only spatial attention.

It should also be noted that there are many other studies, not considered here, that did not analyze the C1 component, possibly because the experimental parameters were not ideal or this component was not of primary interest. For example, because small eye movements alter V1 receptive fields, very strict control of eye movements is important for measuring a C1 effect, whereas later components such as P1 are more robust to small changes in eye position. Therefore, some investigators may not have analyzed C1 spatial attention effects because control of eye position was insufficient. Another potential issue of concern is that extrastriate attention effects could potentially modulate the C1 component, particularly if post-processing filters cause later effects to appear earlier in time.

Conclusions

The present selective review aimed to identify the parameters that may maximize C1 attentional modulation. These parameters include measuring effects at electrodes POz, Pz, and CPz and employing distractors under high perceptual or attentional load. Furthermore, there is evidence that exogenous cuing and upper visual field stimuli may produce more robust C1 spatial attention effects than endogenous cuing and lower visual field stimuli. Future work should systematically manipulate these parameters to assess their impact on C1 spatial attention effects.

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No potential conflict of interest was reported by the author.

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COMMENTARIES

'Tricks' for revealing potential attentional modulations on the C1 component

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ABSTRACT

The t-test formula for a within-subject design suggests that the C1 attentional effect is more likely to be significant if the C1 attentional difference, as the numerator, is large and the standard deviation of the C1 difference that affects the denominator is small. Experimental manipulations for exploring potential C1 attentional effects can be evaluated by their contributions to the numerator and/or the denominator of the t-test formula. 'Tricks' that may enhance the C1 attentional difference and minimize the standard deviation of the sampled C1 are discussed.

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I agree with Slotnick (this issue) that optimal experimental parameters are of importance for studying attentional modulation on C1. The effects of some proposed 'tricks', such as upper-visual-field stimulation, high perceptual/attentional load, distractor-presented stimuli, involuntary attention, and flexible selection of measurement electrode, can be evaluated by their contribution to improving the statistical significance of the C1 attentional effect.

For the purpose of simplicity, let us consider the t-test formula of a within-subject design: $t = (\text{Mean}_{x1} - \text{Mean}_{x2}) / (\text{std of difference} / \sqrt{n})$. The t value basically determines the significance level (i.e., p value). Clearly, enlarging the difference between the means (the numerator), and minimizing the standard deviations of the difference and increasing N (both minimize the denominator) can increase the likelihood of statistical significance. Accordingly, for a better chance to observe a significant C1 attentional effect, three approaches can be taken: (1) enlarging the numerator by enhancing the attentional effect; (2) minimizing the denominator by minimizing

the standard deviation within a group; and (3) increasing N. While increasing N is a straightforward and useful statistical trick, more effort is required for the first two approaches.

There are several tricks for undertaking the first approach, the goal of which is to enhance the C1 attentional difference. The first trick is to make the attentional effect large. As noted by Slotnick (this issue), perceptual load (Dassanayake, Michie, & Fulham, 2016; Fu et al., 2009) and attentional load (e.g., Rauss, Pourtois, Vuilleumier, & Schwartz, 2009) are important factors for eliciting a large attentional effect. The presence of distractors with the target may also enhance attentional modulation, based on the competition hypothesis (Desimone & Duncan, 1995). Intuitively, small and low-contrast stimuli might seem better than large and perceptually salient stimuli, and stimulus offset may be more important than stimulus onset in minimizing automatic attentional attraction, such that more space is available for attentional modulation. However, one needs to strike a balance between enhancing attentional effects (small, faint stimulation and use of distractors preferred) and getting a decent C1 (large and salient stimulation usually preferred). In addition, special homogenous populations (such as professional athletes or other super-attenders) may help to 'amplify' attentional modulation on C1 relative to normal controls (Jin et al., 2010). Importantly, manipulation on a single parameter does not guarantee a C1 attentional effect—the optimal combination of these 'tricks' really matters.

