

Spatial attention facilitates assembly of the briefest percepts: Electrophysiological evidence from color fusion

ELKAN G. AKYÜREK AND E. MANON VAN ASSELT

Department of Psychology, Experimental Psychology, University of Groningen, Groningen, The Netherlands

Abstract

When two different color stimuli are presented in rapid succession, the resulting percept is sometimes that of a mixture of both colors, due to a perceptual process called color fusion. Although color fusion might seem to occur very early in the visual pathway, and only happens across the briefest of stimulus presentation intervals (< 50 ms), the present study showed that spatial attention can alter the fusion process. In a series of experiments, spatial cues were presented that either validly indicated the location of a pair of (different) color stimuli in successive stimulus arrays, or did not, pointing toward isoluminant gray distractors in the other visual hemifield. Increased color fusion was observed for valid cues across a range of stimulus durations, at the expense of individual color reports. By contrast, perception of repeated, same-color stimulus pairs did not change, suggesting that the enhancement was specific to fusion, not color discrimination per se. Electrophysiological measures furthermore showed that the amplitude of the N1, N2pc, and P3 components of the ERP were differentially modulated during the perception of individual and fused colors, as a function of cueing and stimulus duration. Fusion itself, collapsed across cueing conditions, was reflected uniquely in N1 amplitude. Overall, the results suggest that spatial attention enhances color fusion and decreases competition between stimuli, constituting an adaptive slowdown in service of temporal integration.

Descriptors: Attention, Color fusion, Spatial cueing, Temporal integration, ERP, N1, N2pc, P3

As our gaze wanders through the environment, not everything it comes across is treated equally. Particularly when our attention is fixed on something in the visual field, that object and/or its location is thought to enjoy privileged perceptual processing, compared to input from elsewhere. Such differences have often been observed experimentally. Attention helps, for instance, to perceive stimuli close to the detection threshold (Downing, 1988), and it boosts perceptual characteristics such as contrast sensitivity and spatial resolution (Lu & Doshier, 1998; Yeshurun & Carrasco, 1998). Attention is also thought to increase perceptual processing speed, which is reflected in faster behavioral responses (Posner, 1980). One may thus assume that attention affords some kind of acceleration or amplification of the sensory signal, both of which would explain these effects (e.g., Bundesen, Habekost, & Kyllingsbæk, 2005).

Paradoxically, the perceptual acceleration that attention affords has also been associated with reduced performance, namely, temporal inaccuracy. One example is the so-called prior entry effect that occurs particularly when attention is exogenously allocated:

The authors are grateful to Peter Albronda for supporting the electrophysiological data acquisition, and to Michael Wolff for having a look at the data in the frequency domain. We are also indebted to Vince Di Lollo and an anonymous reviewer, whose comments and suggestions have greatly benefited the manuscript.

Address correspondence to: Elkan Akyürek, Department of Psychology, Experimental Psychology, University of Groningen, Grote Kruisstraat 2/1, 9712 TS Groningen, The Netherlands. E-mail: e.g.akyurek@rug.nl

When observers judge the appearance of an attended stimulus to be earlier than it actually was (Shore, Spence, & Klein, 2001). There is in fact more evidence that attention can result in comparatively poor processing of the stimuli at its focus, where the perceived time course of stimuli is concerned. Such effects of allocating attention on processing in the temporal domain, rather than the spatial domain, include an overestimation of stimulus duration (Enns, Brehaut, & Shore, 1999; Seifried & Ulrich, 2011) and a diminished ability to resolve brief, successive stimuli (Rolke, Dinkelbach, Hein, & Ulrich, 2008; Yeshurun & Levy, 2003), both of which have been related to increased visible persistence (Visser & Enns, 2001). The evidence for such temporal deficiencies is rather convincing to date, even though it should be noted that it is not always obtained (Chica & Christie, 2009; Nicol, Watter, Gray, & Shore, 2009).

It has been argued that the differential effects of attention in the spatial and temporal domains might be due to the fact that these are inherently different dimensions (e.g., Wilson, 1980). In more neural terms, it has similarly been attributed to the strengths and weaknesses of parvo- and magnocellular processing pathways in the brain (Yeshurun, 2004; Yeshurun & Levy, 2003). According to the latter proposal, bringing an item within the focus of attention results in it being processed by parvocellular cells to a greater degree. These cells afford more spatially precise and more color-sensitive perception, but are also known to have longer response durations. This has been related quite directly to delays in perceiving stimulus offsets (Rolke, Ulrich, & Bausenhart, 2006). In this

neurophysiological framework, spatial and featural precision are thus traded off for temporal precision.

It may indeed seem plausible that something has to give, if one assumes that the perceptual system is trying to achieve maximal discriminative power (resolution) in both spatial and temporal dimensions. Although this assumption has intuitive appeal, the question may be posed whether trying to maximize resolution actually makes sense in the temporal domain. When spatial resolution is concerned, higher is certainly better, as that not only allows the observer to discern fine details at close range, but also enables more accurate perception across larger distances. By contrast, in the temporal dimension it is doubtful whether being able to resolve very brief segments of sensory input from one another is likely to bring any perceptual advantage. Few meaningful events in our natural environment are likely to require isolated attention within the interval of < 100 ms that is typically studied in the laboratory.

It may thus be argued that the perceptual system would do better not to focus on resolving the shortest possible intervals, but rather on enhancing the interpretation of the longer intervals during which meaningful events are most likely to unfold. The loss of temporal resolution observed with attention may therefore not be an unfortunate side effect of spatial enhancement, but rather an adaptive and intended effect: Ongoing sensory input is allowed to accumulate for a longer period, so that it can be integrated into a comprehensive event. In other words, attention may facilitate temporal integration.

When it comes to processing stimulus features that are distributed in space, rather than in time, attention has indeed previously been given a role as a psychological function that enhances their binding (e.g., Reynolds & Desimone, 1999; Serences & Yantis, 2006). Such binding across a single (static) scene is thought to be necessary to create coherence between both individual stimulus features (e.g., color and shape) that are coded in different brain regions, and more abstract object representations. However, few researchers have studied whether attention might also have a binding role in time, serving to create coherent events. To our knowledge, the only published study so far that has directly investigated the effects of attention on temporal integration was conducted by Visser and Enns (2001). Their study provided at least preliminary evidence for facilitation of integration due to the availability of attention, and will therefore be discussed in some detail.

Visser and Enns (2001) embedded a so-called missing element task (MET; Akyürek, Schubö, & Hommel, 2010; Hogben & Di Lollo, 1974) in an attentional blink task. The MET is a measure of temporal integration, in which small stimuli such as dots or squares are presented in a regularly spaced square grid (e.g., 5×5 , yielding 25 dot locations). A subset of the stimuli in the grid is shown in each of two successive presentations (S1 and S2) with a brief inter-stimulus interval (ISI), so that all but one stimulus out of the full set is presented across both displays (e.g., 12 stimuli in S1, and 12 in S2 yields 24 in total). Observers are typically asked to locate the missing element in the grid, which is easy when the displays are perceptually integrated, but very difficult when they are not. Integration rates depend on the duration of the stimulus sequence, with shorter duration rendering integration more likely. The authors manipulated duration by adjusting the ISI between S1 and S2 from 0 to 80 ms, opting to keep the displays themselves constant at 1 ms each (using an oscilloscope).

The attentional blink task in the study by Visser and Enns (2001) consisted of a briefly presented first target letter, which was masked by a succeeding digit. Then, after a delay of 100, 300, or 700 ms, a second target appeared, which consisted of the pair of

successive MET displays. In this and similar tasks, when both target stimuli must be attended and are presented at short intervals (below about 500 ms), observers often miss the second target, which constitutes the attentional blink phenomenon (Broadbent & Broadbent, 1987; Raymond, Shapiro, & Arnell, 1992). The attentional blink was used by the authors as a manipulation of the amount of attention that was available to process the MET.

When attention was not available, due to the attentional blink, Visser and Enns (2001) observed lower integration performance in their first experiment; observers were less able to locate the missing dot in the MET. Complicating the interpretation of this effect was the fact that the impairment was also present when S1 and S2 of the MET were shown with 0 ms ISI, which suggested the attentional benefit might have been due to improved spatial processing of the stimuli, and not integration (as the latter is not needed when the stimuli are not temporally separated). To remove this factor, the authors conducted a second experiment in which missing element localization was no longer required; observers were now only asked whether an element was missing or not. Detection of the missing element was no longer reliably impaired at 0 ms ISI between S1 and S2, but only at 20 and 40 ms¹, thus implicating changes in temporal integration.

Although some aspects of the reported data might raise questions, such as the spatial effect in their first experiment, the main conclusion drawn by Visser and Enns (2001), which was that attention enhances temporal integration by increasing the perceived duration of S1, seems fair. An attention-induced increase in visible persistence and/or perceived duration has indeed been observed before (e.g., Enns et al., 1999), but that does not yet prove that attention specifically enhances the integration process itself (i.e., by increasing the tendency to bind successive stimuli, regardless of duration), nor that attention would emphasize an event-based mode of perception, trading temporal resolution for coherency rather than for spatial resolution.

The present study. The present study was designed to isolate attentional contributions to the temporal integration process specifically. The main idea was that if the “event-oriented” account of attention holds true, then there must be observable benefits of having the perceptual system act in this way. As mentioned, most studies of attentional effects in the temporal domain to date have focused on discriminative power (e.g., what is the briefest gap between stimuli that can still be detected), in which such benefits will obviously not be observed. Instead, they may be found in measures that reflect the perceptual contents of the interval being considered, cases in which attention facilitates the perception of a comprehensive event. In the present study, one representative case was examined—the perceptual fusion of successive colors. Color fusion entails that a sufficiently rapid succession of two different colors (e.g., red and green) is perceived as if they were presented simultaneously, that is, as a single mixed color (e.g., yellow; Regan & Tyler, 1971; Smith, Bowen, & Pokorny, 1984; Wisowaty, 1981). The report of the fused color can be taken as a relatively unambiguous reflection of the perceptual integration of the individual color stimuli that are involved.

1. It may be noted that in the study of Visser and Enns (2001) missing element detection at 40-ms ISI was also impaired at 700-ms delay between the first and second target of the attentional blink task. This weakens the results in the sense that the attentional blink should no longer have been in effect at that delay. Some doubt is thereby cast on the attentional origin of the deficit at 40 ms.

The principal aim of the present study was thus to test the hypothesis that attention enhances color fusion by favoring an event-oriented analysis of perceptual input. Measuring the frequency of color fusion enables a decisive test of this hypothesis, for two reasons: First, performance on this task cannot be influenced by modulating the degree to which the stimuli are processed by magno- or parvocellular pathways (Yeshurun, 2004; Yeshurun & Levy, 2003); the report of color depends fully on the latter. This ensures that even if any differential activity between parvo- and magnocellular neurons is elicited in the task, this will not reflect on the temporal processing of the critical stimuli. Second, color fusion is insensitive to several potential confounds related to (perceived) stimulus strength, order, duration, and persistence.

To start with the former, perceived stimulus strength (and consequently order as well), is known to be affected by attentional factors. Such effects are described in the “law of prior entry,” which holds that a stimulus is more likely to be reported first if it received more attention than another, primarily because its representation is stronger (Titchener, 1908; for a recent overview see Spence & Parise, 2010). Reports of fused colors, however, would thereby not be enhanced. In fact, if either of the colors is represented more strongly due to the deployment of attention, observers would be more likely to report that individual color, rendering fusion less likely.

Similarly, visible persistence, which is thought of as a visual image that persists after the actual stimulus has disappeared (Sperling, 1960), has been found to increase when attention is available (Visser & Enns, 2001). This may in turn be related to the overestimation of stimulus durations that has also been observed (Enns et al., 1999). Although historically visible persistence has often been associated with temporal integration processes, they are not necessarily the same (Dixon & Di Lollo, 1994). In many integration tasks, increased persistence of the first stimulus results in more temporal overlap of its sensory trace with that of the incoming second stimulus, enhancing their mutual integration. It may be noted, however, that depending on the task, one might also expect a negative relationship between persistence and integration: Perceptually longer-lasting stimuli could lend themselves less well to integration, because integration decreases as duration increases (e.g., Hogben & Di Lollo, 1974). This particular expectation also necessitates the assumption that attention-induced overestimation of stimulus duration is not driven primarily by integration effects, which does remain a possibility. Either way, in the color fusion task, the critical stimuli fully overlap each other in space, effectively preventing persistence beyond the onset of the second stimulus, regardless of the attention condition.

In order to get a firmer grip on the possible mechanisms by which attention might facilitate temporal integration, the ERP was also examined in the last experiment of this study. Because of its ability to track the brain response with high temporal precision, modulations of the ERP can reveal when fusion occurs and when the hypothesized attentional effect might occur in the perceptual process. For the purposes of the present study, three processing phases were considered: First, the perceptual detection and discrimination of the stimuli as reflected in the P1 and N1 components of the ERP (e.g., Luck, Heinze, Mangun, & Hillyard, 1990; Mangun & Hillyard, 1991). Second, the attentional processing of stimulus features at a lateral spatial location, as indexed by the relatively early N2pc component (Eimer, 1996; Kiss, van Velzen, & Eimer, 2008; Luck & Hillyard, 1994). Third, the consolidation of stimulus representations in short-term memory, as indexed by the relatively late P3 component (Kok, 2001; Polich, 2007). Naturally, the

deflections within these components will become most informative only when the hypothesized effect of attention on color fusion is demonstrated. To this end, two behavioral experiments were first conducted.