The second trick is to keep the attentional effect consistent across trials. Peripheral cuing may help to maintain a more focused attentional distribution in a narrower stimulus onset asynchrony (SOA) time range (roughly 100 to 300 ms) relative to central cuing (usually approximately 500 ms). Although both fixed and randomized SOA between the peripheral cue and the target seem to work for eliciting a C1 attentional effect (Fu, Fedota, Greenwood, & Parasuraman, 2010; Fu et al., 2009), the optimal selection of SOA still awaits further investigation. The optimal selection of SOA has not been examined because a fixed SOA is supposed to elicit a more constant attentional effect across trials but requires a linear-hypothesized (which is not guaranteed) subtraction procedure to remove ERP overlap between the cue and the target. In contrast, randomized SOA is better for removing ERP overlap by using the ADJAR algorithm but may elicit a varied and SOA-dependent attentional effect across trials.

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The third trick is to increase the ratio of change. The C1 attentional effect is different from the C1 per se, and the ratio of change between the C1 attentional effect and baseline (usually the C1 of the unattended condition) is of more importance. A small-size C1 attentional effect of 0.5 microvolt is clearly more pronounced for a 1.5 vs. 1.0 microvolt comparison (50% enhanced) relative to a 3.0 vs. 2.5 microvolt comparison (20% enhanced). Again, a large C1 in the unattended condition could be disadvantageous because it may result in automatic attentional attraction and leaves little room for attentional modulation, thereby preventing a high ratio of change by attention.

Other ‘tricks’ can be used in undertaking the second approach, which aims to minimize the standard deviations in the group. Practical operations of this approach include, but are not limited to, the following: excluding participants showing no clear C1 in pilot studies, or showing strong alpha activities; individualized stimulus positioning and individualized electrode location for measurement; upper-visual-field stimulation to avoid ERP overlap from the subsequent P1 component; and selection of a group of homogenous participants (e.g., professional athletes) (Jin et al., 2010). Note that some tricks may contribute to both approaches. For example, individually adjusted stimulation positioning and the selection of a homogenous group mainly help to minimize the standard deviation of the group, but they may also affect the attentional effects. As a rule of thumb, a manipulation that can both enlarge the numerator and minimize the denominator in the t-test formula is definitely worth doing.

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Identifying and removing overlaps from adjacent components is important in investigations of C1 modulation by attention

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ABSTRACT

During recent years, perceptual/attentional load paradigms have been frequently used to investigate whether the initial visual cortical processing can be modified by spatial attention. For example, Rauss and colleagues reported significant modulations of the earliest component (i.e. the C1) of the visual evoked potential (VEP) as a function of attentional load. It may be questioned, however, whether these load effects represent modulations of the C1 or overlaps from other components. Here we summarize some methods to identify and remove the overlaps, which is important to clarify the question of whether the initial visual cortical processing could be modulated by attention.

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Whether the earliest visual evoked activity in the primary visual cortex (V1) as reflected by the VEP component C1 can be modified by attention is an important issue in understanding how the human visual system works. In the paper under discussion, Slotnick (this issue) reviewed recent related studies and proposed several valuable suggestions to investigate the C1 component. For example, the C1 effect should be measured at midline parietal-occipital electrodes where the C1 showed maximum amplitudes, and the early effects from lateral electrodes (e.g., those reported in the study of Kelly, Gomez-Ramirez, & Foxe, 2008) may have reflected modulations on some adjacent early components rather than the C1. These suggestions raised an important issue that an ERP effect during the C1 time window may not necessarily reflect a modulation of the C1 component generated in area V1 (see also Ding, this issue), and overlaps from adjacent components should be seriously considered when interpreting the early ERP effects.

Measuring the effects at midline parietal-occipital electrodes is a good method to reduce overlaps from adjacent components, such as laterally-distributed ones. However, it is not enough in the C1 studies since some other components, such as late components from the preceding stimulus, may also be recorded at midline parietal-occipital electrodes. Thus, detailed spatial-temporal analyses of the early ERP modulations and comparison with the original C1 component (as in the study of Ding, Martinez, Qu, & Hillyard, 2014) may be essential to determine whether these early ERP effects really reflect modulations of the C1. Slotnick (this issue, Table 1) listed several perceptual/attentional load studies which measured and reported C1 effects at midline parietal-occipital electrodes. Unfortunately, none of these studies provided convincing evidence from detailed spatial-temporal analyses of the early ERP modulations. In the attentional load studies of Rauss et al. (2009, 2012), source analyses were conducted on both the C1 components and the early load effects. While the C1 component was localized maximally

within the occipital cortex, the early load effect was significant in prefrontal (Rauss et al., 2009) or frontal/temporal/parietal (Rauss et al., 2012) regions rather than in the occipital cortex. In addition, the reported C1 effect was accompanied by a substantial pre-stimulus baseline shift (Rauss et al., 2012). These results suggest that the reported early load effects on the C1 amplitudes may not actually represent a modulation of the occipitally generated C1 itself, but rather an overlap with other ERP components (e.g., overlapping potentials from previous stimuli) elicited in these tasks. Thus, there is a lack of clear evidence supporting that the earliest visual evoked response in human V1 can be modified by spatial attention. Even if there are attentional modulations in early V1 activity, they may be submerged by much larger overlaps from other components, and cannot be clearly identified.

Since the overlaps from adjacent ERP components may seriously disturb the measurement of the C1 modulation, it is important to remove these overlaps as much as possible before detailed spatial-temporal analyses. Here we provide two efficient methods. The first one is to use the Adjacent Response (ADJAR) Technique (Woldorff, 1993), which is especially useful to remove overlapping potentials from preceding stimuli when measuring the C1 component. The second one is to measure the C1 component in an upper-minus-lower difference wave. This method takes advantage of a well-known characteristic of the C1 component in experimental design and data analyses. That is, the C1 component reverses its polarity for stimuli in the upper visual field (UVF) and the lower visual field (LVF). For most other components, however, such polarity reversal between the UVF and the LVF is absent. Thus, when subtracting the ERPs elicited by LVF stimuli from those elicited by UVF stimuli, most of the overlaps from adjacent components (especially those late components from preceding stimuli) will be eliminated, and a larger C1 with a cleaner baseline will be generated (Miller, Shapiro, & Luck, 2015). Note that when using upper-minus-lower difference waves to get a clear C1, the UVF and LVF stimuli should be presented randomly and with equal probabilities in a block. Otherwise, the overlapping potentials from preceding stimuli may

be different for the UVF and LVF stimuli and cannot be fully eliminated in the upper-minus-lower difference waves. In addition, the upper-minus-lower difference waves may still contain some activities from adjacent components (e.g., early P1) generated in retinotopically organized visual cortex other than the V1 (e.g., V2 and V3). However, these activities usually have different spatial-temporal properties than the C1 component. For example, the early P1 is maximal over contra-lateral scalp sites and starts 10–20 ms later than the C1. Thus, the C1 and these remaining overlaps can be well identified by detailed spatial-temporal analyses on the upper-minus-lower difference waves.

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Endogenous attention to object features modulates the ERP C1 component

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ABSTRACT

Converging neuroimaging and electrophysiological evidence supports the notion that selective attention can modulate neural activity not only in V1 (BA17)—as early as 40–60 ms post-stimulus—but also at the subcortical level (thalamic lateral geniculate nucleus, LGN). V1 modulation has been documented both in space-based and (especially) object-based selection conditions, most of all in endogenous orienting paradigms. It seems then that an attentional modulation of the ERP C1 response—reflecting V1 modulation—would not be especially favoured by exogenous cuing as far as object-based attention is concerned.