Experiment 1

Experiment 1 was designed to investigate the behavioral effects of spatial cueing on perceptual color fusion, across comprehensive presentation intervals from 40 to 80 ms. The critical stimuli were small colored squares, which were successively presented at the same location within a regularly spaced 5×5 grid of black squares, identical to those previously used in METs designed to measure temporal integration (Akyürek, Schubö, & Hommel, 2010). This physical similarity has the collateral advantage that it facilitates comparison of the ERP between the current color fusion task and temporal integration tasks, which may tap into processes that lie on a continuum of temporal perceptual processing (Akyürek et al., 2012).

Method

Participants. Eighteen students (9 female, 9 male) at the University of Groningen participated in the experiment in exchange for course credit. Informed consent was obtained in writing, and the study was conducted in accordance with the Declaration of Helsinki. The study was furthermore approved by the ethical committee of the Department of Psychology prior to its execution. Participants reported normal or corrected-to-normal visual acuity and were briefly checked for color blindness by means of an Ishihara plate. Mean age was 20.1 years (range 18–24 years).

Apparatus and stimuli. Participants were seated individually in sound-attenuated testing cabins with dimmed lighting. Stimuli were shown on a 19” CRT screen, which refreshed at a frequency of 100 Hz, using a resolution of 800×600 pixels in 16-bit color. Viewing distance to the computer screen was not fixed, but was approximately 60 cm. The experiment ran on a Microsoft Windows XP desktop computer, and was programmed in E-Prime 2.0 Professional, developed by Psychology Software Tools. Responses were registered with a USB mouse. A uniform white background was maintained during all trials, as shown in Figure 1. The fixation cross (+) was drawn in 12-point size in Courier New font. The primary experimental stimuli were squares of 10×10 pixels, which were centered within invisible fields of 20×20 pixels. There were 25 of these fields, arranged in a 5×5 grid that was centered on the screen. In the cue display, 25 squares were shown at once within a single grid. The cue itself was a square whose center was bright green (RGB 64, 255, 64), and which was outlined in black (1 pixel width). The remainder of the squares were identically outlined, but had a light gray center (RGB 192, 192, 192). Across the two successive target displays, 23 single black squares appeared in total, as well as 2 colored squares, and 2 gray squares. Unlike the stimuli in the cue display, these were not outlined. There were 6 target colors: red (RGB 255, 96, 96; 74 cd/m^2), yellow (RGB 255, 255, 128; 210 cd/m^2), blue (RGB 96, 96, 255; 48 cd/m^2), green (RGB 128, 128, 32; 46 cd/m^2), orange (RGB 255, 160, 64; 107 cd/m^2), and purple (RGB 192, 48, 128; 37 cd/m^2). The response screen consisted of another 6 squares, one for each color, horizontally aligned in a 2×3 grid of response fields that was centered on the screen, with a random assignment between color and location on each trial.

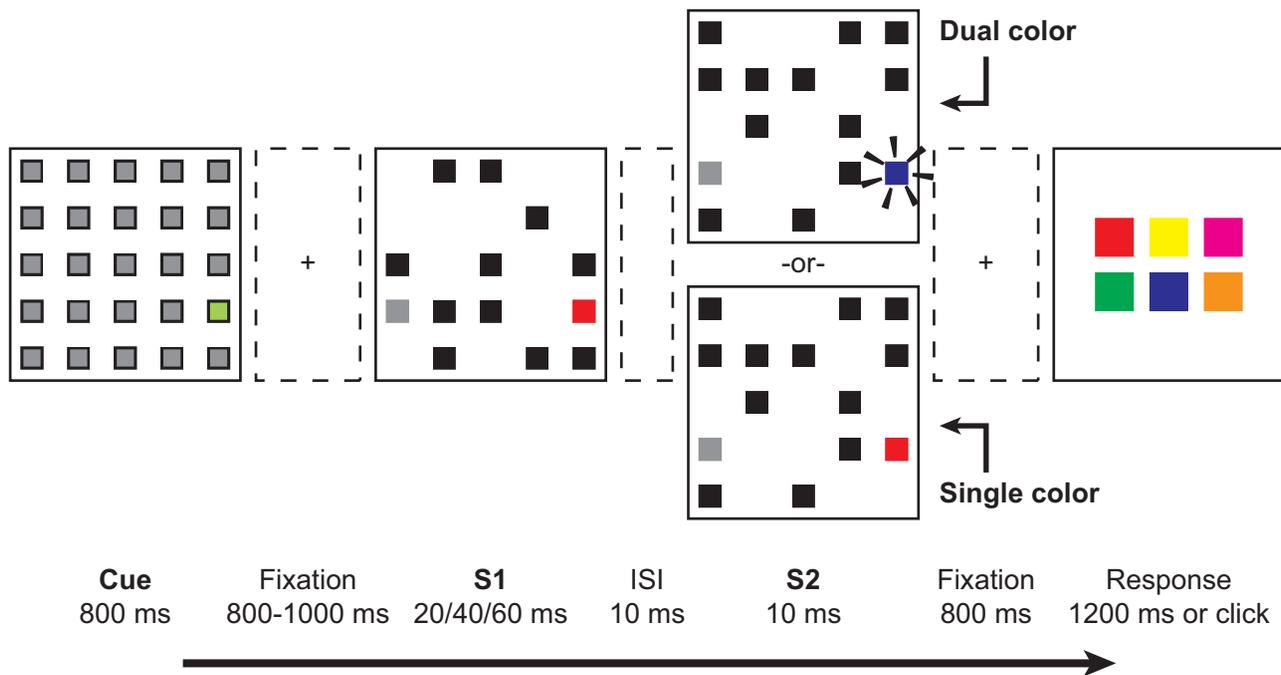


Figure 1. Trial structure of Experiment 1. Two successive rapid target displays containing color singletons were shown after a spatial cue display. The cue either indicated the location of the color stimuli (valid cue; 50% chance), or that of the isoluminant gray square in the opposite side of the visual field (invalid cue; 50%). Depending on the condition, either two different colors were shown across the target displays (dual color trials), or the same color was shown twice (single color trials). The former condition enabled perceptual color fusion. The positions of the individual color response fields were randomized on each trial, and trials concluded with a feedback screen (not shown).

Procedure. The experiment consisted of 864 experimental trials, preceded by 36 practice trials that were not analyzed. Trials continued without interruption within each of six experimental blocks of 144 trials. Participants initiated a block of trials by clicking the right mouse button, and could take a break after each block. Trials started with the presentation of the cue display for 800 ms, followed by the fixation cross for a variable duration of 800–1,000 ms. The cue appeared on the same location as the colored squares that followed on 50% of trials. On the other 50% of trials, it appeared on the location of the gray squares instead.

The first target display (S1) was shown next for 20, 40, or 60 ms. After a fixed ISI of 10 ms, the second target display (S2) was shown for another fixed 10 ms (cf. Akyürek, Schubö, & Hommel, 2010). Each display contained 11 or 12 black squares (so that in total 23 always appeared) at unique and mutually exclusive locations, as well as a single color square, and a gray square. Across the two target displays, the pairs of colored and gray stimuli always appeared at the same location; that is, unlike the locations of the black squares, the locations of the colored and gray stimuli were used twice (once in each target display). Thus, all 25 positions in the grid were filled with stimuli. Across all trials, the colored squares were evenly distributed across the left and right side positions in the grid (i.e., they never appeared in the center column), and presented in random order. The gray squares always appeared in the vertical mirror location of the colored squares, and their luminance was individually adjusted to match that of the actual color shown at the same time on the other side of the visual field, as closely as possible. This luminance adjustment was made to limit possible effects of a lateral stimulus imbalance on the ERP (measured later). There were two color configurations: In the single color condition, one of the aforementioned six colors appeared on both the first and second target display. In the dual color condition,

color pairs consisting of red, yellow, and blue were presented across the two target displays that allowed perceptual fusion into purple (red + blue), orange (yellow + red), and green (yellow + blue). Single and dual color trials were equally frequent and presented in random order.

A delay of 800 ms (with fixation cross) followed the second target display, after which the response screen was shown for 1,200 ms, or until a response was registered. Participants used the mouse to click on the color that best matched the color they had perceived in the trial. The trials concluded with a 200-ms feedback screen, showing “:)” for correct responses, and “:(” for incorrect responses. For feedback purposes, each color that was actually shown, as well as the fused percept (if there was one), was counted as correct, so that any observer bias toward either fused or unfused reports was avoided.

Design. The data were analyzed in four separate repeated measures analyses of variance (ANOVAs) that each featured two variables: S1 duration (20, 40, or 60 ms) and cue (valid or invalid), constituting a 3×2 design. Performance was analyzed separately for single color trials (% correct) and for dual color trials. In the latter type of trials, the frequency of three different reports was analyzed: S1 and S2 color identification rate, and the report rate of fused colors. In case of a significant test of sphericity when a variable contained more than two levels, degrees of freedom were adjusted using the Greenhouse-Geisser epsilon correction.

Results and Discussion

Figure 2 shows color reports in Experiment 1 as a function of S1 duration, plotted separately for valid and invalid cues. In dual color trials, the analysis of fused percepts (Figure 2, left panel) revealed

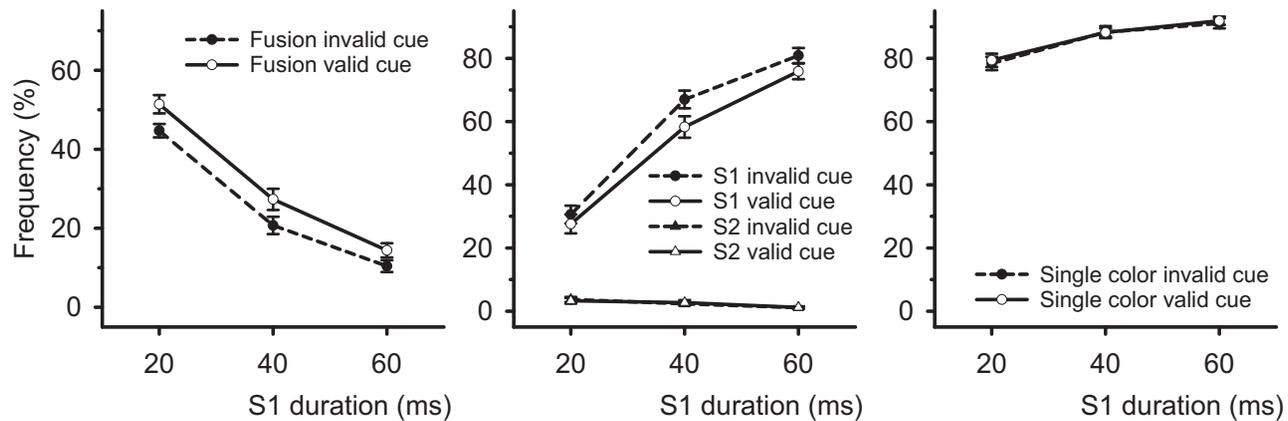


Figure 2. Response frequencies (%) in Experiment 1. The left panel shows the frequency of fused color reports in dual color trials as a function of S1 duration (ms), plotted separately for valid (solid line) and invalid cues (dashed line). The middle panel shows the frequency of individual color reports (S1 color: circles, S2 color: triangles) in dual color trials, for valid and invalid cues. The right panel shows the frequency of correct color identification in single color trials for valid and invalid cues. Error bars represent ± 1 standard error of the mean.

effects of both duration, $F(1,22) = 271.64$, $MSE = .007$, $p < .001$, and of cue, $F(1,17) = 28.29$, $MSE = .003$, $p < .001$, although the interaction was unreliable ($F < 1.2$). As would be expected for a temporal fusion (integration) process, shorter S1 durations led to more fusion reports (48.1% at 20 ms, 24% at 40 ms, and 12.4% at 60 ms). Crucially, a valid cue increased fusion, compared to an invalid cue (31% vs. 25.3%).

S1 color identification rate (Figure 2, middle panel) was affected by duration also, $F(2,34) = 474.57$, $MSE = .005$, $p < .001$. S1 identification was facilitated by longer S1 duration, improving from 29.1% at 20 ms, to 62.7% at 40 ms, and to 78.4% at 60 ms. There was a significant effect of cue as well, $F(1,17) = 23.7$, $MSE = .004$, $p < .001$. Remarkably, the effect indicated that S1 reports decreased when the location of the colored squares was validly cued, compared to trials in which the cue was invalid (53.9% vs. 59.5%). There was furthermore a reliable interaction of Duration \times Cue, $F(2,34) = 3.89$, $MSE = .002$, $p < .05$. The interaction seemed to indicate that there was a relatively small cueing effect at 20 ms (3%), in comparison to the effect at 40 ms (8.7%). The interpretation of this difference is complicated by the fact that the cueing effect seemed to decrease again at 60 ms (5%). By contrast, cue had no effect on S2 color reports ($F_s < 1$), although there was an effect of duration, $F(2,34) = 6.64$, $MSE = .001$, $p < .005$. There were very few S2 reports overall, but they appeared to decrease further when S1 duration increased (3.5% at 20 ms, 2.5% at 40 ms, and 1.2% at 60 ms), which presumably reflected a diminishing forward masking effect produced by S1.