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Slotnick's (this issue) paper has the great merit of overtly addressing the long-standing issue of whether selective attention is able to modulate cortical activity at the earliest level, by concluding that spatial attention specifically enhances V1 excitability, as reflected by the C1 component of ERPs. Indeed an attention modulation for spatial attention has been shown at primary visual cortex and even earlier thalamic levels by fMRI and single cell studies (e.g., Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; McAlonan, Cavanaugh, & Wurtz, 2008), while electrical neuroimaging evidence has been provided that spatial frequency-based selective attention affects V1 activity as early as 40–60 ms in humans (Proverbio, Del Zotto, & Zani, 2010).

However, there is a point raised by Slotnick's (this issue) intriguing paper that needs to be

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further discussed. Indeed, the author states that to maximize C1 spatial attentional modulation there should be stimulus exogenous cuing because the majority of non-significant or marginally significant C1 attention effects employed endogenous cuing. Therefore, exogenous cuing is more likely to elicit C1 attentional modulation. However, this statement deserves a more thorough discussion, and it is certainly not conclusive when considering object-based attention mechanisms. Indeed, there are no theoretical reasons to believe that the C1 component is preferentially involved in exogenous as opposed to endogenous orienting of attention (but the reverse). Indeed, non-spatial attention studies almost exclusively involve endogenous attentional paradigms (e.g., Proverbio, Del Zotto, & Zani, 2007, 2010; Zani & Proverbio, 2009, 2012), in which participants pay sustained attention to a given object-feature (e.g., a spatial-frequency grating or a check-size throughout an experimental sequence, while the specific target is randomly changed across sequences). Interestingly, it has been shown that C1 modulation is stronger in object-based than space-based attention conditions, that is in endogenous cueing conditions (Zani & Proverbio, 2003). Indeed, we observed the functionality of these two attentional networks by inducing different attentional sets in participants while using the same set of stimuli—i.e., lateralized spatial frequency gratings. In different paradigms (Zani, Avella, Lilli, & Proverbio, 1999) participants were requested to pay heed and to respond to a target spatial frequency whatever its spatial location (object-based attention), or to attend and respond to the gratings spatial location, no matter their frequency (space-based attention). In this way, we disentangled the effect of stimulus physical features from that due to the volunteers' top-down attentional strategies on ERPs. Results revealed that spatial selection modulated mainly the extrastriate areas as indexed by a P1 whose arising phase started at about 80 ms post-stimulus, while spatial-frequency selection modulated the amplitude of a very early P/N80 followed by a prominent selection negativity. Overall, these data showed a larger C1 modulation in the object-based attention condition.

Since object-based attention is thought to modulate the activity of brain areas that normally

process a given feature (Kreutzer, Fink, & Weidner, 2015; Maunsell & Treue, 2006), it seems very reasonable to assume that selective attention to grating spatial frequency and orientation (that are the preferred V1 features) strongly modulate striate cortex during the preparatory attentional gating typical of endogenous orienting, as reflected by C1 modulation of ERPs (e.g., Proverbio et al., 2010). Therefore, the notion that C1 modulation is most evident in exogenous cuing does not certainly hold for features and object selection.

Disclosure statement

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Still wanted: a reproducible demonstration of a genuine C1 attention effect

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ABSTRACT

Slotnick (this issue) has specified a number of experimental parameters that appear critical for enabling an attention-related modulation of the C1 component. These include stimulus presentation in the upper visual field, the presence of distractors, a high perceptual or attentional load, and measurements at midline occipito-parietal sites. While we agree with many of these recommendations, we would modify others and even dispute a few. Despite the employment of these parameters in a few existing studies, there has not yet been a convincing, reproducible demonstration of a modulation of the C1 component by spatial attention that can be localized to primary visual cortex.

ARTICLE HISTORY

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KEYWORDS

C1; P1; attention

Commentary

Slotnick (this issue) proposes that C1 attention effects should be measured at midline electrodes POz, Pz, and CPz. However, for the range of stimulus positions considered in the first section of Slotnick's review, stimuli in the left or right upper field elicit maximal C1 amplitudes that are shifted ipsilaterally with respect to the midline, while lower left or right field stimuli elicit C1's with contralateral maxima. This shifting is evident in Slotnick's Figure 1b and is well-known. Instead of measuring C1 at the midline, where its amplitude may be minimal depending upon stimulus position (Clark, Fan, & Hillyard, 1995), we would argue that it is generally preferable to measure C1 at the electrode site where its amplitude is maximal. This is particularly true when stimuli are presented to the upper visual fields, as Slotnick recommends, because measuring C1 at its ipsilateral maximum (as did Di Russo et al. 2003, 2012) will separate it even further from concurrent P1 activity, which has an early contralateral maximum. Dipole

modeling has shown that the negative ipsilateral focus of the upper-field C1 is completely separate from the diffuse far-field sink of the contralateral P1 source in lateral extrastriate cortex (Di Russo et al. 2003; Clark et al., 1995). Accordingly, we disagree with Slotnick's suggestion that 'the electrode sites evaluated by Di Russo et al. (2003, 2012) were not optimal for detecting attention effects (on C1)'.

What kind of experimental evidence is required to establish a true attention effect on the C1? In our view such a demonstration would require that the scalp voltage topography of the component (or its derived intracranial source) when the stimulus is unattended is identical to that of the increment in voltage produced by attention. That is, what needs to be shown is that the neural response arising from a particular generator (such as the presumed source in V1 for the C1) is in fact being amplified by attention rather than being overlaid by a component having a different source. Such an analysis has been carried out for amplitude enhancements of the P1 and N1 components by spatial attention in extrastriate visual cortex (e.g., Di Russo et al. 2003, 2012). To our knowledge, none of the studies purporting to show a C1 increment with attention in primary visual cortex has made such a demonstration.

After reviewing studies by Fu et al. (2009, 2010) and Dassanayake, Michie, and Fulham (2016), Slotnick concludes that exogenous cueing is more likely to elicit attentional modulation of the C1. In our view, none of these studies provides convincing evidence for attentional modulation of the C1 itself. In particular, none of the aforementioned studies made the critical comparison to show an equivalence of the scalp topographies of the unattended C1 and the incremented negativity of the measured C1 with attention. As Dassanayake et al. point out, in all of these exogenous cueing studies the increased negativity in the C1 range 'can be characterized as a protracted negativity superimposed on the C1 and P1m peaks', and the increased C1 on validly cued trials could be 'a third negative component that spans the C1-P1m time range'. In the study of Fu, Fedota, Greenwood, and Parasuraman (2010) the superimposed negativity begins at target onset (i.e., with zero delay) and is fully developed at 30–40 ms, well before the onset of the C1; moreover, this added negativity overlying C1 has a distinctly more anterior

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scalp distribution than the C1 itself. This premature amplitude difference may have resulted from an inadequate removal of the ERP to the preceding cue. Casting further doubt on the proposition that exogenous cueing of attention modulates the C1 is the failure of Hopfinger and West (2006) to find such an effect under cueing conditions very similar to those of Fu and colleagues.

In the second section of his review, Slotnick considers studies where attentional modulations of C1 were measured at lateral rather than midline electrodes. He argues that more lateral occipital recordings might pick up attentional modulations of the P1, which could be confused with those of C1. We agree that the temporal overlap between the C1 and P1 is one of the most significant impediments to measuring C1 attention effects. However, instead of measuring the C1 at what may be less-than-optimal electrode sites (i.e. on the midline), we advocate for the approach used by Kelly, Gomez-Ramirez, and Foxe (2008) in which optimal electrodes are selected for each individual subject based on a separate probe session and all C1 analyses are restricted to only the leading edge of the C1 peak (~50-80ms) to avoid overlap with the P1.