Finally, in single color trials (Figure 2, right panel), duration reliably affected identification performance, $F(1,24) = 68.38$, $MSE = .003$, $p < .001$. As S1 duration increased, performance did also, from 78.9% at 20 ms, to 88.2% at 40 ms, and 91.5% at 60 ms. There was neither a main effect of cue, nor an interaction with duration ($F_s < 1$).

The principal results of Experiment 1 can be summarized as follows. When a single color appeared at a given location, the perception of that color was not affected by the availability of attention. However, when two colors appeared at the same location in rapid succession, color perception was altered by attention. When more attention was available (i.e., when a valid cue preceded the color stimuli), the observers were more likely to perceive the fusion of the two colors, at the expense of individual color reports (primarily

that of S1). Thus, attention seemed to resolve the competition between the two colors and facilitated color fusion.

Experiment 2

The effects of spatial cues can vary substantially over time. The prime example of such variance is the phenomenon of inhibition of return (IOR), which is expressed by a reversal between attentional facilitation and inhibition when the cue-target onset interval is lengthened (for a review, see Klein, 2000). In Experiment 2, the time between cue and target stimuli was varied to investigate whether inhibitory effects might have played a role in the outcomes of Experiment 1, which featured a relatively long cue-target interval.

Method

Participants. Nineteen students (10 female, 9 male) participated in this experiment, under the same conditions as before. Mean age was 21.5 years (range 18–28).

Apparatus and stimuli. Apparatus and stimuli were identical to Experiment 1.

Procedure and design. The procedure and design were identical to those of Experiment 1, with two exceptions. First, the delay between cue and target display was now randomly varied between the original 800–1,000 ms that was used in Experiment 1 and 100–200 ms (50% of trials each). In the analysis, the additional variable delay (short or long) was consequently added. Second, S1 duration was now either 20 or 50 ms, to increase sampling efficiency. As a result of these changes, there were now 768 experimental trials, presented in four blocks, and 24 practice trials.

Results and Discussion

Figure 3A shows color reports for valid and invalid cues in Experiment 2 as a function of S1 duration for the long delay period. Figure 3B shows the same for the short delay period. Fusion reports in dual color trials (Figure 3, left panels) were significantly modulated by duration, $F(1,18) = 107.22$, $MSE = .033$, $p < .001$. At 20-ms S1

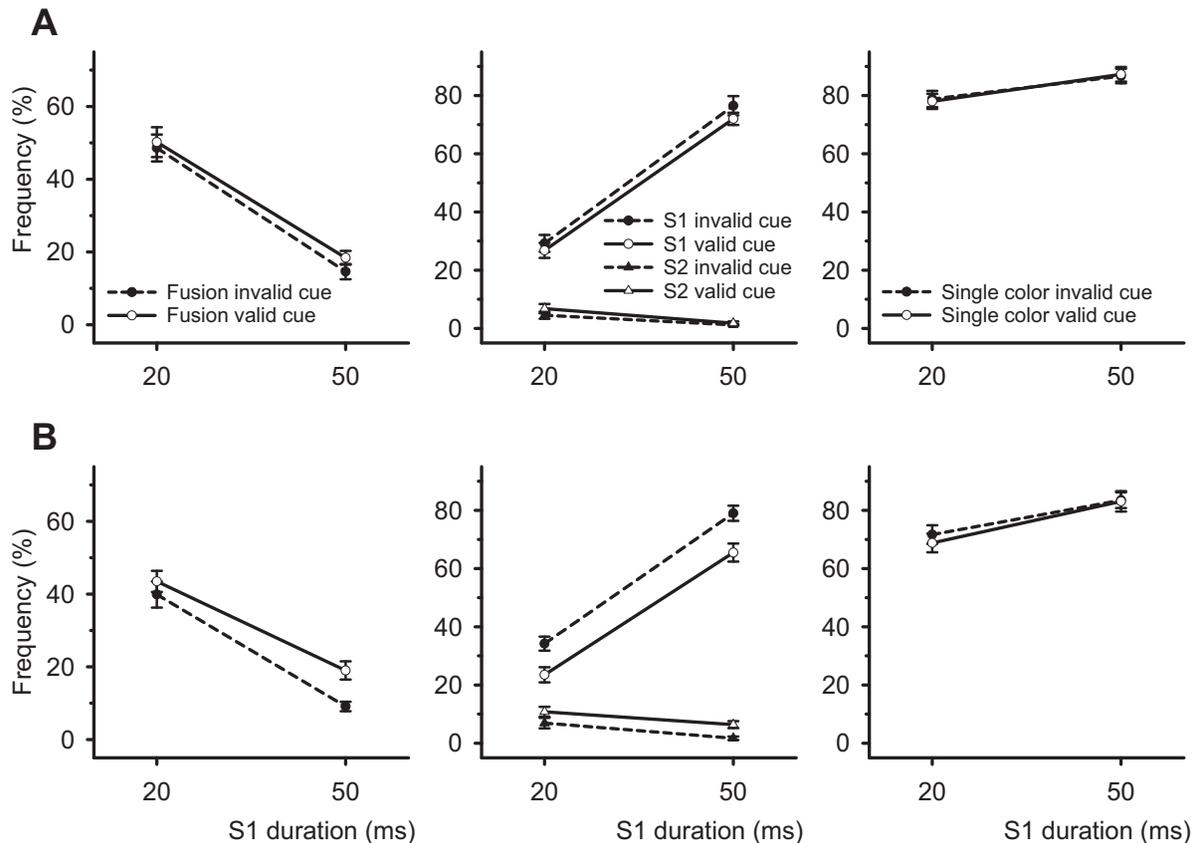


Figure 3. Response frequencies (%) in Experiment 2. Fusion reports, individual color reports, and single color identifications are shown in separate panels from left to right, following previous figure conventions. A: Results of the long cue-target interval (800–1,000 ms). B: The same for the short cue-target interval (100–200 ms).

duration, more fused colors were perceived than at 50 ms (45.6% vs. 15.3%). Delay also had a significant effect, $F(1,18) = 15.42$, $MSE = .007$, $p < .001$. There were more fusion reports overall at the long delay (33%) than at the short delay (27.8%). There was also a main effect of cue, $F(1,18) = 19.77$, $MSE = .004$, $p < .001$. A valid cue again increased fusion (32.8% vs. 28.1%). These main effects were further modulated by two-way interactions; only the three-way interaction was unreliable ($F < 1$). Duration interacted with delay, $F(1,18) = 6.75$, $MSE = .004$, $p < .05$. Duration seemed to have a slightly weaker effect at short cue-target delays than at longer ones; there was 27.7% difference between 20 and 50 ms at short delays, compared to 32.9% at long delays. Duration and cue also interacted, $F(1,18) = 4.4$, $MSE = .004$, $p < .05$. The cueing effect seemed to be larger at 50 ms than at 20 ms (6.9% vs. 2.6%), possibly due to there being more room to improve in the former case. Lastly, the interaction of Delay \times Cue was also reliable, $F(1,18) = 4.72$, $MSE = .003$, $p < .05$. The cueing effect was actually stronger at short delays than at long delays (6.7% vs. 2.7%), contrary to what one might have expected from an inhibition account.

S1 reports in dual color trials (Figure 3, middle panels) were reliably affected by duration, $F(1,18) = 269.26$, $MSE = .028$, $p < .001$. S1 color reports were much more frequent at 50-ms S1 duration (73.3%) than at 20 ms (28.4%). There was no effect of delay ($F < 1$), but cue did have an effect, $F(1,18) = 23.04$, $MSE = .01$, $p < .001$. Again similar to Experiment 1, a valid cue resulted in fewer S1 color reports (46.9%) than an invalid cue did (54.7%). Cue interacted with delay, $F(1,18) = 16.82$, $MSE = .004$,

$p < .001$, so that the cueing effect was again more pronounced at short cue-target delays (12.1%) than at longer ones (3.5%). No further interactions were significant ($F_s < 1.8$). S2 reports were also reliably affected by duration, $F(1,18) = 15.6$, $MSE = .005$, $p < .001$, showing as before more S2 reports at shorter S1 durations (7.2% vs. 2.8%). There was an effect of delay on S2 reports as well, $F(1,18) = 39.71$, $MSE = .001$, $p < .001$. A shorter cue-target delay resulted in more S2 reports (6.5%) than a longer delay (3.5%). Although a short cue-target delay may have weakened the representation of S1, and thereby facilitated S2 reports, the absence of such an effect on S1 reports themselves complicates this interpretation. There was also an effect of cue validity on S2 reports, $F(1,18) = 22.48$, $MSE = .001$, $p < .001$, with a valid cue increasing the likelihood of S2 reports (6.4% vs. 3.6%). This effect was strongly modulated by an interaction with delay, $F(1,18) = 30.91$, $MSE = .001$, $p < .001$. The short delay showed a stronger cueing effect (4.3%) than the long delay (1.5%), which may also explain why this effect was not observed in Experiment 1. No further interactions were reliable ($F_s < 1$).

Finally, in single color trials (Figure 3, right panels), performance was affected by duration, $F(1,18) = 125.29$, $MSE = .004$, $p < .001$, with 50-ms S1 duration resulting in higher performance (85.1%) than 20 ms did (74.3%). There was also an effect of delay, $F(1,18) = 40.61$, $MSE = .003$, $p < .001$. Performance was lower with short cue-target delays (76.8%) than with long ones (82.7%). This effect furthermore interacted with duration, $F(1,18) = 6.21$, $MSE = .003$, $p < .05$, suggesting that it was stronger at 20-ms S1 duration (8.1% difference between short and long delays) than at

50 ms (3.7% difference). As in Experiment 1, there was no reliable effect of cue ($F < 1$), and there were no further significant interactions either ($F_s < 1.2$).

By and large, the results of Experiment 2 replicated those of Experiment 1, particularly in the long delay condition. As in Experiment 1, valid cues decreased S1 reports and increased fusion reports. Short delays between cue and target displays produced a stronger cueing effect on S1 reports than long delays. Furthermore, although short delays resulted in fewer fusion reports, the effect of cueing was actually more pronounced on these reports also. These findings are hard to account for in terms of IOR, which should have been at least less pronounced at shorter cue-target delays, if it were to underlie the effects observed at longer delays. The findings thus support the idea that the (valid) cues in the present study did not have an inhibitory effect even at the longer cue-target interval, but did indeed elicit enhanced attention.

Experiment 3

Experiment 3 was aimed at exploring the electrophysiological mechanisms underlying the effect of spatial cueing on color fusion, and in particular its temporal locus, as well as the locus of fusion itself. Two alternative hypotheses were considered. First, spatial cueing might cause an early attentional differentiation in ERP component amplitude between stimuli that will eventually be fused and those that will not. Second, cueing might differentially modulate the consolidation of fused and unfused stimuli. These hypotheses were investigated primarily by examining P1, N1, and N2pc component amplitude, as well as that of the P3. The former components are known to be sensitive to manipulations of spatial attention, and the N2pc is even uniquely elicited by spatially specific attentional processing (Eimer, 1996; Kiss et al., 2008; Luck & Hillyard, 1994). The P3 component is involved in memory consolidation (Kok, 2001; Polich, 2007; cf. "monitoring," Verleger, Jaśkowski, & Wascher, 2005). Furthermore, although previous attempts to measure these components during color fusion do not seem to have been made, each of them has been implicated in temporal integration before (Akyürek, Schubö, & Hommel, 2010; Akyürek & Meijerink, 2012).

Method

Participants. Thirty-one students (18 female, 13 male) took part in this experiment, following the same procedures as before. Two further participants were excluded: one male due to apparent color blindness, and one female because she withdrew and did not complete the experiment. Mean age was 20.1 years (range 18–25).

Apparatus and stimuli. The experimental sessions were moved to a different room to enable the measurement of the EEG. Participants were seated individually in this new testing chamber at a distance of approximately 50 cm (not fixed) from a 17" CRT screen. The chamber was monitored by means of a video camera, and an intercom system enabled two-way communication between participant and experimenter. Everything else remained the same as before.

Procedure and design. Experiment 3 was identical to Experiment 2, but the short cue-target delay was no longer included, as the cueing effect was similar to that of a long delay, and because the ERP elicited by the cue at short delays would contaminate the ERP of the targets. Dual color trials were also made slightly more frequent

(from 1/2 to 3/5), to anticipate reduced trial numbers due to the response-related classification of the ERP that was performed (described below). The total number of experimental trials was furthermore increased to 960 to increase power.

Electrophysiological recording and analysis. The EEG was recorded at a frequency of 500 Hz with 64 tin electrodes, laid out according to the extended International 10-20 system, and amplified by a REFA 8-72 amplifier that used a 140 Hz cut-off filter. An electrode placed on the sternum served as ground. An average reference was used during recording, and the data were rereferenced offline to the average of both mastoids. Electrode impedance was kept below 5 k Ω . The electrooculogram (EOG) was recorded bipolarly from electrodes placed on the outer canthi of the eyes (horizontal) and from electrodes placed just above and below the left eye (vertical).

Brain Vision Analyzer 2.04 by Brain Products was used to filter the data offline with Butterworth Zero Phase filters, with a 40 Hz low-pass at -12 dB (48 dB/oct roll-off), and a .1 Hz high-pass at -6 dB (24 dB/oct roll-off). The EEG was averaged into segments of 500 ms, starting 100 ms prior to S1 onset and ending 400 ms thereafter. Longer segments were created to examine the P3 component, namely of 800 ms; from -100 to 700 ms poststimulus. Trials with horizontal eye movements (with voltage steps greater than 50 μ V or differences greater than 80 μ V across the segment) were excluded from analysis. Per electrode, trials with artifacts (with amplitudes in excess of ± 80 μ V, or amplitude differences below .1 μ V across 100 ms) were similarly removed. One participant exhibited a bad PO7 electrode, which was corrected using spline interpolation. Blinks and vertical eye movements were corrected by applying the Gratton-Coles procedure (Gratton, Coles, & Donchin, 1983). The 100 ms prior to S1 onset were used for baseline correction.

Trials were classified on the basis of the response given (excluding fully incorrect responses) in order to analyze the associated stimulus-evoked ERP. The first set of analyses was focused on cueing specifically, and included fusion reports at 20-ms S1 duration, single color reports at both 20- and 50-ms S1 duration, and S1 color reports at 50-ms S1 duration. For each of these, there were at least 64 segments of (artifact-free) EEG available for each participant. Categories that did not meet this criterion were excluded from further consideration: S2 color reports were too rare overall (see behavioral results below), and so were fusion reports at 50-ms S1 duration, as well as S1 color reports at 20-ms S1 duration.

The second set of analyses was focused on color fusion by itself, and concerned a subset of physically identical trials of 20-ms S1 duration in which dual colors were shown. These trials were divided dependent on their perceptual outcome, namely, the fused color or either of the individual colors (S1 or S2). This measure of fusion is thus especially sensitive because it excludes any trivial errors from the comparisons: In previous MET paradigms, a correct localization constituted integration, while an incorrect localization constituted nonintegration, and the latter inevitably also includes cases in which the participant accidentally pressed the wrong key, was not properly facing or viewing the screen, and so forth. There were at least 32 segments of artifact-free EEG available in each bin for 29 participants; the two remaining participants were excluded from these analyses.

The earliest electrophysiological measures of interest were mean P1 and N1 amplitude at the PO3, PO4, PO7, and PO8 electrodes, in time windows of 80–130 ms, and 160–210 ms, respectively. Subsequently, mean N2pc amplitude was analyzed at the PO7 and PO8 electrodes in a time window of 160–320 ms. The

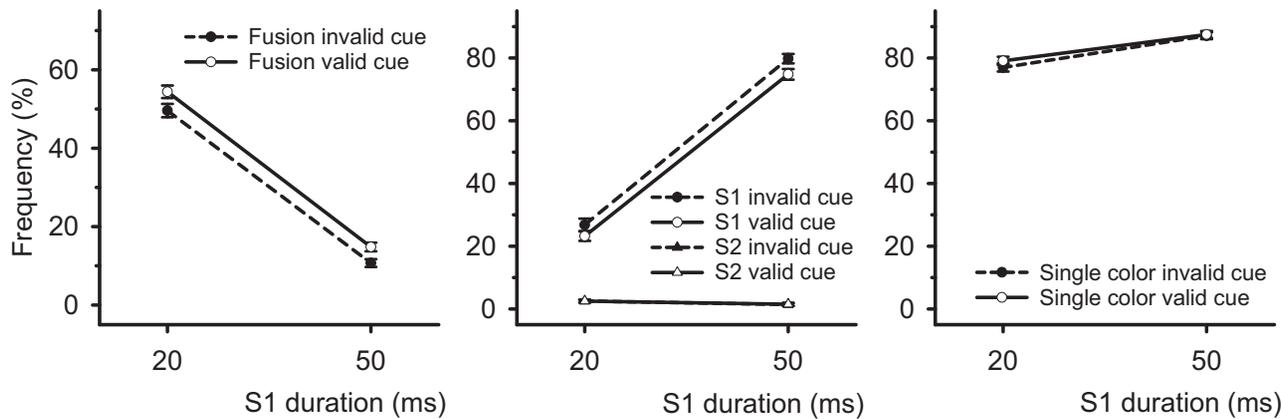


Figure 4. Response frequencies (%) in Experiment 3. Fusion reports, individual color reports, and single color identifications are shown in separate panels from left to right, following previous figure conventions.

differential lateral activity (i.e., the N2pc) was computed by subtracting ipsilateral waveforms (recorded from PO7 when the target stimuli appeared in the left visual field, and from PO8 when they appeared in the right visual field) from contralateral waveforms (recorded from PO7 when the targets appeared in the right visual field, and from PO8 when they appeared in the left visual field). The final measure of interest was mean P3 amplitude, recorded at Pz in an early time window of 370–500 ms and in a late window of 500–630 ms.

The effects of the cue (valid vs. invalid) on the ERP during color fusion and identification were analyzed in four one-way ANOVAs on mean component amplitude in each report condition under consideration. The effects of fusion itself were analyzed in 20-ms dual color trials, in which fusion was contrasted with individual color reports in another one-way ANOVA. In all of the aforementioned analyses concerning the P1 and N1, electrode was added as a variable (four levels: PO3, PO4, PO7, and PO8).

Results and Discussion

Behavior. Figure 4 shows validly and invalidly cued color reports in Experiment 3 as a function of S1 duration. Fusion reports in dual color trials (Figure 4, left panel) showed clear effects of duration, $F(1,30) = 514.4$, $MSE = .009$, $p < .001$, and cue, $F(1,30) = 28.29$, $MSE = .002$, $p < .001$. Fusion reports were substantially more frequent at 20-ms S1 duration (52%), compared to 50 ms (12.8%). A valid cue furthermore enhanced fusion compared to an invalid cue (34.6% vs. 30.2%). There was no evidence for an interaction between the two variables ($F < 1$).

S1 color reports in dual color trials (Figure 4, middle panel) were strongly modulated by duration, $F(1,30) = 839.12$, $MSE = .01$, $p < .001$. At 20-ms S1 duration, report frequency was 25%, compared to 77.3% at 50 ms. The effect of cue was reliable as well, $F(1,30) = 21.23$, $MSE = .003$, $p < .001$, showing reduced S1 reports with a valid cue (49% vs. 53.3% with an invalid cue). The interaction term was not reliable ($F < 1.3$). S2 reports were infrequent overall and only showed a marginal duration effect, $F(1,30) = 3.63$, $MSE = .001$, $p < .07$. S2 reports were more frequent when S1 was 20 ms (2.5%), compared to when it was 50 ms (1.4%). Cue had no effect, and there was no interaction either ($F_s < 1$).

Duration had a significant effect on color identification in single color trials (Figure 4, right panel), $F(1,30) = 93.09$, $MSE = .003$, $p < .001$. Longer S1 duration resulted in higher accuracy (from 78.1% at 20 ms to 87.3% at 50 ms). Cue had a marginal effect,

$F(1,30) = 2.98$, $MSE = .001$, $p < .1$, suggesting a trend toward slightly better identification after a valid cue (82.1% vs. 83.3%). There was no interaction effect ($F < 1.5$).

Taken together, the behavioral results of Experiment 3 clearly replicated those of the previous experiments. In addition to the consistent effects of S1 duration, valid spatial cues produced the same patterns of increased fusion and decreased individual (S1) color report.

Electrophysiology: Cueing. Figure 5A shows the P1 and N1 components for valid and invalid cues in the report conditions that were analyzed, at PO7 and PO8. Figure 5B shows the same at PO3 and PO4. On the P1 in 20-ms fusion as well as 20-ms single color trials, neither cue nor electrode had a significant effect ($F_s < 1.6$). A very similar picture was obtained with 50-ms S1 report and 50-ms single color trials, for which no reliable P1 effects were found either ($F_s < 2.2$).

On the N1, cue had a marginal main effect in 20-ms fusion trials, $F(1,30) = 3.37$, $MSE = 3.287$, $p < .08$, suggesting a trend toward less negative amplitude with invalid cues ($-2.34 \mu\text{V}$) than with valid cues ($-2.76 \mu\text{V}$). Electrode had an effect by itself, $F(2,60) = 3.63$, $MSE = 11.453$, $p < .05$. Mean amplitude on PO3 ($-1.81 \mu\text{V}$) and PO4 ($-2.24 \mu\text{V}$) was less negative than on PO7 ($-2.81 \mu\text{V}$) and PO8 ($-3.34 \mu\text{V}$). The interaction of Cue \times Electrode was also reliable, $F(2,66) = 3.1$, $MSE = 2.613$, $p < .05$. On all electrodes, a valid cue increased component amplitude (i.e., it became more negative), but the effect was stronger on right hemisphere electrodes than on left hemisphere ones. There was $-.81 \mu\text{V}$ difference on PO4, $t(30) = 2.98$, $p < .01$, and $-.6 \mu\text{V}$ on PO8, $t(30) = 2.72$, $p < .01$, compared with $-.04 \mu\text{V}$ difference on PO3 and $-.24 \mu\text{V}$ on PO7 (both $t_s < 1$).

By contrast, in 20-ms single color trials, cue did not have a significant influence by itself, nor by means of an interaction ($F_s < 2$). Electrode did have an effect in this analysis, $F(2,60) = 3.63$, $MSE = 13.258$, $p < .05$. Mean amplitude was more negative on PO7 ($-3.19 \mu\text{V}$) and PO8 ($-3.32 \mu\text{V}$) than on PO3 ($-1.81 \mu\text{V}$) and PO4 ($-2.33 \mu\text{V}$), similar to the previous analysis. The analysis of 50-ms S1 reports did not show reliable effects ($F_s < 1.9$). However, the analysis of 50-ms single color trials showed a marginal effect of cue, $F(1,30) = 3.14$, $MSE = 2.239$, $p < .09$. It is important to note that this marginal trend was opposite to that observed in fusion trials; less negative amplitude was associated with valid

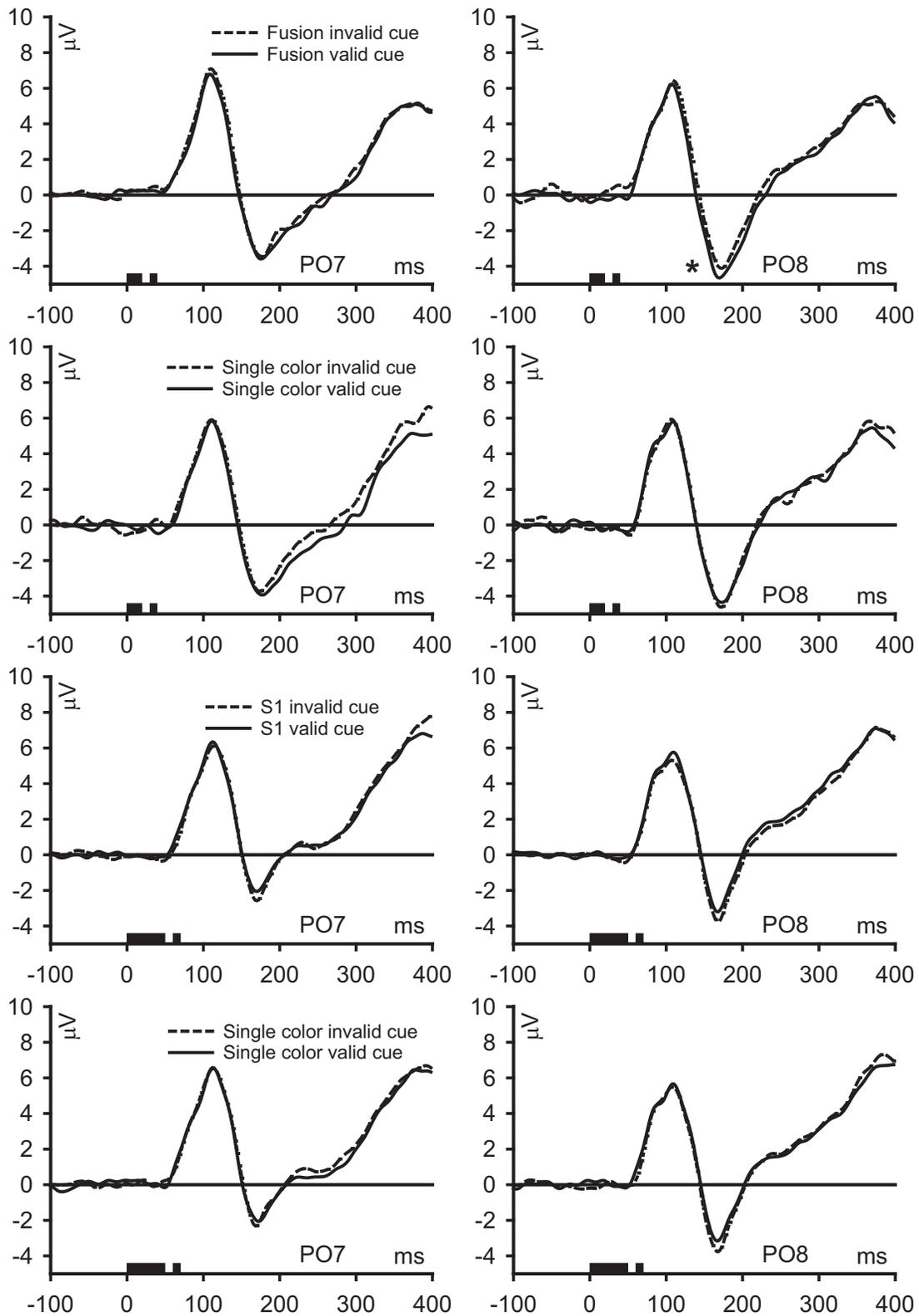


Figure 5. The early ERP showing the P1 and N1 components (in μV) observed at PO7 and PO8 (A), and at PO3 and PO4 (B) in Experiment 3, plotted as a function of time (ms). Top plots represent trials with 20-ms S1 duration, separated by their behavioral outcome: fusion reports (first row) and single color reports (second row). Bottom plots represent trials with 50-ms S1 duration, separated by outcome: S1 color reports (third row) and single color reports (fourth row). Dashed lines represent invalid cues, and solid lines represent valid cues. *Significant pairwise differences.