There are a couple of inaccuracies in Slotnick's review of the study by Martinez et al. (1999, 2001) that should be pointed out. First, he suggested that their stimuli, which spanned the horizontal meridian, would elicit a 'muted C1 response' because the opposing sources in the upper and lower banks of the calcarine fissure would tend to cancel each other out. This is not the case, however, because, as Clark et al. (1995) demonstrated, the C1 does not reverse its polarity at the horizontal meridian but rather at about 20 degrees of polar angle below the horizontal meridian. Thus, both the upper and lower field portions of the stimulus array added to the C1 negativity, which was quite prominent. Second, in his Table 2, Slotnick lists the C1 modulation with attention as being 'marginally significant', which is misleading without further clarification. In fact, this marginal significance was actually due to *reduced* C1 amplitudes for attended relative to unattended stimuli (see Martinez et al., 2001, Figure 4), probably due to overlap with an enhanced P1 component at the lateral occipital site of measurement. When the C1 was measured at a more anterior location (Cz) that was still within the

topographical field of C1 but outside that of P1 (in accordance with Slotnick's excellent recommendation), there was no effect of attention on C1. The bottom line is that the study of Martinez et al. (1999, 2001) demonstrated no attentional modulation of C1 under conditions of high perceptual and cognitive load and thus adds to the mass of evidence favoring the 'majority view' that a C1 modulation with spatial attention has yet to be demonstrated.

We appreciate Slotnick's efforts to identify the optimal parameters for measuring potential C1 attention effects. By taking into account the few modifications suggested here, it is our hope that future experiments will be better equipped to measure C1 attention effects, if they exist.

Disclosure statement

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Insignificant C1 effects cannot be called ‘marginally significant’

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ABSTRACT

Slotnick (this issue) proposes that the earliest ERP C1 component, evoked by visual stimuli, may be affected by attention if certain experimental parameters are used. My opinion on this paper is that some results of previous papers are forced to appear significant even though they were not. This commentary focuses on Slotnick’s description of my cited papers and clarifies that there were not in fact any significant C1 attention effects present. Even though the C1 was often numerically larger in the attended condition, the statistical tests of these effects were far from significance.

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KEYWORDS

ERP; spatial attention; C1

Commentary

Slotnick (this issue) reviews 14 papers studying the effect of visual-spatial attention on the earliest ERP component, called C1, which is considered to originate from the primary visual cortex,

V1 (e.g. Di Russo & Pitzalis 2014). He concluded that to obtain a C1 attention effect, stimuli should be presented in the upper fields with distractors, the task should be cognitively demanding and exogenous cuing should be implemented. Finally, the C1 should be measured at midline (POz, Pz, and CPz) electrode sites.

This commentary focuses on Slotnick’s (this issue) description of the C1 results reported in papers in which I was primarily involved (Di Russo, Martínez, & Hillyard, 2003; Di Russo et al., 2012).

In Di Russo et al. (2003) ERPs to stimuli in three visual quadrants show identical C1 amplitudes in the attended vs. unattended conditions, and in one quadrant (lower-right) the attended C1 was minimally larger than the unattended. Collapsed with the lower-left visual field, the attention effect on C1 was not significant. Slotnick (this issue) suggested that if tested alone the attention effect for the lower right quadrant would have been significant. I have now statistically tested, in the Di Russo et al. (2003) data, the lower-right quadrant alone and found that the attention effect on C1 remained non-significant even though it approached significance ($F(1,29) = 4.06$, $p = 0.0563$). However, if we look at the lower-right quadrant ERP in Figure 3 (Di Russo et al., 2003), it is clear that the attended and unattended waveforms at POz are perfectly superimposed from the C1’s onset up to 90 ms. Starting so late, this effect is likely ascribable to overlap with the extrastriate P1 component and not to an early V1 attention effect.