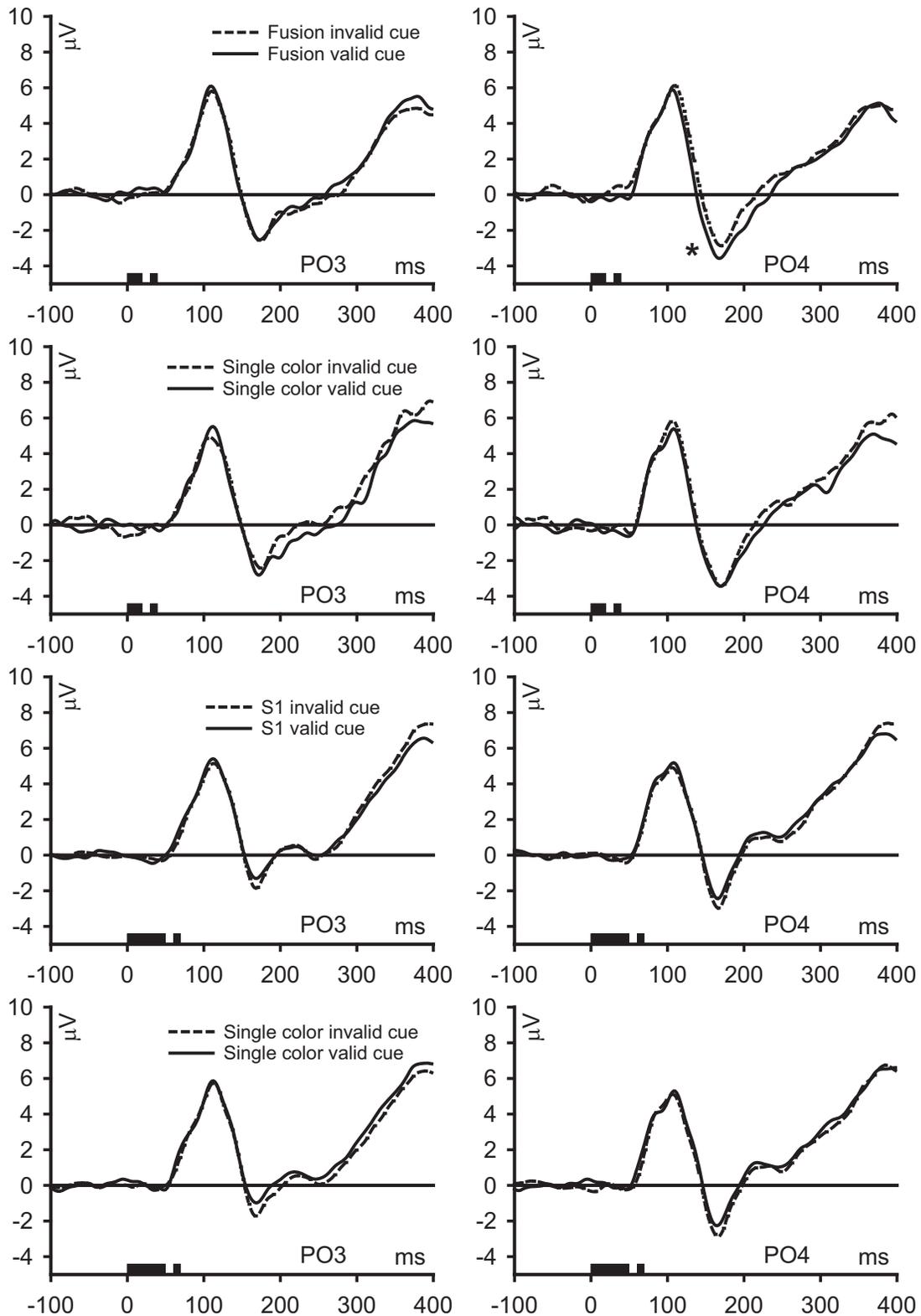


Figure 5. Continued.

cues ($-0.98 \mu\text{V}$), rather than invalid cues ($-1.31 \mu\text{V}$). There was furthermore no interaction with electrode ($F < 1.7$), even though electrode did show a marginal main effect, $F(2,52) = 2.54$, $MSE = 12.3$, $p < .1$, which reflected a trend toward a larger N1 at more lateral sites, as also observed in previous analyses.

Figure 6 shows the N2pc components evoked by valid and invalid cues in each of the analyzed report conditions. Analysis of the N2pc component in 20-ms fusion report trials showed that it was affected by cue, $F(1,30) = 4.38$, $MSE = 1.981$, $p < .05$. Valid cues elicited less negative component amplitude ($-1.14 \mu\text{V}$) than

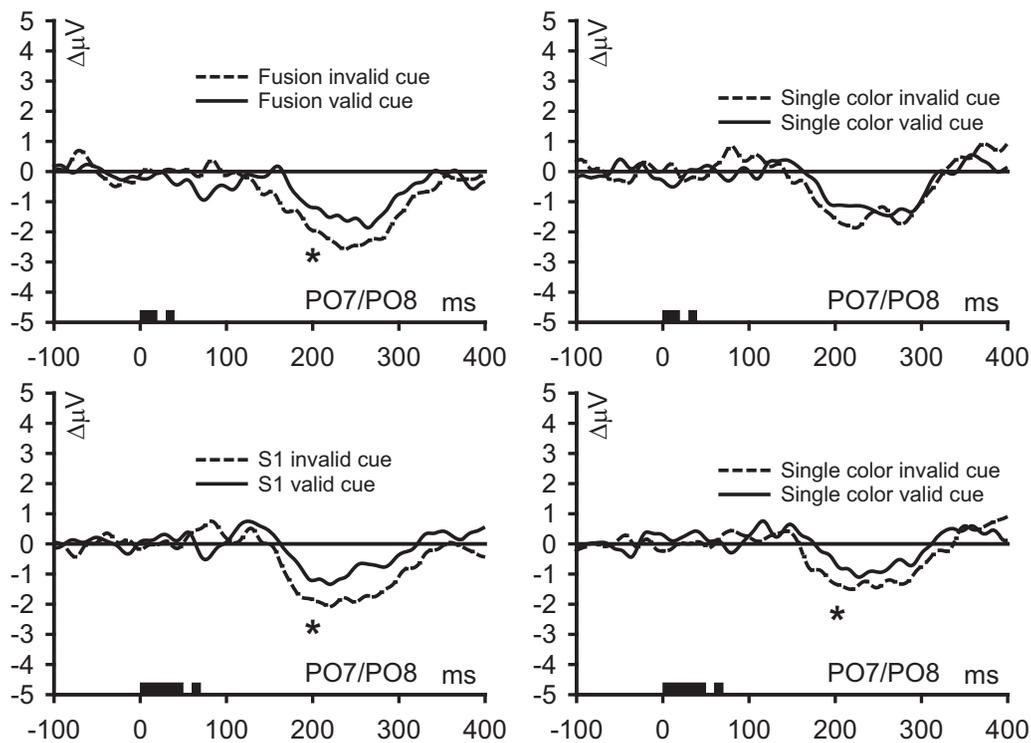


Figure 6. The N2pc component of the ERP (μV difference), computed over PO7/PO8 in Experiment 3. Top: Trials with 20-ms S1 duration (fusion and single color reports). Bottom: Trials with 50-ms S1 duration (S1 color and single color reports). Remaining figure conventions follow Figure 5.

invalid cues ($-1.89 \mu\text{V}$). Correctly reported 20-ms single color trials did not show a cueing effect ($F < 1.6$). By contrast, both 50-ms S1 reports in dual color trials and 50-ms correct single color reports were consistently affected by cueing, $F(1,30) = 11.44$, $MSE = .905$, $p < .005$, and $F(1,30) = 5.53$, $MSE = .876$, $p < .05$, respectively. For 50-ms S1 reports, valid cues elicited less negative amplitude ($-.74 \mu\text{V}$) than invalid cues ($-1.56 \mu\text{V}$). Similarly, for 50-ms single color reports, valid cues also elicited less negative amplitude ($-.53 \mu\text{V}$) than invalid cues ($-1.09 \mu\text{V}$).

Figure 7 shows the P3 component for valid and invalid cues in each of the analyzed report conditions. The analysis of P3 amplitude in 20-ms fusion report trials from 370 to 500 ms did not produce a reliable effect of cue ($F < 1$). The analysis of 20-ms single color correct trials, conversely, did show an effect of cueing, $F(1,30) = 5.41$, $MSE = 1.617$, $p < .05$. Valid cues produced less positive amplitude ($4.71 \mu\text{V}$) than invalid cues ($5.46 \mu\text{V}$). For 50-ms S1 reports, there was also an effect of cue, $F(1,30) = 4.61$, $MSE = 1.809$, $p < .05$. Again, less positive amplitude was associated with valid cues, compared to invalid cues ($5.57 \mu\text{V}$ vs. $6.31 \mu\text{V}$). For 50-ms single color reports, there was no effect of cue ($F < 1.1$). In the window from 500 to 630 ms, P3 amplitude was not modulated by cue ($F < 1.5$) in any of the conditions.

In summary, the first effects of cueing on color fusion were uniquely observed in modulations of N1 amplitude, which seemed to be strongest on right hemisphere electrodes. The analyses of N2pc amplitude showed consistent cueing effects for all conditions, except the 20-ms single color reports. In each case, valid cues decreased component amplitude. Thus, although the cues were clearly having an effect at this stage of perceptual processing, the N2pc pattern by itself did not seem to be predictive of the eventual behavioral outcome. The analyses of P3 amplitude showed different modulations. Cueing affected amplitude in 20-ms single color

trials and 50-ms S1 report trials at the P3. As with the N2pc, when viewed in isolation the P3 effects did not seem to correlate strongly with a specific pattern of behavioral outcomes.

It thus seems that the early interaction between fusion and attention is expressed primarily by N1 amplitude. However, the eventual percept that is generated by the stimuli, as reflected in the observer's behavior, seems to come about through an interplay of different effects observed at different points in time within the chain of perceptual processing (i.e., at the N1, N2pc, and P3). For instance, at 20-ms S1 duration, fusion came with a modulation of the N2pc and an absence of one at the P3, while the opposite pattern was observed for single color reports. At 50-ms S1 duration, the N2pc effects were similar, but S1 reports in dual color trials were associated with a P3 modulation, while single color reports were not. Before these effects are further interpreted, it is useful to consider the effect of fusion itself on the ERP.

Electrophysiology: Fusion. The topography (current source density) associated with fusion is shown in Figure 8. Figure 9A shows P1 and N1 amplitude in 20-ms dual color trials at PO7 and PO8, plotted separately for trials in which fusion occurred and trials in which it did not. Figure 9B shows the same at PO3 and PO4. Similar to the analyses of cueing, there was no reliable effect of fusion on the P1 component ($F_s < 1.5$) in the trials under consideration (recall that the fusion analyses contrasted fusion reports with S1 and S2 reports in dual color 20-ms trials). There was only a marginal effect of electrode, $F(2,54) = 2.47$, $MSE = 6.155$, $p < .1$, showing a trend toward higher component amplitude on the more lateral electrode sites (cf. also the topographic distribution of the P1 in Figure 8).

Fusion reliably modulated the N1, $F(1,28) = 4.74$, $MSE = 2.646$, $p < .05$. Mean amplitude of the N1 was lower (less

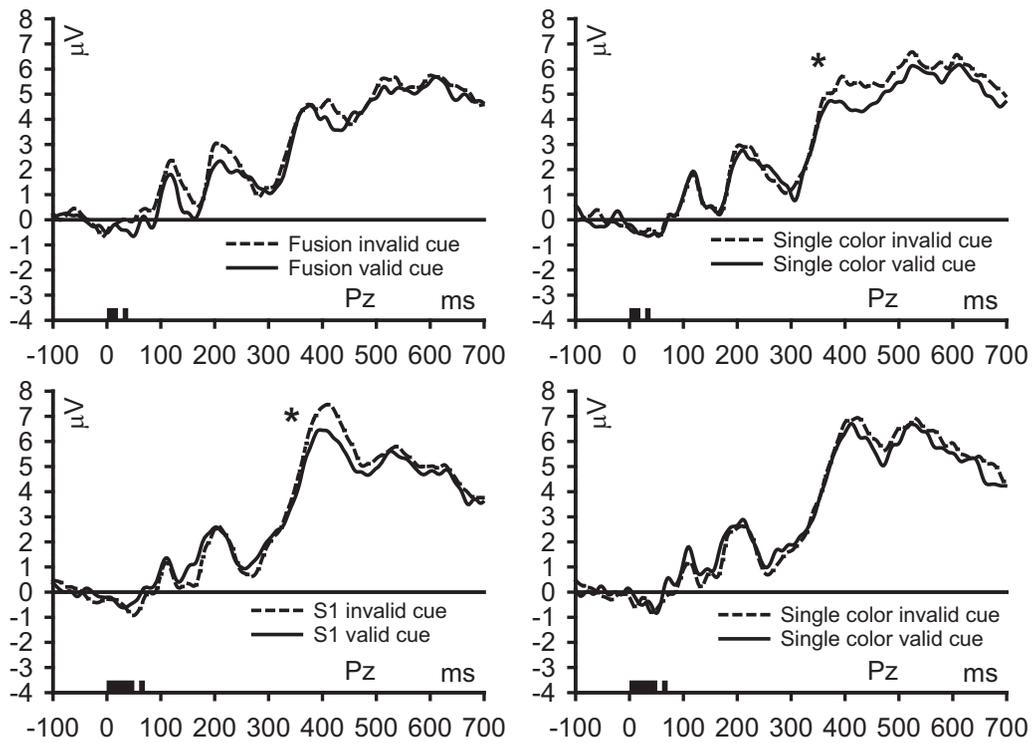


Figure 7. The P3 component (μV) observed at Pz in Experiment 3. Top: Trials with 20-ms S1 duration (fusion and single color reports). Bottom: Trials with 50-ms S1 duration (S1 color and single color reports). Remaining figure conventions follow Figure 5.

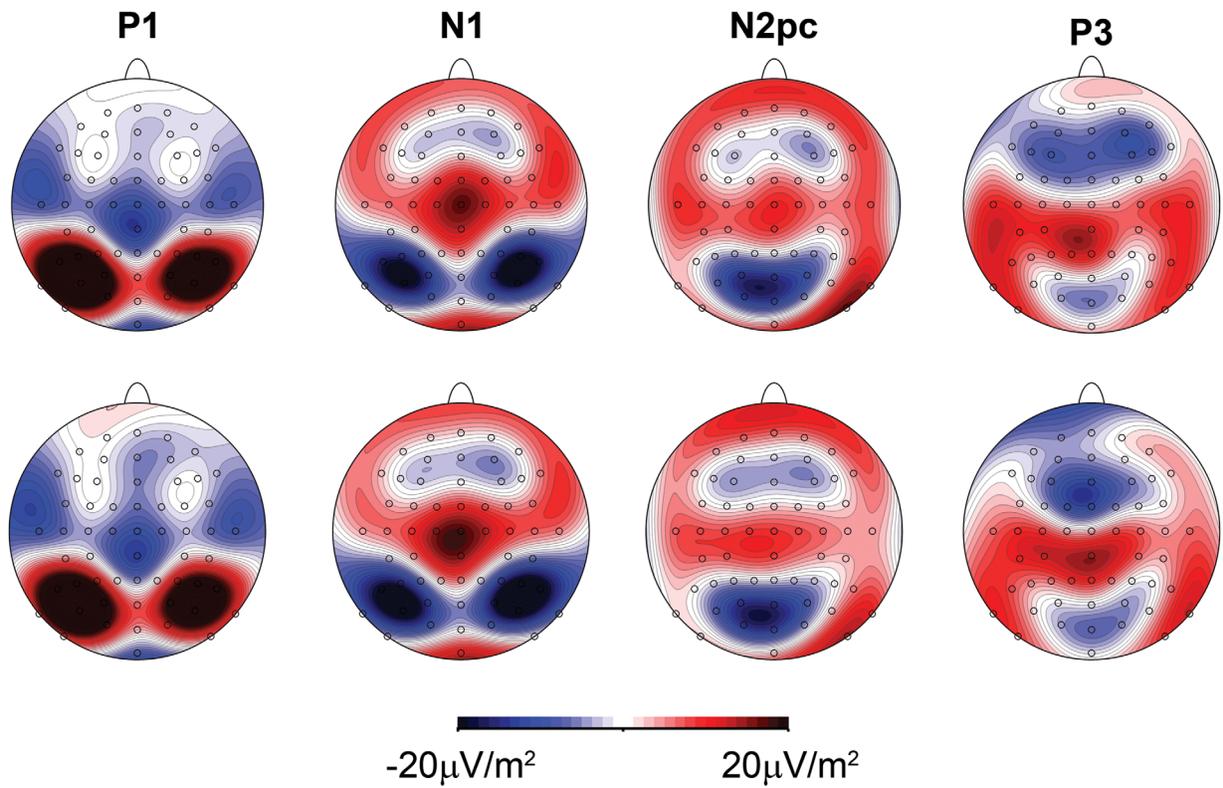


Figure 8. Current source density topographic maps of the 20-ms dual color trials in Experiment 3. Plots were constructed using spherical spline interpolation and represent a 20-ms average centered on the waveform peaks. Top: Trials in which fusion occurred. Bottom: Trials in which it did not (S1 or S2 was reported). From left to right, the plots correspond to the P1 (100–120 ms), N1 (180–200 ms), N2pc (230–250 ms), and P3 (490–510 ms) component peaks.

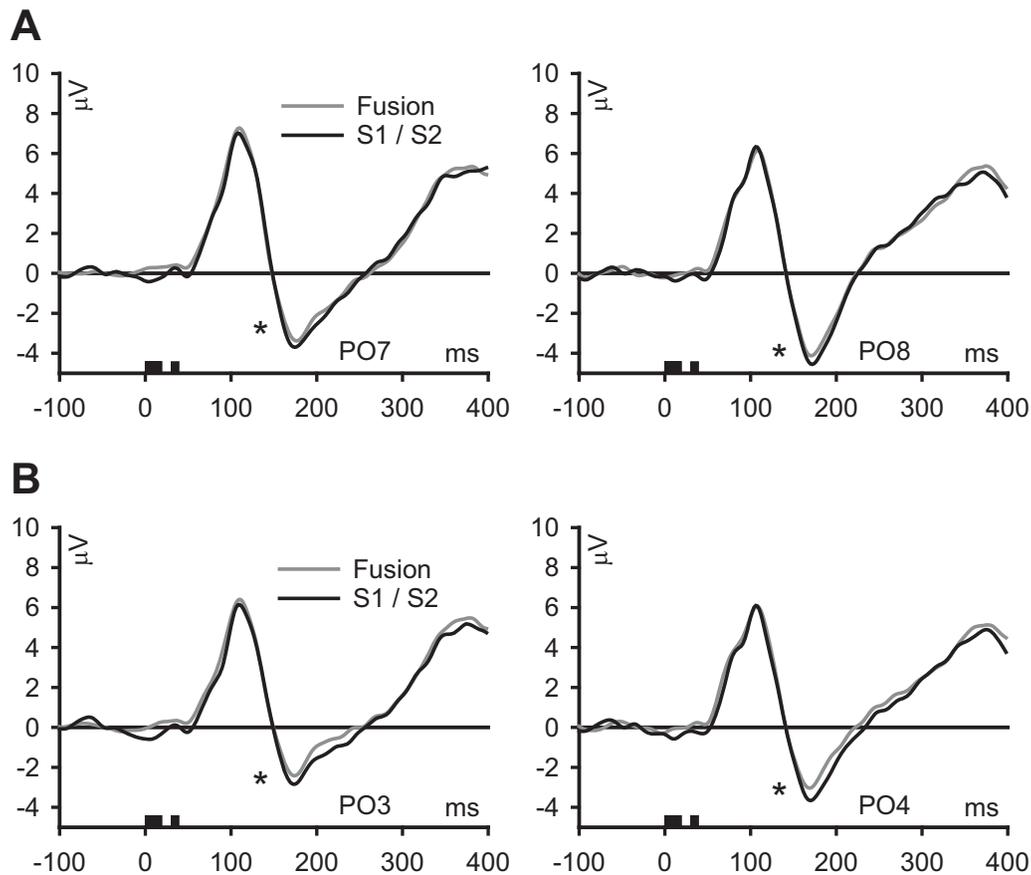


Figure 9. The P1 and N1 components (μV) at PO7 and PO8 (A) and at PO3 and PO4 (B), in 20-ms dual color trials in Experiment 3. Gray lines represent trials in which the fused color was reported, and black lines represent trials in which either of the individual colors (S1 or S2) was reported. *Significant differences (main effect).

negative) for fusion trials, averaging $-2.38 \mu\text{V}$ compared to $-2.85 \mu\text{V}$ for individual S1/S2 color reports. Fusion did not interact with electrode ($F < 1$), and the latter only had a marginal main effect, $F(2,55) = 2.55$, $MSE = 12.53$, $p < .09$, again hinting at a more lateral component advantage.

In contrast to the analyses of cueing, there was no effect of fusion on the N2pc ($F < 1$), which is also apparent from Figure 10A. Figure 10B shows P3 amplitude at Pz in trials in which fusion was reported and trials in which either of the individual colors were reported. Although the means seemed to suggest the existence of some differences in both of the P3 time windows under consideration, neither of these could be substantiated ($F_s < 2.4$).

Thus, fusion seemed to be reflected primarily in a modulation of the N1 component. The locus of the fusion effect corresponded with the earliest locus of the cueing effects, but in contrast to the latter, it was not observed on the subsequent N2pc and P3 components. This might suggest that fusion was complete prior to the processing phases reflected by these later components.

General Discussion

Behavior: Cueing in the Color Fusion Task

There were three principal behavioral outcomes of the present experiments. First, color fusion was consistently enhanced by the presence of a valid cue that directed attention to the location at

which the color stimuli were to appear. Even though there were some exceptions, the majority of these cueing effects was similarly present at each of the tested S1 durations. Second, the identification of individual colors, as reflected in S1 color reports in dual color trials, was impaired by a valid cue. Although S2 color reports did not show the same effect, this can be considered as trivial since these reports were generally invariant and close to zero, presumably due to the comparatively weak sensory impression made by the brief S2 presentation of just 10 ms^2 . Third, there were virtually no effects of attentional allocation on the reports given in single color trials, suggesting that attention did not impair nor enhance color discrimination per se.

The behavioral results thus strongly suggested that, although attention played no appreciable role in single color discrimination

2. According to Bloch's law (Bloch, 1885), for stimuli near threshold, perceived brightness is related to their duration. In the present study, S1 and S2 brightness were not matched for each duration of the former, and S1 was thus generally brighter than S2, which further explains the dominance of S1 reports. If brightness matching had been performed, S2 reports would likely rise. For the purposes of the present study, the main considerations were that the stimuli produced perceptual fusion and that the relative brightness of the stimuli did not confound the experimental manipulations. Nonetheless, it would be an interesting avenue of further research to systematically map the relationship between relative brightness and likelihood of fusion in a parametric design.

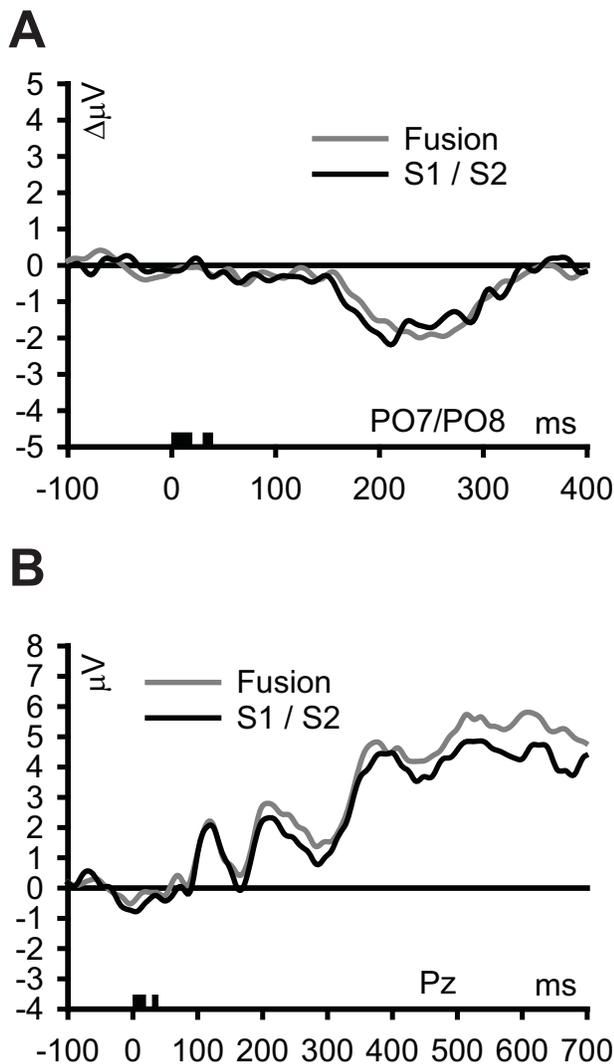


Figure 10. The N2pc component (μV difference), computed over PO7/PO8 in 20-ms dual color trials in Experiment 3 (A). The P3 component (μV) at Pz for the same trials (B). Remaining figure conventions follow Figure 9.

in the current task, it did clearly favor color fusion, and did so at the expense of the perception of the dominant constituent individual stimulus color (i.e., that of S1). This outcome is fully in line with the idea that attention enhances temporal integration, and sheds a new light on previous work that showed attentional modulation of temporal resolution (Rolke et al., 2008; Yeshurun & Levy, 2003), of perceived duration (Enns et al., 1999), and of visible persistence (Visser & Enns, 2001).