In Di Russo et al. (2012), the C1 was numerically larger for the attended ERP for all quadrants, but the differences were very small, ranging from 0.02 to 0.07 μV , corresponding to an amplitude increment from 4% to 12% (see Di Russo et al., 2012 table 1). F values and significance levels were not inserted in that paper, but I report them here to show how these values are far from significance. Statistical comparisons showed that in that study the C1 attention effects had $F(1,29)$ ratios ranging from 0.300 to 1.182 and associated p values ranging from 0.588 to 0.928. Therefore, contrary to Slotnick’s (this issue) assertion on page 10 claiming that the C1 attention effects in Di Russo et al. (2012) were marginally significant, the attended vs. unattended

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differences in that paper were absolutely non-significant.

Regarding Slotnick's (this issue) statement on page 10: 'it is also possible that the electrode sites evaluated by Di Russo et al. (2003, 2012) were not optimal for detecting attention effects', looking at the topographic voltage mapping of C1 in those papers, it is clear that the chosen electrodes well represent the C1 topography, which was clearly more ventral with respect to Cz and Pz.

My general comment is that rephrasing the results of previous studies by claiming that non-significant effects are actually 'marginally significant' does not change the well-substantiated conclusion that the C1 is not affected by attention.

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The spatiotemporal characteristics of the C1 component and its modulation by attention

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ABSTRACT

Slotnick (this issue) provided a selective review of studies on the attentional modulation of the C1 component of the visual evoked potential, and offers a number of guidelines to maximize the likelihood of observing such modulation in terms of electrode choice, stimulus placement, and types of attentional cue and target stimulus. However, the broader literature pertaining to attentional modulation of the C1 does not support many of these guidelines, and the question of why exactly C1 modulations are so rare remains very much open. Here, we provide clarifications that are critical to an accurate appraisal of the current state of this literature.

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KEYWORDS

Spatial attention; visual evoked potential; C1 component; Cruciform model

Interest in the C1 component of the visual evoked potential (VEP) stems from the insight it provides into the first wave of visual information processing by V1 neurons. That the C1 reflects initial V1 activation has been established through a long line of studies (e.g. Clark, Fan, & Hillyard, 1995; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Jeffreys & Axford, 1972) demonstrating that the variation of scalp topography (including polarity) with polar angle in the visual field is uniquely consistent with V1's characteristic 'cruciform' shape. Slotnick (this issue) defines the C1 as reflecting V1 activity, and also as necessarily having a midline occipital-parietal topography with opposite polarity for upper- and lower-field stimuli. As explicated recently (Ales, Yates, & Norcia, 2013; Kelly, Schroeder, & Lalor, 2013a; Kelly, Vanegas, Schroeder, & Lalor, 2013b), these criteria are mutually contradictory. V1 extends over a cortical area both inside and outside the calcarine sulcus, and thus cortical surface orientation varies systematically and quite dramatically across the retinotopic map, as well as randomly across individuals. To take a striking example, the full cruciform model predicts that both upper and lower field stimuli just right of the vertical meridian should yield lateral scalp topographies of the same polarity. This example violates both of the above C1 criteria, highlighting the importance of characterizing the C1 in terms of projections from the relevant segment of calcarine surface, rather than in terms of fixed polarity and topography criteria. Thus, while midline, polarity-inverting topographies are typical of studies

that placed stimuli close to the horizontal meridian (e.g. Clark & Hillyard, 1996; Fu, Fan, Chen, & Zhuo, 2001; Fu, Fedota, Greenwood, & Parasuraman, 2010a, 2010b; Fu, Greenwood, & Parasuraman, 2005; Fu et al., 2008; Johannes, Münte, Heinze, & Mangun, 1995), these features cannot form part of a general definition of the C1 without carefully accounting for stimulus placement.