The present observation that integration is increased in a visual task requiring a response that relies exclusively on parvocellular processing argues against the idea that temporal resolution is diminished exclusively due to decreased magnocellular involvement (Yeshurun, 2004; Yeshurun & Levy, 2003). The occurrence of color fusion in the present task is an instance in which the individual stimuli were not resolved individually, similar to failures of gap detection such as those reported by Yeshurun and Levy (2003). Contrary to their study, however, this apparent decrease in temporal resolution cannot be attributed to parvo/magno trade-offs and must thus have a different origin. Because the fusion effect in the

current study was accompanied by an absence of attentional modulation of single color identification, it also seems unlikely that fusion increased as a consequence of improved color and/or pattern perception. The most parsimonious account for the effect thus seems to be that attention specifically enhances the fusion process itself, similar to binding effects observed previously in the spatial domain (Reynolds & Desimone, 1999). Note that this is not meant to imply that previously hypothesized effects of parvo/magno pathways do not exist—these might still have modulated the temporal dynamics in previous studies, but to a degree that remains to be determined. It seems likely that changes in temporal integration played a role in those studies, too.

Similarly, previous reports of attention-induced increases in perceived duration and visible persistence are not directly disqualified by the present results. It is conceivable indeed that when attention was available in the study by Visser and Enns (2001), the increased persistence of the first integration display contributed to its integration with the second display. By combining a very brief stimulus presentation duration of just 1 ms with a longer variable ISI, the prerequisite conditions for visible persistence to emerge, and to vary, were effectively implemented. What the current results do suggest is that a persistence effect is not necessary to observe enhanced temporal integration. In the present color fusion task, the first display was always masked by the onset of the second, at a constant interval (ISI of 10 ms). The critical first color stimulus itself was furthermore fully replaced at the same location by the second. It is hard to see how increased persistence of the first stimulus might arise in this paradigm, yet attentional facilitation of temporal integration was consistently found.

One might finally consider whether the fusion effect might be explained as a side effect of attention-induced differences in representational strength (cf. the prior entry phenomenon). Yet, even if there would be an attentional modulation of the strength of stimulus representation, it is difficult to envision how this could result in increased fusion, instead of simply more reports of the supposedly strengthened stimuli themselves (recall also that report order was not a factor in the design). The data furthermore showed that virtually no differences in single color identification were observed, and that individual color reports in dual color trials either again showed no differences (S2), or the opposite pattern of attention-induced interference (S1). It thus seems unlikely that variations in representational strength played a mediating role in the current outcomes.

ERPs: Early and Late Effects of Cueing

The attentional modulation of color fusion did not seem to arise in the earliest perceptual phases of visual stimulus processing, such as reflected by the P1. Although the P1 and N1 components of the ERP are both sensitive to spatial attention, and are both associated with initial stimulus detection and discrimination (Luck et al., 1990; Mangun & Hillyard, 1991; Vogel & Luck, 2000), only the P1 was highly similar in valid and invalid cue conditions, while the N1 showed reliable differences. Some caution is warranted when it comes to interpreting the null effect on the P1, which at least suggested that the earliest sensory impression of the stimuli was not reliably changed by the allocation of attention, because the extremely short stimulus durations that were needed to elicit color fusion might be the underlying reason for the lack of an effect on this component. To our knowledge, the present study is the first to report the ERP of rapid successive stimuli of this kind, and so it remains to be determined to what extent this attention-insensitive P1 behavior will generalize.

The effect of spatial cueing on the N1 was rather subtle and seemed to be stronger on right hemisphere electrode sites. The modulation was uniquely reliable in fusion trials, although trends in the same direction could be seen from the grand averages (particularly for 20-ms single color trials). The N1 is known to increase after a valid spatial cue (Mangun, 1995), and this was indeed also observed here. Because the cueing effect was only observed in fusion trials, it might be concluded that attentional facilitation of temporal integration has its locus here. This conclusion is compatible with previous work that has found the N1 to be the first component to be modulated by the temporal integration process (Akyürek, Schubö, & Hommel, 2010). It is further strengthened by the finding that later components (discussed in more detail below) did not show similar uniquely attributable modulations.

It may still be too early to draw highly specific conclusions about the nature of the spatial cueing effect on temporal integration at the N1, but one speculative interpretation might nonetheless be given. Previous work has implicated the right temporoparietal cortex in the temporal coding of visual features, showing that lesions in that area increased the number of temporal binding errors in rapid serial visual presentation (Arend, Rafal, & Ward, 2011). ERPs cannot be firmly attributed to specific brain areas, but the present observation of right hemisphere dominance in the strength of the effect, as observed from electrodes at the scalp, is compatible with the idea that attention could enhance temporal integration (binding) by boosting neuronal activity in temporoparietal cortical regions that harbor temporal perceptual functions.

Later components of the ERP (N2pc and P3) seemed to behave differently in response to cueing, depending on whether S1 was shown for 20 or 50 ms. This need not be surprising, considering that the relative difference in duration was substantial (i.e., a factor of 2.5), and considering that because S2 was always just 10 ms, the balance between the pair of stimuli within a trial was also shifted substantially. In the interpretations of the various effects given below, this distinction in terms of duration has to be kept in mind.

N2pc amplitude in dual color trials at 20-ms S1 duration for validly cued fusion reports was decreased, compared to trials that were invalidly cued. Single color reports at the same duration did not show the same attenuation effect. Prior research that contrasted the N2pc to lateralized target stimuli preceded by informative and uninformative spatial cues has similarly not consistently produced clear differences between these conditions, suggesting that the N2pc to target stimuli might be insensitive to cue-induced shifts of attention (Kiss et al., 2008). Nevertheless, an attenuation was presently observed in validly cued fusion trials. Previous research has shown that N2pc amplitude is reduced when only a single feature dimension is relevant in a visual search task, compared to multiple dimensions (Akyürek, Dinkelbach, Schubö, & Müller, 2010), and that the N2pc can even disappear completely when spatial filtering is not required (Luck & Hillyard, 1994). In other words, the N2pc may be attenuated when there is less competition for selection. In the present study, this explanation would fit very well to the observed pattern. Attentional enhancement of fusion should indeed entail that the competition between the successive S1 and S2 color stimuli is dissolved and a selection between them need no longer be made (see Hommel & Akyürek, 2005, for a similar argument).

In single color trials, the lack of a similar cue-related modulation might simply reflect that the behavioral correlates of reduced competition or enhanced integration are difficult to isolate in this condition (because it does not have a dissociable fusion response option). In single color trials, competition between S1 and S2 is not necessarily resolved when a correct response is made: Because S1

and S2 are identical, a correct report could reflect the perception of either stimulus, or even of fused stimuli. At 20-ms S1 duration, which is relatively short, it is conceivable that the single color reports in this condition contained a number of actual S2 responses.

At 50-ms S1 duration, similar cue effects on N2pc amplitude were observed, both in trials in which the S1 color was reported and in correctly reported single color trials. It is conceivable that attention reduced competition between S1 and S2 in these trials, too, but that because of the longer S1 duration, the outcome was different. In both dual and single color trials, the longer S1 stimulus was likely to dominate, leading to actual S1 reports and to correct single color reports (because here S1 was equal to S2). From the N2pc amplitude pattern at 50 ms, it cannot be excluded that the cue might have facilitated spatial selection itself, reducing the impact of the neighboring black squares in the stimulus grid and thereby contributing to the N2pc amplitude reduction. This account lacks parsimony, however, because it cannot explain the absence of a cueing effect at 20 ms in single color trials. This absence is instead better understood in terms of the comparative survival rate of S2 percepts at 20 ms, which at 50 ms have become extremely unlikely.

The P3 component in fusion trials at 20-ms S1 duration did not differ between valid and invalid cues, while P3 amplitude was increased for invalidly cued single color trials, compared to valid cues. The absence of a P3 modulation in fusion trials might be taken to indicate that fusion both starts and resolves earlier (even before the N2pc time window); afterward, there appeared no further difference in the processing or consolidation of the fused color. The P3 modulation in the 20-ms single color trials is somewhat difficult to interpret, because behavioral measures only showed a marginal trend toward better performance with valid cues. Speculatively, the modulation in this condition might reflect a cue-induced reinforcement of the comparatively weak S1 color (because it lasted only 20 ms), allowing it to win the competition for consolidation with S2 more often (i.e., a case of biased competition; Desimone & Duncan, 1995).

At 50-ms S1 duration, the P3 was modulated by cueing in the S1 report trials only, and not in the single color trials, contrary to what was found at the shorter duration. This might be due to the dominance of the S1 color at 50-ms duration that, when paired with a noncompeting, identical S2 color in the single color condition, might have reached a ceiling that left no further room to modulate the associated activity in this time window. In any case, because no behavioral differences due to cueing were observed in 50-ms single color trials, the lack of a P3 effect in this condition was in line with expectations.

Because S1 reports were facilitated by invalid cues, the associated increased amplitude of the P3 might reflect that. Invalidly cued S1 reports could thus be characterized by increased information transfer (or the monitoring thereof for the purpose of response selection; Verleger et al., 2005), and more certainty with regard to the perceived color (Kok, 2001). In a similar vein, the reduced P3 in validly cued trials might be reflective of increased difficulty. In terms of memory operations, increased amplitude might reflect more successful consolidation (Polich, 2007). These interpretations appear to be equally feasible in the present study and show a considerable degree of convergence.

Summarizing, the ERP results suggested that attentional modulation of color fusion did not affect the earliest phases of stimulus processing, but primarily affected attentional feature processing in the N1 and N2pc time windows. Evidence from the P3 component furthermore indicated that, although single color reports (at 20 ms)

and S1 color reports (at 50 ms) proved to be sensitive to cue-induced task difficulty, fusion was not. The fusion process might have completed prior to later processing phases (including the P3), resulting in the perception of an individual color that is no longer dissociable from that of a truly individual color (i.e., S1 or the single color).

The Locus of Fusion

Color fusion was (uniquely) associated with a modulation of N1 amplitude. As mentioned, in a previous study that examined differences in the ERP as a consequence of temporal integration in a MET (Akyürek, Schubö, & Hommel, 2010), the N1 was also the first component to be modulated. Further considering findings from auditory studies, in which the N1 has been implicated in the integration of successive tones and stream segregation (Loveless, Levänen, Jousmaki, Sams, & Hari, 1996; Müller, Widmann, & Schröger, 2005), it seems the evidence is mounting that the N1 plays an important role in the integration of sensory information across time. The direction of the temporal integration effect on the N1 can apparently differ, however. In the study by Akyürek, Schubö, and Hommel (2010), temporal integration increased N1 amplitude, while color fusion in the present study decreased it. This difference may be due to the stimuli that were used. In the present study, successful fusion may demand less discriminative effort, and hence elicit lower component amplitude, because a single perceived color emerges, instead of two competing colors. In the MET, successful integration results in the localization of the missing element, which contrasts maximally with the actual stimuli in the grid, and may thus increase component amplitude.

The posterior N1 component has been hypothesized to reflect a discrimination process (Vogel & Luck, 2000), but is also associated with attentional analysis of stimulus features (Mangun, 1995). The latter spatial attention effect on the N1 can be eliminated with bilateral stimulus sequences (Luck et al., 1990), which indeed matches the current design when considered across the cue conditions, as done in the present analysis. The N1 discrimination process should thus primarily have been observed. In terms of discrimination, it makes sense that there is less to discriminate when fusion eliminates the competition between the successive colors, which would likely result in reduced component amplitude, as was observed. With the current renewed implication of the N1 in temporal integration processes, it is becoming more clear that the creation of a singular event due to integration may indeed change the way in which the successive stimuli are processed, transitioning from mutual competition to integration, as hypothesized before by Hommel & Akyürek (2005), and that it may do so at a relatively early stage.

The N2pc was not affected by whether the stimuli were fused or not. The processing of visual features at a lateral location (Kiss et al., 2008) thus appears to be similar for fused and veridical color stimuli. This pattern might be expected if the fusion process was complete prior to the onset of the N2pc, which is a distinct possibility, particularly in view of the very brief stimulus presentations that were currently involved. Previous research on temporal integration has shown that the N2pc to veridical and integrated stimuli does have a comparable onset, but that the N2pc of the latter seems to be more sustained in a later phase (Akyürek & Meijerink, 2012). Qualitatively, the current means do bear some semblance to this pattern, but without statistical support this is just a side note, and the conclusion must remain that no difference was observed. This

suggests that previously found differences might thus be specific for temporal integration across longer intervals (i.e., 90 ms, compared to 40 ms in the present study). Akyürek and Meijerink (2012) also showed that a missing element elicited an N2pc that was absent in error trials. This might be explained as a (quite immediate) consequence of integration, rather than the process itself. In the missing element task, integration uniquely affords the appearance of the missing element at a lateral location, which is bound to elicit an N2pc that would otherwise not be observed. In the current task, there was no similar underlying contrast between fusion and S1/S2 reports; in both cases, a color was being processed at the selected location.

The P3 component was also not reliably modulated by fusion. The grand averages did suggest there might be some weak, sustained difference, and so the absence of statistical corroboration should not be taken as strong proof that the P3 components in the fusion and S1/S2 report conditions were perfectly identical. Nevertheless, the current absence or weakness of P3 differences contrasts with findings from previous temporal integration studies (Akyürek & Meijerink, 2012; Akyürek, Schubö, & Hommel, 2010). This might be due to the fact that regardless of fusion, the consolidation of the color that was perceived, and the selection of the appropriate response, were actually similar. Previous P3 differences observed in METs (Akyürek & Meijerink, 2012; Akyürek, Schubö, & Hommel, 2010) might thus reflect the unique consolidation of the integrated percept, including the localization thereof for response purposes. In the MET, none of this information would have been available when integration failed. In other words, such P3 differences may also reflect a consequence of temporal integration, rather than the process itself.

Taken together, the current evidence suggests that fusion might be initiated at the N1, and may also be completed there, in view of the lack of later modulations on the N2pc and P3. Notably, the N1 was also the first component to be modulated by cueing. Subsequent cueing effects may thus reflect attentional processing of temporal events that may be qualitatively similar to our perceptual system, regardless of whether they contain fused or veridical stimuli.

A Role for Recurrent Processing?

Before concluding, it may be worthwhile to briefly consider also the hypothesis that temporal integration might comprise longer intervals if recurrent neural activity is initiated (cf. object substitution masking; Di Lollo, Enns, & Rensink, 2000), which is thought to occur when observers are consciously aware of the stimuli (Favre & Koch, 2014). Top-down control of attention might act similarly by increasing recurrent activity, thereby making integration more likely at the stimulus presentation times tested in the current study. A possible neurophysiological correlate of such control might be found in oscillatory brain activity (Engel, Fries, & Singer, 2001). In the present study, a preliminary view on the time-frequency spectrum of the EEG could not substantiate this conjecture. Nevertheless, before the idea is abandoned too readily, it should be noted that the lack of an apparent effect in the frequency domain might be due to the relatively rapid pacing of the stimuli and trials in the experimental design, which did not lend itself very well for frequency-based analyses. The possible role of recurrent processing in temporal integration thus remains a viable topic for future research.

Conclusion

To our knowledge, the present study was the first to examine the effects of attentional cueing on the perceptual fusion of rapid successive colors and its ERP correlates. The results showed that attention facilitated the temporal integration of the two color stimuli, at the expense of the report of their individual colors. Evidence from the N1, N2pc, and P3 components of the ERP furthermore suggested that color fusion, and the effect of cueing on fusion, can be

placed at a relatively early phase of processing, in line with previous findings (Akyürek, Schubö, & Hommel, 2010). The present outcomes further complement previous research that has shown various kinds of temporal slowdowns due to the allocation of attention (Enns et al., 1999; Rolke et al., 2008; Visser & Enns, 2001; Yeshurun & Levy, 2003), and suggests that such slowing might have an adaptive function that reduces competition between individual stimuli in the process of forming perceptual events.

References

- Akyürek, E. G., Dinkelbach, A., Schubö, A., & Müller, H. J. (2010). Electrophysiological correlates of detecting a visual target and detecting its absence: The role of feature dimensions. *Neuropsychologia*, *48*, 3365–3370. doi: 10.1016/j.neuropsychologia.2010.07.005
- Akyürek, E. G., Eshuis, S. A. H., Nieuwenstein, M. R., Saija, J. D., Başkent, D., & Hommel, B. (2012). Temporal target integration underlies performance at Lag 1 in the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance*, *38*, 1448–1464. doi: 10.1037/a0027610
- Akyürek, E. G., & Meijerink, S. K. (2012). The deployment of visual attention during temporal integration: An electrophysiological investigation. *Psychophysiology*, *49*, 885–898. doi: 10.1111/j.1469-8986.2012.01380.x
- Akyürek, E. G., Schubö, A., & Hommel, B. (2010). Fast temporal event integration in the visual domain demonstrated by event-related potentials. *Psychophysiology*, *47*, 512–522. doi: 10.1111/j.1469-8986.2010.00962.x
- Arend, I., Rafal, R., & Ward, R. (2011). Temporal feature integration in the right parietal cortex. *Neuropsychologia*, *49*, 1788–1793. doi: 10.1016/j.neuropsychologia.2011.03.001
- Bloch, A. M. (1885). Expériences sur la vision [Experiments on vision]. *Comptes Rendus de Séances de la Société de Biologie Paris*, *37*, 493–495.
- Broadbent, D. E., & Broadbent, M. H. (1987). From detection to identification: Response to multiple targets in rapid serial visual presentation. *Perception & Psychophysics*, *42*, 105–113. doi: 10.3758/BF03210498
- Bundesen, C., Habekost, T., & Kyllingsbæk, S. (2005). A neural theory of visual attention: Bridging cognition and neurophysiology. *Psychological Review*, *112*, 291–328. doi: 10.1037/0033-295X.112.2.291
- Chica, A. B., & Christie, J. (2009). Spatial attention does improve temporal discrimination. *Attention, Perception, & Psychophysics*, *71*, 273–280. doi: 10.3758/APP.71.2.273
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222. doi: 10.1146/annurev.ne.18.030195.001205
- Di Lollo, V., Enns, J. T., & Rensink, R. A. (2000). Competition for consciousness among visual events: The psychophysics of reentrant visual processes. *Journal of Experimental Psychology: General*, *129*, 481–507. doi: 10.1037/0096-3445.129.4.481
- Dixon, P., & Di Lollo, V. (1994). Beyond visible persistence: An alternative account of temporal integration and segregation in visual processing. *Cognitive Psychology*, *26*, 33–63. doi: 10.1006/cogp.1994.1002
- Downing, C. J. (1988). Expectancy and visual-spatial attention: Effects on perceptual quality. *Journal of Experimental Psychology: Human Perception and Performance*, *14*, 188–202. doi: 10.1037/0096-1523.14.2.188
- Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, *99*, 225–234. doi: 10.1016/0013-4694(96)95711-9
- Engel, A. K., Fries, P., & Singer, W. (2001). Dynamic predictions: Oscillations and synchrony in top-down processing. *Nature Reviews Neuroscience*, *2*, 704–716. doi: 10.1038/35094565
- Enns, J. T., Brehaut, J. C., & Shore, D. I. (1999). The duration of a brief event in the mind's eye. *Journal of General Psychology*, *126*, 355–372. doi: 10.1080/00221309909595371
- Faivre, N., & Koch, C. (2014). Temporal structure coding with and without awareness. *Cognition*, *131*, 404–414. doi: 10.1016/j.cognition.2014.02.008
- Gratton, G., Coles, M. G., Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, *55*, 468–484. doi: 10.1016/0013-4694(83)90135-9
- Hogben, J. H., & Di Lollo, V. (1974). Perceptual integration and perceptual segregation of brief visual stimuli. *Vision Research*, *14*, 1059–1069. doi: 10.1016/0042-6989(74)90202-8
- Hommel, B., & Akyürek, E. G. (2005). Lag-1 sparing in the attentional blink: Benefits and costs of integrating two events into a single episode. *Quarterly Journal of Experimental Psychology*, *58A*, 1415–1433. doi: 10.1080/02724980443000647
- Kiss, M., van Velzen, J., & Eimer, M. (2008). The N2pc component and its links to attention shifts and spatially selective visual processing. *Psychophysiology*, *45*, 240–249. doi: 10.1111/j.1469-8986.2007.00611.x
- Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences*, *4*, 138–147. doi: 10.1016/S1364-6613(00)01452-2
- Kok, A. (2001). On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology*, *38*, 557–577. doi: 10.1017/S0048577201990559
- Loveless, N., Levänen, S., Jousmaki, V., Sams, M., & Hari, R. (1996). Temporal integration in auditory sensory memory: Neuromagnetic evidence. *Electroencephalography and Clinical Neurophysiology*, *100*, 220–228. doi: 10.1016/0168-5597(95)00271-5
- Lu, Z.-L., & Doshier, B. A. (1998). External noise distinguishes attention mechanisms. *Vision Research*, *38*, 1183–1198. doi: 10.1016/S0042-6989(97)00273-3
- Luck, S. J., Heinze, H. J., Mangun, G. R., & Hillyard, S. A. (1990). Visual event-related potentials index focused attention within bilateral stimulus arrays. II. Functional dissociation of P1 and N1 components. *Electroencephalography and Clinical Neurophysiology*, *75*, 528–542. doi: 10.1016/0013-4694(90)90139-B
- Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 1000–1014. doi: 10.1037/0096-1523.20.5.1000
- Mangun, G. R. (1995). Neural mechanisms of visual selective attention. *Psychophysiology*, *32*, 4–18. doi: 10.1111/j.1469-8986.1995.tb03400.x
- Mangun, G. R., & Hillyard, S. A. (1991). Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. *Journal of Experimental Psychology: Human Perception and Performance*, *17*, 1057–1074. doi: 10.1037/0096-1523.17.4.1057
- Müller, D., Widmann, A., & Schröger, E. (2005). Auditory streaming affects the processing of successive deviant and standard sounds. *Psychophysiology*, *42*, 668–676. doi: 10.1111/j.1469-8986.2005.00355.x
- Nicol, J. R., Watter, S., Gray, K., & Shore, D. I. (2009). Object-based perception mediates the effect of exogenous attention on temporal resolution. *Visual Cognition*, *17*, 555–573. doi: 10.1080/13506280802113860
- Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*, 2128–2148. doi: 10.1016/j.clinph.2007.04.019
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*, 3–25. doi: 10.1080/00335558008248231
- Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: An attentional blink? *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 849–860. doi: 10.1037/0096-1523.18.3.849
- Regan, D., & Tyler, C. W. (1971). Temporal summation and its limit for wavelength changes: An analog of Bloch's law for color vision. *Journal of the Optical Society of America*, *61*, 1414–1421. doi: 10.1364/JOSA.61.001414
- Reynolds, J. H., & Desimone, R. (1999). The role of neural mechanisms of attention in solving the binding problem. *Neuron*, *24*, 19–29. doi: 10.1016/S0896-6273(00)80819-3
- Rolke, B., Dinkelbach, A., Hein, E., & Ulrich, R. (2008). Does attention impair temporal discrimination? Examining non-attentional accounts. *Psychological Research*, *72*, 49–60. doi: 10.1007/s00426-006-0092-0
- Rolke, B., Ulrich, R., & Bausenhardt, K. M. (2006). Attention delays perceived stimulus offset. *Vision Research*, *46*, 2926–2933. doi: 10.1016/j.visres.2006.02.022

- Seifried, T., & Ulrich, R. (2011). Exogenous visual attention prolongs perceived duration. *Attention, Perception, & Psychophysics*, *73*, 68–85. doi: 10.3758/s13414-010-0005-6
- Serences, J. T., & Yantis, S. (2006). Selective visual attention and perceptual coherence. *Trends in Cognitive Sciences*, *10*, 38–45. doi: 10.1016/j.tics.2005.11.008
- Shore, D. I., Spence, C., & Klein, R. M. (2001). Visual prior entry. *Psychological Science*, *12*, 205–212. doi: 10.1111/1467-9280.00337
- Smith, V. C., Bowen, R. W., & Pokorny, J. (1984). Threshold temporal integration of chromatic stimuli. *Vision Research*, *24*, 653–660. doi: 10.1016/0042-6989(84)90206-2
- Spence, C., & Parise, C. (2010). Prior-entry: A review. *Consciousness and Cognition: An International Journal*, *19*, 364–379. doi: 10.1016/j.concog.2009.12.001
- Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General and Applied*, *74*, 1–19. doi: 10.1037/h0093759
- Titchener, E. B. (1908). *Lectures on the elementary psychology of feeling and attention*. New York, NY: Macmillan. doi: 10.1037/10867-000
- Verleger, R., Jaśkowski, P., & Wascher, E. (2005). Evidence for an integrative role of P3b in linking reaction to perception. *Journal of Psychophysiology*, *19*, 165–181. doi: 10.1027/0269-8803.19.3.165
- Visser, T. A. W., & Enns, J. T. (2001). The role of attention in temporal integration. *Perception*, *30*, 135–145. doi: 10.1068/p3089
- Vogel, E. K., & Luck, S. J. (2000). The visual N1 component as an index of a discrimination process. *Psychophysiology*, *37*, 190–203. doi: 10.1111/1469-8986.3720190
- Wilson, H. R. (1980). Spatiotemporal characterization of a transient mechanism in the human visual system. *Vision Research*, *20*, 443–452. doi: 10.1016/0042-6989(80)90035-8
- Wisowaty, J. J. (1981). Estimates for the temporal response characteristics of chromatic pathways. *Journal of the Optical Society of America*, *71*, 970–977. doi: 10.1364/JOSA.71.000970
- Yeshurun, Y. (2004). Isoluminant stimuli and red background attenuate the effects of transient spatial attention on temporal resolution. *Vision Research*, *44*, 1375–1387. doi: 10.1016/j.visres.2003.12.016
- Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature*, *396*, 72–75.
- Yeshurun, Y., & Levy, L. (2003). Transient spatial attention degrades temporal resolution. *Psychological Science*, *14*, 225–231. doi: 10.1111/1467-9280.02436

(RECEIVED December 18, 2014; ACCEPTED July 22, 2015)