Based on this same midline-topography definition of the C1, Slotnick (this issue) argued that the C1s identified by both Kelly, Gomez-Ramirez, and Foxe (2008) and Baumgartner, Grauly, Hillyard, and Pitts (this issue), which were sometimes laterally focused, may instead be P1 components. He specifically pointed to the fact that there was a tendency for upper field stimuli to produce ipsilateral foci and lower field stimuli to produce contralateral foci. This is in fact entirely consistent with V1 anatomy: the calcarine banks are unlikely to be perfectly horizontal and would tend to face contralaterally to some degree. Thus, a dipolar activation in the calcarine floor would project negatively to the scalp over the opposite hemisphere (ipsilateral to the stimulus) whereas a dipolar activation in the calcarine ceiling would project positively to the scalp over the same hemisphere (contralateral to the stimulus), which accords with observations. Slotnick (this issue) argued that the upper-field, slightly ipsilateral C1s may instead reflect the 'voltage sink' of the contralateral P1, but the clear temporally consecutive nature of these foci rule out that they are two ends of the same dipole—the slightly ipsilateral negative focus is indeed greatly diminished by the time the contralateral P1 peaks (Di Russo et al., 2002, 2005). Furthermore, although the C1s measured by Baumgartner et al. (this issue) shared the topographical features of those measured in Kelly et al. (2008), Baumgartner found attentional modulation of the P1 only, implying that these two components were measured independently. Finally, if the P1 does indeed onset at 72–80 ms, the early onset of modulation at 57ms in Kelly et al. (2008) is highly incompatible with a P1 modulation.

The core of the review focuses on nine studies, listed in Table 1 of Slotnick (this issue), investigating C1 modulation at midline electrodes. This particular selection of studies, chosen to explore various experimental factors such as cueing method and load, appear to suggest that spatial attention generally modulates the C1

more often than not. However, of these nine, three (Ding, Martinez, Qu, & Hillyard, 2014; Rauss, Pourtois, Vuilleumier, & Schwartz, 2009, 2012) did not manipulate spatial attention but rather manipulated attentional load. Further, the table leaves out a significant number of other relevant studies that support the overwhelming general trend in the literature of findings of no modulation of the C1 (Gomez Gonzalez et al., 1994; Clark & Hillyard, 1996; Curran, Hills, Patterson, & Strauss, 2001; Fu et al., 2001, 2005, 2008; Hillyard, Teder-Sälejärvi, & Münte, 1998; Johannes et al., 1995; Martinez et al., 1999; Martinez et al., 2001; Wijers, Lange, Mulder, & Mulder, 1997). Four of these studies were indeed discussed, but separately and in the context of doubts regarding correct identification of the C1, which, as explained above, overlook fundamental aspects of the Cruciform model.

Based on the selected studies, Slotnick (this issue) concludes that to maximise the likelihood of finding C1 attentional modulation one 'should' measure from midline electrodes and upper visual field locations, under conditions of exogenous attentional cueing, high perceptual load, and distractor presence. While this represents a useful collation of some recent studies, given that only 6 studies manipulating spatial attention were considered and there exist so many that were not considered, confident inferences cannot be drawn. A more extensive survey of the literature can change many of the claimed dependencies on these factors. For example, upper field locations have been used in many studies finding no C1 modulation but not considered here (Clark & Hillyard, 1996; Fu et al., 2001, 2005, 2008; Johannes et al., 1995). Further, Kelly et al. (2008) used endogenous rather than exogenous cues, and yet observed a clear C1 modulation. Another issue is that the factors have little independent variation across studies. For example, the three studies reviewed that found significant C1 modulation by spatial attention all employed high perceptual load, exogenous attention and upper field locations (Dassanayake, Michie, & Fulham, 2016; Fu et al., 2009, 2010a). There is thus insufficient basis to conclude that all three of these factors moderate the likelihood of C1 attentional modulation. In sum, the determining factors in eliciting a C1 modulation remain very much an open question, not to mention the more important question of *why* such factors would have such an influence. Furthermore, in

advancing on these questions we advocate an approach to characterising VEP components that is founded in neurophysiological principles such as the full cruciform model.

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